
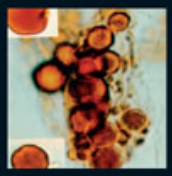
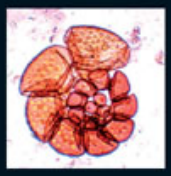
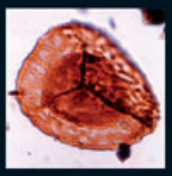

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Paleopalynology

Second Edition

by

Alfred Traverse

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PALEOPALYNOLOGY
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Paleopalynology

second edition

ALFRED TRAVERSE

Department of Geosciences,
The Pennsylvania State University,
University Park (State College),
Pennsylvania, USA

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'He picked up the manila envelope, and got out of the car, slamming the door. He headed for the entrance, shaking his head. Dodgson had been paying him five hundred dollars a day for weeks now, to follow a bunch of scientists around. At first, James had assumed it was some sort of industrial espionage. But none of the scientists worked for industry; they held university appointments, in pretty dull fields. Like that paleobotanist Sattler whose specialty was prehistoric pollen grains. James had sat through one of her lectures at Berkeley, and had barely been able to stay awake. Slide after slide of little pale spheres that looked like cotton balls, while she nattered on about polysaccharide bonding angles and the Campanian-Maastrichtian boundary . . . it was boring.' Quotation from: *The Lost World*, by Michael Crichton, 1995, Ballantine, NY.

Preface to the Second Edition

As soon as the first edition of this book was published, I began thinking of a second edition, in which I planned especially to correct various errors of omission and commission that immediately started being called to my attention. Critical colleagues found things that even the careful editorial process had missed, and dozens of students in my palynology courses found it understandably heartening to discover that the professor was very capable of making even amusing blunders. I started keeping large three-hole binders for the notes about such errors and regarding various suggestions for improvement. By the time the project for this edition finally got into high gear several years ago, there were four binders, crammed with pages well beyond the normal 8 cm. thickness for such books. The revision process has carefully treated every single suggestion, and most of them have resulted in changes.

The first edition had some critics, of course, but it also had some devoted fans, and I have paid close attention to a repeated theme in their communications: what was wanted was a revision of the first edition, not a completely new book. I have therefore concentrated on corrections and revisions in all chapters, and have confined extensive new material to areas where the first edition had become seriously outdated. Specifically, there has been considerable expansion and change of the material about dinoflagellates, acritarchs and cryptospores, as well as about the subjects of palynodebris, palynofacies, paleoecology, thermal alteration of palynomorphs, and the application of palynology to sequence stratigraphy. The glossary has also been extensively revised. I remain convinced that this book provides most of the information necessary to teach a good university/college course on palynology, although I am also aware that it will continue to serve frequently as a handy one-volume reference to palynological subjects.

Preface to the First Edition

This book is intended to fulfill a need which I have recognized through nearly two decades of teaching paleopalynology. My approach in teaching the subject has always been laboratory-centered and has emphasized learning by seeing and doing. This seems natural to me, as paleopalynology is not really a unified subject with an easily definable core of subject matter and a unified approach to its study. Rather, it is the application of a wide variety of techniques to the study of a hard-to-define, extremely diverse set of subjects. Inevitably a professor has favorite approaches and favorite aspects of a subject. Therefore my book obviously does not entirely cover all the possible areas of subject matter, nor does it cover the areas it does treat with an equal degree of thoroughness. Nevertheless, students from my courses have fairly often managed to commence practicing palynology with only my introductory, one-term course, followed by a term of rather independent laboratory work in my problems course. I believe that this book alone will enable even college teachers with little previous experience in the subject to present an adequate course in paleopalynology.

The shape of the book follows that of my course, definition and discussion of the subject matter of paleopalynology, followed by a stratigraphically based survey of palynofloras, and finally by a closer look at "non-pollen" palynomorphs such as dinoflagellate cysts, at "satellite" matters such as carbonization (= "maturation" or coalification) studies, and at some applicable techniques.

Bibliographies are not presented chapter-by-chapter as is often done in this sort of text, because I have frequently been annoyed by this. When one wants to find a certain reference, it is often maddening to have to figure out after which chapter to look. I really see no advantage to the piecemeal bibliography. The reader will find all references together in the back of the book.

Because mine is a laboratory-based approach to the subject, I present in the Appendix applicable laboratory techniques, a flowsheet for processing, and so forth. Ideally, my whole paleopalynology course should be two terms, or a year where the semester system exists. Ideally, also, students taking the course should have a basic understanding of both biology and geology. However, under the circumstances applying at our university, if I were to attempt to realize all of the above-mentioned "ideals," there would not be enough qualified, interested students, with enough spare semester slots for such an elective course, to satisfy the minimum enrollment requirement in force here.

Acknowledgments for the Second Edition

The second edition, as the first, has been a joint project with my wife, Dr. Elizabeth I. Traverse, who since the first edition has earned her Ph. D. in a totally unrelated field, medieval German literature, and in recent years has published more pages in her specialty than I have in mine. Her contributions in helping me convert this palynological work to modern form, via computer programs, scanners, word-processing, etc., and her encouragement, have been critical to whatever success the project has. Personnel in the Earth and Mineral Sciences Library of the Pennsylvania State University have been very generous with their help in tracking down various pieces of literature. William Ammerman, of the Camera Shop, State College, PA, has been generous far beyond the call of duty with his time in helping me get new illustrations, as well as those from the first edition, into suitable electronic form for this edition. Concerning my colleagues in palynology, so many have helped me so much that it is difficult to whittle the list down to one that one can reasonably include in this book. Jan Jansonius began the whole revision process in 1988–89 with a many-page contribution regarding mistakes in the first edition, and he has continued to be a source of wisdom over the years since, right down to a day or two ago. Paul K. Strother, a former student of mine, has assisted me greatly with updating parts of the book dealing with ancient acritarchs and cryptospores. Martin B. Farley, another former student, has also helped me with various matters from time to time, even suggesting wording for several sections. Gordon D. Wood has been helpful in connection with many palynological subjects at various stages of the project, and it is appropriate that one of his chitinozoans is displayed on the book's cover. Speaking of that reminds me of Rodolfo Dino, whose marvelous collage of palynomorphs makes up the main panel of the cover. David J. Batten was extremely generous with his time in helping me bring the palynofacies and thermal alteration sections up to date, especially with preparation of plates of color photomicrographs. Robert A. Fensome and James B. Riding helped me greatly with illustrations and information about dinoflagellates and other matters. W. G. Chaloner, one of the principal editors of, contributor to and fan of, the first edition, continued his assistance into the second edition, especially by allowing me to use his interesting stratigraphic key to fossil palynomorphs. Reed Wicander contributed acritarch illustrations and advice about revising my treatment of the group. Geoffrey Playford, always a booster for the first edition, also provided acritarch and other illustrations. V. A. Krassilov obtained several important illustrations for me. Stewart Molyneux gave me access to early Paleozoic acritarch photomicrographs.

Poul Schiøler permitted use of many of his pictures of Cenozoic dinoflagellate cysts. Oscar A. Abbink permitted me to republish his paleoecology/sequence stratigraphy chart, as did Jorunn Vigran for a chart of palynofacies vs. stratigraphy. Robert K. Booth, a former student, helped me with information about testate amoebae. N. J. Butterfield allowed me to use an illustration of a delicate non-palynomorph ancient microfossil. Carlos A. Jaramillo permitted use of his illustration of the coordinated use of various modern statistical, stratigraphic and geochemical tools in conjunction with palynological analyses. Catherine Duggan helped me adapt her graphical presentation of thermal alteration of Paleozoic acritarchs for my section on T. A. Edith Taylor helped me repeatedly with questions about the literature and about various palynological matters impinging on megafossil paleobotany. John M. McNeill was very helpful with questions relating to my revision and expansion of the section on nomenclatural matters. I am certain that combing my memory at this juncture has failed to turn up a "card" for others who contributed to this project. In some instances it will probably be obvious from captions or statements in the text that I had help from various colleagues I have neglected to list. I apologize in advance to everyone I should have mentioned here but have failed to do so. Finally, I must mention that this project has been underway for so many years that the responsible publishers have changed names and locations several times. I am grateful to all of the editors for their indulgence, but I would especially like to acknowledge the patience and helpfulness in the final stages of the responsible editorial person at Springer, Judith Terpos.

Acknowledgments for the First Edition

Obviously the author of a book such as this has been aided by a great array of people. This particular project has first of all been in many senses a joint effort shared by my wife, Elizabeth Insley Traverse. She has been research assistant, typist, word-processor operator, consultant, adviser, and much more. I am very grateful to her for all of this. The "official" reviewers selected by the publisher, W. G. Chaloner and A. C. Scott, have assisted me immeasurably with suggestions for changes, additions, deletions, and in finding errors. I have incorporated almost all of their recommended alterations. The same is true of C. W. Barnosky, who "unofficially" but very thoroughly reviewed the Cenozoic material and the subsequent chapters on pollen sedimentation and so forth, and the Appendix. Nevertheless, errors that remain are not to be laid to these reviewers' account, as most of them probably stem from either my failure to respond adequately to their criticism, or to material I have added since their reviews. I am grateful to K. J. Hsü for his encouragement of the project while I was at the Swiss Federal Technical Institute ("E.T.H.") Zürich, in 1980–8l. Colleagues at E.T.H., R. Hantke and P. Hochuli, also have been helpful. Dozens of colleagues assisted by providing illustrative material and by reviewing the drafts of resulting figures. These persons are mentioned below in connection with credits for various figures. That sort of mention stands as admittedly far too meagre acknowledgment and expression of thanks for their inestimable help. All of my graduate students during this period have helped me in one way or another, especially by being sounding boards: D. K. Choi, V. S. Ediger, M. B. Farley, N. G. Johnson, R. J. Litwin, E. I. Robbins, D. J. Rue and A. Schuyler. Former students, B. Cornet and D. J. Nichols, helped in a similar way. Dozens of people gave advice over the telephone or by letter (the file of such correspondence runs to many hundreds of items). It is not possible to acknowledge all such valuable help except by this general statement of hearty thanks! However, the patience and goodwill of Roger Jones, Director of Academic Publishing for Unwin Hyman, at all stages of this work, simply must be mentioned. Also, the assistance of D. G. Benson with some troublesome figures of phytoplankton, not one of my areas of expertise, is gratefully acknowledged, as is similar help with fungal spores by W. C. Elsik, and with sporopollenin and chitin diagenesis by K. J. Dorning. For the liberal use of the various excellent facilities in the Department of Geosciences at Penn State, I am also very thankful. (Eight pages of "Specific Acknowledgments to Figures and Tables," being citation

of sources for all illustrations was also placed here in the first edition, but that was an egregious blunder that confused many. One of my esteemed colleagues even asserted in print that I did not acknowledge my sources. In the second edition, all such matter is transferred to the captions, where it belongs.)

Cover Illustration

Main block (1) is a collage of all major categories of palynomorphs: pollen, spores, dinoflagellate cysts, acritarchs, chitinozoans, scolecodont. Prepared by Dr. Rodolfo Dino, Petrobras/UERJ, Brazil. Smaller photomicrographs at the top, from the left, are: (2) *Ramochitina guilloryi* Wood, Devonian chitinozoan, Bolivia. Published by Wood (2004) as a new species. Published by permission of the Assoc. Australasian Palaeontologists.; (3) Ubisch bodies from the pollen of morning glory, *Ipomoea* sp. The principal picture is a mass of ubisch bodies, as released by an acetolysed anther. Lower left is one isolated body, and upper left is a "pseudo-ubisch body," being a detached globose sculpturing element. All of the bodies are in the 10 μm range; (4) Foraminiferal test lining ("micro-foraminifera") from Recent sediment, Great Bahama Bank. The fossil is about 200 μm from top to bottom; (5) *Retispora lepidophyta* (Kedo) Playford, arguably the stratigraphically most important single species of sporomorph ever discovered. This specimen is 75 μm in max. dimension and is from Catskill Fm., uppermost Devonian, Centre Co., PA, USA.

Contents

Chapter 1

What Paleopalynology Is and Is Not

1 Definition of the Subject

There are those who would insist that palynology, and hence also paleopalynology, applies only to pollen and spores or, more specifically even, only to pollen and the spores of embryo-producing (embryophytic) plants. And it is true that Hyde and Williams (l944) had that in mind when they coined the term palynology, a word from the Greek παλυνω ("I sprinkle"), suggestive of "fine meal," which is cognate with the Latin word *pollen* ("fine flour," "dust"). However, that is not the way most paleopalynologists use the term. Instead, they use a pragmatically based working definition, saying in effect that paleopalynology consists of

the study of the organic microfossils that are found in our maceration preparations of sedimentary rocks, i.e. "What my net catches is a fish." This means palynomorphs, the microfossils which are the subject matter of this study, consist at least partly of very resistant organic molecules, usually sporopollenin, chitin or "pseudochitin" (there are some few exceptions). Palynomorphs are also by common consent in the approximately 5–500 μm(= micrometer = micron = μ) size range. Many megaspores are larger, and some "seed" megaspores of the late Paleozoic are much larger. Species of *Tuberculatisporites* are reported by Potonié and Kremp (1955) to be 3000 μm(= 3 mm!), and *Cystosporites* megaspores are even larger–3 × 8 mm (Schopf, 1938). From my pragmatic point of view, such huge spores are beyond the pale of palynology–in megafossil paleobotany. That is not meant in any way to denigrate the study of megaspores! On the other hand, nannofossils are not palynomorphs on two scores. First, they are calcium carbonate ($CaCO_3$) and hence are destroyed by the dilute hydrochloric acid (HCl) we usually employ as a first treatment in palynological maceration of sediments. Secondly, they are also too small, prevailingly less than 5 μm. Diatoms are not palynomorphs, although they are in the right size range, because they are usually siliceous and destroyed by the hydrofluoric acid (HF) that is the major weapon in the paleopalynological armory. The same is true of phytoliths, usually consisting of silica or calcium oxalate, produced typically by grasses and sedges. They are very useful in various forms of environmental reconstruction (cf. Meunier and Colin, 2001; Piperno, 2001; Piperno and Stothert, 2003). These are also in the correct size range but are dissolved by the acids in conventional palynological maceration. A curious oddity is the report of spores and pollen that are apparently permineralized and lack residual sporopollenin (Srivastava and Binda, l984). According to my definition, such fossils, though spores and pollen, are not palynomorphs, because they would not appear in palynological residues prepared with hydrochloric and hydrofluoric acids! Another problem with my definition is typified by work such as that of Butterfield (2005), in which chips of sedimentary rocks are very carefully and gradually treated with hydrofluoric acid, with no crushing of the rock fragments, no centrifugation, as little agitation as possible, no harsh chemicals other than the HF, and handpicking of the very fragile specimens out of water with pipettes and other tools. An illustration of a very delicate late Proterozoic specimen obtained in this manner is displayed here as Fig. 1.1 (see also comments in Appendix, under decantation methods).

Work with such specimens is certainly marvelous paleontological science and very important, but their study is not strictly speaking part of paleopalynology, because the fossils are not robust-walled and therefore are not "fish caught by our nets." Our subject depends on obtaining whole assemblages of abundant, at least relatively robust-walled specimens, data from which we use for stratigraphy, paleoecology and related matters. This is just a fact and does not denigrate the importance of fossils such as the *Tappania* specimen illustrated, in conjunction with paleopalynological studies.

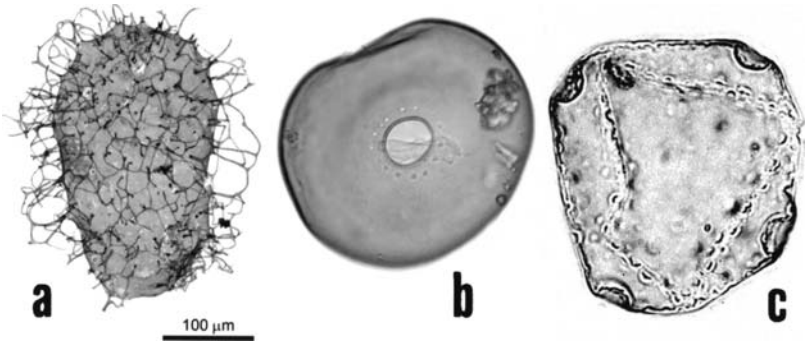


Figure 1.1 How to qualify as a palynomorph. (**a**) *Tappania* sp., from late Proterozoic rocks of northwestern Canada. This beautiful but very delicate organic microfossil of possible fungal origin was recovered by Butterfield (2005) by HF digestion of the rock with no agitation, no centrifugation or other chemical treatments routinely employed in paleopalynology. I processed a sample of the same rock given me by Butterfield, using ordinary paleopalynological techniques and obtained no palynomorphs. Technically, the specimen illustrated here does not qualify as a palynomorph, because it is not robust-walled. That does not detract from its great interest as a fossil. Photo courtesy of N. J. Butterfield. (**b**) *Arcella artocrea* Leidy, a testate amoeba. Holocene peat, Michigan. Tests of this species and some other such amoebae are proteinaceous and moderately resistant to basic palynological processing: centrifugation, the acids used in maceration, etc. At least some testate amoebae are therefore palynomorphs which can be usefully studied for information about environments of deposition, especially of lakes and ponds. Tests of other species of the group are not robust and would not qualify as palynomorphs. Specimen 190 μm in diameter. Photo courtesy of R. K. Booth. (**c**) Zygospore of *Mougeotia* sp., a zygnemataceous green alga from late Pleistocene of the Netherlands. This algal zygospore contains enough sporopollenin to render it somewhat robust-walled. Zygnemetaceous zygospores are typical of some fresh-water sediments and although rather atypical both taxonomically and environmentally, they are definitely palynomorphs. Specimen 45 μm in maximum dimension. Photo courtesy of Bas van Geel.

Palynodebris is organic "junk"=organic matter ("OM") found in palynological preparations along with palynomorphs, even though not consisting to any significant extent of sporopollenin or chitin. Some of it is more or less structured plant material, such as charcoal or even cellulosic tissue fragments that escaped hydrolysis or acid digestion. Some of it is amorphous ("AOM"). Palynodebris is now an important subject matter of paleopalynology for its relevance to questions of palynofacies/environment relationships. Charcoal in particular is a very abundant and frequent constituent of palynodebris and can be analyzed as to quantity and type, potentially revealing much about the environment at the time of deposition (see Whitlock and Larsen, 2001).

There is a small problem related to the "paleo" part of our subject's title. That means that paleopalynology deals specifically only with palynomorphs that are fossils. I take a very liberal view of what constitutes a fossil palynomorph, defining it as any body that answers to the requirements given above for palynomorph, and which comes from some sort of sediment or debris in the earth's crust, representing past life. How far past? I don't think that is worth arguing about– I would regard pollen, spores, dinocysts found in any sample of the earth's crust, including spores found in surface sediment, water or ice as fossils. The current edition of the AGI *Glossary of Geology* (Neuendorf, 2005) only insists that fossils represent the geologic past, but that includes yesterday as well as the Precambrian. I therefore reject as hair-splitting the term "subfossil," which is defined in the same *Glossary* as being what would otherwise be a "true" fossil, but is less than 6,000 yrs. old. It is self-evident that paleopalynology, but not other aspects of palynology, is a subset of micropaleontology and thus of paleontology. Fig. 1.2 illustrates the common sorts of palynomorphs, and Fig. 1.3 presents the range in time of the various categories of fossils. See also color illustrations of palynodebris later in the book.

The word palynology should be pronounced pal-ih-nol-o-jee. The first "a" is pronounced as a in map. Avoid "pahl…" or "pohl…", as if directly taken from the word pollen. Avoid also "pail…", suggesting by the beginning of the word that it comes from "paleo-", as in paleontology. That restriction applies to paleopalynology, but not to branches of palynology such as the morphology of modern pollen.

The textual material that follows describes the categories of things included in the subject paleopalynology, more or less in order of stratigraphic appearance.

1.1 Acritarchs

(Fig. 1.2f. Range: Proterozoic to present.) The term means "of undecided or doubtful origin" (Greek: ακριτοσ-αρχη). It was introduced by Evitt (1963) as part of a package to replace an older grab-bag term, hystrichosphaerid ("spiny sphere"; also by analogy to the genus, *Hystrichosphaera* Wetzel, a synonym for *Spiniferites* Mantell). Many of the former hystrichosphaerids were shown by Evitt and by Wall to be dinoflagellate cysts. The "hystrichosphaerids" which could not be shown to be dinoflagellate cysts were then left as "acritarchs." However, the term now includes a very large range of presumably algal bodies, mostly marine (but there are many brackish-water or freshwater forms including probable green algal akinetes and hypnozygotes), ranging from less than 10 μm to more than 1000 μm, but mostly 15–80 μm, well within the palynomorph size range. (cf. Wicander, 2002). The wall contains sporopollenin or a very similar compound. They may be more or less psilate, scabrate, spiny, reticulate, and a nearly bewildering array of other sculpturing types. They first appear in the Proterozoic as simple more or less spherical, more or less featureless monads

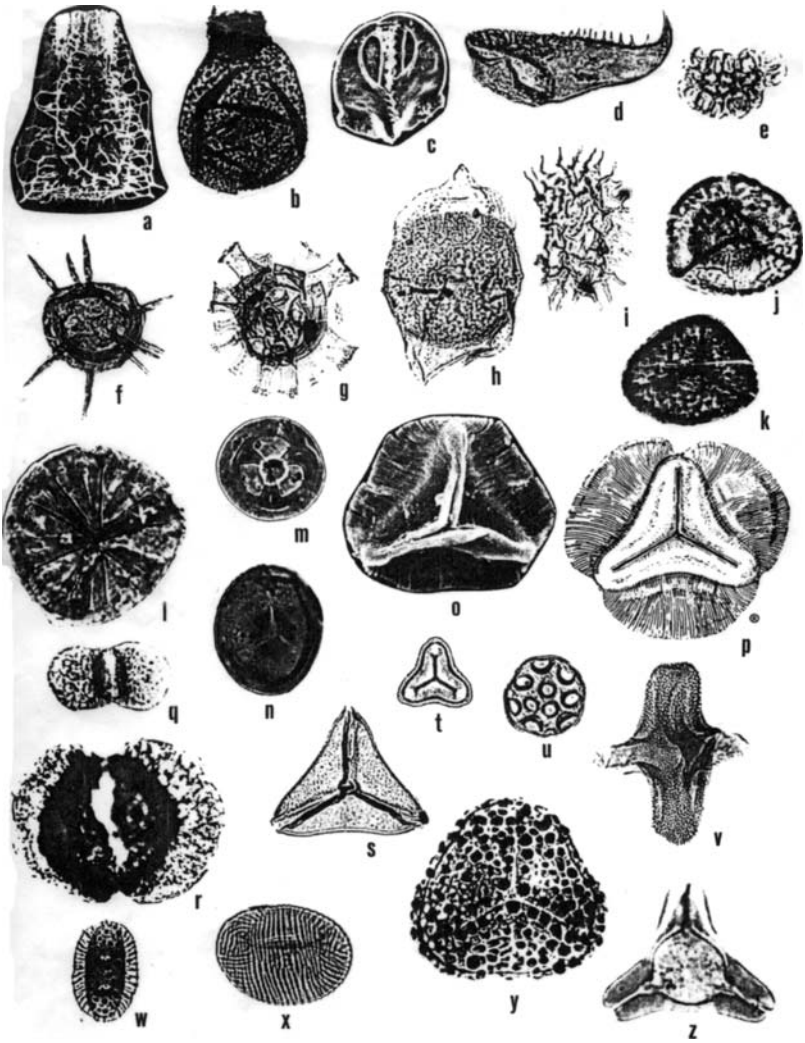


Figure 1.2 *(See caption on page 7)*

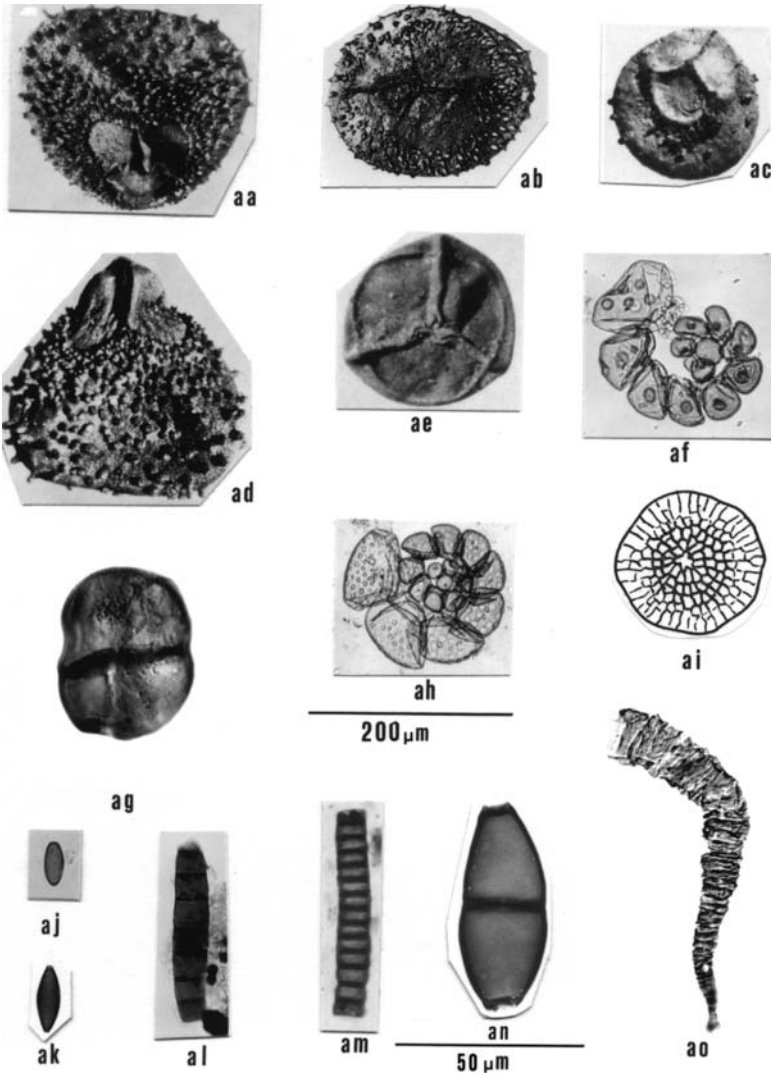


Figure 1.2

Figure 1.2 Palynomorphs of various categories and geologic ages, illustrated by photomicrographs (PM) (= transmitted light, made with a light microscope–LM), microphotographs (MP) (= reflected light, relatively low power), scanning electron micrographs (SEM) and line drawings. All major categories of palynomorphs are included: "microforams," chitinozoans, scolecodonts, colonial algae, acritarchs, dinoflagellates, cryptospores, isospores, microspores (cannot be distinguished on morphology alone from isospores), megaspores, pollen, and fungal spores. Because the fossils come from many sources and represent specimens in many different size ranges, the magnification varies considerably. Approximate size of each specimen is indicated in micrometers, except that a bar is provided for the fungal spores (ai)–(an). (**a**) Chitinozoan: *Herochitina* sp., Upper Ordovician, England. SEM by W. A. M. Jenkins, length 200 μm. (**b**) Chitinozoan: *Kalochitina multispinata* Jansonius. Upper Ordovician, Oklahoma. PM by R. W. Hedlund, length 150 μm. (**c**) Scolecodont: *Xanthoprion albertensis* Jansonius and Craig. Dorsal view of partial apparatus. SEM by J. Jansonius, length 350 μm. (**d**) Scolecodont: *Arabellites* sp., Upper Ordovician, Oklahoma. PM by R. W. Hedlund, length 150 μm. (**e**) Colonial alga: *Botryococcus* sp., Oligo-Miocene, New South Wales, Australia. PM, length 40 μm. (**f**) Acritarch: *Baltisphaeridium* sp., Upper Ordovician, Oklahoma. PM by R. W. Hedlund, diameter 100 μm. (**g**) Dinoflagellate cyst: *Hystrichokolpoma unispinum* Williams & Downie, Lower Cretaceous, Ellef Ringnes Island, Arctic Canada. PM by C. J. Felix, diameter 85 μm. (**h**) Dinoflagellate cyst: *Deflandrea granulifera* Manum, Upper Cretaceous, Ellef Ringnes Island. PM by C. J. Felix, length 120 μm. (**i**) Algal coenobium (special kind of colony): *Pediastrum* sp., Upper Pleistocene, Black Sea. PM, length 50 μm. (**j**) Spore: *Retispora lepidophyta* (Kedo) Playford (= *Spelaeotriletes lepidophytus* (Kedo) Keegan, Uppermost Devonian, Pennsylvania. PM, diameter 70 μm. (**k**) Spore: *Rugospora flexuosa* (Jushko) Streel, Uppermost Devonian, Pennsylvania. PM, diameter 70 μm. (**l**) Spore: *Emphanisporites robustus* McGregor, Upper Devonian. PM by R. W. Hedlund, diameter 65 μm. (**m**) Spore: *Knoxisporites stephanephorus* Love, Upper Mississippian, Oklahoma. PM by C. J. Felix, diameter 55 μm. (**n**) Spore: *Calamospora* sp., Uppermost Devonian, Pennsylvania. PM, diameter 70 μm. (**o**) Spore: *Reinschospora speciosa* (Loose) Schopf, Wilson & Bentall, Upper Mississippian, Iowa. SEM by J. B. Urban, diameter 65 μm. (**p**) Spore: as (o), Carboniferous. Line drawing by R. Potonié (Potonié and Kremp, 1954, p. 139) adopted as trademark of *Catalog of Fossil Spores and Pollen*. (**q**) Pollen grain: *Pityopollenites pallidus* Reissinger emend. Nilsson, (al. *Vitreisporites* and *Caytonipollenites*), Upper Triassic, Texas. PM, length 30 μm. (**r**) Pollen grain: *Platysaccus nitidus* Pautsch, Upper Triassic, Texas. PM, length 55 μm. (**s**) Pollen grain: *Expressipollis ocliferius* Khlonova, Upper Cretaceous, Ellef Ringnes Island, Arctic Canada. PM by C. J. Felix; diameter 65 μm. (**t**) Pollen grain: *Expressipollis accuratus* Khlonova, Upper Cretaceous, Ellef Ringnes Island. Compare with (s)–forms referred to the same form-genus of dispersed spores are often very heterogeneous. PM by C. J. Felix, diameter 30 μm. (**u**) Pollen grain: *Kuylisporites lunaris* Cookson & Dettman, Middle Cretaceous, Lougheed Island, Arctic Canada. PM by C. J. Felix, diameter 40 μm. (**v**) Pollen grain: *Aquilapollenites trialatus* Rouse, Upper Cretaceous, Alaska. PM by C. J. Felix, length 95 μm. (**w**) Pollen grain: *Wodehouseia spinata* Stanley, Upper Cretaceous, Alaska. PM by C. J. Felix, length 50 μm. (**x**) Spore: *Schizaeoisporites* sp., Middle Cretaceous, Oklahoma. PM by R. W. Hedlund, length 50 μm. (**y**) Spore: *Trilobosporites sphaerulentus* Phillips and

about 30 μm in diameter. Some palynologists follow Diver and Peat (1979) in separating off such bodies lacking spines, plates or other features suggesting algal affinity as *cryptarchs* (see Glossary and later discussion). However, it is as yet more common to include the types in the one category, *acritarch*. Acritarchs range to the present time, but their greatest significance and high point of abundance was reached in the early Paleozoic. Tappan (1980) shows that, after the early Jurassic, spiny acritarchs are rare and unimportant, and though leiospheres and some other forms continue to the present, acritarchs as a whole are not an important factor among extant phytoplankton. The statement in Pflug and Reitz (1985) that acritarchs "... finally disappear in the Pleistocene" is, however, too extreme. There are even some leiospheres and acanthomorphs in modern sediments.

Figure 1.2 Felix, Lower Cretaceous, Louisiana. PM by C. J. Felix, diameter 80 μm. (**z**) Pollen grain: *Nudopollis* sp., Paleocene, Gulf Coast, USA. PM by R. W. Hedlund, diameter 30 μm. (**aa**)-(**ae**) MP of megaspores; sizes are approximate. (**aa**) *Lagenicula acuminata* (Dijkstra) Dybová-Jachowicz *et al.*, Lower Carboniferous, Moscow Basin, Russia, 1, 800 μm. Proximal view showing prominent contact structure or gula. Although the parts of the gula look as though they could represent aborted spores, they are actually expanded contact faces. (**ab**) *Tuberculatisporites mammilarius* (Bartlett) Potonié & Kremp, Carboniferous (Westphalian), Belgium. 1, 800 μm. Proximal view showing laesura and contact faces. (**ac**) *Triletes grandispinosus* Dijkstra, Lower Carboniferous, Moscow Basin. 1, 100 μm. Proximal view, showing trilete laesura with curvaturae perfectae and contact faces. (**ad**) *Triletes acuminata* (Dijkstra) Dybová-Jachowicz *et al.*, Lower Carboniferous, Moscow Basin. 1, 800 μm. Lateral view for comparison with (aa). Note prominent proximal gula (see comment under (aa)). (**ae**) *Triletes patulus* Dijkstra, Lower Carboniferous, Moscow Basin. 800 μm. Proximal view showing trilete laesura and contact faces. Raised figure of laesura has characteristic flaps near center which are sometimes called "tecta." (**af**) PM of the chitinous inner tests of spiral foraminifera, recent sediment, Great Bahama Bank. Size indicated by bar under (ah). (**ag**) Cryptospore: cf. *Pseudodyadospora* sp., Lower Middle Ordovician, Saudi Arabia. Maximum dimension 35 μm. (**ah**) PM of the chitinous inner tests of spiral foraminifera, recent sediment, Great Bahama Bank. See also (af). (**ai**)-(**ao**) PMs of chitinous palynomorphs of fungal origin. Magnification as shown under (an). (**ai**) Drawing of characteristic flattened, multichambered, fruiting body (ascostroma) of a sort produced by some ascomycetes. *Asterothyrites* sp., Cenozoic (from Elsik, 1979). (**aj**) Small, non-aperturate fungal spore, recent sediment, Gulf of Mexico. (**ak**) Small diporate fungal spore, Pleistocene, Black Sea. (**al**) Chain of fungal spore units, with characteristic thickenings on septa, Pleistocene, Black Sea. (**am**) Chain of fungal spore units, with very thick septa, recent sediment, Gulf of Mexico. (**an**) Diporate, two-celled (septate) fungal spore body, Pleistocene, Black Sea. (**ao**) Organic-walled tentaculite zoomorph, Late Devonian, Poland. Maximum dimension 400 μm. (cf. Wood *et al.*, 2004). a-z reprinted by permission from Traverse, 1974a; aa and ac-ae reprinted by permission of Rijks Geologische Dienst, Heerlen, The Netherlands, from Dijkstra and Piérart, 1957; ab reprinted by permission from Piérart, 1955.

1.2 Chitinozoans

(Figs. 1.2a,b. Range: Late Cambrian to Latest Devonian.) These are pseudochitinous palynomorphs for which there have been several suggestions as to the source organisms. One of these is graptolites (see Jenkins, 1970), for which relationship the arguments are circumstantial but interesting (chemical similarity, frequent association, close agreement in stratigraphic limits). The suggestion of fungal relationship (Loquin, 1981) seems improbable. The best known experts on the groups at present (Paris *et al.*, 2004) will go only so far as "...eggs of soft-bodied marine metazoans." They first appear in Cambrian rocks, are most abundant in the Ordovician and become extinct by the end of the Devonian time. They are found only in marine rocks, unless reworked. They sometimes occur in chains, but usually as single "individuals." Because of their thick, more or less opaque walls, they are usually best studied by scanning electron microscopy (SEM), although LM study of broken surfaces frequently reveals important structural details. Because they are not present in the abundance often seen for spores/pollen and acritarchs (about 10^2/g range instead of 10^3–10^5/g range), larger samples must be processed. For this reason and because large specimens are easily broken, somewhat different processing techniques must be employed.

1.3 Scolecodonts

(Figs. 1.2c,d. Range: Lower Ordovician (Arenigian) to present.) These are chitinous mouthparts of polychaetous, mostly marine annelid worms. Although they range from Cambrian to the present, they have been mostly studied in Paleozoic rocks. As is true of chitinozoans, scolecodonts mostly occur in the range up to 10^2/g and require different processing techniques from those for spores/pollen, though fragments are frequently encountered in slides from conventional macerations. As pointed out by Jansonius and Craig (1971), the mouthlining parts from one worm may exist united or dispersed, and the dispersed parts may not all be alike. The taxonomy is therefore difficult.

1.4 Microscopic Algae and Algal Parts

(Figs. 1.2e,i. Range: Ordovician to present.) *Botryococcus* (Fig. 1.2e) is a colonial alga occurring in a wide range of freshwater to brackish aquatic environments. The walls of the colonies that are preserved apparently consist partly of hydrocarbons; the hydrocarbon "mineral," coorongite, consists largely of *Botryococcus* colonies. There is some evidence that the walls also contain sporopollenin. Although I once described a "new species," I now regard all *Botryococcus* colonies as representing *B. braunii* Kutzing, which would be, if this is correct, a candidate for the oldest surviving species of Plantae, ranging from Ordovician to the present.

Niklas (1976) has shown *Botryococcus*, both extant and fossil, to possess an extraordinarily diverse suite of organic compounds. Stratigraphically and paleoecologically almost worthless, *Botryococcus* must nevertheless be treated here, as it is found so commonly in palynological preparations. The other principal "colonial" alga occurring as a palynomorph is *Pediastrum* spp. (Fig. 1.2i), the various species of which range from early Cretaceous to present. Although it is multicellular, it is more precise and technically correct to call it a green algal coenobium, as the number of cells is fixed at the origin of the organism. The resistance to biodegradation of *Pediastrum* is one of the puzzles of palynology. The wall seems to be fairly delicate and cellulosic and should be hydrolyzed quickly. Obviously the walls must be impregnated with something additional, presumably sporopollenin The various species of *Pediastrum* are all freshwater forms. Sporopollenin-containing microscopic parts of various green algal forms such as Zygnemataceae zygospores (see Fig. 1.1) and Prasinophyceae phycomata (see Fig. 12.1 and associated text) are found occasionally as constituents of terrestrial and near-shore marine sediments of Paleozoic to present age. For an introduction to various other microscopic algal bodies that appear from time to time as palynomorphs, see Colbath and Grenfell (1995) and Van Geel (2001). Prasinophyte algal phycomata such as the tasmanitids are also commonly found algal palynomorphs (see Fig. 12.1).

1.5 Cryptospores

(Fig. 1.2a–g. Range: Cambrian to Silurian.) Cryptospores are spore-like bodies in the normal spore size range, with walls containing sporopollenin, but lacking the haptotypic characters, such as a trilete laesura, that typify true spores. Cryptospores presumably are spore-like reproductive bodies of plants representing an intermediate stage between aquatic algae and land plants. Some of the producing plants may well have been comparable to modern bryophytes, especially to liverworts.

1.6 Embryophyte Spores

(Figs. 1.2j–p, x,y. Range: Upper Ordovician to present.) Embryophytes are all plants that make true embryos in their life cycle: Bryophyta, Pteridophyta, and all seed plants. Embryophytic plant spores actually include pollen, in the sense that the exines of pollen we study as sporomorphs are the microspore walls of seed plants (see Pollen below, and presentation of life-cycles in Chapter 4). However, for palynologists, "spore" as usually employed refers to sporopolleninous microspores and homospores (= isospores) of embryophytes. Embryophyte pollen, megaspores, and fungal spores are thought of as "different," despite the fact that pollen and free megaspores are sporopolleninous and clearly

are part of the same category as "spores." Fungal spores are equally clearly another story, as the fungi are more closely related to animals than to plants.

1.7 Pollen

(Figs. 1.2q–w, z. Range: latest Devonian to present.) The definition of pollen is not morphological but functional: the microspore wall of seed plants, plus the microgametophyte that develops within the wall. Only the outer microspore wall survives as a fossil. The earliest pollen grains were not at all different morphologically from isospores or microspores, and they had haptotypic features like a spore and even germinated proximally like a spore in order to release their gametes. Such pollen is called "prepollen" (Chaloner, 1970b). We would not realize that they are pollen except for the fact that they are known from paleobotanical investigations to be the fecundating element of seed plants. Later gymnosperm, and especially angiosperm, pollen differ markedly in morphology from spores. Chemically, the walls are apparently the same, that is, sporopolleninous. Biologically, a whole mature pollen grain represents a plant generation and is therefore, in a sense, a haploid plant. In fact, whole (haploid) plants can be grown in culture from a single pollen grain. Nitzsch and Nitzsch (1969) produced tobacco plants by culture from single pollen grains. The plants mature normally and flower but, as they are haploid, they do not undergo meiosis properly and cannot set seed.

1.8 Dinoflagellates

(Figs. 1.2g,h. Range: (Cambrian?)–Late Triassic to present.) Sporopolleninous cysts of dinoflagellates are common from Late Triassic rocks to present, mostly in marine environments, but also in sediments deposited in fresh and brackish water. The range problem indicated above has to do with the difficulty of proving that a given cyst is a dinoflagellate. This requires certification of the presence of dinoflagellate-type archeopyle-operculum, and/or dinoflagellate plates and related morphological features. Many Paleozoic cysts from as early as the Cambrian may be of dinoflagellates, but the required proofs are not present in sufficiently convincing manner. Molecular and other chemical studies in recent years strongly support pre-Triassic existence of the group (see Hackett *et al.*, 2004). On the other hand, many brackish-water or freshwater dinoflagellate cysts are more or less featureless "bags" that require examination of thousands of specimens to prove that a dinoflagellate made them, e.g., in Black Sea Deep-Sea Drilling Project (DSDP) cores (see Traverse, 1978a).

1.9 Chitinous Fungal Spores and Other Fungal Bodies

(Figs. 1.2ai–ao. Range: Jurassic (?) to present.) Although the kingdom Fungi ranges from Proterozoic to present, these organisms did not until the Jurassic

(Elsik, pers. comm., 1981) commonly produce chitinous walls in hyphae or spores, permitting preservation as maceration-resistant fossils. There are some Permo-Triassic exceptions, but they are scarce as a rule. An alleged "spike" of them in some places near the Permian/Triassic boundary (see Steiner *et al.*, 2003) has been challenged on the basis that the "fungal fossils" are probably algal (Foster *et al.*, 2002), but a spike of fungal spores and hyphae at or near the Cretaceous/Cenozoic boundary, probably as a result of huge volumes of dead vegetable matter (Vajda and McLoughlin, 2004) seems plausible. The fact of chitinous fungal remains found in the Late Jurassic onward and becoming abundant in the Cretaceous coincides with the rise of the angiosperms, and it is tempting to think that the development of abundant chitinous walls by fungi is somehow related to their exploitation of the flowering plants. "Spore" in the fungi is a far different concept from "spore" in embryophytic plants. There are many kinds of fungal spores: conidiospores, ascospores, basidiospores, etc. Some are sexually produced, others asexually. They may be single-"celled" or multi-"celled". Many of the things loosely called by paleopalynologists "fungal spores" are actually not strictly spores, e.g., ascocarps and ascomata. Also, pieces of chitinous-walled vegetative tissues of fungi occur as palynomorphs: hyphae and mycelia (see Fig. 1.2ao). It would be good to check the hypothesis that resistant-walled fungal parts are really always chitinous. The statement that they are is based mostly on the knowledge that chitin does occur in the Fungi and is a resistant substance. Fossil fungal spores are almost all derived from Ascomycetes.

1.10 Microforaminiferal Inner Tests (= "Microforaminifera")

(Figs. 1.2af, ah. Range: Devonian (?) to present.) These frequently occur in paleopalynological preparations of marine rock, especially in Cenozoic sediments. They represent the chitinous inner tests of foraminifera, almost always of planispiral forms. The size range is very much less than that of the foraminifera from which they are presumed to have come. The jury is still out on the question of how they are produced and how they should be treated taxonomically: are they in general referable to particular existing foraminifera taxa (some certainly are), etc.? (See Tappan and Loeblich, 1965; Traverse and Ginsburg, 1966; Cohen and Guber, 1968.) The assertion that they are chitinous is based on the fact that the substance behaves and looks like chitin. In some papers, microforaminiferal tests are referred to as "Scytinasciae," citing Deák (1964), but I regard this as systematically unnecessary and not helpful.

1.11 Megaspores

(Figs. 1.2aa–ae. Range: Lower Devonian to present.) Megaspores are the spores of heterosporous embryophytes, inside of the walls of which the megagametophytes

develop. The common practice in paleopalynology is to follow Guennel (1952) in setting an arbitrary lower size limit at 200 μm. The first such large spores occur in the Emsian stage of the latest Lower Devonian. They represent an evolutionary stage or "experiment" largely superseded by development of seeds, and reached the peak of their development in Carboniferous time. There have remained some heterosporous lycopsids and ferns producing free megaspores ever since, and hence fossil megaspores have been preserved in sediments. After the Cretaceous they are not abundant, but they can be common locally and paleoecologically useful. Chemical constitution is apparently sporopollenin. In fact, sporopollenin even occurs in some gymnosperm megaspores that are a developmental stage in producing seeds. Such megaspores are not dispersed as such but are encountered as relicts in developed seeds. N.B. Some palynologists use the term "mesofossil" for a particle of plant material larger than 200 μm, clearly not a palynomorph, yet requiring microscopy for study, such as a tiny seed (Batten, pers. comm., 2003). As could be deduced from my definition of palynomorph, I regard the term "large palynomorph," used by some authors for things in the millimeter size range as an oxymoron. "Small palynomorph," for palynomorphs smaller than 200 μm, on the other hand, is useful for referring to palynomorphs in that size range that are not miospores, such as some foraminiferal linings, for example.

1.12 Palynodebris

(Figs. 18.4–18.5a Range: Proterozoic to present.) Palynological preparations always contain more-or-less organic "junk" not referable to specific palynomorph classes. Coal petrologists and palynologists have made a virtue of this by studying the color and/or reflectivity of pellets of such things (plus palynomorphs) to determine the geothermal history of a sedimentary rock. Such material is collectively designated palynodebris. Four categories of such particles are especially common and are occasionally useful to paleopalynologists: (1) wood (tracheids, wood fibers, vessel elements), (2) cuticular-epidermal leaf fragments, (3) ubisch bodies (orbicules), and (4) variously degraded algal and other plant tissues. Wood fragments in palynological preparations can seldom be systematically identified, almost never closer than to a class, e.g. "conifer tracheids." Their abundant presence in a shale, however, usually indicates lagoonal or deltaic environment. When carbonized, such woody material is charcoal, and counts of the abundance of charcoal is sometimes an important environmental indicator. Cuticular fragments, especially if well preserved stomata are present, on the other hand, can often be identified. However, their identification is a complex matter, a field of its own, and few palynologists do more than report presence. Very abundant presence in shale usually indicates lacustrine or fluvio-lacustrine deposition. Some palynologists use relative amounts of cuticles, wood fragments, sporomorphs, dinoflagellate cysts, etc., for "palynofacies" (more specifically this

is palynolithofacies) studies: (see discussion in Chapter 18). Ubisch bodies, also called orbicules, are tiny bits of sporopollenin about 1–5 μm, which consist at least in part of sporopollenin left over by the tapetum in laying down the exine of spores and pollen. They are occasionally abundant in paleopalynological preparations. I am not aware that they are at present regarded by anybody as indicating much paleoenvironmentally. Degraded algal and other plant tissues can sometimes indicate probable marine deposition. The total organic content of sedimentary rock found in palynological preparations is called OM for organic matter, and it can be sub-classified into categories that include the sorts of things mentioned above, as well as amorphous organic matter (=AOM, degraded plant and animal structures, which can be abundant in some sedimentary rocks).

1.13 Varia

In addition to the categories named above and illustrated in this chapter, additional kinds of organic particles are continually being found in palynological preparations. Most of them turn out to be animal remains of various kinds. Lepidopteran insect wing scales, for example, are chitinous and regularly show up, are in the palynomorph size range, and have a quite characteristic fan shape. So far, they are only curiosities for the palynologist, but one can imagine their becoming significant some day. Other sorts of chitinous arthropod remains such as insect skeletal parts, and crustacean parts of many sorts (see Korhola and Rautio, 2001) and even eurypterid cuticle pieces (cf. Miller, 1996a) also are frequently seen by paleopalynologists in their preparations, especially if the more corrosive treatments have been avoided. Van Waveren (1992, 1993) described and illustrated many more or less ovoid to spherical bodies in the palynomorph size range, evidently chitinous, which she identified as copepod eggs, and other copepod parts, from Holocene sediments of Indonesia. They survived full-scale palynological maceration. She also described tintinnid, apparently chitinous remains from the same sediments. In recent years there have been a number of studies of testate amoebae (see Fig. 1.1) in palynological preparations. These protozoans have shells at least partly in the palynomorph range; (some are larger). The shells that survive maceration have proteinaceous binding material either as a discrete wall material or as a binder for miscellaneous organic and inorganic particles. Study of testate amoebae in sediments can reveal important facts about the local hydrology during sedimentation (Beyens and Meisterfeld, 2001; Booth, 2002). Wood *et al.* (2004) report odd ribbed stocking-like bodies within palynomorph size range, from Devonian rocks, that represent the linings of tentaculites (see Fig. 1.2ao), an extinct animal ranging from Lower Ordovician to Upper Devonian, possibly related to molluscs. Hochuli (2000) has described robust organic-walled, microfossils found in macerations of Oligocene siltstones and resembling in

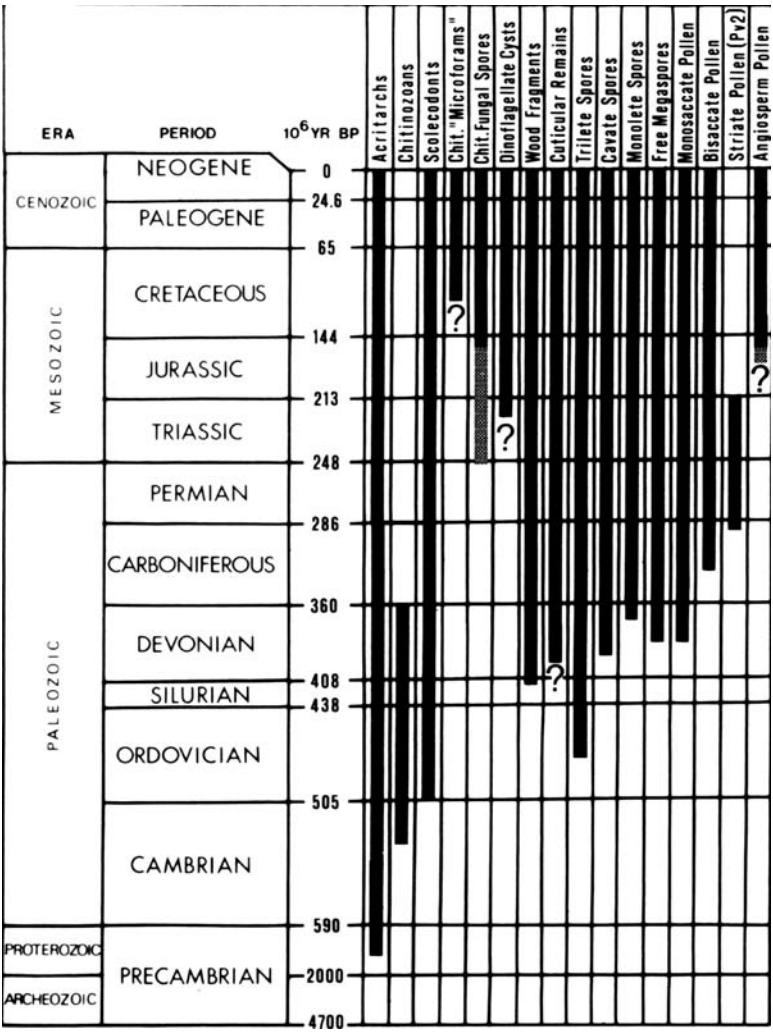


Figure 1.3 Range of occurrence in time of all major categories of palynomorphs, derived from the current literature. "Cuticular remains," column 8, refers to plant cuticular coverings. Depending on interpretation of problematic structures, such structures go back to early Silurian. "Pv2" after "striate pollen" means bisaccate. Striate (= taeniate) pollen other than bisaccate ranges to the present.

morphology the calcareous nannofossil taxon, *Braarudosphaera*, although five times as large. They presumably represent a stage in the life cycle of some algal species, and they must be considered palynomorphs, although nannofossils are not. Doubtless there are more such surprises in the rocks, but it is by now pretty

certain that the major groups of things belonging in the palynomorph category are those mentioned in this chapter.

The general stratigraphic range of palynomorphs is shown in Fig. 1.3. A liberal view of what is a palynomorph is assumed, in order to be as complete as possible.

2 Historical Matters

Wodehouse (1935) presents a marvelous history of the study of extant pollen grains and spores, and this book should be consulted by those who need more information about the early history of palynology-proper = "pollen analysis." A more modern summary of the history of pollen studies is presented by Ducker and Knox (1985). The development of pollen research follows the history of plant anatomy and morphology in general and is dependent to a large degree on developmental stages of the microscope. Nehemiah Grew first observed pollen microscopically in Britain about 1640. Malpighi noted differences in size and color of pollen about the same time. Various people later studied the biology of pollen and spores, especially with reference to the function of pollen in fertilization of ovules, in the 18th century. Camerarius usually gets credit for proving the maleness and fertilizing function of pollen in the late 17th century. Curiously, ancient peoples knew what pollen was for, and such aboriginal people as American Indians have understood the maleness, and the precise function, of pollen, apparently for thousands of years: pollen played a prominent role in some Indian puberty ceremonies. Southwestern Indians seem also to have understood the dietary advantage of eating pollen, long before health-food stores began promoting it (see Fig. 1.4). The Indians perhaps noticed that various insects, especially beetles and hymenopterids, use pollen as a major food staple.

In the 19th century, with the coming of much improved microscopes, the anatomy of pollen and spores was carefully studied and catalogued by German scientists, e.g., von Mohl (d. 1872), Fritsche (d. 1871) and Fischer (pollen work published in 1889). Robert Brown noted in 1809 that pollen could be used to advantage for systematic studies of seed plants, and Brown's illustrator, F. Bauer, described 175 species of pollen for this purpose (see Graham and Barker, 1981). Pollen morphologists of today continue the work of Brown, Fritsche and Fischer, employing better optical microscopes, and especially scanning and transmission electron microscopes (SEM, TEM). Ultramicrotome techniques, in conjunction with transmission electron microscopes (TEM) have played a critical role in recent years in elucidating the internal structure of the exine. The study of spore/pollen morphology has had impact on paleopalynology, of course, but the history of paleopalynology is in practice a separate matter.

The first person to describe fossil spores/pollen, and figure them in line drawing, was apparently Goeppert in Germany in 1838. *Alnus*-like and *Betula*-like pollen are easily recognizable in Goeppert's plates. Ehrenberg (Fig. 1.5a),

Figure 1.4 The vital, dynamic nature of pollen has long been recognized by humans in many cultures. The symbol shown above, from Silas John's Western Apache writing system (Basso and Anderson, 1973) bespeaks the ceremonial use of pollen by American Indians, symbolizing fertility, among other things. The pollen used by Silas John (a shaman) was apparently *Typha*, although the symbol would seem to represent a *Zea* tassel, the pollen of which was and is also used ceremonially by Indians. The jars illustrate the widespread modern use of pollen as a dietary supplement. Such pollen is sometimes harvested by human vacuum cleaners, sometimes taken from domesticated bees, which use pollen for hive nutrition. The human use is based on the vitamin, mineral, and nutritive (lipids, carbohydrates, amino acids) content of pollen. Apiaries sell untreated bee leg loads stripped from worker bees by a device at the hive entrance–hence the variously colored blobs in the jar, each being one leg-load. "Vibrant Health Bee Pollen" is compressed into tablets, for a considerable elevation in price per gram.

who pioneered almost everything in micropaleontology, certainly also saw them, and described what we later were to discover are acritarchs and dinoflagellate cysts in the 1830s. By 1867, Schenck was illustrating with good line drawings the *in situ* fossil spores he removed from fossil fern compressions. Reinsch in 1884 published the first photomicrograph of a fossil spore. It was of Carboniferous age, and the genus to which it belonged was long afterwards named, in his honor, *Reinschospora*, by Schopf *et al.* (1944). Bennie and Kidston published in 1886 descriptions of megaspores from the Carboniferous of Scotland. Actually, that is about where the paleopalynological matter ended for many decades, with somewhat peripheral exceptions, such as studies in the early 1900s by Thiessen of spores seen in Pennsylvanian coal thin-sections, and unpublished studies by Wodehouse of about the same time of pollen and spores in thin-sections of the Paleogene Green River Oil Shales.

However, the investigation of possible use of fossil (as some would say, "subfossil") spores/pollen in investigation of "post-glacial" or "Holocene" ("present interglacial" would perhaps be a preferable term for the last approximately 10,000 years) sediments went off rather independently, more or less unheeded by paleobotanists, about 1900. Details of this story are related by Erdtman (1954). A Swedish botanist, Lagerheim, realized that the pollen in, e.g., peats of Sweden, told the story of the vegetation in the vicinity of the

Figure 1.5 Important founding figures of paleopalynology: (**a**) Christian Gottfried Ehrenberg, 1795–1876; (**b**) E.J. Lennart Von Post, 1884–195l; (**c**) left, Gunnar Erdtman, 1897–1973; right, William S. Hoffmeister, 1901–80. From Saxony in Germany, Ehrenberg was originally a mycologist, but in 1837 he presented a paper to the Berlin Academy of Science, in which most of the major categories of what we now call palynomorphs

peat deposition, and he published some brief notes on preliminary studies based on rather primitive pollen spectra. Lagerheim himself depended on previous work based on geological and paleobotanical studies of Blytt, Sernander, and others, showing that vegetational changes marked the climatic history of the latest Neogene (Faegri 1974, 1981). It remained, however, for a Swedish assistant and student of Sernander, a protégé of Lagerheim, Lennart Von Post (see Fig. 1.5b), to put the subject on a sound footing with thorough studies of a number of cored sequences of Holocene peat in Sweden. The publication of Von Post's dissertation work in 1916 is usually accepted as the beginning of pollen-analysis or pollen-statistics, as such studies came to be known. Von Post was apparently not as versatile in languages as some Scandinavians (he published only in Swedish and German), and did not widely popularize the new subject outside of Scandinavia. That task fell to the one man who has probably most influenced the subject, Von Post's doctoral student, Gunnar Erdtman (Figs. 1.5c and 1.6a). A very gifted musician (flutist) and surrealist artist (see frontispiece "self-portrait" sketch in Fig. 1.6a of pollen analyst with flute!), Erdtman was urbane and very skilled at languages. (He was, in fact, so good at English and so confident of his talents that he would argue nuances of the language even with well educated, native speakers of English such as this writer! He was often, but not always, right!) He traveled widely, indeed he loved to travel, and wherever he went he practiced and "sold" palynology, e.g., trapping pollen grains with a vacuum cleaner on a transatlantic cruise. He was responsible for a great expansion of pollen-analytical/statistical studies in many parts of the world in the 1920s, 1930s and 1940s. The terminology he developed for pollen morphology came to be dominant, partly because of the pre-existing void, partly because of his talent for coining new terminology, sometimes even in anticipation of the discovery of features not yet found! Also,

◄

Figure 1.5 were described. The science of palynology is usually reckoned as commencing in 1916 with the introduction by Von Post of analytical pollen diagrams for post-glacial sediments. Von Post, a Swede, was developing ideas actually pioneered earlier by Gustav Lagerheim and others in Scandinavia. Von Post did not publicize pollen analysis much outside of Scandinavia, partly for linguistic reasons.

Erdtman, a younger one-time associate of Von Post's in Sweden, was urbane, fluent in various languages; he traveled very widely, evangelizing for the new scientific method. To Erdtman should go most of the credit for putting fossil spores/pollen studies on the map, over much of the world. He was very conscious of his contribution and would not have liked appearing beneath Von Post here, as Erdtman felt Von Post never sufficiently recognized his work. Hoffmeister, a paleontologist for Esso (Exxon), more than any other one person in industry was responsible for recognition that palynomorphs were a critically important group of microfossils that could be used for practical correlation, where other microfossils failed or were less satisfactory. (**a**) reproduced from Sarjeant, 1978, courtesy of AASP Foundation; (**b**) reprinted by permission from Erdtman, 1954; (**c**) courtesy of W. R. Evitt.

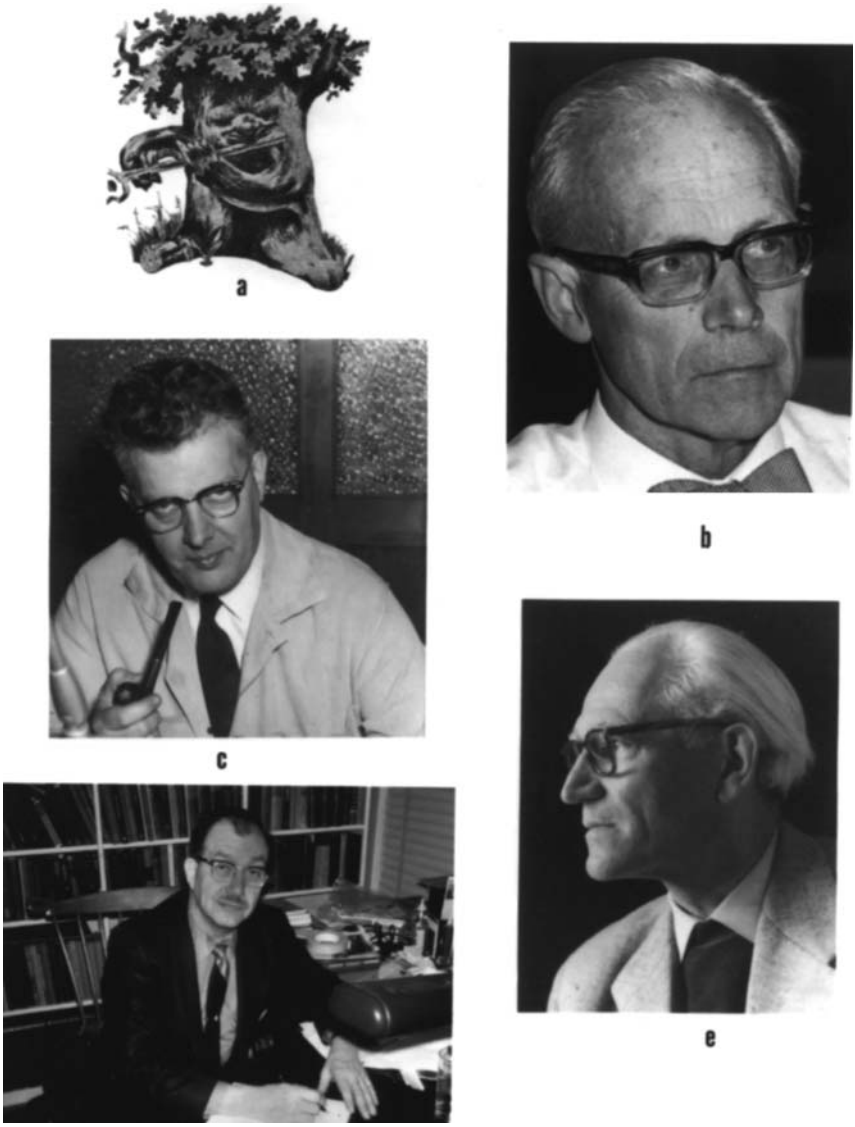


Figure 1.6 A few guiding spirits, and one poltergeist, of paleopalynology: (**a**) Gunnar Erdtman's (1897–1973) self-portrait as a wood-gnome. One must not deduce from this bit of whimsy that Erdtman was jovial and light-hearted. He could excoriate a younger palynologist for such a self-defined infraction as publishing a trilete spore photo with no radius of the laesura pointing up; (**b**) Knut Faegri (1909–2001), a keen student of pollination mechanisms, was the leading Norwegian Pleistocene-Holocene palynologist for decades. Though not primarily a paleopalynologist, he especially contributed to paleopalynology by his justly famed *Textbook of Pollen Analysis* (the first edition co-authored by J. Iversen);

his prolific production of publications served to popularize and establish his ideas. In his later years he became rather intolerant of what he regarded as deviant, i.e., non-erdtmanian, practices in spore/pollen work and frequently wrote letters to errant authors, dressing them down for their sorry ways. (I have such a letter scolding me for orienting spores/pollen upside down: the laesura ray of a trilete laesura must point up at 90', the long axis of bisaccate pollen must be parallel to the bottom of the page with the distal side up, etc.) Nevertheless, it must be acknowledged that Erdtman's impact on palynology is unequaled, and we all owe his memory a great debt.

After Von Post and Erdtman, came many other Holocene pollen analysts in Scandinavia such as Iversen, Jessen, and Faegri (see Fig. 1.6b) but also Godwin in Britain, Sears and Potzger in America, Neustadt in the (former) USSR, Firbas in Germany, and a long list of others. But from the time of Erdtman and Von Post, this subject, linked to plant geography, ecology generally, paleoclimatology, and archeology-anthropology, tended to go its own way, as it still does today. Most of the practitioners are botanically rather than geologically oriented, and the field and laboratory techniques for taking cores of the relatively shallow, usually unindurated post-glacial sediments and processing them to obtain the usually well preserved palynofloras are more or less special to Holocene palynologists. The pollen/spore types studied are 100% extant species.

Unfortunately, because of all these factors, and other, more personal ones, there tends to be little contact between pollen-analysts and paleopalynologists. This was not always the case, and some pioneer paleopalynologists, such as A. Raistrick in Britain, L. R. Wilson (Fig. 1.6c) in the USA, and others, worked in both Pleistocene/ Holocene pollen analysis and with palynomorphs as old as Paleozoic.

As already noted, coal petrologists studied spores/pollen seen in coal thin-sections long ago, and the American coal petrologist, Thiessen, early in the 20th century even suggested the use of spores for coal-bed stratigraphy. Raistrick,

Figure 1.6 (**c**) Leonard R. Wilson (1906-1998), one of the first American palynologists (usually called "Dick" or "Doc") published papers on what we would now call paleopalynology soon after Erdtman's visits to North America in the 1920s; (**d**) James M. Schopf (1911–78), American paleobotanist, coal petrologist and paleopalynologist, made very important early contributions to establishing the systematic study of palynomorphs on a sound basis. For example, Schopf, *et al.* (1944), largely his work, became a model for such studies; (**e**) Robert Potonié (1899-1974), son of the well-known German paleobotanist, Henri Potonié, was one of the first people to recognize and apply the stratigraphic possibilities of paleopalynology, especially in the German coal fields and, through students and associates, elsewhere. After World War II, Potonié's encyclopedic studies of fossil spores/pollen, including introduction of his suprageneric "turmal" system of classification, had great importance in emphasizing the potential for systematic work in the field. (a) reprinted by permission from Erdtman, 1954.

in Britain in the 1920s, was a pioneer in the use of spores for this important task (see Chaloner, 1968a; Marshall, 2005). Unfortunately, coal beds are very difficult to correlate by spores because coal is primarily derived from woody swamp peat. The spore/pollen flora of such a sediment is notoriously local in derivation, e.g., as compared to deltaic silts, which have a rich, fluvially derived pollen flora representing a large area. Also the palynofloras of coals of an area usually represent a persistent biofacies that tends to recur mostly in response to the environment. Thus, within a given time frame, it is not always possible to correlate coal beds by correlating the facies, as almost identical palynofloras may occur in widely separated horizons. Nevertheless, because the "original" palynologists were the Holocene pollen analysts who preferred to work with post-glacial peats, the idea persisted for decades that paleopalynologists should be looking at fossil peats, that is, coals. Even now it is hard to convince some field geologists that it is usually better to collect the associated shales than coals for palynology, and that presence of plant megafossils in a shale does not necessarily correlate with presence of palynomorphs! It should be noted that some palynologists (Kosanke, 1950; Smith and Butterworth, 1967; Peppers, 1996) have successfully correlated coal beds by their spore-content, despite the attendant difficulties.

In the late 1920s and early 1930s, Robert Potonié (Fig. 1.6e), son of the paleobotanist, Henri Potonié, began to study spores/pollen from German coals and associated sediments, especially at first the Cenozoic lignitic coals, but later the Carboniferous coals as well. Potonié and his students and coworkers made a very significant contribution to paleopalynology with systematic and biostratigraphic studies. Just before the outbreak of World War II, in the late 1930s, Potonié was engaged by the Royal Dutch/Shell petroleum interests to investigate the possibility of using palynology as a biostratigraphic tool. The war ended that, but soon after the war Shell remembered Potonié's work and began palynological research in earnest, employing especially Dutch palynologists such as Waterbolk, whose ultimate palynological roots were in Holocene pollen analysis. Other, more geologically oriented persons such as Kuyl were soon involved, however, and even such botanists as Jan Muller were geologically adept enough to assure a sound geological approach. By the early 1950s, Shell had employed paleopalynology very successfully in the Maracaibo Basin in Venezuela, where marine micropaleontology (= study of foraminifera and ostracodes mostly) was not fully satisfactory because of the extensive non-marine sections (see Kuyl *et al.*, 1955). In North America, Esso (Standard Oil of New Jersey = Exxon) also began looking at palynology as a biostratigraphic tool quite early. By the late 1940s, they also had a laboratory in Venezuela under R. H. Tschudy, but the center of their palynological operation soon shifted to Oklahoma, where W. S. Hoffmeister (Fig. 1.5c), a micropaleontologist working for Esso's research subsidiary, Carter Oil Co., and L. R. Wilson (Fig. 1.6c), an academic palynologist working as a consultant, together developed Esso's palynostratigraphic program. American paleopalynology owes a great debt also to J. M. Schopf (Fig. 1.6d),

who started his career with the Illinois Geological Survey and later served with the U. S. Bureau of Mines and the U. S. Geological Survey. He recognized in the early 1930s the great potential of spores/pollen studies for solution of geologic problems. The classic work of Schopf *et al.* (1944) was one flowering of Schopf's pioneer efforts. By 1955 when I joined Shell Development Company (a research subsidiary of the Royal Dutch/Shell group of companies) as a palynologist, Shell's palynological operations were worldwide, from Nigeria to western Canada. About the same time, nearly all the other oil companies in the world of any size introduced palynology, at least into their research programs. Esso (now Exxon-Mobil) and the Shell group were in the thirties and remain today the giants of the oil industry worldwide, and the early use by them of palynology for stratigraphic and paleoecological purposes was in my opinion pivotal, though others also contributed, such as J. W. Durham, through his connection with oil operations in the 1940s in Colombia (see Langenheim, 1989). The 1950s were the time of greatest expansion of the subject.

A treatment such as this cannot claim to be complete, and I clearly should discuss at length the important and early contributions of the many Soviet (mostly Russian) paleopalynologists: Naumova, Bolkhovitina, Zaklinskaya, and many others. Near the end of the 20th century the Chinese also began to be heard from in large numbers and with many publications. In the English-speaking world, probably no other one institution has had the impact of the University of Sheffield, under L. R. Moore, Charles Downie, and their many students, now practicing the profession all over the world (see Sarjeant, 1984). My treatment of the subject also tends to emphasize the pollen and spore part of the subject more than the "non-spore" aspects. Sarjeant (1998) published an important summary of his extensive contacts with paleopalynological leaders in the study of acritarchs and dinoflagellates, including photographs of many of them.

As far as I am aware, my 1951 Ph.D. dissertation on Paleogene spores/pollen was the first one dealing exclusively with paleopalynology in North America; it certainly was one of the first, but I never had a course specifically in palynology because there were none at Harvard or Cambridge Universities. However, Sir Harry Godwin's ecology course at Cambridge, England, and E. S. Barghoorn's paleobotany course at Harvard, both of which I took, contained some of what is now called paleopalynology. By the 1960s, Ph.Ds in palynology were common, and by 1981, the American Association of Stratigraphic Palynologists had over 800 members. There were something on the order of 3,000 professional paleopalynologists in the world at that time (see Traverse, 1974a, for a history of palynology to 1972). When I was working on my doctoral dissertation in the late 1940s, there was no journal specifically for palynology, and the relatively manageable number of publications in the subject appeared in a wide variety of journals. There was an informally mimeographed newsletter about pollen/spore research in the 1940s called the *Pollen Analysis Circular*, later the *Pollen and Spore Circular*, edited and distributed by a Holocene pollen analyst, P. B. Sears

(in the later numbers assisted by L. R. Wilson). It was chiefly intended to inform "friends of pollen" about new developments, but it has achieved lasting recognition, mostly because of the fortuitous circumstance that the word "palynology" was coined by Hyde and Williams in No. 8, October, 1944. (As of mid-2005, the Center for Environmental Science, Northern Arizona University, made it possible to download from the Internet all of the numbers of the PSC. See: www.envsci.nau.edu/faculty/ScottAnderson/Pollen & Spore Circulars.htm. Then click on the desired circular.) Erdtman's *Grana Palynologica* (now *Grana*) began in 1954, and the French *Pollen et Spores* (now moribund) in 1959. There are quite a number of other journals worldwide (see Annotated Bibliography at the end of this chapter). It is now impossible to "stay on top" of the whole palynological literature, even with the aid of the many society newsletters and bibliographies (see abovementioned bibliography). This is dramatized by the explosion in numbers of contributions and pages now being published primarily in Chinese, and requiring those of us who read only languages in greco-Roman alphabets and their derivatives, to wait for translations.

The work of Evitt, Wall, Williams, Norris, Fensome, Edwards, Wood and many others, beginning in the early 1960s, put a new face on paleopalynology by showing that dinoflagellates (apparently almost always their cysts) can be used biostratigraphically. Evitt (Fig. 12.4a) has had an especially important impact on this work. Dinoflagellate cysts are in the same size-range as spores/pollen, and apparently possess a resistant sporopollenin framework in their walls, as do spores/pollen. Most (but by no means all) of the cyst-producing dinoflagellates are marine, and their study has greatly expanded the usefulness of paleopalynology by providing more control for marine rock sequences where spores/pollen may be rare or absent, and because dinoflagellate cysts are often far better chronostratigraphic indicators. The pioneer in this field was G. Deflandre (Ehrenberg, as noted above, had seen dinoflagellate cysts in the 1840s), when palynology was in its infancy in the 1930s. However, it was the proof that many of what had been known as "hystrichosphaerids" are in part dinoflagellates that opened up this field. Dinoflagellate palynologists mostly started as spore/pollen palynologists, and perhaps this and the fact that spores/pollen and dinoflagellate cysts occur in the same preparations is responsible for keeping spore/pollen and dinoflagellate people closely allied. The "hystrichosphaerids" which were not transferred to the dinoflagellates were then recognized as acritarchs ("unknown" origin), following a proposal of W. R. Evitt. The study of these, mostly algal cysts or reproductive bodies, was pioneered especially by Alfred Eisenack (1891–1982; see Fig. 12.4d) in Germany, by Charles Downie (1923–1999; see Fig. 6.4a) in England, and by F. H. Cramer and M. d. Carmen R. Diez (Fig. 6.4b), working primarily in Spain and the USA. In recent years, the publications of Fensome, Wood, and Wicander have been especially important.

Pleistocene (including Holocene, as used here) pollen analysis researchers tend to go their own way, now as before. Their orientation has always been ecological,

paleoclimatological, and archeological, and still is. Paleopalynologists have been oriented to biostratigraphy and especially to its economic application. Paleopalynology owes its origins to present interglacial ("post-glacial" = Holocene) pollen analysis, and even the very name "palynology" to exponents thereof, but very few paleopalynologists have managed to remain closely associated with Pleistocene pollen analysis as well.

3 Annotated Bibliography of Readily Available Publications

The following short bibliography is intended to assist the student to get "established in the neighborhood," by helping him/her find the way around in the basic literature. It is aimed primarily at readers who use the English language. The principal weakness this occasions is that the coverage of the Russian (and the earlier Soviet, Russian–language) literature is practically nil, despite the great volume of Russian/Soviet palynological publication. In recent years the Chinese palynological literature has exploded in quantity. Much of it provides at least brief English summaries. English-speaking students will, in my experience, mostly not attempt to read any foreign language publications, and even the adventurous ones will not try to cope with non-Roman alphabets, to say nothing of Asiatic pictographs.

3.1 Textbooks, Review Articles and Other General Works

Al-Hajri, S., and Owens, B., eds., 2000, *Stratigraphic Palynology of the Palaeozoic of Saudi Arabia*, Gulf PetroLink, Spec. GeoArabia Publ. 1. Although this book deals exclusively with the palynology of the Arabian Peninsula, and only with Paleozoic material (Ordovician to Permian), a wide range of palynomorphs is covered and profusely illustrated in the various separately authored chapters: acritarchs, chitinozoans, miospores, cryptospores. This makes the book a handy item for comparison purposes.

Berglund, B. E., ed., 1986, *Handbook of Holocene Palaeoecology and Palaeohydrology*, Wiley, Chichester. This bulky collection of papers includes many that have direct bearing on paleopalynology, especially on Pleistocene studies. Contributions by Birks (general background and statistical methods), Aaby and Digerfeldt (coring and other sampling techniques), Berglund and Ralska-Jasiewiczowa (pollen analysis and pollen diagrams), Prentice (forest-composition calibration of pollen data), and other chapters will all be useful to the student.

Birks, H. J. B., and Birks, H. H., 1980, *Quaternary Palaeoecology*, Edward Arnold, London. Although now dated, this is a very informative work as

to palynological methods for Pleistocene/Holocene studies, from laboratory techniques to multivariate analysis.

Brooks, J., ed., 1981, *Organic Maturation Studies and Fossil Fuel Exploration*, Academic Press, London. Papers presented at a symposium at the 5th International Palynological Conference, Cambridge, U.K., 1980. Deals with "carbonization" studies of organic matter in sediments, a subject that grew out of palynology, is still more or less satellite to it and coal petrology, and has considerable importance in organic geochemistry. Level of "carbonization" (= maturation or thermal alteration) is a useful geothermometer.

Cleal, C. J., ed., 1996, Studies on early land plant spores from Britain, *Spec. Papers in Palaeont*. **55**, Palaeont. Assoc., London. Contains a wealth of information by J. B. Richardson, C. H. Wellman and others, about the early spores and cryptospores from the Ordovician and Silurian. Profusely illustrated.

Dimbleby, G. W., 1985, *The Palynology of Archaeological Sites*, Academic Press, London. A rather brief summary of the methods of, problems encountered in, and potential application of, palynology in archeology.

El-Arnauti, A., *et al.*, eds., 1988, *Subsurface Palynostratigraphy of Northeast Libya*, Garyounis Univ., Benghazi, Libya. This book can be compared with the later Al-Hajri and Owens volume on the Arabian Peninsula, treated above, in that it contains a number of separately authored chapters on a variety of palynofloras, ranging from Precambrian to Cretaceous in age and from leiosphaerid and other acritarchs to chitinozoans, miospores, gymnosperm pollen and dinoflagellate cysts, as well as illustrations of the microscopic appearance of various sorts of palynofacies residues in palynological preparations.

Elsik, W. C., 1992, *The Morphology, Taxonomy, Classification and Geologic Occurrence of Fungal Palynomorphs*, Amer. Assoc. Strat. Palynol. Short Course. This volume, along with the Kalgutkar and Jansonius book listed below, make a fine reference combination for working with fungal spores.

Erdtman, G., 1952–71, *Pollen Morphology and Plant Taxonomy: Angiosperms–An Introduction to Palynology*, vol. 1, Almqvist and Wiksell, Stockholm (vol. 2, 1957; vol. 3, 1965; vol. 4, 1971.) An attempt to present a complete catalog of flowering plant pollen, plus an introduction to pollen morphology is given in vol. 1. Erdtman's trouble was diarrhea of terminology, but the pictures are very good, and the book as a whole is indispensable to anybody studying pollen. Vols. 2 and 3 treat in much briefer fashion than vol. 1 (for angiosperms) the conifers, the bryophytes, and the lower vascular plants. Vol. 2 is mostly composed of illustrations. Vol. 3 mostly consists of text covering the illustrations in vol. 2. Vol. 4 has descriptions and illustrations (SEM pictures and TEM pictures of sections, but most palynologists use light microscopes most of the time, and such pictures have limited use for identification) of spores of Lycopsida, Psilopsida, Sphenopsida, and ferns (mostly of the latter). These volumes, and the one that follows are now old and out of date, but still of great importance to palynology. They still may be found in many libraries.

Erdtman, G., 1954 (1943), *An Introduction to Pollen Analysis*, Chronica Botanica, Waltham, MA. The first real palynology text. Still very useful for getting an overall picture of Pleistocene/Holocene palynology (= "pollen analysis").

Evitt, W. R., 1985, *Sporopollenin Dinoflagellate Cysts: Their Morphology and Interpretation*, Amer. Assoc. Strat. Palynol. Foundation, Dallas, TX. Presents in book form and in great detail the information from Evitt's justly famous Stanford short courses on dinoflagellates. This book is a must for any palynological library, even though it is now a little out of date.

Faegri, K., and Iversen, J., 1989, *Textbook of Pollen Analysis*, 4th ed., by Faegri *et al.*, Wiley, Chichester, New York, etc. This book, despite the heavy emphasis on Pleistocene/Holocene palynology, is probably still the most useful single book, page for page, on palynology. Terminology, directions for lab work, and interpretations of research results, are clear, simple and easy to understand and apply.

Faegri, K., and Van der Pijl, L., 1979, *The Principles of Pollination Ecology*, 3rd ed, Pergamon Press, Oxford. For background information about pollen as it operates in nature, you can do no better than to read this. Of course, the pollen of most significance to us (wind-propelled) is not much considered! When I visited Faegri in Nov., 2001, just a few weeks before his death, he said that he was well along in producing a 4th edition of this marvelous work, but I suppose it is now unlikely that it will ever appear.

Fatka, O., and Servais, T., eds., 1996, *Acritarcha in Praha*, Acritarch Subcommission, CIMP. *Acta Univ. Carolinae, Geologica* **40**:293–717. This volume, which grew out of a CIMP-sponsored meeting, contains many papers of significance to acritarch studies.

Fensome, R. A., *et al.*, 1993, *A Classification of Living and Fossil Dinoflagellates*, Micropaleontol. Spec. Pub. **7**:351 pp. This is a landmark publication presenting a suprageneric classification for dinoflagellates, including both extant and fossil forms. The explanatory line-drawing illustrations in the Introduction are very helpful. This work, as well as Fensome, Riding and Taylor, Chapter 6 in Vol. 1 of the Jansonius and McGregor (1996) work cited below, provide useful summaries with exhaustive information for dinoflagellate studies, more up to date than the Evitt book listed above, which is, however, still useful reading.

Ferguson, I. K., and Muller, J., eds., 1976, *The Evolutionary Significance of the Exine*, Linnean Society of London Symposium Series **1**. This volume is a diverse assortment of papers. Chaloner on adaptive features of spores/pollen and Walker on angiosperm pollen evolution are important to our concerns.

Gradstein, F. M., *et al.*, eds., 1998, *Sequence Stratigraphy–Concepts and Applications*, Elsevier, Amsterdam. This book is very useful in understanding the history and nature of sequence stratigraphy, which has been widely applied in stratigraphic and sedimentological studies with palynological input.

Harley, M. M. *et al.*, eds., 2000, *Pollen and Spores: Morphology and Biology*, Royal Botanic Gardens, Kew, UK. This book includes instructive articles by

many authors on a wide variety of subjects on the evolution of and structure of spores and pollen.

Head, M. J., and Wrenn, J. H., eds., 1992, *Neogene and Quaternary Dinoflagellate Cysts and Acritarchs*, Amer. Assoc. Strat. Palynol. Foundation, Dallas, TX. Contains much valuable information about late Cenozic dinocysts and acritarchs from enough different points of view to make the whole very instructive.

Jansonius, J., and McGregor, D. C., eds., 1996, *Palynology: Principles and Applications*, vols. 1–3, Amer. Assoc. Strat. Palynol. Foundation, Dallas, TX. The thirty-two chapters of this set of books covers practically everything in palynology, though as usual with multi-author books, somewhat unevenly and lacking in linkage. The chapters are mostly very well and profusely illustrated. This 3-vol. set is a must for reference to practically anything in paleopalynology.

Jell, P. A., ed., 1987, *Studies in Australian Mesozoic Palynology*, Assoc. Australas. Palaeontol. Mem. 4. This volume and its later companion (see under Laurie and Foster, below) provide beautifully documented and illustrated, largely dinoflagellate-based information on the palynostratigraphy of the Mesozoic of Australia.

Jones, T. P., and Rowe, N. P., eds., 1999, *Fossil Plants and Spores: Modern Techniques*. Geol. Soc., London. 60 chapters on most aspects of paleobotany and plant-derived palynomorphs, with special emphasis on research methods. Much invaluable palynological information.

Kalgutkar, R. M., and Jansonius, J., 2000. *Synopsis of Fossil Fungal Spores, Mycelia and Fructifications*, Amer Assoc. Strat. Palynol. Foundation, Dallas, TX. This book is a must for the bookshelf of every paleopalynologist. Fungal spores are an important constitutent of many palynofloras from Cretaceous to present, and this book treats and illustrates them in depth. See further description under Catalogs.

Kapp, R. O., Davis, O. K., and King, J. E., 2000, *Pollen and Spores*, 2nd ed., Amer. Assoc. Strat. Palynol. Foundation, Dallas, TX. This spiral bound book presents basic information about and illustrates with good line drawings many sorts of modern pollen and spores, as well as some other sorts of palynomorphs that might be encountered in simple preparations of sediments. The illustrated forms are organized as a dichotomous key. The book includes only a few hundred forms, so it will not replace a reference collection, but it provides a good start to identification.

Koutsoukos, E. A. M., ed., 2005, *Applied Stratigraphy*. Springer, Dordrecht, Netherlands. Chapters by specialists in many aspects of stratigraphy and related matters, such as taphonomy, palynofacies, paleoclimatology–very important concepts for palynostratigraphy and paleopalynology generally.

Kremp, G. O. W., 1965, *Morphologic Encyclopedia of Palynology*, University of Arizona Press, Tucson. Kremp's glossary or dictionary of palynologic terms is

useful in trying to read palynological papers, especially older ones, in which a variety of terminology is employed. Its usefulness is limited by its lack of critical comment on the terms listed and by incompleteness; one term used in the foreword to the book is not defined in the Encyclopedia! See reference below to the Punt glossary.

Kurmann, M. H., and Hemsley, A. R., eds., 1999, *The Evolution of Plant Architecture,* Royal Botanic Gardens, Kew, UK. This contains many papers of considerable usefulness in the understanding of the structure of fossil pollen and spores and their evolution.

Last, W. M., and Smol, J. P., eds., 2001, *Tracking Environmental Change Using Lake Sediments,* Kluwer, Dordrecht. Vol. 1, *Basin Analysis, Coring, and Chronological Techniques*; Vol. 2, *Physical and Geochemical Methods*. [Vol. 3, *Terrestrial, Algal, and Siliceous Indicators*, and Vol. 4., *Zoological Indicators*, are edited by Smol, J. P., *et al.*, q. v.] This four-volume set of books about study of pond and lake sediments contains a wealth of information for paleopalynologists. The books each have multiple chapters by various qualified authors on many different subjects, such as non-pollen/spore palynomorphs and sediment coring techniques. Nearly all the chapters contain information useful to our subject.

Laurie, J. R. and Foster, C. B., 2001, *Studies in Australian Mesozoic Palynology II*, Assoc. Australas. Palaeontol. Mem. 24. This volume, and its companion (see Jell, 1987, above) provide invaluable information on the palynostratigraphy of the Australian Mesozoic. The Jell volume is mostly, and this one is entirely, devoted to dinoflagellate palynology.

Lipps, J. H., 1993, *Fossil Prokaryotes and Protists,* Blackwell Sci. Pub., Oxford. This book contains interesting chapters by various experts on protists. Two of the protist chapters are of interest to paleopalynology: A very useful presentation by C. V. Mendelson on acritarchs and prasinophytes, and a very clear, well illustrated treatment of dinoflagellates by L. E. Edwards. N. B.: A second, revised edition of this book is in press with Columbia University Press, New York.

Mann, K. O., and Lane, H. R., eds., 1995, *Graphic Correlation,* SEPM Soc. Sed. Geol. Spec. Pub. **53**. This book pulls together in chapters by a variety of people information about the history and applications of graphic correlation. Palynologists have used this method widely for stratigraphic work, and this book is useful in helping understand what the technique entails and can produce.

Muller, J., 1981, Fossil pollen records of extant angiosperms, *Botanical Review* **47**:1–146. Though preliminary, biologically oriented, and now dated, this little book is an essential aid for paleopalynogical work in the Cenozoic.

Panova, L. A. *et al.*, 1990, *Practical Palynostratigraphy*, Nedra, Leningrad. In Russian. This book is in succession to the very useful but no longer available three volume set by Pokrovskaya, 1966, in presenting 80 plates of sporomorph

illustrations from Devonian to Neogene, which can be used for getting a general idea of the stratigraphic position of a palynoflora of uncertain age.

Playford, G., 2003, *Acritarchs and Prasinophyte Phycomata: A Short Course*, Amer. Assoc. Strat. Palynol. Contr. Ser. **41**. This short booklet presents much useful information about acritarchs of all ages, as well as about prasinophyte "cysts" [=phycomata].

Powell, A. J., and Riding, J. B., 2005, *Recent Developments in Applied Stratigraphy*, Micropalaeont. Soc., Spec. Pub., London, Geol. Soc. My copy of this important compendium unfortunately arrived too late for the chapters to be treated in the text. Dale *et al.*, Gary *et al.*, and Jaramillo *et al.*, are all important as examples of the use of graphic correlation and multivariate statistical techniques in palynostratigraphy.

Punt, W. *et al.*, 1994, *Glossary of Pollen and Spore Terminology*, LPP Foundation, Utrecht, Netherlands, Contrib. Ser. **1**. A very useful glossary of terms used in palynology, including paleopalynology. Unlike the much larger Kremp glossary, this one takes a stand on what the authors of the booklet consider correct. Sometimes this means that Punt is, in my opinion, wrong. N. B.: a second, revised edition of this glossary, compiled by P. Hoen is maintained as a very useful website: http://www.bio.uu.nl/~palaeo/glossary/glos-int.htm.

Riding, J. B., and Kyffin-Hughes, J. E., 2004, A review of the laboratory preparation of palynomorphs with a description of an effective non-acid technique, *Rev. Brasil. Paleontologia* **7**:13–44. A thorough survey of most of the principal methods for extracting palynomorphs from rock samples, including one of the methods for maceration without use of acids.

Servais, T., and Paris, F., eds., 2000, Ordovician palynology and paleobotany. *Rev. Palaeobot. Palynol*. **113**, *Special Issue.* This issue of "RPP" includes instructive articles on several of the prominent kinds of Early Paleozoic palynomorphs, especially acritarchs and chitinozoans.

Smith, A. H. V., and Butterworth, M. A., 1967, Miospores in the coal seams of the Carboniferous of Great Britain, *Palaeontological Assoc. London Spec. Papers in Palaeontology*. Although dated, this book is a must for work with spores of Mississippian-Pennsylvanian age.

Smol, J. P. *et al.*, eds., 2001, *Tracking Environmental Change Using Lake Sediments*.Vol. 3, Terrestrial, Algal, and Siliceous Indicators; Vol. 4., Zoological Indicators, Kluwer, Dordrecht. See information on the four-volume set to which these belong under Last, W. M. and Smol, J. P.

Song, Z. *et al.*, 1999, *Fossil Spores and Pollen of China*, Vol. 1, *The Late Cretaceous and Tertiary Spores and Pollen*, Science Press, Beijing. This massive volume contains descriptions and illustrations of pollen and spores of Late Cretaceous (beginning with Cenomanian Stage) and Cenozoic rocks of China. The text is mostly in Chinese, but there is an English summary (pp. 822–824), and the 207 plates of photomicrographs are self-explanatory, as the names are

in Latin. The volume is valuable for comparisons with sporomorphs of similar age from anywhere in the Northern Hemisphere.

Song, Z. *et al.*, 2000, *Fossil Spores and Pollen of China*, Vol. 2, Science Press, Beijing. Comments for preceding book apply also to this one (English summary on pp. 614–616). Covers Triassic, Jurassic and Cretaceous through Albian Stage.

Stewart, W. N., and Rothwell, G. W., 1993, *Paleobotany and the Evolution of Plants*, 2nd ed., Cambridge University Press, Cambridge, UK. Basic paleobotany text competitive with Taylor and Taylor (1993). However, this one differs in the inclusion of much information, some of it speculative, about paths of plant evolution. Little palynology.

Tappan, H., 1980, *The Paleobiology of Plant Protists*, W. H. Freeman, San Francisco. This is an invaluable reference book for the paleopalynologist because we deal constantly with dinoflagellates, acritarchs and occasionally with diatoms and other protists treated in Tappan's book. The information about dinoflagellates and acritarchs must now be supplemented by more up-to-date references found in this bibliography.

Taylor, T., and Taylor, E. L., 1993, *The Biology and Evolution of Fossil Plants*, Prentice Hall, Englewood Cliffs, New Jersey. This book is now regarded as the standard text in general paleobotany. It is well written and comprehensive, including considerable information about paleopalynology generally, and the linkage between fossil spores and pollen and the related megafossil groups.

Traverse, A., ed., 1994, *Sedimentation of Organic Particles*, Cambridge University Press, Cambridge, UK. Similar in subjects covered to Tyson (1995). Covers some subjects that were not treated by that book or has a different slant, for example on palynofacies and palynodebris.

Tyson, R. V., 1995, *Sedimentary Organic Matter: Organic Facies and Palynofacies*, Chapman and Hall, London. This book is a must for working with palynofacies and sedimentation of palynomorphs. Covers much of the same ground as Traverse (1994), but is a one-author book with the resultant better integration and thoroughness.

Visscher, H., and Warrington, G., eds., 1974, Permian and Triassic Palynology, *Rev. Palaeobot. Palynol.* **17**, *Special Issue*. Contains a number of useful papers for Permian and Triassic research, edited by two of the fathers of the field of palynology.

Wicander, R., 2002, Acritarchs: Proterozoic and Paleozoic enigmatic organic–walled microfossils, in: *Instruments, Methods, and Missions for Astrobiology IV* (R. B. Hoover *et al.*, eds.), *Proc. Soc. Photo-Optical Instrumentation Engineers* **4495**:331–340. This rather short article is important in presenting an up-to-date survey of acritarch studies from the older rocks.

Williams, G. L. *et al.*, 2000, *A Glossary of the Terminology Applied To Dinoflagellates, Acritarchs and Prasinophytes, With Emphasis On Fossils,* 3rd Ed., Amer. Assoc. Strat. Palynol. Contrib. Ser. **37**. This glossary, like the Kremp

glossary for pollen and spores, presents all the alternative definitions without taking a position on correctness. This completeness makes this volume an indispensable source for delving into the various meanings of some terms, and the 42 plates of line drawing illustrations are marvelously instructive.

Wodehouse, R. P., 1935, *Pollen Grains*, McGraw-Hill, New York. (Reprint by Hafner, New York, 1959). The first modern book on pollen morphology and its history, plus information on the state 70 years ago of what we now call palynology. For pollen morphogenesis, this is still important reading.

3.2 Catalogs, Keys, etc.

(See also the following section for computer databases and websites.) In addition to the few atlases listed below as examples, there are now literally hundreds of them for pollen and spores of local or regional floras for all parts of the world. Most of them can be found with the various computer search engines. The Jones *et al.* atlas listed below has a good list of atlases of North America. However, the Jones atlas, and various other of the newest ones, illustrate the forms only with SEM pictures, which is not desirable because the instrument used for practically all palynological analytical work is the light microscope (LM). The best atlases provide LM illustrations, as well as SEM. The electron micrographs often are very useful in clarifying sculpturing patterns that are difficult to resolve with the LM alone. An important list of Pleistocene/Holocene pollen and spore atlases of the world can be found in Hooghiemstra and van Geel, 1998.

Bassett, I. J., Crompton, C. W., and Parmalee, J. A., 1978, *An Atlas of Airborne Pollen Grains and Common Fungus Spores of Canada*, Canada Department of Agricultural Research Branch, Monograph **l8**. Profusely illustrated (LM, SEM, light interference-contrast pictures), provided with keys. Useful for Pleistocene studies of temperate North American and Eurasian sediments.

Beug, H.-J., 2004, *Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende Gebiete*, Verlag Dr. Friedrich Pfeil, München. This is a superb atlas of the pollen types of Europe, but includes many, especially American, species and genera not found wild there. Profusely illustrated with magnificent photomicrographs (no SEM), this book is for this reason valuable for pollen identification, and the fact that the text is exclusively German is not an insuperable barrier.

Boros, A., and Járai-Komlódi, M., 1975, *An Atlas of Recent European Moss Spores*, Akadémiai Kiadó, Budapest. Despite the title, includes also hornworts and liverworts, as well as mosses, sensu stricta. Very interesting presentation of spores of bryophytes, profusely illustrated, though the SEM and light pictures average only fair.

Charpin, J., Surinyack, R., and Frankland, A. W., 1974, *Atlas of European Allergenic Pollens*, Sandoz, Paris. Never mind the error ("pollens") in the

title. This is a good reference if you wish to know what kinds of pollen to expect in the air at a certain time and place in Europe. Many of the forms are also found in North America.

Chester, P. I., and Raine, J. I., 2001, Pollen and spore keys for Quaternary deposits in the northern Pindos Mountains, Greece, *Grana* **40**:299–387. This is a good example of a modern, local pollen atlas. The presentation of it as a key will be helpful to many beginners in palynology.

Eisenack, A., 1964, *Katalog der fossilen Dinoflagellaten, Hystrichosphären und verwandten Mikrofossilien*, vol. 1, *Dinoflagellates* (3 parts), vol. 2, *Dinoflagellates*, cont. (2 parts), vols. 3–6, *Acritarchs* (4 parts), E. Schweizerbart'sche Verlag, Stuttgart. This fine catalog is intended to cover fossil dinoflagellates and "hystrichosphaerids" (many of the latter are now called acritarchs). Original descriptions in originally published languages. See also the New Series of Eisenack Catalog, by Fensome *et al.*

Fauconnier, D. and Masure, E., Eds., 2004, Les dinoflagellés fossiles: Guide pratique de determination les genres à processus et à archeopyle apical, BRGM, Orleans (France). This book is an encyclopedic treatment of dinocysts with processes and apical archeopyle, from all levels in which fossil dinoflagellates are found. The book is so profusely illustrated and the descriptive material so clearly presented that non-francophone readers should have few linguistic problems with this very valuable work.

Fensome, R. A., *et al*., 1990, *Acritarchs and Fossil Prasinophytes: an index to genera, species and infraspecific taxa*, Amer. Assoc. Strat. Palynol. Contrib. Ser. 25. This 771 pp. compendium is essential to anybody working with fossil phytoplankton. It has an exhaustive bibliography and treats names of acritarchs and prasinophyte phycomata in great detail.

Fensome, R. A., *et al.*, 1991–1996, *The Eisenack Catalog of Fossil Dinoflagellates*, new series, vols. 1–4. E. Schweizerbart'sche Verlag, Stuttgart. This continuation of the very valuable Eisenack Catalog provides in loose-leaf binders detailed descriptions from the original publications, with helpful interpretative information and in some but not all cases illustrations of the forms described. There are abundant literature references in each description, keyed to the reference lists in the back of each volume. Better have a supply of hole-reinforcements when using these volumes. The sheets tear VERY easily. The four volumes contain 2548 pages of dinocyst information!

Fensome, R. A., Lentin, J. K., and Williams, G. L., 2004, *The Lentin and Williams Index of Fossil Dinoflagellates: 2004 edition*, Amer. Assoc. Strat. Palynol. Contrib. Ser. **42**. This massive, 6 cm-thick, three-hole notebook of 909 pages replaces the previous eight volumes of the Lentin and Williams Index, going back to 1973. Unlike most such compendia, each of the editions after 1973 is not a supplement to the original version, but an entirely new Index. According to Fensome, there is no reason to keep previous editions after acquisition of the newest one, unless you might need to check the exact

literature references for new names and other nomenclatural changes that have occasionally been introduced directly in the volumes. For each generic name of a dinoflagellate, the currently recognized species with supporting information and commentary is given. A very complete bibliography is provided at the end of the volume.

Jansonius, J., Hills, L. V., and Hartkopf-Fröder, C., 1976–, *Genera File of Fossil Spores and Pollen*. Department of Geology, University of Calgary, Alberta, Special Publication. As originally published in 1976, this was a set of 3287 "cards" (= paper sheets), usually one per genus of fossil spores and pollen, with very good line drawings and "diagnosis" (description) along with bibliographic reference to type species, and comments. Absolutely invaluable for paleopalynological taxonomy. Beginning in 1977 there have been 13 Supplements to the original set, totalling 2247 additional sheets. Supplement 13 was published in 2002, and Supplement 14 will probably appear in 2005. I recommend organizing the sheets alphabetically in ring notebooks to prevent loss or misplacement of the individual "cards." The newest member of the triumvirate of editors, Hartkopf-Fröder, now makes available free to subscribers an online index of the whole catalog from which one can download an alphabetical or numerically organized list of all of the units. Inasmuch as the generic units are often referred to by number, this is an invaluable aid to the person who organizes the set alphabetically. Similarly, if the "cards" are organized numerically, Hartkopf-Fröder's alphabetical index will also be helpful. The index includes also supplementary information about the generic units. People who wish to use the electronically available index should contact Hartkopf-Fröder at: christoph.hartkopf-Froeder@gd.nrw.de for current instructions.

Kalgutkar, R. M., and Jansonius, J., 2000, *Synopsis of Fossil Fungal Spores, Mycelia and Fructifications. AASP Contrib. Ser.* **39**. This is a very complete compilation of data about all fossil fungal palynomorphic remains that the authors could discover. Systematic descriptions and comments on them are featured. At the rear of the large 3-hole binder are many pages of very useful illustrations and a very comprehensive glossary of terms applicable to microscopic fossil fungal remains.

Jones, G. D. *et al.*, 1995, *Pollen of the Southeastern United States: With Emphasis on Melissopalynology and Entomopalynology*, *AASP Contrib. Ser.* **30**. This atlas is not as useful as it could be for practical palynological analysis because the illustrations are almost all SEM pictures. Most analyses are still routinely done with the light microscope. While the SEM illustrations help elucidate some otherwise difficult points of pollen morphology they are quite different from what one sees with the LM. The ideal atlas would provide LM as the default illustrations, with SEM and phase-contrast/Nomarski type LM to clarify otherwise difficult morphology.

Kremp, G. O. W. *et al.*, 1957–1967; Traverse, A. *et al.*, 1968–1976; Traverse, A., and Ames, H. T., 1979; Ames, H. T., and Spackman, W., 1981–1985, *Catalog of Fossil Spores and Pollen*, 44 vols., Pennsylvania State University. Intended as a systematic compendium of original (specific) descriptions and illustrations for the specialist, and very incomplete, but nevertheless one of the best ways for a starting student to get an impression of the sorts of fossil pollen to be found at various stratigraphic levels. I have found it useful for teaching purposes to have two sets, one of cards filed stratigraphically and (secondarily) morphologically (the "strat file") in a filing cabinet, and the other, a set of bound shelf volumes. I realize that today a palynologist could only organize this by massive photocopying.

Lentin, J. K., and Williams, G. L., 1973–1998, *Fossil Dinoflagellates: Index to Genera and Species*. See Fensome *et al.*, 2004.

Marret, F., and Zonneveld, K. A. F., 2003, Atlas of modern organic walled dinoflagellate cyst distribution, *Rev. Palaeobot. Palynol*. **125**:1–200. This publication plots the distribution of extant dinoflagellate cysts in relation to water condition: temperature, salinity, currents, etc., and is useful in interpreting distribution of fossil cyst populations.

McAndrews, J. H. *et al.*, 1973, *Key to the Quaternary Pollen and Spores of the Great Lakes Region*. Royal Ontario Museum Miscellaneous Publication. For identification of modern pollen and spores from peats, etc., of northeastern North America, this key is still an indispensable aid. Good photomicrographic illustrations.

Nilsson, S., ed., 1973–2004, *World Pollen and Spore Flora (WPSF)*, Almqvist and Wiksell, Stockholm. Treated pollen and spores of various groups of plants, rather randomly. For some years the various numbers, such as no. 12 on the Onagraceae, were provided to subscribers by the journal *Grana* (q.v. under journals, below). As of 2004, the editor of *Grana*, Else Marie Friis, announced that articles which formerly would have been part of *WPSF* will henceforth be just articles in *Grana.*

Potonié. R., 1956–1975, *Synopsis der Gattungen der Sporae Dispersae*, 7 vols: I-VI: *Beihefte zum geologischen Jahrbuch*, **23**, 1956; **32,** 1958; **39**, 1960; **72**, 1966; **87**, 1970; and **94**, 1970; VII: *Fortschritte in der Geologie von Rheinland und Westfalen,* **25**, 1975. These monographs outline Potonié's system of spore classification (Turmas, etc.), and list with commentary (in German) most of the genera of fossil spores that had been published up to 1975. The classification is primarily of use for Paleozoic and (to a much lesser extent) for Mesozoic spores, and has been somewhat revised by M. E. Dettmann (1963) "Upper Mesozoic microfloras from South-eastern Australia", *Proceedings of the Royal Society of Victoria*, **77**(1), among others. Related works that should be consulted are Potonié and Kremp (1954, 1955, 1956a, 1956b) (see General Bibliography). Despite their relative antiquity, all of these publications are still vital to doing paleopalynological systematics.

Punt, W. *et al.*, eds., 1976–2003, *The Northwest European Pollen Flora I*, Some nos. published by Elsevier directly, others in *Rev. Palaeobot. Palynol.* (e.g., no. 8 in *R.P.P* **123** as a special issue). The eight numbers so far published present the pollen in the form of keys, with very good illustrations and descriptions. Is handy for Pleistocene/Holocene studies, especially of European materials, but many of the forms are important also in North America. The future of the *NEPF* is uncertain.

Rawson, P. F. *et al.*, 2002, *Stratigraphical Procedure,* Geol. Soc. (London) Prof. Handbk. Very readable and useful summary of the meaning of the many stratigraphic methods and terms found in palynological literature, including even sequence stratigraphy and graphic correlation.

Reille, M., 1992, *Pollen et spores d'Europe et d'Afrique du Nord*, Lab. Bot. Hist. et Palynol., Marseille. Also published for this atlas are two supplements and a general index. One needs all four items, and this massive work has literally thousands of very good LM photomicrographs that are very useful in identification of Northern Hemisphere Neogene pollen forms.

Stachurska, A., Szczypek, P., and Sadowska, A., 1965–, *Kartoteka Palynologiczna Roslin Polskich* (The Palynological Card Index of Polish Plants), Opolskie Towarzystwo Przyjaciol Nauk. Begun in 1965, this ongoing project still continues, with Sadowska listed as first author in recent editions. Each edition provides light and scanning electronic micrographs of the pollen of a number of Polish plants. The whole collection is a big help in learning the morphology of a variety of Northern Hemisphere temperate plants.

Stuchlik, L. *et al.*, eds., 2001, *Atlas of Pollen and Spores of the Polish Neogene,* Vol. 1: *Spores*; and 2002, *Atlas of Pollen and Spores of the Polish Neogene*, Vol. 2: *Gymnosperms*, W. Szafer Inst. of Bot., Pol. Acad. Sci., Krakow. This atlas is very well illustrated and although the forms are identified with morpho-taxon names, the botanical affinity is stated in the generic descriptions and is usually obvious from the names. Because all of the genera are extant, the atlas is useful for study of fossil floras from Miocene to Holocene.

Thanikaimoni, G. *et al.*, 1972–, *Index bibliographique sur la morphologie des pollens d'angiospermes*, Inst. franc. de Pondichéry [India] Sect. Sci. Tech. These volumes, published at least through the eighth Index volume of 1999, provide useful bibliographic references to studies of the pollen of extant angiosperms, arranged by genus and species.

Tryon, A. F., and Lugardon, B., 1990, Spores of the Pteridophyta: Surface, Wall Structure, and Diversity Based on Electron Microscope Studies, Springer-Verlag, New York. This book is a very valuable aid in determining which extant spore-bearing vascular plants are most closely related to the plants producing fossil spore morphotaxa.

3.3 Bibliographies, Databases, Websites, Software

At the time of publication of the first edition of this book, computer-based databases were just beginning to become important in paleopalynology. There were then many hard-copy bibliographies and similar aids available, and it was important to know about and use them. In the meantime, many of the hard-copy bibliographies have stopped publishing, and palynologists who want to stay abreast of the field need to consult Internet databases and use the online bibliographic services available for the more important journals. A further service now available that has contributed to hard-copy bibliography obsolescence is search engines. Google, Yahoo and other search engines can often find even quite obscure pieces of information, such as geographic information. In my recent research I have found Google searches invaluable. There are also more specialized search engine/databases designed specifically for geology and biology, which are useful in finding palynological references. Thus, in what follows I need only cite the relatively few hard-copy bibliographies and bibliographic services that are still of importance to the palynologist, and a few computer databases of special significance for our field. I have found in editing this chapter that when the websites mentioned don't work easily, "googling" the title (such as *Pollen and Spore Circular*) of the item almost always solves the problem.

AASP. The most important American palynological society sponsors a website, www.palynology.org, with frequently updated, easily accessible information on a wide variety of palynological subjects, including all phases of paleopalynology. Especially interesting is this site's "Palydisks," each of which covers some important aspect of palynology.

Bibliography and Index of Geology and *GeoRef* (continuing), American Geological Institute, Washington. Monthly in magazine form, published annually in hardback, as bibliographic and index volumes. Available in most good geological libraries, it is as useful for literature searches in palynology as in any branch of geology. Now worldwide in coverage and available online, as *GeoRef*, as well as in the traditional hard copy form. Formerly published (until vol. 43, 1979) by the Geological Society of America. Incorporates the former U. S. Geological Survey Bibliography of North American geology, and the former Geological Society of America Bibliography of geology outside of North America. (Pre-1966, you must search both of these!) This database, which as *GeoRef* can be searched online, is the biggest database there is with application to paleopalynology.

California, University of, Museum of Paleontology. This museum has a very useful website: www.ucmp.berkeley.edu for dinoflagellate work. It is recommended, for example, by Lucy E. Edwards of the U. S. Geological Survey. Go to the home page and search directly on dinoflagellates.

CHRONOS At the time of preparation of this edition, this system is pulling together databases from all fields related to stratigraphy, including paleopa-

lynology. Palynostratigraphic studies of the future will presumably need to use the system: www.chronos.org See also *PaleoStrat*.

Erdtman, G., 1927–60, *Literature on Palynology*. Stockholm. Mostly published in *Geologiska Föreningens i Stockholm Förhandlingar*. This goes back in coverage to the beginning of palynology. If you have access to a complete set, you can find everything (well, practically everything) ever published on a certain aspect of palynology up to 1960. For a time, this was continued in the journal *Grana Palynologica* (q.v.). This bibliography was eventually abandoned by Erdtman because of the emergence of *Pollen et Spores* bibliographies (q.v.).

Geobase This is an Elsevier (www.elsevier.com) for-pay online search engine for geology covering 2000 scientific journals. If it is available in your library, use it in combination with *GeoRef*. The coverage of papers is more critical than that of the much larger *GeoRef*, and a search may pick up something that would be missed by more routine searches. See also *Scirus*.

GeoRef An online search engine invaluable for literature searches in paleopalynology. It is now associated with the *Bibliography and Index of Geology*, q. v., and the coverage is enormous.

Geoscience World (www.geoscienceworld.org) This is an online journal aggregate encompassing most of the journals important worldwide to paleopalynology. The subscription price is in the thousands of dollars, and in practice one must access it through a library that is a subscriber.

Global Pollen Database (http://www.ngdc.gov/paleo/pollen.html) This database now covers much of the world and is part of the World Data Center sponsored by NOAA. Go to the website and get connected not only to the GPD but to many other pollen databases.

Hulshof, O. K., and Manten, A. A., 1971, Bibliography of actuopalynology, 1871–1966, *Special Issue, Rev. Palaeobot. Palynol.*, **12**. Does same thing for extant spores/pollen that Manten (1969) does for fossil sporomorphs.

International Federation of Palynological Societies (IFPS) website: www.geo.arizona.edu/palynology/ifps.html. Information on palynological activities in all parts of the worlds.

Library of Congress: has a free database (www.loc.gov.) that is sometimes worth trying in searches that haven't worked elsewhere. Tends to be slow.

Manten, A. A., ed, 1969, Bibliography of Palaeopalynology 1836–1966,. *Special Issue, Rev. Palaeobot. Palynol.*, **8** (1–4). A very handy bibliographic tool. If you have this, and the *Pollen et Spores* (q.v.) bibliographies, you are fairly complete (see also Hulshof and Manten) up to about 1965.

North American Pollen Database=NAPD. This is part of the World Data Center for Paleoclimatology–Modern and Fossil Pollen Data. Use the following home page to visit the pollen database: www.ncdc.noaa.gov/paleo/pollen.html. When you get to the home page you will discover also links to pollen databases for most of the world. This

means data on modern pollen distribution. Also provided is considerable other valuable palynological information.

Paleobotanical Section, Botanical Society of America: Bibliographies (continuing). These are sent out free to members of the section (q.v., under societies, below), and deal only with North America. They are quite complete and up to date.

PaleoStrat. An information system for, among other thing, stratigraphic data of all sorts. www.paleostrat.com. At the time of this writing, *PaleoStrat* is in the process of being integrated with *CHRONOS*, q. v. Paleopalynologists will need to keep abreast of the constantly changing internet handling of palynostratigraphic information.

PALYNODATA=PDTA. This database was began by G. O. W. Kremp in 1977 with cooperation of many oil companies. Separate bibliographies for various time segments were at one time available. For example, no. 13 is "Jurassic palynological literature..." Gradually the publication effort was supplanted by a computer-operated database with stratigraphic ranges, nomenclatural-taxonomic information, and very complete data on stratigraphic and geographic occurrence, for most taxa of fossil palynomorphs. This service is now available online for an annual fee. As of June, 2004, the cost for subscription to *PDTA* was very modest for individuals or libraries, and considerably more for commercial enterprises. There are some restrictions on the use subscribers may make of the database. Contact John H. Wrenn at wrenn@geol.lsu.edu for more information about this unique database and its applications.

Palynology Page. A website, http://www.geo.arizona.edu/palynology/, is maintained by Owen K. Davis at the University of Arizona. It emphasizes pollen, but does provide information about many aspects of palynology.

Pollen et Spores. Bibliographies were published once a year as part of the journal, *Pollen et Spores* (q.v.), defunct since 1989. These overlapped Erdtman's bibliographies at first but were more nearly current. For a time they were alone in the field as a comprehensive, exclusively palynological bibliography. If you can get at them in your library they still are useful.

Scirus. This is a search service of Elsevier, for which, unlike Elsevier's *GeoBase*, q. v., there is no subscription charge for doing searches, but there is one for accessing material. Trial searches I have made with it have been quite impressive.

Tilia Graph. A widely used and very helpful software program for drafting palynofloral distribution graphs in connection with stratigraphic and climatic zones, etc. It was devised by Eric Grimm at the Illinois State Museum. Although originally designed for Pleistocene pollen graphs, the program is quite versatile for different sorts of palynological graphing. It is now known as *TGView*, and the current program is Version 2.0.2. TG must be

paid for and registered to an owner. For information, contact E. Grimm (grimm@museum.state.il.us).

World Data Center [=WDC] for Paleoclimatology: see *NAPD=North American Pollen Database*.

3.4 Journals

Important palynological articles appear in hundreds of journals worldwide, such as *Eclogae Geologicae Helvetiae* in Basel, Switzerland, or *Alcheringa* in Australia, too numerous to list here, but the following are worth special note. Note also that many journals that used to appear in hard copy now appear online, either as an alternative to hard copy, or exclusively in that form. This is especially true of society newsletters, which more and more are available only in an online version. For example, the newsletter of the American Association of Stratigraphic Palynologists, for some decades a very informative paper, regularly appearing in one's mailbox, is now available only online unless one can demonstrate urgent need of hard copy. This trend makes it especially important not only to track journals on library shelves but to use computer-based search engines to be abreast of new developments.

Grana (formerly *Grana Palynologica*). Originally published by G. Erdtman's laboratory in Stockholm, now under the editorship of E. M. Friis, at the Swedish Museum of Natural History. In the past the emphasis was mostly on extant pollen, but now the journal is publishing more paleopalynology.

Journal of Micropalaeontology. British Micropalaeontological Society, London. Publishes many palynological papers and has had several special all-palynology issues. Dinocyst palynology stressed. Two numbers per year.

Micropaleontology. American Museum of Natural History, New York. Older numbers have more paleopalynology than has been the case in recent years.

(The) *Palaeobotanist*. Birbal Sahni Institute of Palaeobotany, Lucknow, India. Has numerous palynological papers. Quite irregular in publication.

Palaeontographica, Abteilung B, Paläobotanik. This German publication (Stuttgart) is too expensive for individual subscribers. Contains numerous, some important, survey papers in sporomorph palynology.

Palaeogeography, Palaeoclimatology, Palaeoecology. This periodical, published in Amsterdam by Elsevier, as is the *Review of Palaeobotany and Palynology*, includes many paleopalynological articles that could just as well have been published in the latter journal. Both contain plenty of paleopalynology.

Palaeontology. British journal that has published many important papers in our field, especially of British palynologists.

Palynology. This is in effect a proceedings volume for the American Association of Stratigraphic Palynologists, as it appears once a year and contains

the abstracts of papers presented at the previous year's annual meeting. However, the journal also includes research papers that are not based on contributions to the annual meeting. This is a very important journal and is provided to members as one benefit of their annual dues. Many libraries do not regard *Palynology* as a periodical, and thus it does not appear with other scientific periodicals in the current issues section. Note also that before 1977 the first seven proceedings volumes of the AASP appeared in *Geoscience and Man*, LA Sta. Univ., Baton Rouge. AASP Proceedings Vol. 1 is *Geoscience and Man* Vol. 1, AASP. Vol. 2 is *Geoscience and Man* Vol. 3, AASP vol. 3 is *Geoscience and Man* Vol. 4, etc.

Palynos. This is the newsletter of the International Federation of Palynological Societies and contains much valuable palynological information. See Societies, below.

Pollen et Spores. This journal was produced for many years, ending in 1989, in Paris by M. Van Campo-Duplan's laboratory. Very productive and important. One needs to have some access to these volumes. Unfortunately, there is now a tendency for major libraries to ship all such older publications to the "annex" or "archives," usually located far from the main library.

Review of Palaeobotany and Palynology. Elsevier, Amsterdam. The first five volumes consist entirely of papers presented at the 1966 2nd International Conference on Palynology in Utrecht. Since then it has become the journal with the most paleopalynology by far. There have been many special issues devoted entirely or mostly to work with fossil palynomorphs. The magazine is nicely printed and edited and is a must to have around, but it is expensive.

Newsletters–Most societies (see next section) have newsletters. Many of them are very useful sources of information. Also, some working groups and some individual laboratories produce valuable newsletters. However, newsletters, except those for societies, tend to come and go, and it is not practical to list them here. There is a recent tendency for them to be delivered to the membership only electronically, as an e-mail attachment. There are also nowadays many websites for labs, projects, organizations, and even individuals, that one may visit for information. One may use Google, Yahoo!, etc., to find practically any of them with a little resourcefulness.

3.5 Societies (USA, Canada, UK)

If one wants to keep abreast of what is going on in paleopalynological research one should belong to at least one palynological organization, in order to get the newsletter(s) and other publications. If one belongs to the American Association of Stratigraphic Palynologists (AASP), the Canadian Association of Palynologists (CAP), or the British Micropalaeontological Society (BMS) [Palynology Group], for example, one gets the various publications of the societies, as well as the

newsletters, and through membership in one of the societies also the newsletter, *Palynos*, of the International Federation of Palynological Societies. *Palynos* 24:2, Dec., 2001, has a useful list of palynological societies on p. 18.

American Association of Stratigraphic Palynologists (AASP). At its foundation, this society almost got the better name, Society of North American Palynologists . Emphasizes pre-Pleistocene, applied palynology, but really covers just about the whole field. Puts out a *Newsletter*, proceedings volumes (*Palynology*), and through the AASP Foundation, a *Contributions* series on a wide range of paleopalynological subjects, and other special publications. To join, see information in *Palynology*.

Coal Geology Division, Geological Society of America. The annual meetings of this group, held with GSA, almost always include palynological papers dealing with coal-oriented problems. Join by first joining GSA and then informing the current Division Secretary (name available from GSA, Boulder, Colorado, USA).

Paleobotanical Section, Botanical Society of America. This group includes both megafossil and microfossil people, but the emphasis is now on megafossil plants. Nevertheless, palynologists are paleobotanists and find it significant to be associated with PSBSA. An annual bibliography including much paleopalynology is provided to members. Members first join the Botanical Society of America at the regular fee, or one may be an associate member of just the Section by paying a single fee. In either case, to join, write to the current Secretary (listed in *American Journal of Botany*).

There are about 25 paleobotanical-palynological societies worldwide. Some are national, e.g. the Canadian Association of Palynologists (CAP) Others are linguistic, e.g., Association des Palynologues de Langue Française (APLF), which has a number of members in Quebec, Canada, for example. Still others are subject matter oriented, e.g., the important Commission Internationale de Microflore du Paleozoique (CIMP), devoted to Paleozoic studies. One can join by contacting the current Secretary-General. The International Association for Aerobiology (IAA) has mostly to do with airborne pollen and spores, and especially their impact on human health. Nevertheless, the IAA Newsletter contains much of interest and importance to paleopalynologists, for example regarding the relation of pollen and spore "rain" to meteorological conditions. Palynologists who are mostly interested in the Pleistocene tend to belong to such organizations as the American Quaternary Association (AMQUA) or the International Quaternary Association (INQUA), and their papers appear in journals such as Quaternary Research, or Ecology. The newsletters are often of paleopalynological interest. If you want a list of all societies now affiliated with the International Federation of Palynological Societies (IFPS), write the current Secretary-Treasurer (name and address available from IUBS Secretariat, Paris), requesting a copy of the current Federation Newsletter, *Palynos*. (As for IFPS and most of the other societies mentioned here, current information can be obtained from

the Secretariat of the International Union of Biological Sciences (IUBS), or of the International Union of Geological Sciences (IUGS), both quartered in Paris.) Some societies that are not affiliated with IFPS nevertheless have a palynological section section. At this writing the IFPS newsletter, *Palynos*, is edited by Anne-Marie Lézine, whose e-mail address is lezine@lsce.saclay.cea.fr. IFPS web site: www.geo.arizona.edu/palynology/ifps.html.

Chapter 2

Why One "Does" Paleopalynology and Why It Works

1 Purposes

The primary reasons for doing paleopalynology are as follows.

1.1 Geochronology

Palynomorphs represent parts of the life-cycles of various plants and animals that have at times evolved quite rapidly, with the result that such palynomorphs are characteristic of a fairly narrow time-range and hence are useful for age dating (geochronology). (See also biostratigraphic correlation of strata, below.) Academic palynologists are often given pieces of sandstone, siltstone or claystone which are "unfossiliferous"–meaning no megafossils–with the request that they use palynological methods to determine the relative age. Before palynological study was available, geologists often did not know, even within a period or two, what the age of the rock was. Paleopalynology has now been practiced on countless thousands of samples of sedimentary rocks from Precambrian to present (about two billion years; see Fig. 2.1), so that well established, well dated (by study of contained radioactive minerals and other geological and paleontological methods) reference palynofloras are readily available. In studies conducted at

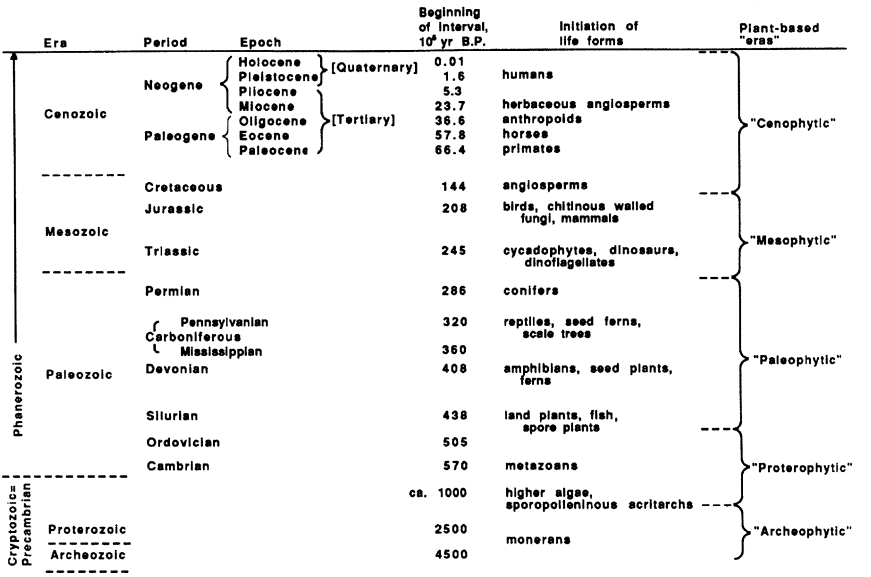


Figure 2.1 General geological timescale. (B.P. = before present; 10^6 yrs.= million years; Precambrian = "Cryptozoic"; all time since the Cryptozoic = "Phanerozoic".) Time not to scale. Sources of dates: DNAG Geologic Time Scale, *Geology*, September, 1983. Plant-based "eras" (= "phytic" eras) are discussed at various places in the text–see also Fig. 6.1. (Gray, 1993, published a different version of the -phytic chronology, without reference to this one, which was originally published in 1988.) The last epoch of the Cenozoic is labeled Holocene, as it appears in the DNAG Scale. However, in the text the Western European term "Flandrian" and the expression "present interglacial", are also sometimes used for the last approximately 10,000 years. "Recent" and "Post-glacial" are avoided. Note that the Cenozoic era is divided into major subdivisions in two different ways: (1) Tertiary (about 65 My) plus Quaternary (about 2 My), which is the traditional way; and (2) Paleogene (about 43 My) plus Neogene (about 24 My). The Neogene, as usually defined in the past, does not include the Pleistocene and Holocene (sometimes collectively called the "Anthropogene"), but in this book Neogene is treated in the original and more logical sense, including all the time from the end of the Oligocene to present, as indicated by the dotted bracket (cf. Berggren, 1998).

Penn State, for example, the Mississippian/Devonian boundary in Centre County, Pennsylvania, was shown from well preserved palynofloras to lie within the local Pocono Formation, which is otherwise not very fossiliferous. We also showed from well preserved palynofloras that the Newark Supergroup rocks in the Hartford-Springfield Basin of Connecticut and Massachusetts range over a very large time-span from Late Triassic to well up into the Jurassic, whereas formerly most geologists regarded these rocks as Triassic only. Most geologists thought the time-span of deposition was much narrower than it is.

A good example of precise palynological dating that is more characteristic of palynomorphs derived from marine organisms than it is of sporomorphs was presented by Grahn *et al.* (1996). Three Ordovician impact craters in Scandinavia could be accurately dated because the chitinozoan organisms invaded the waters of the craters soon after the impact events.

Each student in my beginning course in paleopalynology was issued an "unknown" sample of sedimentary rock near the beginning of the course. In the final week the student handed in a report, in which he/she established from work in the laboratory and library the age of the rock, among other things, such as the environment of deposition. The students almost invariably succeeded in determining the age to the correct stage of the correct period (one student issued a Cretaceous coal even succeeded in identifying the coal-bed from which the sample originated, but he used some non-palynological, albeit scientific, sleuthing in the final stages of his investigation!).

1.2 Biostratigraphy

Paleopalynology has become economically important mostly because palynofloras can be used, beginning with about one-billion year old rocks (acritarch palynofloras), to show correlation of a section of rocks from one place with another section of rocks, from a different locality and of perhaps quite different thickness and quite different lithology. This work of biostratigraphic (in this case, palynostratigraphic) correlation is what oil company palynologists mostly have done. The sections to be correlated may be hundreds of kilometers apart. More often they are not widely separated, and may be in the same oil field, where it is very important to know at what level one is drilling, not in meters of depth, but with reference to known gas or oil production levels. Sometimes this sort of stratigraphy is attempted across a whole continent, but this is risky, and intercontinental correlation is only possible with great caution and with appropriate concern for the paleolocation of the continents concerned. Paleopalynology is particularly well suited for correlation, because palynomorphs of one kind or another are found in sedimentary rocks of all ages from about two billion years ago to present, and in all sorts of environments, from freshwater lacustrine deposits to deep-marine sediments. Palynomorphs from land-dwelling organisms are the only abundant microfossils that link marine and non-marine environments–pollen from trees in the Mississippi drainage will be found in lake sediments in Arkansas, lagoon sediments in Louisiana, and in marine sediments of the Gulf of Mexico.

Stratigraphic applications of palynology have included many successes in getting age estimates for sedimentary and even metamorphic rocks that are otherwise unfossiliferous or nearly so, and stratigraphically challenging, such as the displaced chunks of continents called terranes or suspect terranes.

Maziane-Serraj *et al.* (1999) reported such a study in the Lower Paleozoic of Ireland. The small size and chemical durability of palynomorphs are in such cases very advantageous.

A curiosity in the history of paleopalynology is that the earliest pre-Pleistocene use of palynostratigraphy was the attempt to correlate coal beds. It is probable that the success of Holocene (= present interglacial = "post-glacial") pollen analysis of peats encouraged the belief that coals were the things to look at. Furthermore, there was economic incentive, because both coal and peat were mined in Europe and North America. As mentioned earlier, however, coals are nearly all autochthonous deposits of woody swamps. As such, the palynoflora reflects almost entirely the very local swamp environment, and correlation of coals by palynology is therefore very tricky. Variations in spore/pollen content of coal beds are likely to be palynofacies (specifically, palynobiofacies per later discussion), depending on the impact of local conditions in the swamp on the vegetation that produced the peat.

1.3 Paleoecology

For a variety of reasons it may be important to know as much as possible about various sorts of environments represented by a sedimentary rock. Palynology can help here in several ways. Palynomorphs can be sensitive indicators of the processes of sedimentation and the source of sediments. The source organisms of some palynomorphs, e.g. dinoflagellates and other marine algae, are primarily marine organisms, and their fossils (dinocysts, various other algal remains attributable to specific groups, and acritarchs) may be indicators of the biological environment of the organisms when alive. Spores/pollen occurring as sporomorphs originate almost exclusively on the continents. They indicate therefore the presence of source vegetation. Because plants are sensitive indicators of continental environments (mostly climates), spores/pollen have much to tell us about climatic paleoenvironments. This is, of course, the reason for the original successes of palynology/pollen analysis in Holocene vegetational analysis. On a micro-scale, the same sort of reflection in the palynoflorules of climatically caused vegetational change (first noted by Von Post and other Europeans) in the Holocene can be seen, e.g., in Carboniferous coals. Fig. 2.2 shows such an example for Pennsylvanian age coal in Illinois. *Lycospora granulata* is the spore of *Lepidophloios*, and *Cappasporites* that of *Lepidodendron,* both lycopsid trees, whereas *Thymospora* was produced by *Psaronius* tree ferns.

A plant succession depending on conditions in the swamp is probably reflected, though one must always be cognizant of a spore succession depending on paleo-sedimentological factors (these are related to palynolithofacies, per later discussion).

Specht, Dettmann and Jarzen (1999) showed that in Late Cretaceous rocks of Australasia and Antarctica plant taxa identified from their fossil pollen could be

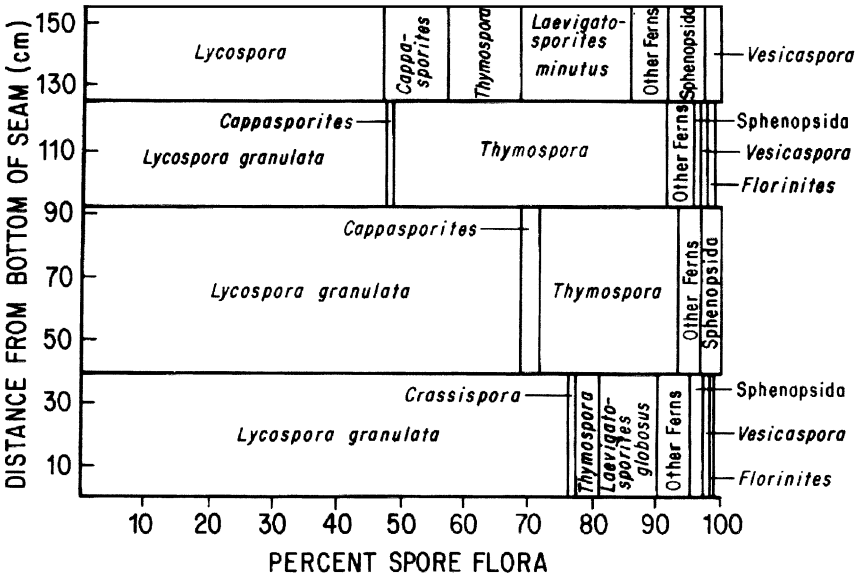


Figure 2.2 Spore succession in Herrin (No. 6) coal, Illinois (Pennsylvanian). Redrafted from R. A. Peppers in Phillips and DiMichele (1981) and reprinted by permission from K. J. Niklas, ed., *Paleobotany, Paleoecology, and Evolution*, ©1981, Praeger Publishers.

used to trace vegetation and its relationship to climate with considerable precision. Even pollen in human and animal coprolites has been used (see Waldman and Hopkins, 1970; Carrión *et al.*, 2001; Carrión, 2002) to deduce the climate and other aspects of the environment in which the producing animals lived! Such spore- and pollen-rich coprolites from Paleozoic rocks studied by Cutlip and Raymond (1999) have established that arthropods were already specialized to feed on sporomorphs in the Carboniferous.

Fedorova (1977) has pointed out that in large sequences of sediments deposited over a considerable time span, the complexes of associated palynomorphs reveal much about sedimentation regimes and the coordinated climatic conditions. She has shown that these broad scale relationships can be plotted as triangular diagrams (see Fig. 2.3), which succinctly demonstrate the coordination of sedimentation and general environmental conditions on land (per spores/pollen) and in the marine environments (per phytoplankton, especially dinoflagellates). Fedorova studied the Lower Cretaceous rocks of the then USSR, but similar sorts of relationships can be demonstrated for other time and space frames. Martin (2004) has summarized the significant contribution that micropaleontology, of which paleopalynology is obviously an integral part, can make to environmental studies concerned with potential anthropogenic influences on the

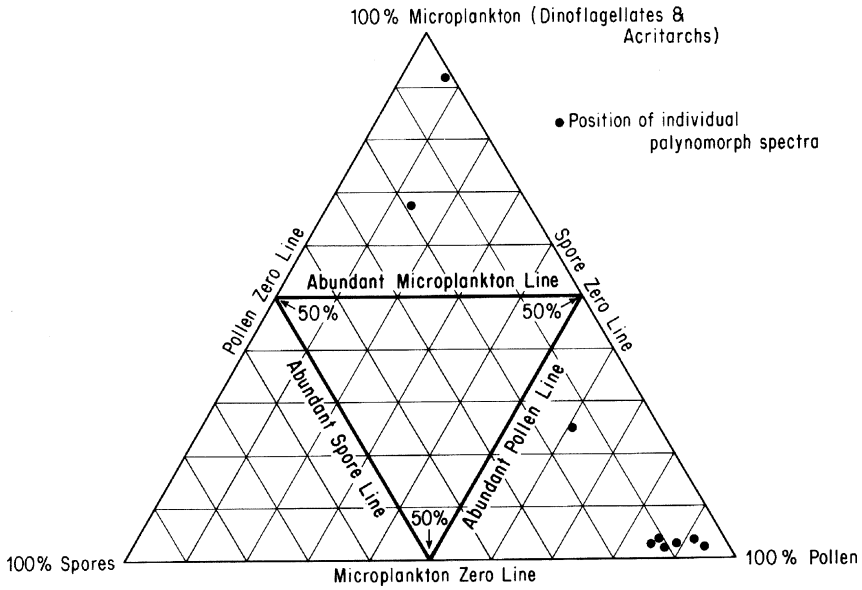


Figure 2.3 Phase diagram for showing paleoecological relationships for palynofloras. Dots represent position of nine Berriasian-Valanginian (Lower Cretaceous) palynomorph assemblages from the Pre-Caspian Depression, (former) USSR. Translated and adapted from Federova, 1977.

modern environment. He sees a new field of "environmental micropaleontology" emerging.

For a very able citation of practical, commercially valuable applications of palynology, mostly related to paleopalynology, see McGregor *et al.* (1996).

2 Why Paleopalynology Works

2.1 Ubiquity of Palynomorphs

Beginning with Precambrian acritarchs up to 1.4 billion years old, sporopollenínous and chitinous palynomorphs (and some consisting of other, also very robust organic compounds) occur in sedimentary rocks of all ages and from many different sedimentary and biological environments (but there are problems–see *Disadvantages and Limitations*, below). They originate both on land (spores/pollen = sporomorphs) and in fresh water (*Botryococcus* and other algae, some dinoflagellates and a few sporomorphs) and salt water (most dinoflagellates, acritarchs, and other algal microscopic remains, the extinct chitinozoans, scolecodonts, foraminiferal test linings, a few sporomorphs).

2.2 Abundance and Durability of Palynomorphs

Most palynomorphs, especially spores/pollen and dinoflagellates (when present at all), tend to be much more abundant than most other fossils, even than other categories of microfossils. I have worked on a sample of silt containing five million dinoflagellates per gram and one containing four million pollen grains per gram. That is exceptional, but 10,000–100,000 palynomorphs per gram is common for siltstones. It is routine for palynological strew slides to contain 5,000 specimens. A 100-place slide box often contains, therefore, 500,000 specimens, more than the specimen catalog of most museums! This provides possibilities for statistics and population studies nearly unique in paleontology. A large part of the explanation for this abundance in sediments is the tiny size of palynomorphs, which is illustrated in Fig. 2.4 Fungal spores, plant spores and anemophilous (=wind pollinated) plant pollen are significant parts of the primary biological aerosol particle ("PBAP") load of the atmosphere (cf. Jaenicke, 2005). It is incidental to our concerns here, but all sorts of airborne spores and pollen are potentially allergenic to humans, and this is the basis for much palynological research under the banner of aerobiology. The author just cited also asserts that pollen in the atmosphere because of its affinity for water is a likely source of nuclei for cloud condensation and thus can directly affect climates.

Further, sporopollenin (dinosporin of dinocysts is a similar compound) and chitin, the principal components of the walls of palynomorphs, are among the most, probably *the* most chemically inert of the major naturally occurring organic compounds. Palynomorphs thus not only tend to be preserved despite chemical vicissitudes during and subsequent to deposition, but also can be readily separated by relatively easy laboratory procedures from the enclosing sedimentary rock.

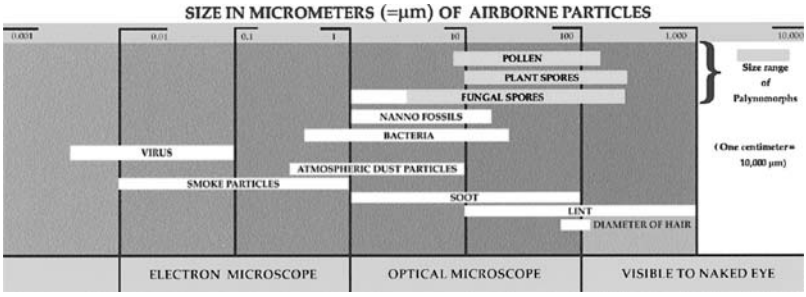


Figure 2.4 Palynomorphs are very tiny! This diagram shows the size range of pollen, plant spores, and fungal spores in comparison with other sorts of very small objects with which people are familiar, such as the cross-sectional diameter of a human hair. Note that the smallest fungal spores are too small to qualify as palynomorphs. The diagram is based on an advertisement used some years ago by an air-cleaning equipment manufacturer.

2.3 Fast Evolution

Palynomorphs of various sorts represent preserved parts of the life cycles of various organisms that, during one or more segments of Earth history, were comparatively fast evolving, as well as abundant and easy to collect. This is a "must" for biostratigraphy and is true of acritarchs for the latest Precambrian, Cambrian, and Ordovician, scolecodonts and chitinozoans in marine sediments of the Ordovician and Silurian, spores in the Devonian, spores/pollen in all periods since the Devonian, and dinoflagellates in marine rocks since the Triassic. However, it should be noted that, although paleopalynology for the first time brought into the field a paleontological discipline in which a single slide of a single preparation may contain easily 5,000 specimens, paleopalynology has not as yet provided compelling evidence for gradual evolution. Though centimeter-by-centimeter sampling is possible, taxa caught in the act of gradually turning into other taxa have not been widely reported. On the other hand, some palynologists, e.g., de Jersey (1982) for the genus *Aratrisporites*, deduce evolutionary change in quanta–supporting the concept of punctuated equilibria–"saltating" evolution.

3 Disadvantages and Limitations

It is not fair to oversell! Paleopalynology has disadvantages and limitations! Palynomorphs are silt-sized and are therefore sparse or absent in well-sorted, coarse-grained sandstones and fine-grained claystones.

Palynomorphs are sensitive to oxidation and to high alkalinity and therefore are not usually recoverable from red bed deposits, "clean" limestones generally, evaporitic deposits generally, or weathered rocks, although there are exceptions. Furthermore, most other sorts of fossils are far more lithologically restricted.

Palynomorphs are sensitive to high temperatures and pressures and apparently to crystallization processes in rocks, and are therefore not usually studied with profit from metamorphosed rock, e.g., slate, or rocks in which the organic matter has been carbonized by heat and/or pressure (anthracite or very low-volatile bituminous coals; shales near a lava flow) or secondarily cemented or re-crystallized rock such as dolomite.

Pollen and spores of modern plants can ordinarily be determined with certainty in routine light microscopy only to genus of producing plant, sometimes, e.g., Chenopodiaceae, Poaceae, and Cyperaceae, only to family. Almost certainly, the same situation applied in, say, the Permian. Obviously this is a handicap to both biostratigraphy and paleoecology, because different species of the same genus can mean very different things ecologically. Also, only certain species of a genus may become extinct, and the extinction would be useful stratigraphically if it could be observed. Actually, in a limited number of special cases, species

of pollen within the same genus can even be distinguished in light microscopy. For example, Ammann (1977) did it for two species of *Pinus* based on nodules under the sacci, Holloway and Bryant (1984) have separated some species of *Picea* on sculpturing differences, and others have done the same sort of thing with size, or the ratio of one measurement to another, but this kind of procedure is seldom practicable. However, much more important is the fact that in recent years electron microscopy of modern pollen has made possible specific determination on morphological and structural features not observable by the light microscope. Transmission electron (TEM) microscopy demands preparation techniques and sectioning that make its routine use unlikely in the foreseeable future, but scanning electron microscopy (SEM) can be done with relatively easy preparation procedures that can be applied to a sizable sample of a microscopic residue, and the same is true of fluorescence microcopy, which also shows promise for revealing features of palynomorphs at the specific level not observable by light microscopy (LM). Nevertheless, light microscopy is the workhorse method for study of palynomorphs, and this will remain the case for the immediate future. Thus, it is limiting that with the methods in routine laboratory use, pollen and plant spores are not routinely determinable below the generic level. Another problem with plant spores and pollen is that they tend to be heteromorphic, even within a species, or even within the same spore or pollen organ of the same plant. Lindstrom *et al.* (1997), for example, have shown that individual Permian glossopterid sporangia, can contain as many as four morphologically disparate sorts of pollen, probably reflecting developmental stage differences. Although one type of pollen greatly predominates in each sporangium, this news does indicate the ease with which dispersed fossil pollen floras could be over-speciated and over-interpreted on analysis.

Dinoflagellate cysts are usually not subject to the generic level limitation characteristic for pollen and spores, and they are therefore intrinsically better suited to biostratigraphic use in general. Unfortunately dinoflagellate cysts are not regularly found in non-marine sediments, and sporomorphs remain the best microfossils for non-marine sediments and for connection of non-marine and marine levels in the same set of sediments.

All palynomorphs are subject to reworking, just because they are so sturdy. They can be weathered and eroded out of the original sediments, sometimes in multiple cycles of redeposition. As we shall see later, there are ways of compensating for this, but it is a very devilish problem. A paper by Utting *et al.* (2004) reports an especially distressing example of massive reworking of Devonian, Carboniferous and Permian palynomorphs into Lower Triassic rocks over very large parts of the world. Utting *et al.* point out that this situation does not make palynostratigraphic work impossible in the affected groups of rocks. In fact, the phenomenon itself has stratigraphic and paleoecological usefulness if correctly interpreted, but it unquestionably greatly complicates work in all of the affected sedimentary formations.

However, despite the caveats discussed above, some negative opinions about the applicability of paleopalynology to solution of geological problems are ill-informed and misleading. It is sometimes stated (cf. Mader, 1990, v. 1, p. 170), for example, that palynofloras are exclusively allochthonous taphocoenoses, which ignores peats, coals derived from them, and many other non-marine sediments, in which the sporomorphs are essentially autochthonous.

Chapter 3

The Natural History of Palynomorphs

1 Introduction

Palynomorphs are derived from four "kingdoms" of eukaryotic organisms: Protista, Plantae, Fungi, and Animalia, now usually referred to as subdivisions of the "domain" Eukarya–see simple diagram of relationships in Fig. 3.1 The study of prokaryotic organisms has been greatly expanded since the first edition of this book, and they are now recognized as representing two separate "domains," Archaea and Bacteria, with very long and complex histories. In this way of classifying all life forms, the eukaryotes represent the third "domain." However, the two "domains" of prokaryotic organisims produce no or essentially no palynomorphs. (There have been claims of resistant-walled fossil filaments representing Cyanobacteria, cf. Vecoli, 2004, and their akinete-spores have occasionally been reported in palynofloras–cf. Ralska-Jasiewiczova and van Geel, 1992.) Representatives of all four of the productive eukaryotic kingdoms include organisms that have some part of the life cycle that produces a cell, tissue or organ with some sort of "wall" that is highly resistant (= inert, robust) to organic decay or inorganic degradation, e.g., attack by enzymes, oxygen, or high or low pH. *Botryococcus* (Fig. 1.2e) colonies are preserved apparently mostly because the "skeletons" contain waxy hydrocarbons, though they may also contain some sporopollenin, and certainly contain a complex mix of other compounds (Niklas, 1976). *Pediastrum* (Fig. 1.2i) colonies (coenobia) occur commonly as fossils even though they seem to be cellulosic; they must contain in their walls something other than pure cellulose, which easily hydrolyzes and is very sensitive to attack by microorganisms. This "something else" is probably small amounts of sporopollenin. Chitinozoans (Fig. 1.2a, b) occur as well-preserved palynomorphs in marine

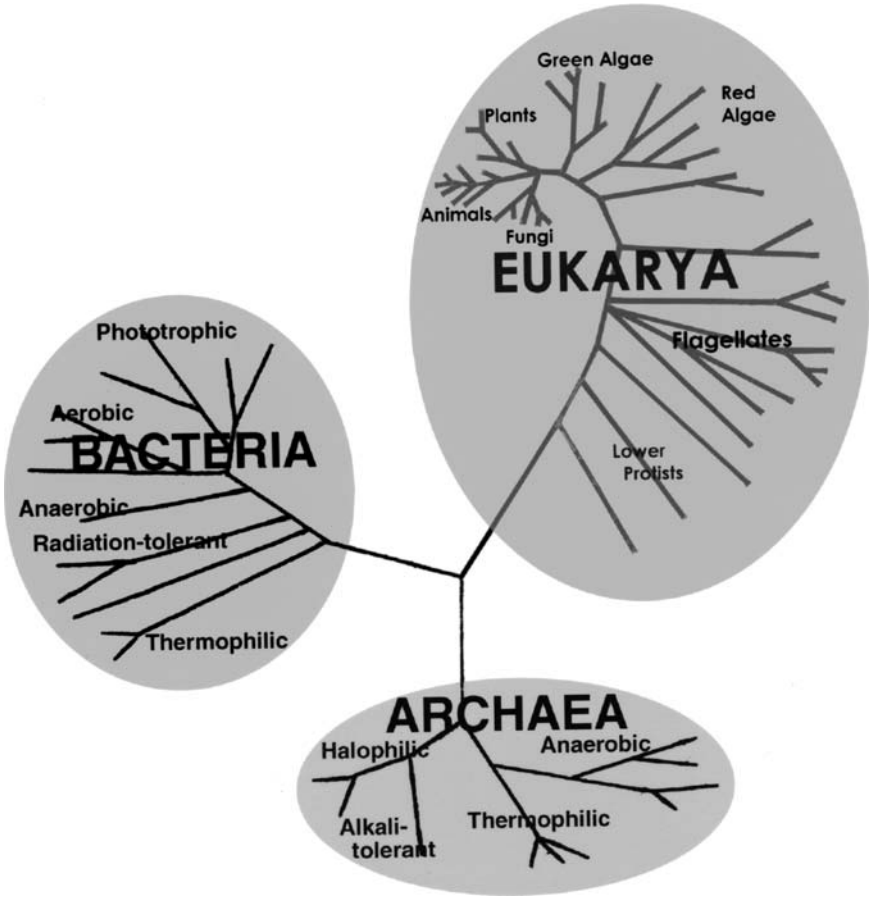


Figure 3.1 The three "domains" of life forms. Eukarya domain includes all of the subdivisions, sometimes called "kingdoms," that produce palynomorphs: animals, fungi, plants/green algae, flagellates/other protists. From Drexler *et al*., 2001, Fig.1, pg. 44; see also Knoll, 1999. The Eukarya is a huge and complex plethora of life forms. See Baldauf, 2003, for a consensus phylogeny, or Futuyma, 2005, for an easy to grasp chart of the relationships.

early to middle Paleozoic sediments. Their relationship to the kingdom Animalia is certain, though some in the past have considered them fungal. In any event, their walls are generally agreed to consist not of "true" chitin but of another complex C-H-N-O compound, which has been dubbed "pseudochitin."

However, the walls of the "main line" of palynomorphs consist of two compounds, or perhaps better stated, two families of compounds: chitin and

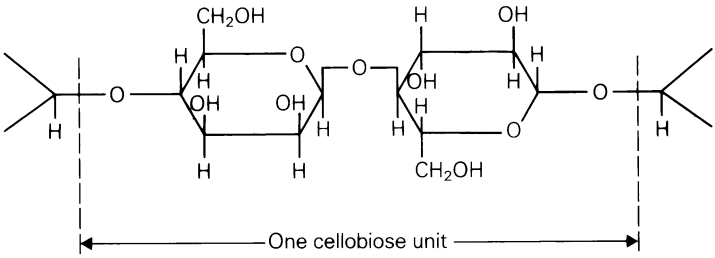
sporopollenin. In an important summary work on chitin (Jollès and Muzzarelli, 1999) chitin is referred to as "the chitins," to stress that not all chitin is the same. Sporopollenin displays a similarity of diversity. The geological history of the families of compounds is caricaturized in Fig. 3.4 Both substances were undoubtedly part of the armament used by organisms to protect living protoplasm from enemy substances and sources of energy, such as oxygen and UV light. They later were adapted to different functions, such as protection against dehydration in the air, structural integrity and the necessity to be flexible in action. An essay on resistant cell walls in charophyte algae and bryphytes by Kroken *et al*. (1996), although dealing primarily with cells other than spores, provides interesting insights into the evolution of robust compounds in the primitive green organisms ancestral to all higher plants.

2 Chitin

Chitinous palynomorphs include spores, mycelia and other organs of certain fungi (mostly ascomycetes), scolecodonts, arthropod organs such as insect mouthparts and lepidopteran wing scales, and certain foraminiferal inner tests or test linings ("microforaminifera"). Van Waveren (1992, 1993) also describes abundant copepod eggs and other copepod parts from Indonesian marine sediments. Copepods are crustaceans, and their hard parts are surely chitin. Van Waveren also describes tintinnid fossils from the same sediments. They are protozoans, and the tests described are also almost certainly chitin. It is somewhat startling that Muzzarelli (1999), one of the world authorities on chitin, writes that "Detection of chitin in fossils is not frequent . . .." Certainly, as fungal spores and mycelia, chitin seems to be almost ubiquitous in post-Jurassic sedimentary rocks. In the modern environment chitin is said to be more abundant than any other organic compound except only cellulose. This is largely due to the chitin produced by marine animals, especially zooplankton.

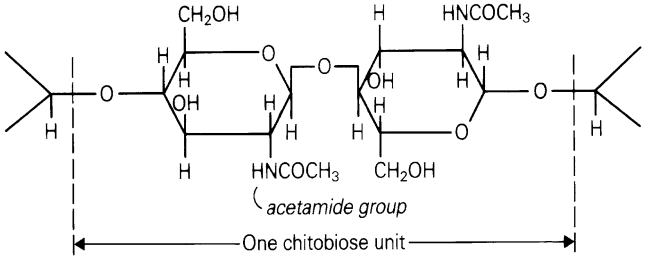
Chitin is a close "relative" of cellulose. This is puzzling, because cellulose is normally quite easily degraded in nature to simple sugars such as glucose, by microorganisms, by oxidation, by enzymes of certain animals, and by hydrolysis. For example, lye (KOH) is quite destructive of cellulose. On the other hand, various celluloses from different organisms are quite disparate in resistance to chemical and microbiological attack. Household bleach (5.25% NaOCl, sodium hypochlorite) attacks linen, but not so readily cotton–both fabrics consist almost entirely of cellulose. The cellulosic primary wall of some fossil wood may persist even after the lignified secondary wall has been destroyed. The structural formula of cellulose is shown below, and the structure of chitin (" . . . the insoluble polymer of N-acetylglucosamine . . . .," per Jollè and Muzzarelli, 1999) is very similar to cellulose, differing in the presence of side acetamide groups:

Cellulose



Molecule has 2,000–3,000 cellobiose units.
Empirical formula for cellobiose: $C_{12}H_{22}O_{11}$
(Glucose: $CH_2OH–CHOH–CHOH–CHOH–CHOH–CHO = C_6H_{12}O_6$)

Chitin

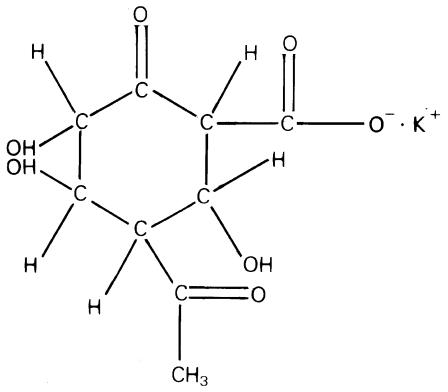


Chitin and sporopollenin behave very similarly in sediments and in laboratory procedures. In unconsolidated sediments sporopollenin is a very pale yellow color, whereas chitin can be almost clear, but often is darker: brown or orange-brown to grayish brown. Other properties seem similar to sporopollenin, although I have noticed some tendency for some chitinous palynomorphs to be a bit more resistant to both chemical and biological attack and to change in color on carbonization (= "thermal maturation," or coalification).

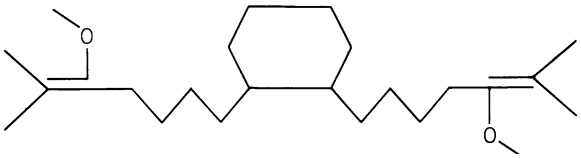
3 Sporopollenin

Sporopollenin is probably a "family" of similar substances making up the basic structure of the resistant wall of most palynomorphs: dinoflagellates, acritarchs, plant spores (isospores, megaspores, microspores) and pollen. It is also present in a number of algae, e.g., in the walls of *Phycopeltis opiphyton*, a green alga (see Good and Chapman, 1978). Acritarchs are almost certainly algal and have a sporopollenin type of substance which makes them degradation-resistant. The

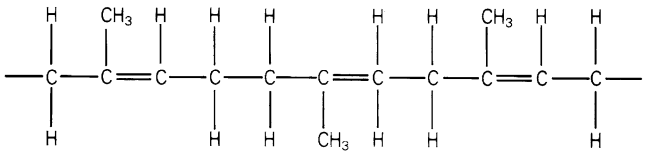
form of sporopollenin occurring in the resistant walls of many dinoflagellate cysts is known as dinosporin. Dinosporin is a substance similar to sporopollenin-proper, like it a macromolecular robust organic compound, but responds differently to various stains, and has different fluorescence properties from sporopollenin of spores and pollen (Fensome *et al*., 1993). Sporopollenin in its broad sense, including dinosporin and other algal variants, is a very interesting substance, probably the most inert organic compound known. It resists acetolysis, but is degraded by strong oxidants such as H_2O_2 or CrO_3, and exhibits secondary fluorescence when stained with primuline (Good and Chapman, 1978). With even slight elevation of temperature over long periods of time it changes color in transmitted light from an almost colorless very light yellow to orange, brown and finally black. However, spore and pollen exines can survive temperatures of 200° C with intact structure for short periods. It was first observed and named (as "sporonin") by John in 1814, and characterized by Berzelius in the 1830s (see Zetsche and Huggler, 1928). Much later, Zetsche and co-workers (Zetsche, 1932; Zetsche and Kalin, 1931; Zetsche and Vicari, 1931) were able to establish an approximate (and arbitrary) empirical formula of $C_{90}H_{142}O_{27}$ for the resistant wall compound of *Lycopodium*, and similar numbers for *Picea, Pinus* and *Corylus* sporopollenin. It was apparently Zetsche who broadened John's term "sporonin" to the more inclusive "sporopollenin." Characterization of the structural formula is very difficult because procedures which break down the substance (oxidation, "solution" in monoethanolamine) produce simple sugars and other compounds that do not prove the structure of the original molecule. Further, preparation techniques used to remove the other constituents of spores and pollen (KOH-lysis, acetolysis) also change the sporopollenin, as it has a marked tendency to pick up halogens, metallic ions, and other groups when treated. In a series of analyses I did long ago, sporopollenin of *Beta vulgaris* pollen, a very resistant exine type, was prepared by prolonged KOH-lyzing. Infrared absorption spectra of the sporopollenin so prepared matched quite well with the K salt of glucuronic acid:



Inasmuch as I also was able to show that the breakdown of beet sporopollenin by oxidation (by H_2O_2) produced hydroxycarboxylic acids, I thought at the time that sporopollenin was probably a condensed carbohydrate of some sort. (That chitin is a carbohydrate derivative is certainly interesting in this connection.) In the meantime many others have used more sophisticated tools on this substance. Shaw and coworkers, Heslop-Harrison, Brooks and others (see Brooks *et al*., 1971) have published research done by following the buildup of compounds in the tapetum in anthers of flowers at the time that sporopollenin is seen to be deposited in the exines of pollen. Based on these studies, it has been suggested that sporopollenin is a copolymer of ß-carotene, a xanthophyll such as anther axanthin, and fatty acids. If true, the substance should have repeating units of an isoprenoid sort. Given (1984) notes that the predominance of straight chains over isoprenoid structure in fossil spore walls makes it difficult to accept the Brooks *et al*. theory. Given *et al*. (1985) have also noted the presence of aliphatic chains with little or no branching in samples of modern sporopollenin, as well as considerable structural variability in samples from different plant groups. Potonié and Rehnelt (1971), for example, suggested the structural unit:



This would make sporopollenin a sort of "cousin" of rubber. They share much in common: elasticity, sensitivity to oxidation and alkalinity, general "durability". However, rubber's structure contains no oxygen, and the analogy is really only a caricature. The structure of rubber is:



The structural manner in which sporopollenin occurs in spores/pollen is very diverse. In general, it is limited to the outer wall, the exine. Most fern spores and some gymnosperm pollen have an additional sporopollenin-bearing wall, the perine or perispore (seldom seen in fossils). Some, mostly aquatic, flowering

plants have abandoned the production of sporopollenin altogether, and others, e.g. the family Lauraceae, manage to operate with very little sporopollenin in their exines, meaning that these exines seldom are preserved as fossils and that reference preparations of such pollen cannot be prepared by the usual method of acetylation. Other sporopollenin-containing elements associated with spores/pollen are the following:

(a) Viscin threads (Hesse, 1981), ektexinous extensions, producing a sticky (but not viscous) webbing. Such threads are produced by various, entomophilous (insect-pollinated), ornithophilous (bird-pollinated) and chiropterophilous (bat-pollinated) angiospermous pollen. The threads cause adherence to animal vectors. Viscin threads were described for a fossil onagraceous pollen by Traverse (1955, 1994). They are especially complex and prevalent in that family of plants (cf. Skvarla *et al*., 2005). Note that anemophilous pollen and spores generally are not sticky. The stickiness of animal-dispersed pollen is usually provided by an external coating of a tapetal derivative (see Table 3.1). Pollenkitt has even been described from *Tilia*-like pollen in fossil flower buds of Miocene age (Zetter *et al*., 2002).
(b) Elaters, perispore-like bands attached to *Equisetum* spores, probably used for dispersal by air currents.
(c) Ubisch bodies = orbicules, small ($2-5\,\mu m$) pieces of sporopollenin apparently produced by the tapetum as a "throw away" during formation of the exine-proper, though it would be unwise to assume that they have no function. Ubisch bodies are often loosely attached to the surface of fossil spores/pollen exines and therefore are found as free bodies in palynological macerations (see Taylor, 1976a, b). They also have been described from pollen in megafossil, *Tilia*-like flower buds of Miocene age (Zetter *et al*., 2002), and they were found by Archangelsky and Taylor (1993) to be extremely abundant on the surfaces of *in situ* pollen of Cretaceous *Clavatipollenites*. It is not surprising that they are seldom found still attached to fossil dispersed pollen. (Suggesting that orbicules are "throw away" products, makes me recall that Tournefort and other early botanists considered pollen itself a "waste product" of flowers!– Bernasconi and Taiz, 2002, p. 99). See illustration of ubisch bodies on cover of this book.

Measurement of the amount of sporopollenin in spores and pollen is usually achieved by acetolyzing them and assuming (as microscopic examination shows to be generally true) that only exine is left. Table 3.2 shows a representative list for a variety of spores/pollen producers. The range is very considerable. In general, the more sporopollenin, the more resistant to decay, oxidation, etc. However, the distribution of the sporopollenin also makes a difference: the more sporopollenin concentrated in the outer part of the exine (ektexine or sexine), the more durable

Table 3.1 Origin and characteristics of pollenkitt and viscin threads. From Hesse (1981)

Characters	*Pollenkitt*	*Viscin threads*
occurrence in angiosperms	in all families investigated up to now	only in a few distinctly entomophilous families
origin	synthesis by plastids of the anther tapetum, mostly during the tetrad stage and later on	like the material of the ektexine, long before the pollenkitt synthesis
chemistry	a complex mixture of lipid substances	similar or equal to the ektexine, containing sporopollenin
state of aggregation	fluid, viscous, sticky, partially with crystalline inclusions	firm, elastic, not fluid, not sticky, without crystalline inclusions
sculpture	no sculpturing	often smooth surfaces, but partially species–specific knobs or furrows
fine structure	opaque, but with varying homogeneity and electron density, partially with lamellae	the same homogeneity and electron density as the ektexine, without lamellae
distribution on the pollen surface	in entomophilous angiosperms mostly as an electron-dense, homogeneous film on the pollen surface; in anemophilous angiosperms usually as small and heterogeneous lumps in the cavities of the exine	the threads often originate near the apertures, but otherwise they are not connected with the exine
mode of pollen attachment	the pollen grains (or tetrads) adhere only by their stickiness	the pollen grains (or tetrads) become entangled by the threads, pollen attachment by friction or adhesion

the exine. Elemental analysis of the exinal material remaining after acetolysis or KOH-lysis is interesting in several respects (see Table 3.3). Acetolysis obviously destroys some carbonaceous matter in the exines that KOH treatment leaves intact. KOH treatment introduces some potassium to the exine, whereas acetolysis introduces sulfur from the sulfuric acid in the acetolysis mixture. Some sorts of spores/pollen, e.g., *Juniperus*, contain much more non-combustible (mostly mineral) matter than others. Chitinous fungal spore walls, e.g., *Calvertia*, contain

Table 3.2 Proportion of various species of pollen and spores that consist of sporopollenin, as calculated by residue from acetolysis

Species	*Percent of weight of air-dried pollen lost in acetolysis*	*Percent sporopollenin*
Spores		
moss (mixed sample of commercial origin)	69.0	31.0
Lycopodium sp.	69.5	30.5
Equisetum sp.	95.0	5.0
fern (mixed sample of commercial origin)	87.0	13.0
Pollen		
Pinus silvestris	74.1	25.9
Poa pratensis	85.6	14.4
Alnus incana	82.2	17.8
Populus trema	94.4	5.6
Ulmus scabra	84.7	15.3
Ulmus scabra (2 h maceration with 10% KOH)	93.1	6.9
Trifolium pratense	90.8	9.2
Beta vulgaris	82.6	17.4
Brassica napus	90.9	9.1

much more nitrogen than sporopolleninous exines, as might be expected from the acetamide content of chitin. Acetolysis, however, largely strips the acetamide groups away. Pocock and Vasanthy (1986) showed that the substrate on which plants grow can be reflected in the mineral content of pollen walls, including the exine.

Sporopollenin's propensity to pick up oxygen is so great that it will "autoxidize" on microscope slides. The observable effect on exines is swelling, eventually grotesque swelling and dissolution. Some have suggested that this effect is due to hydrolysis rather than oxidation, but my observation is that it does not occur if O_2 is excluded. Some years ago I re-measured the modern spores/pollen illustrated in Traverse (1955) after ten additional years on microscope slides in glycerin jelly. The results are shown in Table 3.4. Havinga (1971) showed that exines of spores/pollen buried in soils of various sorts were attacked progressively, presumably by bacteria and natural hydrolysis. Table 3.5 shows the results of some of Havinga's experiments.

Havinga (1984) has also shown that spores/pollen of different taxa have conspicuously different rates of corrosion (usually observable as thinning). *Lycopodium* spores are the most resistant, followed by conifer pollen and various angiosperm pollen. That generalization is difficult is illustrated by the fact that one of the most sensitive forms to corrosion is *Polypodium*, a fern spore. The observation from experiments by Campbell and Campbell (1994) that pollen exines

Table 3.3 Elemental analysis (%) of spores/pollen exines obtained by various treatments of whole spores/pollen

Species	*Treatment*	*Ash*	*C*	*H*	*O*	*S*	*N*	*K*
Calvertia gigantea (puffball fungus spores)	acetolysis	0.4	45.3	6.3	35.9	6.5	0.9	*
	KOH	0.2	43.3	6.6	33.3	0.8	5.6	*
Lycopodium sp.(club-moss spores)	acetolysis	3.0**	57.8	7.4	28.0	3.3	0	*
Juniperus communis (juniper pollen)	acetolysis	11.5	46.7	6.8	29.5	3.1	0	*
Pinus silvestris (Scots pine pollen)	KOH	2.3	55.2	7.6	27.2	0.1	0	*
Typha latifolia (cattail pollen)	KOH	0.7	62.1	8.7	24.6	0	0	*
Poa pratensis (bluegrass pollen)	KOH	6.1	51.5	7.4	28.8	0	0	*
Ulmus scabra (elm pollen)	acetolysis	6.1	50.5	6.6	31.8	5.9	0.4	*
	KOH; H_2O wash	8.4	55.3	9.1	25.7	0	0.2	5.0
	KOH; HCl, H_2O washes	0.5	60.0	9.4	30.8	0	0.5	0.04
Quercus robur (oak pollen)	acetolysis	3.1	51.7	7.5	30.7	4.2	0	*
	KOH; H_2O wash	11.8	51.3	7.8	28.5	0	0.5	0.5
	KOH; HCl, H_2O washes	2.2	63.5	9.6	27.6	0	0.4	0.1
Artemisia vulgaris (mugwort pollen)	KOH	23.5	44.9	6.4	19.1	0	0	*
Beta vulgaris (beet pollen)	acetolysis	10.9	47.7	7.0	32.0	5.1	*	*
	KOH; HCl, H_2O washes refluxed 1 week in	11.3	48.2	4.8	34.0	0.2	*	*
	benzene-alcohol-KOH, 1 week in HCl, 3 weeks in monoethanolamine	11.6	62.6	8.2	13.0	*	*	*

* = not analyzed.
** = estimated.

Table 3.4 Degradation of pollen/spore exines on microslides, 1951–61 (= "autoxidation")

Amount of swelling (%)	*Number of species*
0–1	13
1–5	7
6–10	11
20	16
> 20	1

are degraded by wet-dry cycles in sediment that dries out completely in the dry phases, probably involves both mechanical breakage and oxidation of the exines.

The evolutionary history of sporopollenin is very long (see Fig. 1.3). The oldest sporopolleninous acritarchs occur in Precambrian rocks 1.2–1.4 billion years old. In these organisms sporopollenin probably played the role of protector of protoplasm against ultraviolet radiation. The green algae are presumably responsible for the development of sporopollenin and its introduction into the armament of most higher green plants, where its principal function is protection against oxidation and desiccation (while sporopollenin can be oxidized, it is more resistant to O_2 than are most other organic compounds).

I would now like to summarize the salient features. Sporopollenin is a highly inert C-H-O compound, probably of the carotenoid-terpenoid sort (though in my opinion, some sort of condensed carbohydrate structure has not been altogether excluded). Its natural color is pale yellow, but with thermal maturation, as the

Table 3.5 Unaffected (u), intermediately affected (i) and severely affected (s) pollen grains and spores in various soil types for different lengths of time. (November 1964 is eight months after placement of the pollen in the soils.) From Havinga, 1971

Dates	*Percentages*														
	Spagnum peat			Carex peat			Podsolized sand soil			River clay soil			Leaf mould in greenhouse		
	u	i	s	u	i	s	u	i	s	u	i	s	u	i	s
November 1964	92	8	0	84	16	0	63	37	0	26	61	13	23	60	17
March 1965	78	21	1	48	45		45	51	4	–	–	–	21	31	48
November 1965	–	–	–	7			26	61	13	17	36	47	16	25	59
November 1969	68	31	1	–	–	–	24	58	18	4	26	70	4	27	69

sporopollenin increases in "rank," with loss of O and H and increasing percentage of C (parallel to the coalification series of other organic matter), the color deepens through dark yellow, orange, reddish brown, finally to black. See Fig. 19.2 later in this book showing fossil spores/pollen color changes as related to organic thermal maturity. During this series, the reflectance increases. The agents of thermal maturation are temperature-elevation plus time. Time alone does little. Pressure alone does little. Gutjahr (1966) showed that *Quercus* pollen darkens in the manner described slowly at 100° C, and more rapidly at 150 and 200° C (so dark that 90% of transmitted light is absorbed by exines treated less than 3 days at the latter temperature). Other experiments show that 150° C over very long periods will eventually blacken exines, and that the geothermal gradient alone is sufficient to do the job completely at depths of 5,000 m or so. The specific gravity is about 1.4, close to that of solid wood substance (because of air spaces, most whole wood is commonly less than 1.0 and floats in water, which woods with little air space will not–similarly, a block of pure sporopollenin would not float). The index of refraction is 1.48. Sporopollenin is sensitive to oxidation, though not as much so as is most organic matter in sediments. It is also sensitive to high pH over prolonged periods of time. Enzymes mostly do not affect sporopollenin, so pollen and spore exines pass through most animal guts (including human) unchanged, though the non-sporopollenin constituents of the grains are digested (Scott *et al*., 1985a). However, I once heard the noted paleobotanist, Tom Harris (1974b), relate that he fed pollen from his beehives to his geese, through which the pollen passed unscathed, but that by the third "pass" through the recycling ruminant stomachs of his goats, the exines were attacked, and by the sixth day they were destroyed by enzymes. Harris's experiment with exines of pollen passing through goose and goat digestive systems showed that it takes the multiple cycles of a goat's ruminating digestive system plus a goat's powerful enzymes to destroy sporopollenin over a six-day period. There are species of fruit bats that subsist largely on nectar and pollen (Kunz, 2003), but I have seen no published evidence that the bat digestive enzymes attack the pollen exines. I can add that bat guano I have studied in Texas contained abundant pollen exines in excellent condition, but those bats were not fruit bats, and it would be interesting to study feces of such animals more thoroughly.

Chaloner (1976, 1984) has shown that fern spores remain alive and can germinate in fair numbers after passing through the gut of a locust (American: "grasshopper;" see Fig. 3.2).

The poor preservation of pollen in reptilian coprolites reported by Waldman and Hopkins (1970) was not likely due to corrosion of the sporopollenin by the animals' enzymes, as supposed by the authors. In fact, others report abundant and well-preserved sporomorphs in coprolites as old as Devonian (Habgood, 2002) and Carboniferous (Cutlip and Raymond, 1999). Krassilov *et al*. (1999) have dramatically proven that "sporomorphivory" was a way of life for Paleozoic insects by discovering beautifully preserved monosaccate pollen in the guts of

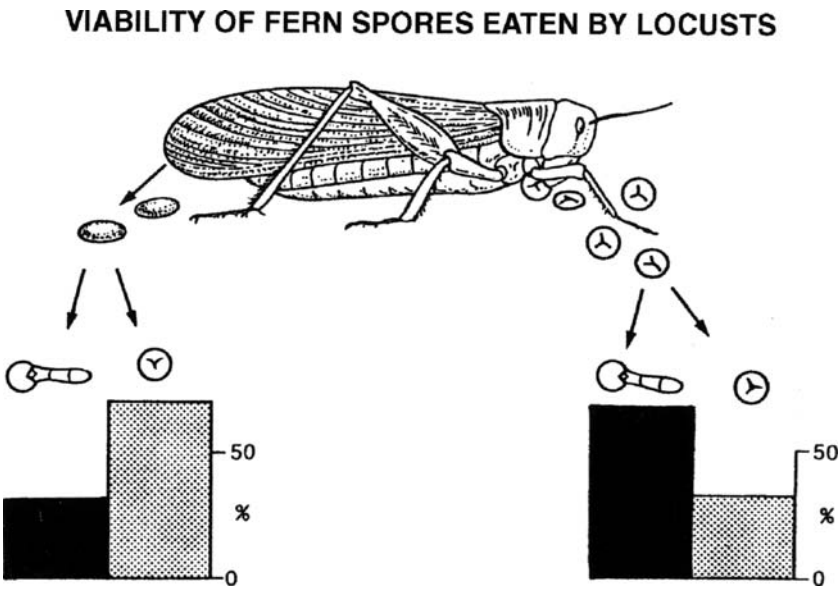


Figure 3.2 The sporopollenin-rich exine of some fern spores is so tough and protects the sporoplast so well that even after passing through an insect's digestive system, many spores can still germinate. About half as many spores germinate in the feces (left) as germinate from fresh spores (right). The dot pattern below the trilete spores represents ungerminated spores, and the black pattern below the sporelings represents germinated spores. From Scott *et al*., 1985a.

Permian booklice. Krassilov *et al*. (2003) have even found an early Cretaceous hymenopterid insect with massive amounts of *Eucommiidites*-like pollen in the gut and around the anus, demonstrating pollinivory flourishing at the time of origin of the angiosperms (see Fig. 3.3).

Angiosperm pollen is rich in vitamins and other nutrients and has been consumed by humans for centuries and is still favored by some humans as a dietary supplement (see Fig. 1.4). Fungal spores are also a source of nourishment for at least some beetles, which have very specialized comb-like mouthparts for the harvesting and opening of fungal spores. Such mouthparts have obviously required millions of years of evolution (cf. Betz, 2004).

Elsik (1966) and Srivastava (1976a) have shown that some fungi can digest sporopollenin and can therefore attack spores/pollen, apparently after deposition in sediments. (*In situ* fossil spores/pollen showing fungal attack of the spore *contents* have been described by Stubblefield and Taylor, 1984, but the exines were apparently not the fungal target.) Havinga (1967) has demonstrated that some soil bacteria can also accomplish this difficult trick. Various people, e.g. Southworth (1974), have noted that sporopollenin "dissolves" in 1-ethanolamine

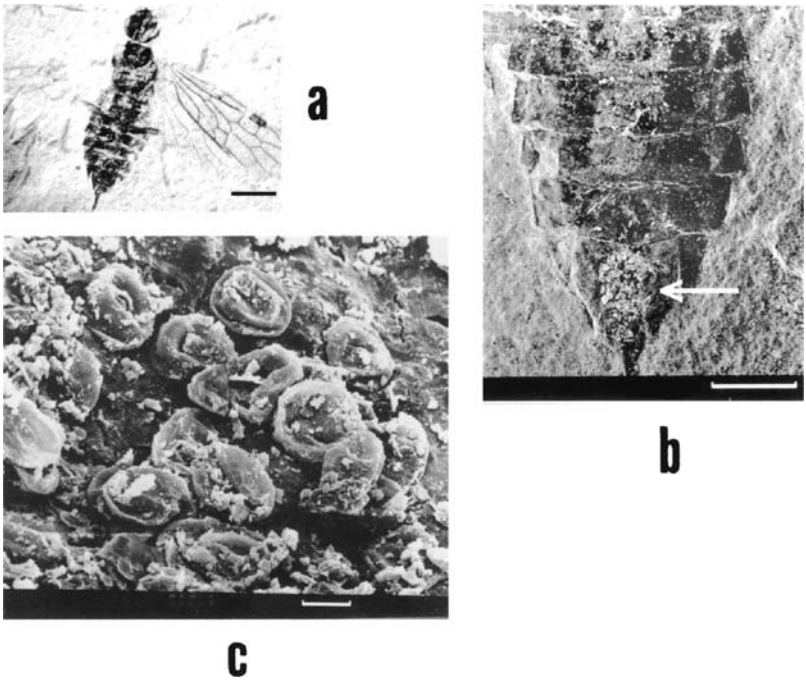


Figure 3.3 Investigation of an Early Cretaceous hymenopterid (xyelid) insect from Transbaikalia, Russia, shows that insect consumption of spores and pollen was practiced on pollen of plants during the period of development and expansion of the angiosperms, as it had already for hundreds of millions of years. The digestive processes of really specialized pollinivores are not likely to pass viable pollen grains in their feces, but the exines come through intact. (**a**) Whole insect on rock surface. Scale bar 2 mm. (**b**) Rear end of insect showing clustering of pollen around the anus (arrow). Scale bar 1mm. (**c**) Mass of pollen exines from area illustrated in b. All are specimens of one species of a *Eucommiidites*-like form. Scale bar 30μm. From Krassilov, 2003.

(monoethanolamine), especially if the exines treated are pretreated by acetolysis (Denizot, 1977). Kedves and numerous co-authors have published many papers on research (e.g., Kedves and Horváth, 2000; Tripathi *et al*., 2004) in which 2-aminoethanol or diethylamine was used to strip away parts of exines in order to investigate the structure of the remaining parts. However, what really happens in such cases is the breakdown of the sporopollenin, producing among other things, sugars (see Fig. 3.1), not the solution of the sporopollenin, as frequently stated by Kedves and co-authors (see Kedves *et al*., 2001). Loewus *et al*. (1985) report that 4-methylmorpholine N-oxide monohydrate ($MMNO.H_2O$), a patent polysaccharide solvent, "dissolves" sporopollenin, a technique which is used for

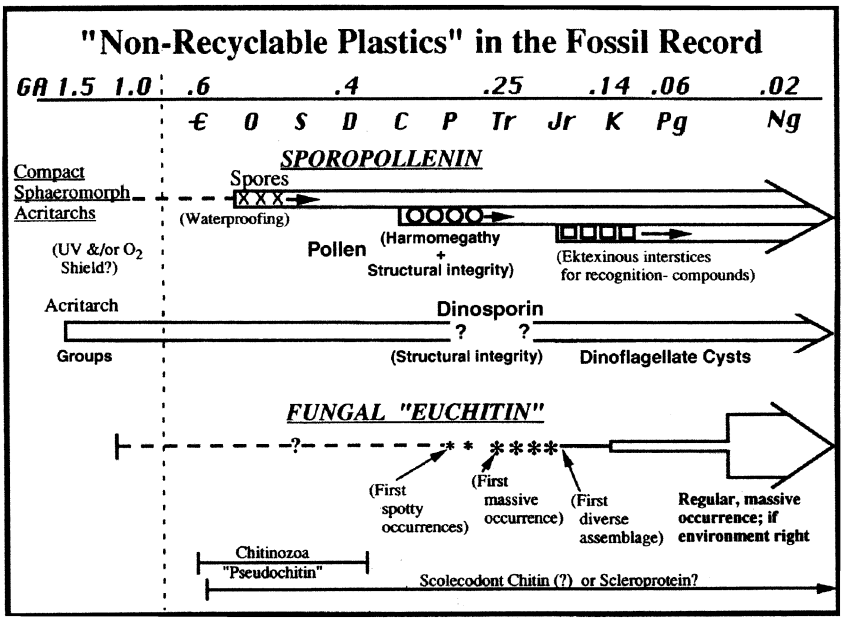


Figure 3.4 *Durability of sporopollenin and similar substances.* If sporopollenin (including the similar, resistant substance of dinoflagellate cysts, known as dinosporin) and the forms of chitin occurring in palynomorphs could be readily synthesized, they would be classified as plastics and industry would undoubtedly find uses for them. Non-scientists are astonished that hard rocks millions of years old can be dissolved with acids, but that microscopic fossils contained in the rocks survive such treatment. These compounds were synthesized by organisms in response to various stimuli and adopted for walls of reproductive bodies then and later as a result of still other requirements.

freeing pollen sporoplasts by removing the exine. Presumably this also represents disintegration, not solution.

From a paleopalynological point of view, the significance of the properties of sporopollenin is that sporopollenin-bearing palynomorphs, once delivered to a sediment, tend to stay there, though the cell contents of the palynomorphs and constituents of the wall layers other than sporopollenin are quickly lost. That small ($1-3\,\mu m$) sporopollenin bodies produced by plants as a by-product of exine formation are frequently preserved and are indeed often quite abundant in sediments further demonstrates the resistance of sporopollenin. These bodies are called ubisch bodies or orbicules.

Indeed, the robustness of sporopollenin, its close relative, dinosporin, and the form of chitin I call euchitin (the chitin of the walls of fungal spores, mostly of ascomycetes, occurring since the Late Jurassic) explain the usefulness of paleopalynology–without those compounds we have no subject. Fig. 3.4 displays

an effort to show diagrammatically the history of the compounds as "non-biorecyclable" plastics of geological history.

It is clear that all of the compounds have been adapted by organisms to a variety of uses. For example, when first found in the Precambrian as acritarch wall constituents, sporopollenin was probably a protector against UV radiation and/or oxygen. Since then it has been adapted to other functions, such as structural integrity, dehydration protection and elastic response to changes in volume from moisture uptake or loss (= harmomegathy). The fact that euchitinous fungal spores are coterminous with the angiosperms makes it interesting to consider if its emergence as a kind of chitin represents development of resistance to angiosperm defenses.

In formation of a sediment, original and post-depositional factors can destroy the sporopollenin: (a) oxidizing environment, (b) highly alkaline environment, (c) carbonization (= coalification, thermal maturation, as a result of even relatively low temperature elevation over a long time), (d) high temperature (over a relatively short time, as a result, e.g. of volcanic intrusion), and (e) re-crystallization of the minerals in the sediments.

The effect of re-crystallization on sporopollenin has not to my knowledge been directly studied, but I have observed from study of several dozens of dolomite samples from most continents that dolomites almost never contain palynomorphs. Limestones are not as a group very good sources of palynomorphs, presumably in large part because of formation in an alkaline environment. (In studies of recent sediments of the Bahamas, I showed progressive loss of palynomorphs in lime muds with time.) But limestones are not as a class barren of palynomorphs. In fact (Blome and Albert, 1985), some limestones contain excellently preserved palynomorphs. Therefore, as dolomites are usually barren, I conclude that the $CaCO_3$ to $CaMgCO_3$ (limestone to dolomite) re-crystalization conversion process destroys palynomorphs.

4 Palynomorphs in Petroleum

A number of studies have turned up the interesting fact that spores/pollen are capable of being swept along with migrating petroleum as it moves through porous sedimentary rocks. De Jersey (1965), for example, was able to show in Australia that petroleum in the producing sands of the Moonie oil field in Queensland contained a characteristically Jurassic palynoflora, whether the reservoir rocks were Permian, Jurassic or Triassic. A Jurassic source for the petroleum was therefore assumed, though previous information had favored a Permian source. Jiang (1984), and Jiang and Yang (1989) in China have described a taxonomically diverse palynoflora of Jurassic age in crude oils from reservoir rocks of Jurassic, Cretaceous, and Cenozoic age. Jiang (1990, 1991) has also made important contributions to the general application of studies of palynofloras from petroleum

in relation to the source rocks from a variety of basins in China. A number of palynologists in the former Soviet Union worked on palynomorphs in petroleum, using them, for example, to demonstrate the direction of oil migration (See Jankauskas and Sarjeant, 2001). A valuable summary of the whole subject is to be found in McGregor (1996a).

5 General Occurrence of Palynomorphs in Time

As we have seen (Fig. 3.1), the palynomorphs commonly studied include representatives of four "kingdoms" of organisms, all belonging to the eukaryotic domain. This information is very briefly presented in Table 3.6. This book emphasizes embryophytic (= archegoniate, i.e., Bryophyta and Tracheophyta) spores/pollen ("sporomorphs"), although dinoflagellates and acritarchs, chitinozoans, scolecodonts, fungal spores, and miscellaneous other forms that make the rest of the "palynomorphs" are also treated. One of the strong selling points for paleopalynology is that from about one billion years ago (late Precambrian) to present, sporopolleninous or chitinous palynomorphs of one group or another are always present in sedimentary rocks of suitable lithology and lithification/metamorphic history, and they are often biostratigraphically useful (that is, rapidly evolving, ubiquitous, abundant). The range of the main groups is shown in Fig. 1.3.

The oldest sporopollenin-containing palynomorphs are sphaeromorph acritarchs over one billion years old from the former Soviet Union and from other parts of the world. The oldest chitinous and pseudochitinous palynomorphs are Cambrian scolecodonts and chitinozoans, respectively. (Chitinous fungal spores appear much later. With a few exceptions in the Permian and Triassic, they do not occur regularly until the Late Jurassic and are not abundant until mid-Cretaceous.) Precambrian sphaeromorph, sporopolleninous acritarchs were joined by hordes of acritarchs with processes and other modifications in the Cambrian and Ordovician. Even non-marine sediments began to contain sporopolleninous fossils in late Ordovician. Some of these are cryptospores, spore-like bodies lacking the haptotypic marks typical of true spores. The earliest unquestioned embryophyte spores are Ashgill (Late Ordovician) trilete spores.

In referring palynomorphs to their appropriate stratigraphic level we use the general geological time scale presented in Fig. 2.1. However, it is very helpful to one's understanding of the plant history involved to speak (informally!) of plant-based "eras", shown on the right side of Fig. 2.1, based on events in plant evolution. The "Archeophytic" extends from about 3.5 billion years (and the earliest known fossils) to the level of the first robust-walled acritarchs and the eukaryotes, at about 1.2 billion years ago. The "Archeophytic" had only prokaryotic organisms, which produced no robust-walled fossils. With the first sporopolleninous acritarchs begins the "Proterophytic," extending up to the level of the first spores or spore-like tetrads of the Late Ordovician-early Silurian.

Table 3.6 A classification of organisms showing palynomorphs occurring as fossils. The makeup of the kingdoms is per Margulis (1981). More recently (cf. Morell, 1997) the classification has been made much more complicated and diverse with the taxonomic expansion of non-eucaryotic life forms into Archaea and Bacteria, with many subdivisions and much splitting of the one-celled eucaryotes. However, as neither Archaea, Bacteria, or the newly recognized protist subdivisions include significant palynomorphs, there is for our purposes no urgency to revise the classification

Palynomorphs produced	*Organisms*
	KINGDOM MONERA (Prokaryotes)
	bacteria
No palynomorphs produced	
	cyanobacteria (= "blue-green algae")
	KINGDOM PROTOCTISTA
Foraminiferal chitinous inner tests	Subkingdom Protozoa
	Subkingdom Thallophyta
Dinoflagellate cysts	Pyrrophyta
Frustules of SiO_2 (diatoms), platelets of $CaCO_3$ (coccoliths and discoasters = nannofossils) are in the correct size range, but are not palynomorphs because of chemical composition	Chrysophyta (diatoms, coccoliths, probably discoasters)
No palynomorphs produced	Phacophyta (brown algae)
$CaCO_3$ deposited, but no palynomorphs	Rhodophyta (red algae)
Desmid zygospores, e.c., *Staurastrum, Pediastrum* coenobia (cellulose, ?sporopollenin). *Botryococcus* colonies (fatty-waxy). Characeae oögonia (cellulosic, often mineralized, not considered palynomorphs) Zygnemataceae zygospores, Prasinophyceae phycomata, and many acritarchs (all of these sporopollenin)	Chlorophyta (green algae)
No palynomorphs produced	Myxomycophyta (slime molds)

Table 3.6 *(Continued)*

Palynomorphs produced	*Organisms*
	KINGDOM FUNGI
Fossil fungi range from Precambrian to present. Robust chitinous-walled fungal "spores" and mycelia occur commonly from Jurassic to present, with a few earlier occurrences, especially at the Permian/Triassic interface	Eumycophyta
	KINGDOM ANIMALIA
Spicules (SiO_2) and other skeletal parts sometimes seen in preparations, not here regarded as palynomorphs	Porifera (sponges)
No palynomorphs produced	Coelenterata
No palynomorphs produced (bryozoan statoblasts sometimes seen in preparations, not considered palynomorphs)	Ctenophora, Platyhelminthes, Nematohelminthes, Bryozoa, Brachiopoda
Paleozoic tentaculite remains possibly belong here; they are palynomorphs	Mollusca
Chitinous mouth-lining parts often occur as palynomorph fossils from Lower Paleozoic to present	Annelida (class Polychaeta)
Chitinous exoskeleton parts, from carapaces of cladocereans to butterfly scales, frequently occur in preparations and are considered palynomorphs when in proper size range	Arthropoda
Possibly the pseudochitinous Chitinozoa from the Lower Paleozoic belong here (if graptolite-related)	Chordata
	KINGDOM PLANTAE
Isospores: trilete in many hepatics and some mosses; mostly alete or monolete. The latter are thin-walled. (Cryptospores?)	Atracheophyta (non-vascular plants) Bryophyta (mosses and hepatics)
Trilete and monolete(?) isospores	Tracheophyta (vascular plants) Primitive, extinct mid-Paleozoic plants: rhyniophytes, trimerophytes, etc.

Table 3.6 (*Continued*)

Palynomorphs produced	*Organisms*
Monolete and trilete isospores	Psilotales (two living genera, no megafossil records)
	Lycopsida
Trilete isospores	Lycopodiales
Trilete microspores and megaspores	Selaginellales
Trilete microspores and megaspores (approaches seed habit)	Lepidodendrales (scale trees–extinct)
Presumably as just above	Pleuromeiales (extinct, reduced lepidodendrids)
Monolete microspores, trilete megaspores	Isöetales (quillworts)
	Sphenopsida
Trilete isospores(?)	Hyeniales (extinct)
Trilete isospores	Sphenophyllales (extinct)
Equisetum: apparently alete isospores with elaters and perine. Calamitaceae: apparently alete to trilete, isospores or microspores and megaspores. Some approach seed habit	Equisetales (living: *Equisetum*–herbaceous; extinct: Calamitaceae–woody)
	Pteropsida
	Filicineae (ferns)
Mostly monolete and trilete isospores, many with perine, some (e.g., *Stauropteris*) with megaspores and microspores	Coenopteridales (extinct)
Isospores, trilete	Ophioglossales (extinct and living)
Isospores, trilete or monolete	Marattiales (some living ferns, some extinct tree ferns)
Mostly isospores (Marsileaeceae and Salviniaceae heterosporous!), trilete to monolete, often with perine	Filicales (most modern ferns)
Trilete microspores and megaspores	Progymnospermopsida Archaeopteridales: *Archaeopteris*
	Gymnospermae
Prepollen, monolete or trilete (and leaf cuticles)	Cycadofilicales (=Pteridospermae = "seed ferns"–extinct)
Pollen, monosulcate (and leaf cuticles)	Bennettitales (extince, cycad-like)
Pollen, monosulcate (and leaf cuticles)	Cycadales (modern cycads and fossil relatives)

Table 3.6 (*Continued*)

Palynomorphs produced	*Organisms*
Pollen, monosulcate to vesiculate (which is monosulcate also) (and leaf cuticles)	Cordaitales (extinct progenitors of conifers)
Pollen, monosulcate (and leaf cuticles)	Ginkgoales (living *Ginkgo* and extinct relatives)
Pollen: saccate (*Pinus et al.*), inaperturate (*Juniperus et al.*), "monosulcate" (*Larix et al.*), "monoporate" (*Sequoia et al.*) (and leaf cuticles)	Coniferales (pine, juniper, etc.)
Pollen: mostly polyplicate(*Gnetum*; others?)–inaperturate. Some fossils probably polyplicate-vesiculate (and leaf cuticles)	Gnetales (living *Ephedra* and associates, living and fossil)
	Angiospermae (flowering-fruiting plants)
Pollen: monosulcate, trichotomosulcate, inaperturate (and leaf cuticles)	Monocotyledonae (one seed leaf, parallel venation, floral parts usually in threes or derivative)
Pollen: monosulcate (primitive Ranales), tricolpate, triporate, periporate, syncolpate, etc. (and waxy leaf cuticle particles)	Dicotyledonae (two seed leaves, net venation, floral parts usually in fives or derivative)

[1.] Homospore = isospore, i.e., spores all of one type. Contrasts with types which have microspores and megaspores, of which pollen-seed plants are the extreme example. Pollen consists of a microspore coat, inside of which a male gametophyte develops.

[2.] Saccate pollen is also prevailingly monosulcate, though the sulcus is often obscure, especially in Cenozoic forms

[3.] Larger taxa, five kingdom view of Margulis (1981). Note that recently the prokaryote classification has been much expanded, with many new members, but none of them produces palynomorphs.

Kingdoms	Major members
Monera (prokaryotes)	bacteria
Protoctista (lower eukaryotes)	protozoans, protists, nucleate algae, slime molds
Fungi	mushrooms, molds, yeasts, lichens
Planta	green plants (bryophytes, tracheophytes)
Animalia	metazoans

This marks the commencement of the "Paleophytic" which is typified by ancient sorts of vascular plants and persists until the Upper Permian, when conifers, cycadophytes, and other advanced gymnosperms came to dominate the land flora, and the "Mesophytic" began. The "Mesophytic" gave way to the present "Cenophytic" in the very early Cretaceous, with the first significant appearance of angiosperms. It is interesting that the "Paleophytic," "Mesophytic," and "Cenophytic" each began well before the animal fossil-based "-zoic" eras with the same prefix. Remy, e.g., in Gothan and Remy (1957), presented practically the same "-phytic" classification many years ago. Gray (1993) published a somewhat different version of the -phytic story, but did not mention either Remy's work or the first edition of this book.

Chapter 4

Spores/Pollen Basic Biology

1 Introduction

Embryophytic spores, and pollen grains (which begin as spores, but become more than just spores), are a principal focus of this book. It is unavoidable at this point to explain what they are in some detail. This is best done by examination of life-cycles of embryophytic plants (Figs. 4.1, 4.2).

2 Bryophyte Life Cycles

The Bryophyta comprise the mosses and liverworts (and the less known hornworts as well). They are non-vascular green plants, apparently related to the green algae on the one hand, and to the vascular green plants on the other. Their general need for a wet environment to effect reproduction invites comparison with the amphibians, and it is tempting to regard them as survivors of the transition from aquatic green algae, probably via liverworts, to land plants, in Ordovician time, and evidence is building (Wellman, 2003) that this is the case. That some of the first certain sporopolleninous embryophytic spores and sporangia of the Ordovician resemble certain liverwort spores is fascinating, but the bryophytes have practically no megafossil record, and what they had to do with land-plant evolution is as yet somewhat controversial. Nevertheless, the Bryophyta are "right" for a primitive, non-vascular embryophytic land plant. (Some green algae

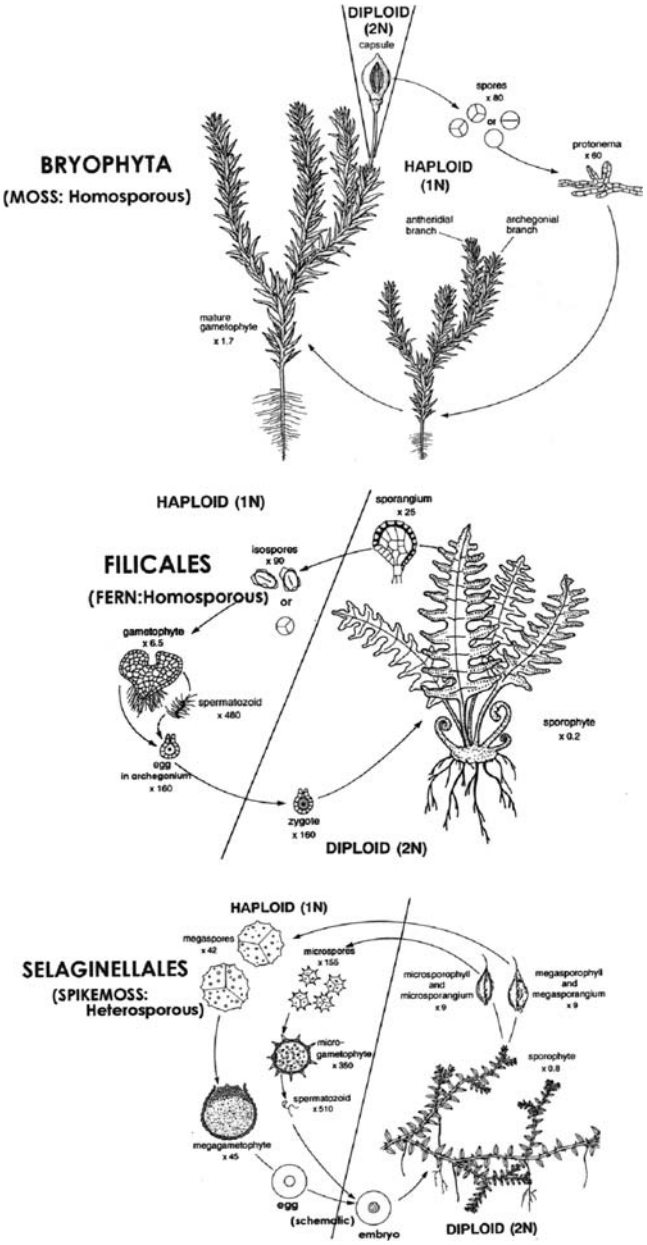


Figure 4.1 Life cycles of free-sporing embryophytic plants. Contrast with Figure 4.2. Note that the spore-bearing organ (= sporangium) of the bryophyte is usually called a capsule by bryologists. It is diploid and is in a sense a parasite on the haploid "parent plant." See explanations in text.

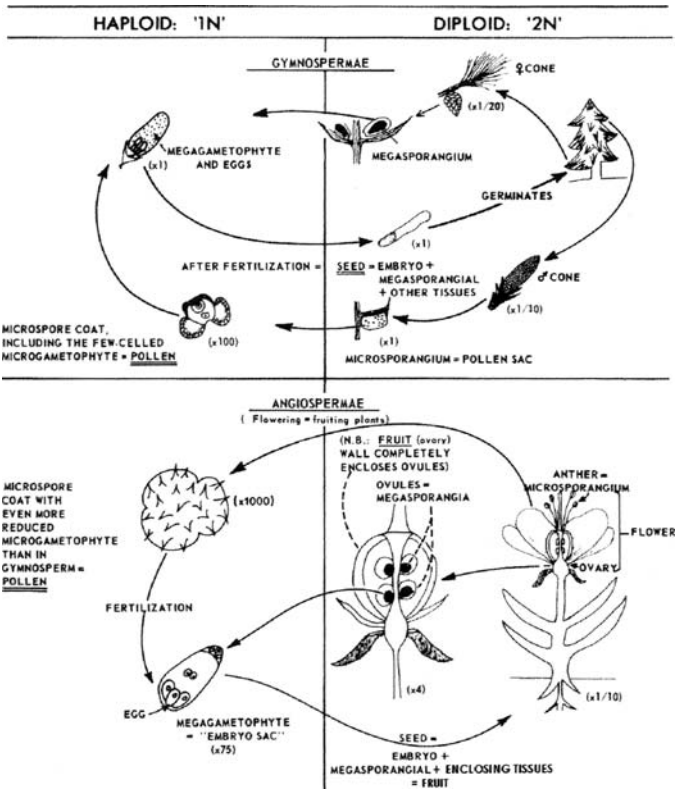


Figure 4.2 Life cycles of pollen-bearing (= seed-bearing) plants. Note that fossil pollen consists only of the exine, which is homologous with the microspore exine (exospore) of a heterosporous "pteridophyte" (see Fig. 4.1). Although not shown in the angiosperm diagram, it should be emphasized that when the pollen arrives at the stigma of the flower it germinates, if accepted by the stigma, on the basis of recognition compounds associated with the exine, and a pollen tube grows through the style (directly beneath the stigma) to reach the embryo sac, where the nuclear fusions leading to zygote and triploid endosperm occur.

produce sporopolleninous zygospores and some have alternating generations with a prevailingly haploid life cycle, as a bryophyte ancestor "should"!)

The typical moss shown diagrammatically in Fig. 4.1 is a small, haploid (1N = gametophytic) plant with no true roots or vascular system. It thus is bound closely to water, both because it cannot easily obtain, store or transport it, and because its reproduction depends on water. This plant has female and male sex organs, which produce eggs and spermatozoids, respectively. The fertilized egg (zygote) develops into a small, diploid plantlet which remains attached to

the parent plant and is generally not as green as the parent because it is in a sense a parasite; its only function is to produce a capsule (sporangium). In the capsule, tetrads of spores are differentiated through meiosis (two-stage reduction division). The spores are haploid and are isospores (or homospores, a synonym), meaning that all the spores are alike. Liverwort spores are often but not always trilete (having a Y-shaped contact scar from the contact in the original tetrad). This is the primitive or original structure for true embryophyte spores. Some liverwort spores, however, are monolete. Moss spores are typically small, are sometimes trilete (*Sphagnum, Andreaea*), but are more often alete or, in a few cases, monolete. Most moss spores contain rather little sporopollenin and are not, therefore, good candidates for fossilization. *Sphagnum* is an exception and this sort of moss spore has a fossil record reaching back at least 150 million years, as the genus *Stereisporites*. Moss spores can produce perispores (Brown and Lemmon, 1984), and sporopollenin deposition in moss spores in exine and perine during sporogenesis is not unlike that of vascular cryptogams. Bryophyte spores are ejected from or fall from the capsule (sporangium). In order to germinate, they must land in a moist place or a place that will later be moist. When they germinate, a new moss or liverwort plant may eventually result. Water remains important to the plant, as the spermatozoids must swim in "casual" water to the egg in order to bring about fertilization.

3 Pteridophyte Life Cycles

"Pteridophyta" is not a natural division in plant classification–it is not monophyletic. Nevertheless, for paleopalynological palynology it is a convenient category, including all vascular embryophytes that do not produce true seeds.

3.1 Isosporous Pteridophytes

In Fig. 4.1 the example displayed is a homosporous fern, but the basic plan is good also for what used to be called the homosporous "fern allies": psilopsids, some lycopsids, and sphenopsids. (These are rather insignificant in modern vegetation, but apparently at least collaterally ancestral forms were much more important in the Paleozoic.) Here the conspicuous plant that comprises more than 99.9% of the life cycle is diploid (2N = sporophytic). It produces sporangia, 2N of course, as in the case of the bryophytes, but the sporangium is an organ of the main plant, not a 2N "parasite"! In the sporangia, spore mother cells divide meiotically to produce ultimately tetrads of haploid (1N) spores. Again they are isospores: all alike, trilete most commonly, but in some instances monolete or alete. Actually, there may be considerable range of size and other morphological features in the spores from one sporangium, but the critical matter for the spores to be "iso-" is that when they germinate in a moist place, a tiny, separate gametophytic plant is

produced which produces both male and female sex organs. Again, as in bryophytes, a little water is necessary at this stage in order for the spermatozoids to swim to the egg-bearing organ for fertilization. From the fertilized egg grows a 2N adult spermatophyte. Most non-botanists never see gametophytes, as they are very tiny, but gardeners are usually aware that one may "plant" pteridophyte spores on moist soil or a wet filter paper and get gametophytes and eventually adult ferns.

It should be noted that, as fossils, isospores (= homospores) are indistinguishable from the microspores of heterosporous plants (see below). Paleopalynologists should always use the term "miospore" (explained later in this chapter) or "small spore," not "microspore," for small dispersed spores whose life-cycle function cannot be determined. Regrettably this dictum is often disobeyed, and the student will find small spores in the literature described as "microspores," when in fact they are more probably isospores.

3.2 Heterosporous Pteridophytes

Some living pteridophytes, such as the fern, *Marsilea*, and the lycopsid, *Selaginella*, displayed in Fig. 4.1, are heterosporous. This suggests that the spores produced are of two different types, which is correct. Usually, as shown in Fig. 4.1, there is a conspicuous size difference between the two spore types, the microspore (male) being smaller, and the megaspore (female) being larger. However, the critical matter is that the microspores (usually numerous, smaller) produce on germination a male gametophyte, which makes in its sex organs spermatozoids. The megaspores (usually very reduced in number, larger), on the other hand, produce a female gametophyte, which makes eggs in its sex organs. The germination of the megaspores occurs on moist ground, and produces a very tiny megagametophyte, confined, or mostly confined, to the exine of the germinated spore. The microgametophyte also germinates on the ground, producing a very tiny male gametophyte which makes spermatozoids. These swim in films of water to the eggs and cause fertilization. From the embryo so formed grows an adult (2N) sporophyte. Heterospory confers emphasis in the life cycle to the sporophyte and obviously has evolutionary advantages, as it evolved independently many times (DiMichele and Bateman, 1996).

4 Seed Plant Life Cycles

4.1 Gymnosperms

Suppose that the megaspores in the sporangium of the heterosporous pteridophyte in Fig. 4.1 were reduced in number to one, and that the germination of this one spore to produce a reduced mega- (female) gametophyte occurred in the megasporangium while this is attached to the "parent" plant. Then suppose that

the egg of the female gametophyte is fertilized by a spermatozoid from a reduced micro- (male) gametophyte that landed, still in its microspore coat (exine) near the opening of the megasporangium. (The spermatozoid swims in a liquid drop provided by the adult plant at the mouth of the megasporangium.) Further suppose that the embryo resulting from the fertilization develops before the megasporangium and its supporting "maternal" tissues are shed from the "parent" plant. What is produced is a seed: the megasporangium and its protective maternal structure, and remains of the megagametophyte, and the embryo (see Fig. 4.2). The microspore exine with its included, very reduced (ultimately in angiosperms to three nuclei; more in gymnosperms) microgametophyte is then called a pollen grain! This is a functional, embryological, not a morphological definition! Actually, a pollen grain occurring as a fossil is only the microspore exine. Hence, it really is not wrong to call it a microspore. Note however that it is wrong, though frequently done, to call an isospore a "microspore," because "microspore" refers exclusively to the male spores of heterosporous plants! The gymnosperms are a huge group, possibly but not certainly monophyletic, ranging from the first seed and pollen producers of the uppermost Devonian through the various Paleozoic and Mesozoic seed-fern groups (Pteridospermae or Cycadofilicales: Paleozoic medullosans, Mesozoic caytonialeans, corystospermaleans, and others), cycadeoids and true cycads, ginkgoaleans, gnetaleans, and, more familiar to most people, coniferaleans. The pollen is usually sulcate, but there are many variants. In the Paleozoic, the pollen of primitive gymnosperms often resembles morphologically the microspores of heterosporous plants, including trilete laesurae. Such primitive pollen with spore-like morphology is usually called prepollen. Later gymnosperm pollen is usually monosaccate, bisaccate, multisaccate, monosulcate, trichotomosulcate, inaperturate, or a variant of one of these morphological types (see Chapter 5). In some extinct gymnosperms, such as the cycadeoids, the megasporangia and microsporangia were produced in a single strobilus, but in living gymnosperms, such as conifers, there are separate male and female strobili ("male cones" and "female cones"). Sometimes, e.g., in *Ginkgo*, these are even produced by separate, male and female trees. In primitive gymnosperms the spermatozoids were presumably flagellate and motile, because they are in living cycads and *Ginkgo*. However, in living conifers and gnetaleans, a pollen tube is produced which penetrates into the megagametophyte of female cones and introduces nonmotile fertilizing nuclei into the vicinity of the egg. (Pollen tubes have naturally not often been preserved as fossils, but Rothwell, 1972, described one from a saccate gymnosperm grain of Pennsylvanian age.)

4.2 Angiosperms

This group of plants dominates the modern vegetation in terms of numbers of species as only the insects do among animal groups. (It is interesting in this connection that the modern insect fauna has closely co-evolved with the

angiosperms.) Estimates of the number of species of angiosperms have about doubled during my scientific career and are now getting close to a half million. Conifers cover some vast areas of the world but are two orders of magnitude less diverse than the flowering plants. Angiosperms apparently first appear in the fossil record in the Late Jurassic, and already dominated the world's flora by early Late Cretaceous time. The group is referred to as the "flowering plants," but the angiosperm flower is not really unique. Bisexual cycadeoid (gymnosperm) strobili of the Mesozoic are really flowers, too. The carpellate fruit is a more distinctively angiosperm structure, in which the seeds are enclosed by carpel walls, and this is the reason for the name angiosperm, "seeds in a vessel," but some gymnosperms approximate this, and, on the other hand, a few apparently primitive angiosperms have incompletely closed carpels. The ovules or megasporangia (see Fig. 4.2), plus the enclosing carpel walls, in a flower comprise the ovary, and the ovary plus accessory "maternal" tissues make up the fruit. The megasporangium produces by reduction-division a several-celled megagametophyte or embryo sac, one of the cells of which is the egg (see Fig. 4.2). The embryo sac is the really distinctive angiosperm feature. We really should call the angiosperms the embryo sac plants, or some Latin equivalent! The flowers (or sometimes separate male flowers) also have microsporangia (anthers), which with their stalks are called stamens. In them, meiosis produces from spore mother cells the tetrads of microspores, within which 3-nucleate, fully enclosed microgametophytes develop. The microspore wall, plus the enclosed gametophyte, is the pollen grain. This agent of fertilization is carried by various vectors–wind, water or animal–to an extension of the ovary (stigma) of the same or different flower. Some angiosperms have elaborate biochemical and structural features to prevent self-fertilization. Others are even cleistogamous, with flowers that do not open but pollinate themselves. Still others are open to normal pollination in good times but self-pollinate in poor times. Some make pollen, and the flowers have nectar reward for insect visitors which take the pollen to other flowers, where it germinates, but the whole act is a farce: the ovules are fertilized apomictically, and the apparently normal pollen has nothing to do with it! The common dandelion is such a plant. Angiosperms also are wind- or animal- (usually insect) pollinated in very variable patterns. Some species are even partly wind-pollinated, partly insect-pollinated. Meeuse and Morris (1984) present a good and entertaining discussion of these matters.

On the stigma, the pollen germinates, producing a pollen tube. The pollen tube penetrates the stigma and grows down inside the style, from which it derives nourishment, to the ovule (in *Zea mays* this incredible journey may be up to 50 cm!), where two of the three nuclei of the pollen grain enter the embryo sac. The guidance of the pollen tube to its goal–the mouth, or micropyle, of the ovule, is directed by compounds in the style and ovule. Some of the cells of the embryo sac act very precisely in guiding the tube to the egg and then shutting off the attraction when fertilization occurs (cf. Higashiyama *et al*., 2001). Another uniquely (well, almost uniquely–the Gnetales have an analogous feature)

angiospermous event then occurs: double fertilization, in which one sperm nucleus fertilizes the egg to produce the 2N zygote, and the other sperm nucleus combines with two other nuclei of the embryo sac to produce the triploid nucleus from which a 3N tissue, the endosperm, develops. This in many angiosperms is later the major source of nutrients to the embryo during germination. (In the form of cereal grass endosperm, it also produces the principal source of nourishment for human beings.) All angiosperm pollen probably derives from monosulcate-trichotomosulcate forms. From that base, however, practically all imaginable structural variants of pollen derive, except saccate pollen, which seem to be confined to gymnosperms.

Pollination biology ("anthecology") is a fascinating field in itself, with much to tell paleopalynologists. One of the nestors of paleopalynology, K. Faegri, was also co-author of a fundamental book in this field (Faegri and Van der Pijl, 1979). The subject has a hoary history within biological history generally (Baker, 1983), and the co-evolution of angiosperms with their pollination vectors (Crepet, 1983) is a very important aspect of the evolution of the plant kingdom.

5 Spores, Pollen, "Miospores," and Other Terminological Troubles

The reader has already noticed that we have some difficulty with what inclusive term to use for those palynomorphs that are spores/pollen of embryophytic plants. I have already stressed that various such things with sporopolleninous exines that occur as fossils include (possibly some cryptospores), homospores (= isospores), microspores, megaspores, prepollen, and pollen. I will use "sporomorphs" because it is a handy term, and there are difficulties with other suggested words. Grayson once proposed "polospore", but it never caught on, perhaps because the suggested sport is not very common. Guennel's (1952) proposal of "miospore" was more popular: this makes all pollen or spores less than 200 μm "miospores", those more than 200 μm "macrospores". There are a few problems with the term "miospore". First, it is pronounced the same as "meiospore", a term mostly used for meiotically produced algal spores such as zoospores and aplanospores (Scagel *et al*., 1965). Secondly, the 200 μm boundary, while reasonably good as a biological division between functional microspores and functional megaspores, is not completely dependable for that purpose. Some functional megaspores are smaller than 200 μm, some extant and fossil pollen grains are occasionally larger than 200 μm, e.g., *Cucurbita* spp., *Oenothera* spp., and *Schopfipollenites* prepollen. "Miospores" include pollen, isospores, microspores, and some (only a few) small megaspores. It is essentially equivalent to the older expression "small spore". As was stressed earlier, however, it is not correct to use "microspore" in this sense, despite the fact that it "sounds right". The arbitrary 200 μm boundary was selected by Guennel because of the use

of ca. 200 μm screens in sedimentological screening for particle size. Guennel intentionally used "macrospore" for his class of spores larger than 200 μm, in order to emphasize that the group was not coterminous with megaspores in the biological sense, but this aspect of Guennel's proposal has been confused by many, including me in the first edition of this book. Macrospore is, in any case, a synonym for megaspore, per such authorities as Jackson's (1928) *A Glossary of Botanic Terms*. Zerndt (1934) in a classic megaspore monograph had already proposed 200 μm as the formal boundary between "small spores" and megaspores, so the Guennel miospore/macrospore separation was following an existing suggestion in the palynological literature.

Chapter 5

Spores/Pollen Morphology

1 Introduction

As we noted earlier, paleopalynology's subject matter includes far more than embryophytic spores/pollen. Nevertheless, spores/pollen are the original "heart" of the subject and are a major emphasis of this book. I found in over 30 years of teaching the subject that beginning the study of paleopalynology with both laboratory and lecture exposure to extant spores/pollen is the "correct" approach, because the study materials are abundant and relatively easy to work with, even though it seems to be putting the cart before the horse to study Holocene things first. Some would urge early and coordinate exposure to study of extant dinoflagellate cysts–the other major paleopalynological subject matter, but I think this would tend to confuse and discourage the student. Better to crawl first with trilete and tricolpate and walk and run later with precingular plate arrangement and so forth.

Fig. 5.2 provides a very general glance, without exact time, of the evolution (presumably monophyletic) of spores/pollen types, beginning with Late Ordovician trilete spores. Most, but perhaps not all, of the types listed are still extant. (At the moment I cannot think of an extant plant that produces pseudosaccate pollen grains.)

The appearance in time of the major morphological novelties in spores/pollen is depicted in Fig. 5.3. There is a substantial complex of older sporopolleninous walled spore-like bodies called cryptospores. They lack haptotypic features, but some of them certainly represent the plants ancestral to embryophytes with true spores. Cryptospores are known from rocks as old as Middle Cambrian (Strother *et al.*, 2004), and they range to Lower Devonian. See discussion in Chapter 7.

2 Morphological Types

The basic morphological types encountered in extant embryophytic spores/pollen are shown diagrammatically in Figs. 5.4 and 5.5. The fossil spore/pollen is basically a hollow, tough, variously ornamented and grooved bag, ball, or case, from which the contents (inner wall layers and protoplasm) have been removed through biodegradation by bacteria, by fungi and possibly also by non-biological lysis. (Fig. 5.5 shows schematically what a section of the whole grain, before removal of contents, looks like.) As a fossil, the bag or ball

Figure 5.1 Roger P. Wodehouse, 1889–1978. Wodehouse was a pioneer in many aspects of pollen and spore study. Especially known in connection with aerobiology and the importance of pollen and spores as vectors of human allergy diseases (cf. his book, *Hayfever Plants,*1971), Wodehouse also made very important contributions to our knowledge of pollen morphology and morphogenesis, via his book, *Pollen Grains* (1935, 1959). In paleopalynology he was also a pioneer, per his studies of the Eocene Green River Formation and Pleistocene pollen of Kashmir, India (Wodehouse, 1932, 1933, 1935a). Photo by W. R. Taylor, 1930, published here by permission of the Hunt Institute for Botanical Documentation, Carnegie-Mellon University, Pittsburgh, PA.

is usually found squashed flat and variously contorted. Students first encountering fossil sporomorphs in an uncovered preparation, e.g., in attempting to pick them up for single-grain mounts, are usually startled to discover that these fossils are not spheres as idealistically drawn, but wafers that twist and turn in liquid mountants, like snowflakes or, better, tiny pancakes. The bag consists of a wall (exine) of sporopollenin which retains considerable resilience until much of the hydrogen and oxygen has been removed during increase of rank ("coalification" = "carbonization" = "maturation"). Therefore, during palynological processing of the enclosing rock, low-rank palynomorphs will often re-expand to some extent. Preparations of modern spores/pollen are usually produced by acetolysis (see Appendix), which removes the contents and inner walls in much the same way as fossilization, and also slightly carbonizes the wall, therefore changing the color from pale yellow to a darker yellow or orange.

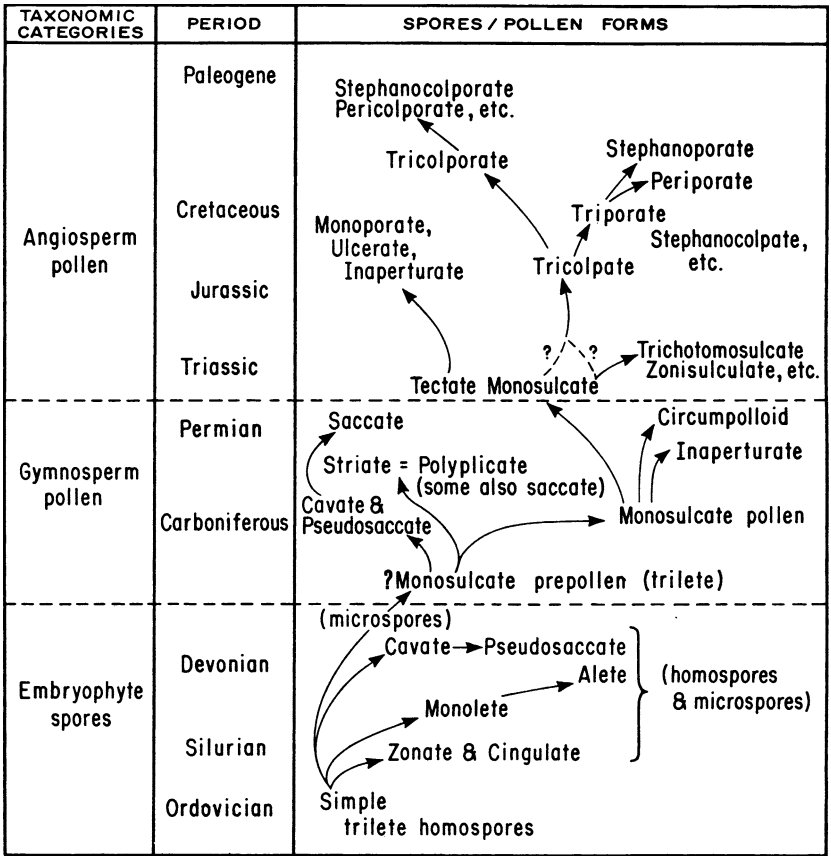


Figure 5.2 Probable evolutionary pathways of major spores/pollen morphological types. Time periods not to scale. Spores/pollen of course do not evolve independently of the taxa producing them, but, for example, logic and the fossil record indicate that plants producing monolete homospores were derived from plants producing trilete spores, etc. There is inevitably oversimplification in a diagram such as this. For example, at the interface between spores and pollen, prepollen represents the stage at which microspores still germinated proximally, as defined by Chaloner (1970b). However, some trilete forms representing this stage also seem to be sulcate, suggesting that haustorial pollen tubes probably formed.

However, unless the wall was very thin (as in Juncaceae or *Populus*), the prepared grains are not much collapsed or folded. In any event, the diagrams of major types presented in Fig. 5.4 are of hypothetical, non-collapsed forms. Study of these morphological types is best accomplished with a set of accompanying slides representing a majority of the types. It should be stressed that the details of structure and sculpture of exines presented in this chapter apply primarily to spores and pollen

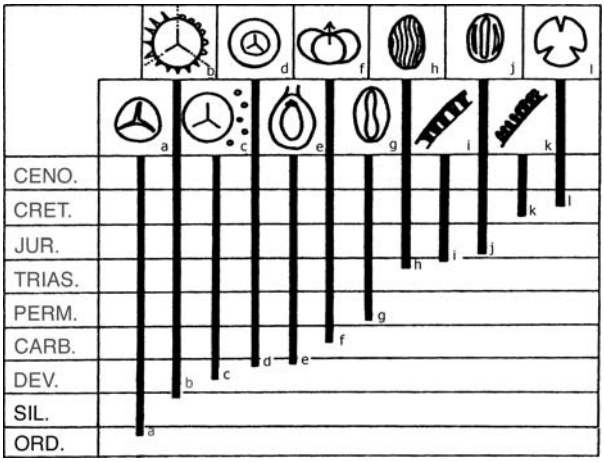


Figure 5.3 Major events in the appearance of features of spore exines. The bottom of each bar represents the time of first appearance of each item. Not all of these exine features (e.g., (e),(i), and (j) persist to the present time. (**a**) Spores with evident triradiate aperture (now known from at least upper Ordovician). (**b**) Triradiate spores, showing diverse sculpture of the exine (now known from late Silurian). (**c**) Size differentiation indicative of heterospory. (**d**) Spores with markedly cavate exine. (**e**) Megaspore tetrad with three members aborted, retained in seed-like structure (*Archaeosperma*). (**f**) Bisaccate pollen (of seed ferns) with distal germinal area. (**g**) Monosulcate pollen of unknown (presumably gymnospermous) origin. (**h**) Polyplicate pollen, comparable to that of modern *Ephedra*. Early records of this type of pollen have been attributed to a conifer, but later (Tertiary) occurrences probably represent Gnetales. (**i**) Pollen exine with inwardly directed columellae simulating angiospermous tectate structure (as seen in the conifer *Hirmerella*). (**j**) Assymetrically tricolpate pollen (*Eucommiidites*) of gymnospermous origin. (**k**) Incompletely tectate angiospermous monosulcate pollen. (**l**) Symmetrically tricolpate (presumed angiospermous) pollen. Names of geological periods and eras abbreviated from Ordovician through Cenozoic. Modified from Chaloner, 1976.

of extant plants, with emphasis on the angiosperms. The farther back from the present one goes, the more different structure and sculpture were, and aspects of the differences will be dealt with at various places as we examine the fossil record.

The basic morphological categories shown in Fig. 5.4 depend on obvious differences in external organization. Of these differences, the most common are "haptotypic features": scars representing former contact with other members of the original tetrad (e.g., laesurae), or thin places or openings in the wall, which are usually the site of exit of pollen-tube or other germinal material (pores, sulcus, colpus). As Chaloner (1984) has noted, various authors have stressed different functions of the laesurae, sulci, pores, etc. For some, e.g., Potonié, the "exitus" function is the most significant, and it is true that even laesurae normally serve this function. For others, e.g., Wodehouse, the accordion-pleat action of the colpi to accommodate

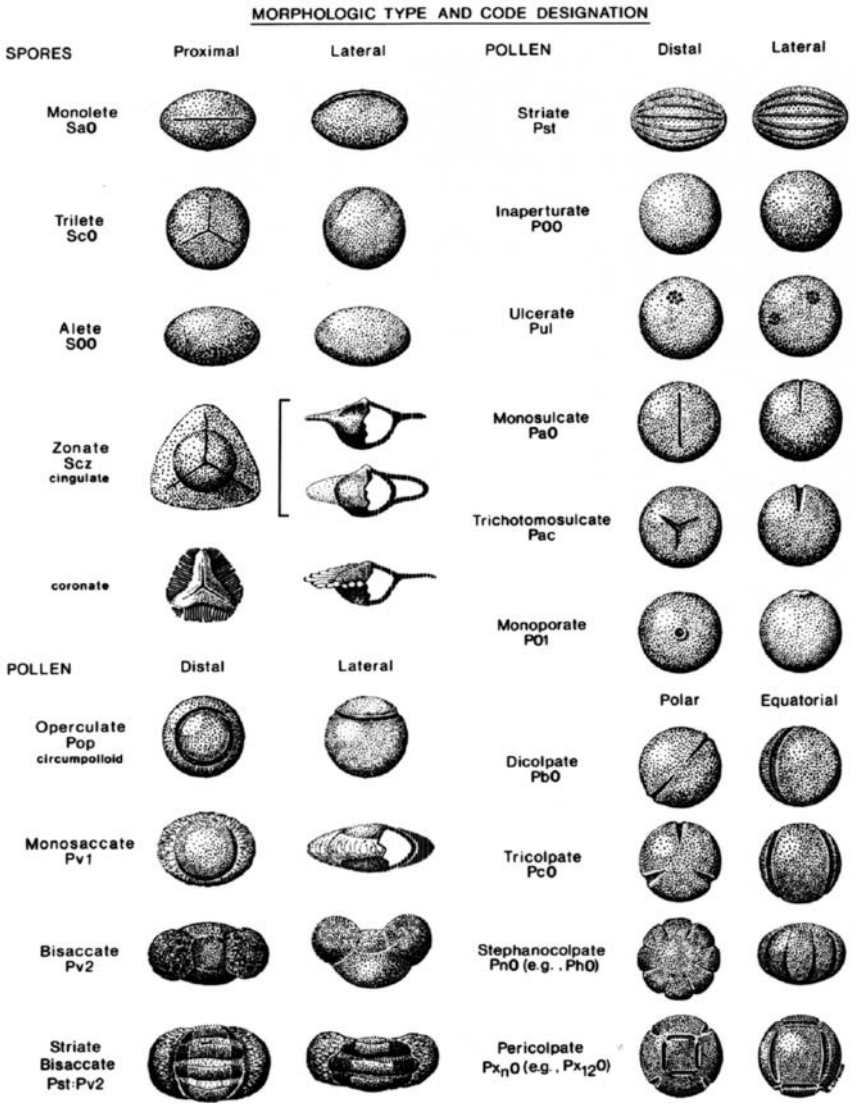


Figure 5.4 *(See caption on page 94)*

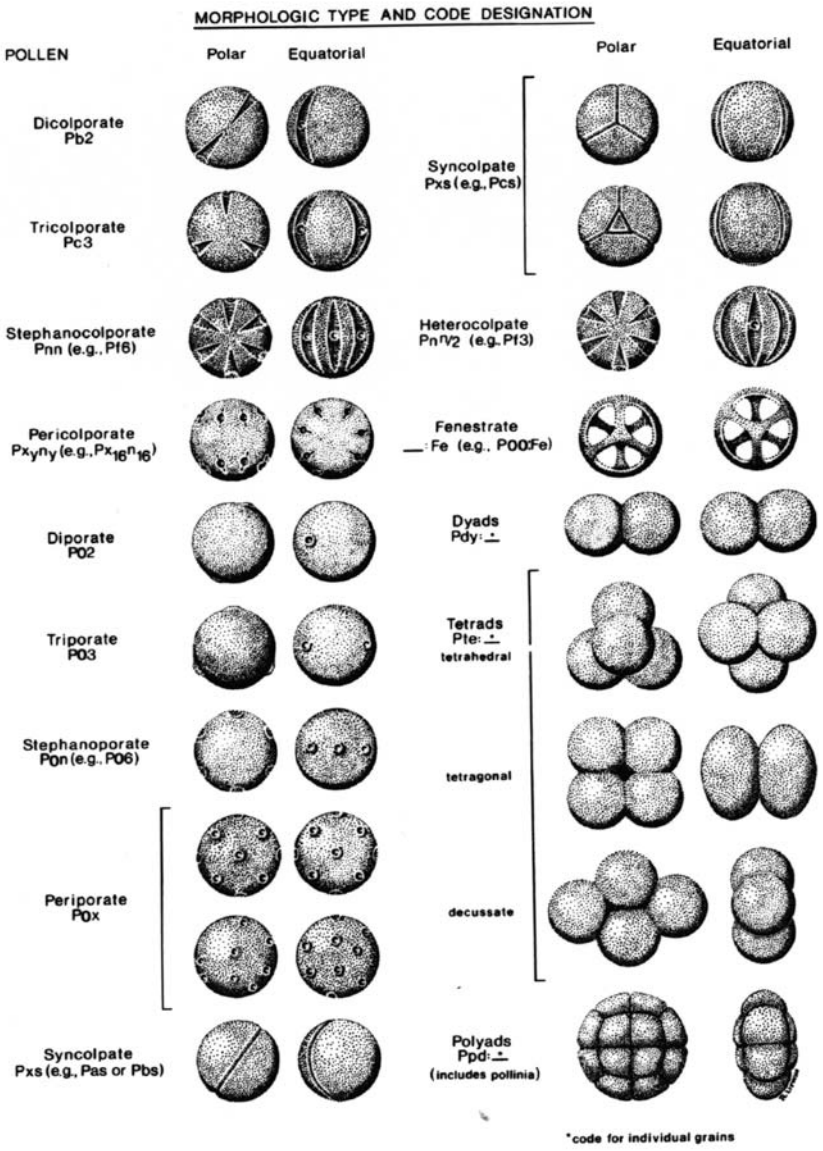


Figure 5.4 General morphological types of embryophytic spores and pollen, plus "Shell code" designations. These are letters-and-numbers symbols for the various types, as explained in the text. The classification depends to some extent on Iversen and Troels-Smith (1950) and Faegri and Iversen (1975 edition). Note under zonate (Scz) the lower form shown in diagrammatic section would be considered by some as camerate-cavate (see Glossary), but such forms are included as zonate in this classification. The sectional view of monosaccate pollen (Pv1) is intended to demonstrate that the saccus of saccate pollen is not completely hollow but contains a more or less webby inner lining.

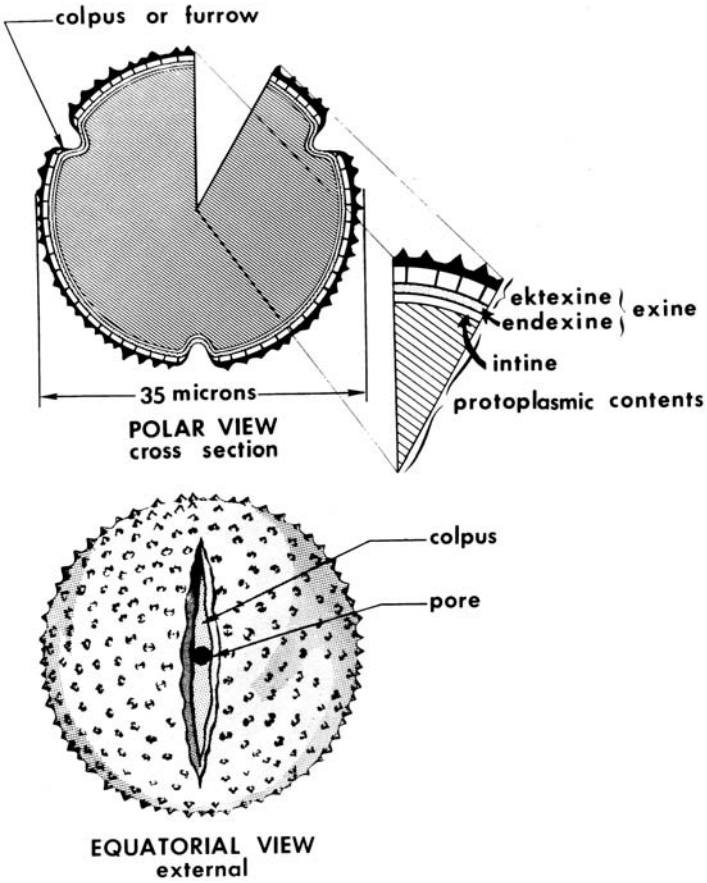


Figure 5.5 Diagrammatic view of typical tricolporate pollen grain in section, above, and external view, below.

for moisture-related harmomegathic expansion and contraction is more significant. For still others, e.g., Heslop-Harrison, the colpi of at least the angiosperms are pathways for chemical recognition signals. In any event, these features, plus a few other major morphological characteristics such as possession of sacci (the function of which is primarily orientation of the pollen grains in liquid drops at the opening of the megasporangium) provide a convenient means for classifying spores and pollen.

This is a good place to emphasize that spores/pollen, unlike dinoflagellate cysts, unfortunately do not have anything like perfect integrity as to size and morphological type per species. They are very variable as to size, and even as to morphological type in a single sporangium, or anther; in exceptional cases, monolete and trilete spores are found in one sporangium, or triporate, tetraporate, and pentaporate pollen in one anther, or (very commonly) pollen of very different

size in one species. Manicacci *et al*. (1995) report that pollen of *Eichornia*, which has dimorphic stamens, is larger in the elongated stamens. Furthermore, it is well documented that many angiosperms are regularly ("intentionally") dimorphic or even polymorphic as to size and morphological type, presumably as an anti-self-pollinating mechanism.

Chinappa and Warner (1982) found 13 species and varieties of *Coffea* to be di-, tri-, tetra-, penta- and polymorphic! *Coffea arabica*, the source of commercial coffee, for example, was found to have six pollen types, ranging from 3-zonocolporate to spiraperturate, with irregularly disposed ora and colpal-like apertures. Ferguson (1984) reports just as great "lack of integrity" among the palms. The genus *Daemonorops*, for example, has diporate, disulcate, and monosulcate pollen, with intectate echinate or tectate psilate, rugulate, foveolate or reticulate sculpture! Till-Bottraud *et al*. (1995) found that heteromorphic pollen in *Nicotiana* was correlated with the polyploid condition. (It has long been known that pollen abnormally large for a family of plants is also related to polyploidy.) Teratological, abnormal pollen and spores occur frequently in extant plants and also are found as fossils, where they have been interpreted as indicating ecological stress of the producing plants (Levkovskaya, 1999; Kedves, 2002). Dzuba and Tarasevitch, 2002, report that *Tilia cordata* trees in St. Petersburg, Russia, produced about ten times as many teratoid, abnormal pollen in 1992 as in 1892. At least some species are very sensitive to atmospheric pollution and reflect this sensitivity by producing teratoid pollen. Nevertheless, it has been recognized almost since Linnaeus' time that pollen morphology can be used to show indication of generic and family relationships of plants (Graham and Barker, 1981), though plant systematists have only irregularly availed themselves of this opportunity. Various studies such as Oberlander *et al*. (2004) have shown that palynological data are sometimes on a par with DNA sequence data, and better than plant morphology for indicating relationships. Many of the morphological features of spores/pollen probably have some sort of adaptive significance, but Wodehouse (1935), Muller (1984) and others have pointed out that some characters are determined by the mathematical-physical constraints imposed by development in the anther. Nevertheless, it is fair to assume that the sacci of saccate pollen do serve a flotation function for some reason, and it turns out to be connected to orientation for germination of the pollen grain on the megasporangium–for some marvelous illustrations see Zizka and Schneckenburger (1999, p. 114). Hughes (1994, p. 36) has a very clear explanation of the situation in relations to pollination. Various sorts of pleats (sulci, colpi, taeniae) serve an accordion-like expansion-contraction function (harmomegathy) related to moisture loss and gain.

Table 5.1 presents data on the numbers of representatives of various morphological categories and sculpturing types in my reference core collection of modern spores/pollen. The collection has been assembled since 1947 in connection with various Cenozoic research projects and is broadly representative of the common

plants of the North American flora, with some cultivated forms and many forms from other continents. (The total collection is over 5,000 species, but only the core collection was tallied.) Table 5.2 gives size information for the same core collection. (The total number of species under "size" is a bit less, because size was not measured for a few forms at the time of study.) Note that the "super-typical" spore/pollen in the modern flora is tricolporate (27%), reticulate (26%), and 2l–40 μm (52%) in maximum dimension.

Chaloner (1984) has noted that, whereas the evolutionarily basic homospore is often sculptured, gymnosperm pollen seldom has much sculpture, and angiosperm pollen varies enormously, from strongly sculptured to smooth, with all sorts of intermediate stages. Pollination-mechanisms study and the adaptive significance of the size, shape and other features of pollen are mostly beyond the scope of this book. One should be aware that features he/she observes mostly if not always had significance for the producing plant. Large and/or ornately sculptured pollen ordinarily means insect-pollination, though *Picea* and *Zea* pollen are both examples of wind-pollinated pollen that can be near or over 100 μm in one dimension. Smooth and/or small pollen is ordinarily wind-pollinated, though, as Basinger and Dilcher (1984) point out, the very tiny pollen (as small as 8 μm!) of a Cretaceous flower they describe was likely not wind-pollinated, because particles that small do not have sufficient impact velocity to adhere to a stigma. Some smooth pollen, such as *Prosopis* sp., is clearly insect-pollinated. Nevertheless, despite exceptions, it is pretty safe to assume that ornately sculptured fossil pollen, or pollen greater than 40 μm in size (or less than 10 μm?) was insect-pollinated, and that relatively smooth pollen in the 15–35 μm range was wind-pollinated. Chaloner (1984) has pointed out that the sculpture of angiosperm pollen in some instances is related to static electricity: the negative charge of pollen, in part given it by insect vectors, means that pollen is attracted to the (induced) positive charge of the stigma, and protruding sculptural elements such as spines protect the charge from premature grounding. Wind-pollinated forms seem even to have evolved features on the female side adapted to reception of pollen: aerodynamically tuned structures of female cones or inflorescences to deflect air flow containing pollen in such a way as to maximize pollination success (Niklas, 1985).

It should also be emphasized that spores/pollen of extant plants are characteristically determinable with the light microscope only to genus, not to species. In a few unfortunate cases (Poaceae (=Gramineae), Chenopodiaceae, and others) only the family can be determined in routine LM analysis. SEM, TEM, fluorescence and other forms of more demanding microscopy do show differences on which differentiation in such cases would be possible. On the other hand, Tiwari (1984) and de Jersey (1982) both emphasize that, for fossil sporomorphs, even such a seemingly minor feature as sculpture may be of great significance in separating fossil genera from each other. Nevertheless, it is clear that the lack

Table 5.1 Numbers of representatives (species) of morphological categories and sculpturing types in Traverse's reference core collection of extant spores/pollen. Note percentage figures after the principal morphological categories. (* = includes Retirugulate)

		Sculpturing type													
Morphological category	*Total species for class*	*Psilate*	*Micropitted*	*Foveolate*	*Fossulate*	*Scabrate*	*Gemmate*	*Clavate*	*Verrucate*	*Baculate*	*Echinate*	*Rugulate**	*Striate*	*Reticulate*	*Mixed/Other*
Trilete	142 (6%)	38	4	2	2	21		2	28	2	6	16		21	
Monolete (spore sculpture sometimes of exospore, sometimes of perispore)	136	72			3	15			20	2	3	10	1	4	6
Alete	52	4	3			31	2		3		3	1		5	
Saccate (= prevailing sculpture of corpus)	54			20		1			3					27	3
Polyplicate	15	15													
Inaperturate	138	15	14	1	2	39	1		4	2	21	1		29	9
Monosulcate (includes Pac)	219 (9%)	45	34	13	2	17	6	3	6			14	4	66	9
Ulcerate	3		2												1
Monoporate	63	5	19	2		16			4		2	1		11	3
Dicolpate	7	2												3	2
Tricolpate	282 (12%)	21	24	19	31			10	5	2	19		9	129	13

Stephanocolpate (Pd0–Pe0, etc.)	43	11	6			4								13	9
Pericolpate	15		1	2		2					3			7	
Dicolporate	2			1		1									
Tricolporate	614 (27%)	117	33	44	1	104		1	13	3	73	6	14	190	15
Stephanocolporate (Pd4–Pe5, etc.)	58	21	5	2		7		3	2				1	17	
Pericolporate	2								1		1				
Diporate	20	5	4	1		4									6
Triporate	165 (7%)	35	40	9		35	1		7	1	7	2	3	19	6
Stephanoporate (P04-P05, etc.)	40	11	2		1	9			2	1	3	3		8	
Periporate	97	9	19	4		15	2		2		24	1		15	6
Syncolpate (Pbs–Pcs, etc.)	42	11	5		1	5			1		4		1	12	2
Heterocolpate	5	3				1						1			
Fenestrate	11	1								2	4			4	
Dyads	1													1	
Tetrads	63	12	1		1	31		1	4	1	4			8	
Polyads (includes massulae)	17	9	1		2	2								3	
TOTALS	2306	462 (20%)	217	120	46	360 (16%)	12	20	105	16	177	56	33	592 (26%)	90

Table 5.2 Numbers of species in various size groups in Traverse's reference core collection of extant spores/pollen

		Maximum dimension														
Morphological category	*Total species*	*<11 μm*	*11-15 μm*	*16-20 μm*	*21-25 μm*	*26-30 μm*	*31-35 μm*	*36-40 μm*	*41-45 μm*	*46-50 μm*	*51-60 μm*	*61-70 μm*	*71-80 μm*	*81-90 μm*	*91-100 μm*	*>100 μm*
Trilete	139			1	3	5	13	23	17	20	22	17	8	6	1	3
Monolete	131					4	13	12	24	14	28	18	8	2	3	5
Alete	50	5	11	13	3	1	2	1	3	2	3	3	1	1	1	
Saccate	54						1	1		2	3	3	6	8	8	22
Polyplicate	15						1	2	5	1	5	1				
Inaperturate	133	1	7	12	12	20	23	12	7	4	11	6	5	8	3	2
Monosulcate (includes Pac)	214	1	1	7	10	30	30	29	29	11	27	12	7	7	3	10
Ulcerate	2				1		1									
Monoporate	68			2	5	15	13	11	9	5	6		1			1
Dicolpate	6					2	2									
Tricolpate	266	1	5	28	44	51	39	26	18	9	13	14	7	6	2	3
Stephanocolpate (Pd0–Pe0, etc.)	41			1	10	14	4	3	4		2	1	2			
Pericolpate	15			1	1		2	3			3	2			1	2
Dicolporate	2									1	1					
Tricolporate	612		30	62	132	120	69	74	33	36	31	9	5	5	1	5
Stephanocolporate (Pd4–Pe5, etc.)	56		1	6	11	8	4	14	1	2	3	2	1	2	1	

Pericolporate	3											1			1	1
Diporate	22		2	4	3		4	3	1	1	3		1			
Triporate	157		1	9	12	32	28	19	10	9	12	3	8	6	4	4
Stephanoporate (P04–P05,etc.)	37			2	1	4	14	11	3	1	1					
Periporate	96		2	7	9	14	11	9	5	8	6	4	3	2	1	15
Syncolpate (Pbs–Pcs,etc.)	39		4	4	8	8	4	5	2	1	1	2				
Heterocolpate	5			1	3		1									
Fenestrate	9			2	1	1			1	2	2					
Dyads	1					1										
Tetrads	61	1	1	4	4	15	6	9	4	3	3	2	5	3	1	
Polyads (includes massulae)	17	1	2	3		1		3	1	3		1	1			1
TOTALS	2251	10	67	169	273 (12%)	346 (15%)	284 (13%)	272 (12%)	177	135	186	101	69	56	31	75
						(52%)										

of distinctiveness at the specific level implies that fossil spores/pollen species seldom really coincide exactly with plant species.

Fig. 5.6 shows part of a plot of size-ranges of common grass pollen. Note that the overlap is too great to permit use of size alone for identification. It is possible to exclude some taxa that lie at the extremes of the range. For example, a grass pollen measuring 70 μm cannot come from *Sorghum bicolor.* Most grass pollen is smaller than the species shown. All grass pollen is monoporate (P01). Most of the largest grass pollen classes are of cultivated cereals, presumably reflecting polyploidy. Use of SEM and other sophisticated techniques to separate species or species groups of large genera such as *Pinus* or *Quercus* is possible, though it is doubtful that this will be practicable on a routine basis in the near future (see Fig. 5.13). Efforts have been made to separate pollen of species of various

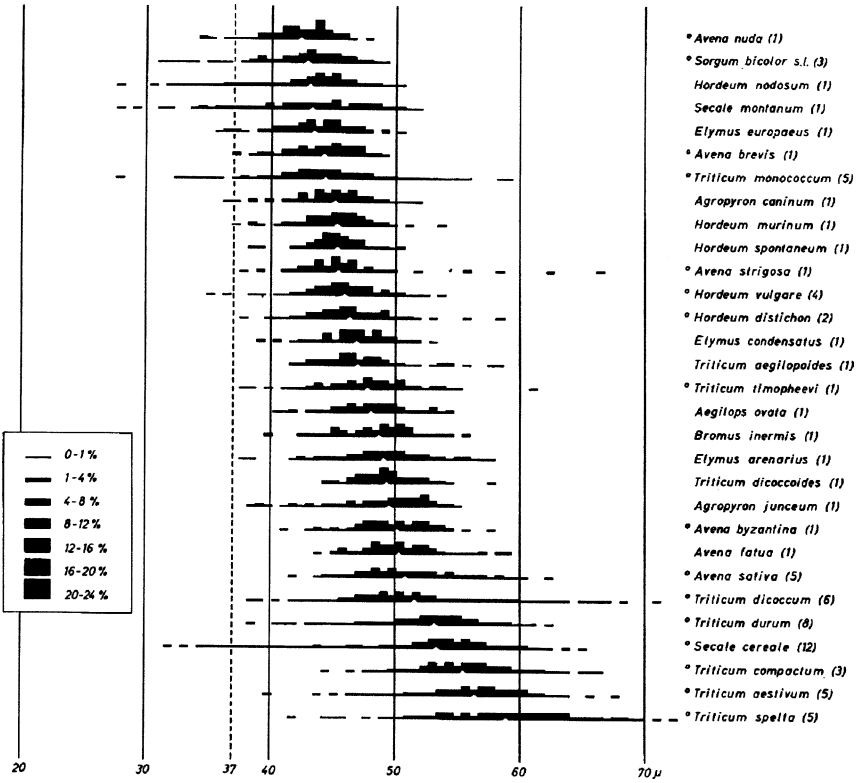


Figure 5.6 Pollen sizes of selected grass taxa. Cultivated cereal grasses are marked with a small circle. These tend to be larger than average for grass pollen. The original entire diagram includes many forms in the 20-40 μm range. From Beug, 1961.

genera on the basis of size or other measurement-ratios, but they are seldom really reliable, just because of the great plasticity that characterizes pollen and spore morphology.

3 "Shell Code"

The diagrams in Fig. 5.4 are accompanied by the name of each morphological type, plus a letter-and-number shorthand "code" designation for each type. The diagrams were originally developed by Iversen and Troels-Smith (1950), and have appeared in the first edition (1950) of Faegri and Iversen's famous *Textbook of Pollen Analysis*. The Shell group of oil companies used this basic chart and the code-designations in its practical paleopalynology for many years, beginning in the mid-1950s (Hopping, 1967). For easy reference, Shell developed the three-symbol code for designation of the morphological types. When I was a Shell palynologist, I learned this "code" and have employed it ever since. The principle is very simple, and I have found it helpful to have a shorthand, mnemonic, way of referring to the many morphological groups. (In the original publication of Iversen and Troels-Smith cited above, a different letter and number convention was proposed for most of the units later given the "Code" designations described here. The symbols used here were adopted in the Shell labs because they have mnemonic qualities and logical coherence that the older code lacked; P always stands for pollen, and S always for spore, for example.)

3.1 Spores

1st symbol: "S" for spore
2nd symbol: laesura type
- "c" for trilete (the basic type)
- "a" for monolete
- "b" for dilete, or "chevron" (but this is very rare)
- "0" if no laesura (note: here and elsewhere 0 is really zero, not o, though it is usually spoken "o")

3rd symbol: special features, if any
- "0" if none, "z" for zonate

Thus, Sc0 is for ordinary trilete spores, S00 for alete spores, Sa0 for monolete spores, Scz for zonate, trilete spores. "Sc0", "Scz", etc., were used by Shell

palynologists and in my Penn State laboratory as if they were super-genera. A number following the code designation was the locally used "species": thus Sc0-12, Scz-29, etc.

3.2 Pollen

1st symbol: "P" for pollen
2nd symbol: usually refers to number of colpi (or sulci)
"a" for monocolpate (monosulcate)
"c" for tricolpate, "d" for tetracolpate, etc.
"0" for none
3rd symbol: usually refers to number of pores:
"1" for one pore
"3" for three pores, "4" for tetraporate, etc.

Thus, a monocolpate pollen grain is Pa0, a tricolporate pollen grain is Pc3, a triporate pollen grain is P03.

3.3 Saccate Pollen. A Special Problem

1st symbol: "P" for pollen
2nd symbol: "v" for vesiculate (= saccate)
3rd symbol: number of sacci

Thus, a bisaccate is Pv2, a monosaccate is Pv1.

Other features of the shorthand code are more easily understood by referring to the figures than by more textual explanation.

Paleozoic and Mesozoic spores/pollen present many features that are difficult to handle with the code. In its basic form the code does not distinguish between pseudosaccate and saccate, for example, nor does it provide for the possibility that a pollen grain may have laesurae, as prepollen do. Nevertheless, the code is a handy shorthand way of referring to morphological types, both fossil and extant, and a palynologist will easily invent his own extra symbols for forms of importance to him/her. In my own laboratory when working up a new palynoflora I usually use the Shell code designations, plus an abbreviation for sculpture, plus a number for unnamed forms, e.g. P0x-ret-4 (for a certain reticulate periporate pollen grain form). Erdtman and others have provided far more complicated classifications, which are useful for detailed morphological studies, but the one presented here worked well for practical purposes in our Penn State laboratory for over 30 years.

4 Morphological Types in Detail

The reader should consult Figs. 5.4–5.5 and 5.7–5.8 when reading this section.

4.1 Spores (See Figs. 5.4, 5.7, and 5.8)

4.1.1 Trilete (Sc0)

This is the basic spore type, first appearing in the Late Ordovician. It owes its trilete laesura to the contact between it and the other three members of the tetrad of spores produced by meiosis from a spore mother cell in the sporangium. The trilete laesura is also called a "Y mark". Trilete is an adjective, not a noun. Thus, a spore has a trilete laesura, not "a trilete". Laesurae are haptotypic features, resulting from position in the spore tetrad. Extant examples: *Lycopodium, Botrychium, Aneimia* (Fig. 5.8a–g).

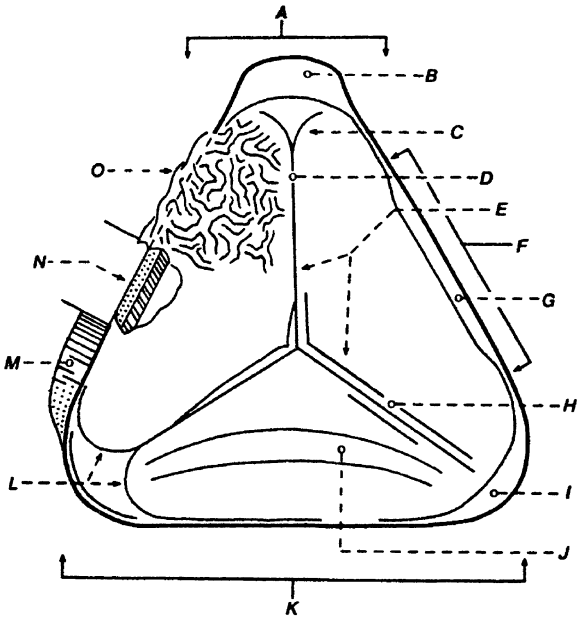


Figure 5.7 Schematic representation of principal morphological features of trilete spores (monolete spore terminology is basically the same): **A**, radial region (area); **B**, auricle (radial thickening; a limited zona); **C**, curvatura imperfecta (does not join other radii); **D**, commissure (center of the suture of "dehiscence mark"); **E**, radii (arms) of laesura; **F**, interradial region (area); **G**, interradial thickening; **H**, labrum (lip of suture); **I**, valva (slight to moderate radial thickening); **J**, torus (= "kyrtome", often a fold feature); **K**, equatorial diameter (= spore size); **L**, curvatura perfecta (joins other radii); **M**, cingulum or zona (equatorial thickening or flange); **N**, exospore in cross-section (= exine; often double layered); **O**, perispore (= perine).

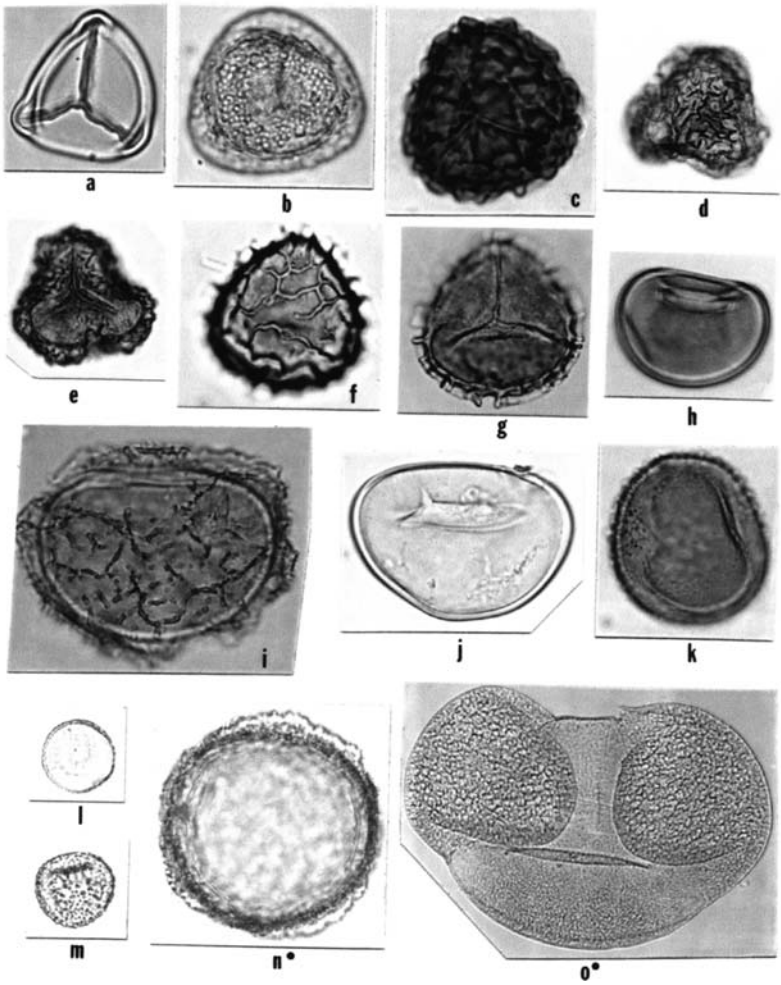


Figure 5.8

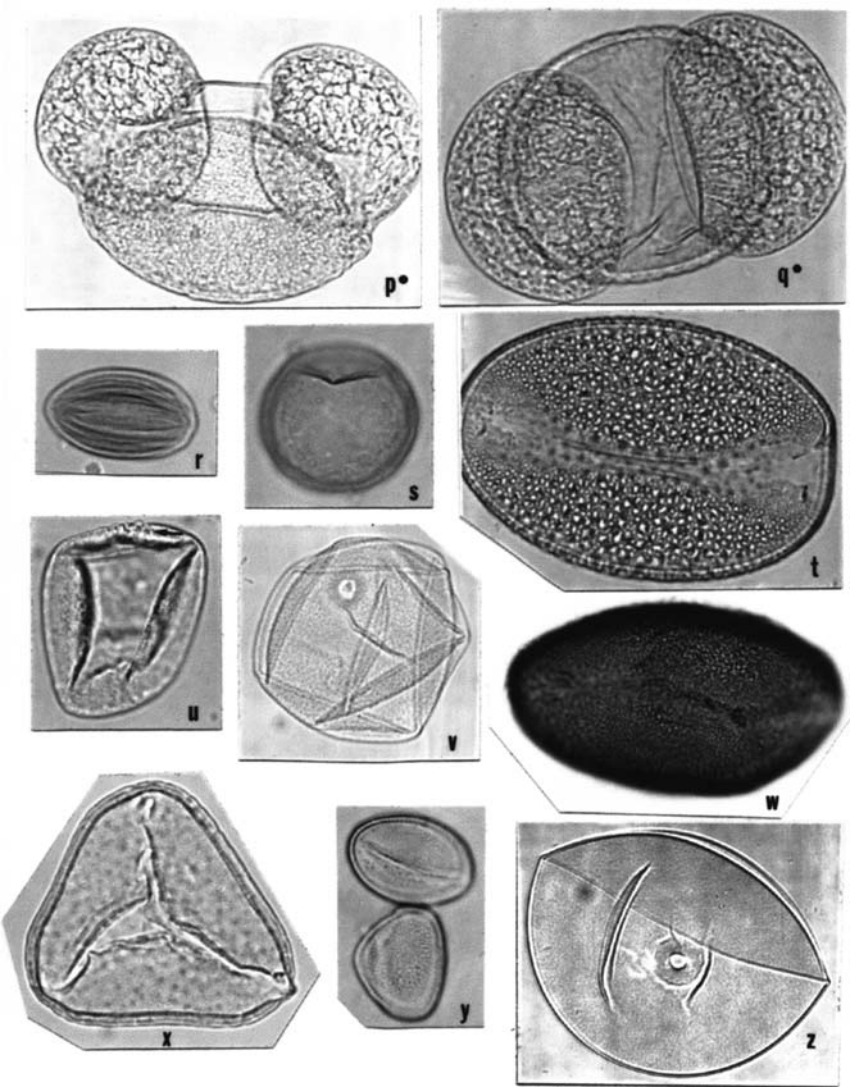


Figure 5.8 *(See caption on page 110)*

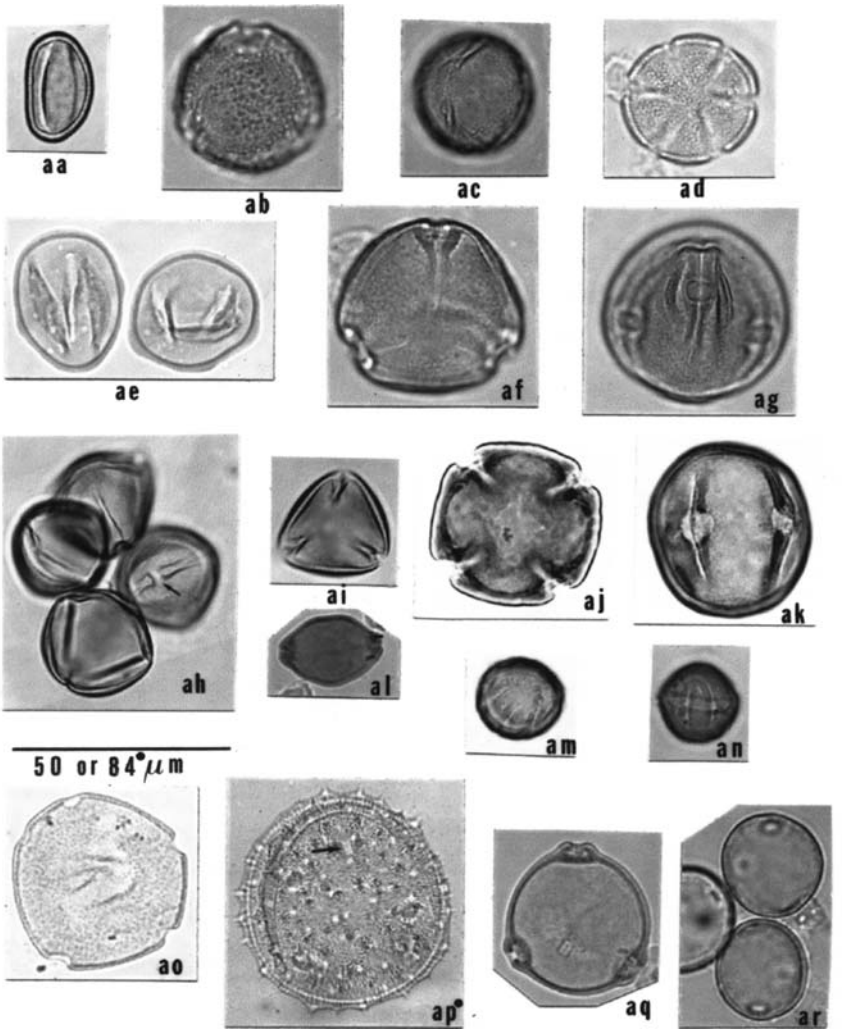


Figure 5.8

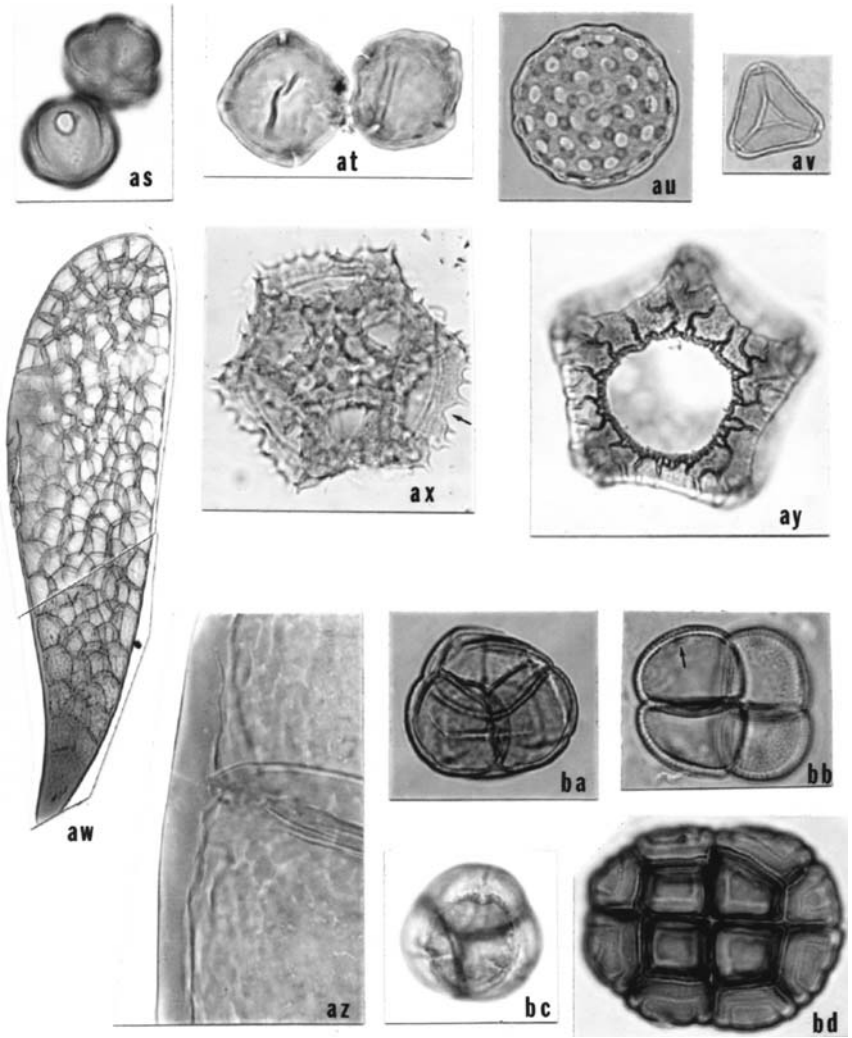


Figure 5.8 *(See caption on page 110)*

Figure 5.8 Photomicrographs of principal spores/pollen morphological types. All from acetolyzed preparations. Magnification indicated by bar under (ah). Items with a dot after the letter are 0.6x as magnified as those with no dot. Item (aw) is at very low magnification. For it, the reference bar represents 440 μm. Erdtman suggested conventions for illustrating spores and pollen, and he felt quite strongly that they should be followed. Some consistency *is* a good idea, and I have followed Erdtman, e.g., in orienting trilete spores with one radius of the laesura always pointing up, and in placing bisaccates in lateral view with the distal side up, as well as in orienting equatorial views of colp(or)ate grains with the colpi pointing up. However, I have oriented polar views of triporate and tricolp(or)ate grains with one colpus or pore at the top, whereas Erdtman oriented them with a colpus or pore pointing *down*. I didn't realize when I adopted this custom that I was being non-erdtmanian in this respect. Regarding monolete and monosulcate forms, Erdtman was uncharacteristically inconsistent, except that the laesura of a monolete form is never portrayed on the up side, but is either on the down side and parallel to the bottom of the page, or pointing up at exactly 90°. For illustrating monoletes with laesura on the up side and triporates-tricolp(or)ates upside down, one would hear from Professor Erdtman, were he still alive. (**a**) Trilete (Sc0): *Hemionitis palmata* L., Guatemala. Psilate exospore in proximal view. Auriculae developed at ends of radii of laesurae. (**b**) Same taxon as (a). Perispore in proximal view with rugulate-reticulate sculpture enclosing exospore. (**c**) Trilete (Sc0), trending to zonate (Scz): *Pityrogramma triangularis* (Kaulf.) Maxon, California. Rugulate sculpture presumably on perispore, proximal view. (**d**) Trilete (Sc0): *Botrychium lunaria* (L.) Sw., Pennsylvania. Perispore, distal view, rugulate-reticulate sculpture. (**e**) Same taxon as (d). Proximal view showing trilete laesura and outline of exospore within the perispore. (**f**) Trilete (Sc0): *Lycopodium annotinum* L., Quebec. Loosely reticulate sculpture of exospore, distal view, mid-focus. (**g**) Same taxon as (f), proximal view showing trilete laesura, high focus. (**h**) Monolete (Sa0): *Dryopteris hexagonoptera* (Michx.) C.Chr., Pennsylvania. Psilate exospore, lateral view, but showing monolete laesura. (**i**) Monolete (Sa0): *Thelypteris gongylodes* (Schkuhr) Kuntze, Florida. Beady rugulate perispore, partly abrading away, showing exospore, lateral view, high focus. (**j**) Same taxon as (i), exospore without perispore, psilate sculpture, proximo-lateral view showing that this "monolete" laesura is really more or less trilete, indicating origin of the monolete condition. (**k**) Operculate (P0p) (= zonisulcate), a variant of monosulcate (Pa0): *Nymphaea candida* Presl (cult.). Single encircling sulcus (= sulculus) seen in distal view, high focus. Sculpture scabrate and baculate. (**l**) Alete (S00): *Bryum bimum* Schreb. (Colorado). Scabrate and verrucate sculpture. (**m**) Alete (S00): *Anoectangium anomalum* Bartr., New Guinea. Scabrate and verrucate sculpture. As (l), both are moss spores. (**n**) Monosaccate (Pv1) or inaperturate (P00): *Tsuga heterophylla* (Raf.) Sarg., Washington. Mid-focus. Sporopolleninous envelope of internally alveolate structure is interpretable as a single saccus with rugulate sculpture, or the grain can be interpreted as simply inaperturate. (**o**) Bisaccate (Pv2): *Picea likiangensis* Pritzel var. *purpurea* Dallimore & Jackson, China. Lateral view. Sacci reticulate sculpture, corpus psilate on distal surface (= cappula), reticulate on proximal surface (= cappa). (**p**) Bisaccate (Pv2): *Pinus resinosa* Ait., New Hampshire. Lateral view, high focus. Sculpture information as for (o). (**q**) Same taxon as (p), distal view, high focus (**r**) Polyplicate (= striate) (Pst): *Ephedra foliata* C.A.M., India. If the plicae are interpreted as morphological features, the sculpture is psilate. Lateral or proximal-distal view. (**s**) Inaperturate (P00): *Populus* sp., Pennsylvania.

Figure 5.8 See (n). Sculpture scabrate. (**t**) Monosulcate (Pa0): *Hippeastrum vittatum* Herb. (cult.). Distal view. Mid-high focus. Sculpture reticulate. Columellate structure observable in section around the edge and in small light dots on the surface. (**u**) Ulcerate (Pul): *Carex variabilis* Bailey, Colorado. Lateral view. Sculpture scabrate. Ulcus (arrow, at top) is a place where the exine is incomplete; it serves as a pore. (**v**) Monoporate (P01): *Arundinaria tecta* (Walt.) Muhl., Louisiana. Distal view. Note thickening (annulus) around the pore, and the small block of ektexine (operculum) in the center of the pore membrane. Sculpture scabrate. (**w**) Monosulcate (Pa0): *Yucca* aff. *louisianensis* Trel., Texas. Distal view, high focus, very thick exine, hence darkness. Sculpture reticulate. (**x**) Trichotomosulcate (Pac): *Cocos nucifera* L., Yucatan, Mexico. Distal view, high focus. The single sulcus is tricornered, sometimes closely simulating a trilete laesura. Sculpture micropitted. (**y**) Monosulcate (Pa0): *Xerophyllum tenax* (Pursh) Nutt., Montana. Two specimens, upper one is distal view showing sulcus, lower one a proximal view. Sculpture reticulate. (**z**) Monoporate (P01): *Zea mays* L. (cult.). See comments for (v). Cereal grass pollen is usually larger than non-cereal grass pollen, probably because of polyploidy. Sculpture classifies as psilate, is actually microscabrate–meaning that the scabrae are too small to make the sculpture scabrate. (**aa**) Dicolpate (Pb0): *Pontederia cordata* L., Florida. Sculpture psilate. (**ab**) Tricolpate (Pc0): *Quercus phellos* L., District of Columbia. Polar view, high focus. Sculpture scabrate and verrucate. (**ac**) Same taxon as (ab), equatorial view. Note that colpus is somewhat modified equatorially, a condition called tricolporoidate, if more pronounced, as in (ah),(ai). (**ad**) 6-stephanocolpate (Pf0): *Mentha rotundifolia* (L.) Huds., North Carolina. Polar view. Microreticulate sculpture. (**ae**) Pericolpate (Px0): *Batis maritima* L., Yucatan, Mexico. Equatorial views, showing that colpi are not located on lines connecting the poles. Psilate sculpture. Note knobby thickenings of ektexine. (**af**) Tricolporate (Pc3): *Nyssa ogeche* Marsh., Georgia. Polar view. Sculpture counts as psilate per Faegri classification, although very small pits and granae are visible. LO analysis at 1,000x reveals columellate structure. (**ag**) Same taxon as (af), equatorial view. Note costae (thickenings) on edges of colpi, and the complex equatorial structure with an inner aperture (= os) with a thickened exinous rim (see those out of focus, both here and in ag). (**ah**) Tricolpate-tricolporoidate (Pc0): *Phoradendron serotinum* (Raf.) M.C. Johnston, Texas. Variety of equatorial views, various focal levels. Note (arrow) equatorially modified colpus. Psilate sculpture. (**ai**) Same taxon as (ah), polar view. Note that from polar view alone, even with critical focusing, it is hard to prove whether it is Pc0, Pc0 or Pc3. (**aj**) 4-stephanocolporate (Pd4): *Melia azedarach* L., Texas. Polar view. Sculpture "counts" as psilate per Faegri classification, though a slightly verrucate texture is observable. See (ak). (**ak**) Same taxon as (aj), equatorial view. Note costate thickenings along the colpi and the large equatorial pore structure. (**al**) Diporate (P02): *Itea virginica* L., Alabama. Polar or equatorial view (in P02s, hard to distinguish). Sculpture psilate. (**am**) n-stephanocolporate (Pnn): *Spermacoce glabra* Michx., Texas. Obliquely polar view. Sculpture psilate. (**an**) Same taxon as (am). Note that the equatorial "pore" structure is actually an equatorial band of thinning (= "transverse colpus") (Faegri and Iversen, 1975: colpus transversalis). In some stephanocolporate pollen the transverse colpus is separate for each longitudinal (meridional) colpus, so that the two present a cruciate appearance. The colpi in (an) are not syncolpate, though from this photo one might draw that conclusion. (**ao**) 5-stephanoporate (P05): *Pterocarya stenoptera* DC., China. Polar view. Sculpture scabrate. (**ap**) Pericolporate (Pxx): *Malvastrum spicatum* (L.) Gray,

4.1.2 Monolete (Sa0)

Appears much later in the fossil record, seemingly derived from the trilete condition by change of tetrad form so that the 3-pronged laesura is not formed. (An intermediate, dilete form (Sb0) with a v-shaped laesura exists but is rare.) Examples: *Marattia, Lorinseria* (Fig. 5.8h–j).

4.1.3 Alete (S00)

Apparently derived from monolete or trilete condition by non-formation of haptotypic marks. Example: many moss spores (Fig. 5.8, l–m).

Figure 5.8 Texas. Sculpture echinate plus microreticulate. The colpi and associated rectangular "pores" are small and scattered over the surface (see arrow). Pxx is a relatively rare condition. (**aq**) Triporate (P03): *Betula nigra* L., Tennessee. Polar view. Sculpture psilate. Ektexine and endexine separate at pores producing a vestibulum. Erdtman called the outer, ektexinous pore the "pore", the inner endexinous one the "os", and he would call *Betula* pollen "pororate". (**ar**) Triporate (P03): *Maclura pomifera* (Raf.) Schneid. (cult.). Oblique, mostly equatorial views. Sculpture psilate. Pores annulate (surrounded by thickened rim). (**as**) Heterocolpate (Pf3): *Lythrum salicaria* L., Quebec. Polar (top) and equatorial views. Sculpture psilate. Equatorial *Figure 5.8, concluded.* pores occur in only half the colpi. (**at**) 4-stephanocolpate (Pd0): *Haloragis erecta* (Murr.) Schindler, New Zealand. Polar views. Sculpture psilate. This is a good example of form with very short colpi often described as "pores". (**au**) Periporate (P0x): *Salicornia virginica* L., New Jersey. Sculpture psilate (micropitted). (**av**) 3-Syncolporate (Pcs): *Melaleuca quinquenervia* (Cav.) S.T. Blake (cult.). Polar view. Sculpture psilate. Colpi unite to an "island" comprising the polar area. "Pcs" includes both the syncolpate and syncolporate forms. (**aw**) Pollinium (Ppd:P00): *Asclepias tuberosa* L., Georgia. Composite of two photomicrographs at very low magnification–bar under (ah) represents 440 μm. All of the pollen of one chamber of a stamen is shed as a single mass. This is thus a special sort of polyad. The individual grains are P00. Sculpture psilate. See (az). (**ax**) Fenestrate (Pfe:Pc0): *Sonchus arvensis* L., Pennsylvania. Polar view. Echinate sculpture. The large "windows" (hence, fenestrate) dominate, but the grain is also tricolpate, though the colpi are hard to see (arrow). (**ay**) Fenestrate (Pfe): *Passiflora incarnata* L., Texas. Sculpture loosely reticulate. The "windows" are left by opercula dropping out. The opercula are sporopolleninous and also appear by themselves in pollen preparations. (**az**) Same pollinium as in (aw). 1,000x. Outer edge of pollinium showing that outer exines of individual grains tend to fuse with each other. (**ba**) Tetrahedral tetrad, tricolporate (Pte:Pc3): *Phyllodoce caerula* (L.) Bab., Finland. Lateral view, high focus of tetrad, showing colpi running toward each other from adjoining grains (Fischer's rule). Sculpture verrucate. See (bc). (**bb**) Tetragonal tetrad, monoporate (Pte:P01): *Typha latifolia* L., Texas. "Top" view of tetrad, mid-focus in which out-of-focus pore shows for only one grain (arrow). Sculpture reticulate. (**bc**) Tetrahedral tetrad, tricolporate (Pte:Pc3): same taxon as (ba). See "top" view of tetrad, high focus. (**bd**) Polyad, syncolpate (Ppd:Pcs-?): *Acacia* sp. (cult.). Sculpture psilate. Sixteen grains comprise the polyad. Each grain is undoubtedly syncolpate, but that they are 3-syncolpate is a guess.

4.1.4 Zonate (Scz, rarely Saz)

Trilete (rarely monolete) spores with an equatorial extension. More common in Paleozoic than since. Extant example: *Gymnogramme* (Polypodiaceae).

This general category includes variants, such as the following:

4.1.4.1 Cingulate In which the zone is thick, more of a flange than a thin zone. Extant example: *Lophosoria*.

4.1.4.2 Coronate In which the zona is feathery or broken up to a tattered fringe. The best examples are all fossils, such as *Reinschospora*, a Carboniferous spore shown in SEM picture and diagrammatically in Fig. 1.2o,p.

Grebe (1971) has produced an excellent compendium of standard terms for, and methods of, spore description, which the student should consult for more information. Unfortunately, the publication is not available in every library. Also useful is the *Glossary of Pollen and Spore Terminology* (Punt *et al.*, 1994), and the glossary of this book.

4.2 Pollen (See Figs. 5.4, 5.5, and 5.8)

4.2.1 Operculate (P0P)

Has an encircling sulcus or pseudosulcus. The circumpolloid Mesozoic pollen group including *Classopollis* could conceivably be put here, as can pollen of the extant pond lily, *Nymphaea*. The encircling feature in the latter is a true sulcus, and that of *Classopollis is* not (Fig. 5.8k)–it is termed a rimula, and sometimes *Classopollis* pollen does break apart at it. Note also that some palynologists follow Walker and Doyle (1975) in terming pollen with ring-like, encircling, apertures "zona-aperturate." Various subdivisions of this condition are in use, such as "zonasulculus" for the ring-like aperture of *Nymphaea*, which is an equatorial feature.

4.2.2 Saccate (Pv2, etc.)

Having at least one saccus (= "vesicle," "bladder," "wing"). Strictly speaking, a true saccus is not a hollow sack; it has an internal spongy or "webby" lining of varying thickness and density. If a similar vesicle is present but lacking the internal "webbing", the grain is pseudosaccate, a common form in the Paleozoic. In practice, I include pseudosaccate in Pv1, Pv2, etc. The function of sacci is still debated, but the "idea" was already on the go in the Devonian and this was a very dominant type in the Mesozoic. The function of the spongy lining of the true saccus would seem clearly to be at least partly to provide firmness to the saccus, to prevent its collapse, and the saccus obviously makes a saccate grain float better in water, perhaps even significantly in air, because of the reduction in total specific gravity. It is now generally agreed, however, that flotation in

liquid at the mouth of the megasporangium for better germination orientation is the primary biological purpose of the sacci. Extant examples: *Pinus, Picea, Podocarpus* (Fig. 5.8n–q).

4.2.3 Striate (= Polyplicate) (Pst)

Pollen grains with multiple grooves (striae), plicae ("pleats"), or straps (taeniae) dominating the surface. Such grains in the Paleozoic and Mesozoic are often also saccate, and one can use a double code reference, e.g., Pst-Pv2. The plicae, etc., may have a harmomegathic (expansion-contraction) function, especially in connection with gain and loss of water content. Extant examples: *Ephedra, Welwitschia* (Fig. 5.8r).

4.2.4 Inaperturate (P00)

No haptotypic features. Unfortunately not easy to distinguish from S00 or even from "baggy" acritarchs and dinoflagellate cysts. Extant example: *Populus* (Fig. 5.8s).

4.2.5 Monosulcate (= Monocolpate) (Pa0)

Having a single germinal furrow or colpus or sulcus. Technically, a sulcus is such a furrow when located on the distal surface, usually with the distal pole as its center, whereas a colpus is a longitudinal furrow on a "meridional line" crossing the equator. In day-to-day work palynologists do not usually trouble with this erdtmanian distinction. For example, some of the "colpi" of pericolpate grains (Fig. 5.4) are not technically colpi but sulculi (see Glossary). In any event, the code designation is Pa0. In, for example, the Arecaceae (=Palmae), there are forms in which the distal sulcus has extended its two termini around the grain until they join. This variant of monosulcate is sometimes called zonosulcate, which could be given the code symbol of Paz Extant example for Pa0: *Lilium* (Fig. 5.8t, w, y).

4.2.6 Ulcerate (Pul)

Grains with no well-organized pores or colpi, but having one or more areas with thinned or partially broken exine. Extant example: Cyperaceae (Fig. 5.8u).

4.2.7 Trichotomosulcate (-colpate) (Pac)

A variant of Pa0, in which the germinal furrow is drawn out to a three-pronged shape, like the outline of a tricorn hat, but resembling sometimes a trilete laesura. As such a furrow is always a distal feature, some would insist on the use of trichotomosulcate not trichotomocolpate, but the distinction as of little practical importance. Extant examples: many palms, e.g., *Cocos*, which sometimes has Pac and Pa0 in the same anther (Fig. 5.8x).

4.2.8 Monoporate (P01)

Obviously a modification of Pa0. P01 grains are especially a feature of Poaceae, in which they are found in all species. Grass pollen always has a thickened rim of exine around the pore, the annulus, and a small pad of ektexine, the operculum, on the pore membrane (Fig. 5.8z).

4.2.9 Dicolpate (Pb0)

Uncommon type of angiosperm pollen. Extant example: *Pontederia* (Fig. 5.8aa).

4.2.10 Tricolpate (Pc0) and Tricolporoidate (Pc0)

This is the basic type of dicot angiosperm pollen, with three meridional colpi, 120° apart as viewed from the pole. Extant examples: certain *Quercus* spp., *Ilex* (Fig. 5.8ab,ac). (Many *Quercus* spp. and *Ilex* are actually tricolporoidate, meaning that the colpal membrane is narrowed and/or somewhat modified at the equator. See comment under Tricolporate.)

4.2.11 Stephanocolpate (Pn0: Pd0, Pe0, Pf0, etc.)

Colpi arranged on meridians connecting the poles of the grains, perpendicular to the equator, evenly spaced and greater than three in number. Extant example: Labiatae (e.g., *Mentha* is usually Pf0) (Fig. 5.8ad,at).

4.2.12 Pericolpate (Px_n*0:* Px_4*0, etc.)*

Colpate pollen in which the colpi are not located on "meridians" but are in quite other positions or are skewed with reference to lines connecting the poles. (According to Erdtman, such "colpi" should be called either sulculi or colpoids depending on orientation.) Extant example: *Batis* (Fig. 5.8ae).

4.2.13 Dicolporate (Pb2)

Dicolporate pollen (with colpi and pores), an uncommon pollen type. Extant example: some Acanthaceae.

4.2.14 Tricolporate (Pc3)

One of the fundamental dicot angiosperm pollen types, with three equally spaced colpi on "meridians" (see Pc0), each colpus also provided with an equatorial pore, os, ulcus, or other membranal modification. There are literally thousands of extant examples, e.g., *Nyssa* (Fig. 5.8af-ag).

Note that many species make pollen grains with colpal configuration intermediate between tricolporate and tricolpate. Erdtman and others call these tricolporoidate. Such -colporoidate grains lack a well defined equatorial pore or an

ulcus, but a thinning of some sort of the membrane, or a shallowing or other modification of the colpus, is apparent. I normally include these with -colpate, but underline the *0*. Thus, a tricolporoidate grain is a Pc0. Extant example: some species of *Quercus* (see Fig. 5.8ac, ah,ai).

4.2.15 Stephanocolporate (Pnn: Pd4, Pe5, etc.)

As Pc3, but more than 3, equally spaced meridional colpi, each with equatorial pores or other membranal modifications. Extant example: *Citrus* (Fig. 5.8aj-ak, am-an).

4.2.16 Pericolporate (Px_yn_y*:* Px_4n_4*, etc.)*

Colporate pollen in which the colpi (Erdtman: colpoids) are not arranged meridionally but otherwise, or at least are skew to lines connecting the poles (see Pxn0). Extant example: *Malvastrum* (Fig. 5.8ap).

4.2.17 Diporate (P02)

Pollen with two more or less isodiametric germinal apertures, including both pores and ulci (if the latter are regularly arranged–otherwise grains with ulci are Pul). Extant examples: *Itea*, some *Ficus* (Fig. 5.8al).

4.2.18 Triporate (P03)

One of the most common dicot angiosperm pollen types, having three equatorial, more or less isodiametric germinal apertures, including pores and ulci (if the latter are arranged as just described–otherwise such grains with ulci are Pul), including forms with complex apertures, with an outer pore, an inner opening (os) and an intervening chamber (vestibulum) between them. (Erdtman calls the latter "-pororate".) Extant examples: *Urtica, Maclura, Celtis* (simple pores), *Betula* ("vestibulate-triporate") (Fig. 5.8aq-ar).

4.2.19 Stephanoporate (P0n: P04, P05, etc.)

Similar to P03, but with more than three equatorial, equally spaced pores or ulci. Extant examples: *Alnus* (sometimes P03, usually P04-5), *Pterocarya* (usually P06 or P07) (Fig. 5.8ao).

4.2.20 Periporate (P0x)

With pores arranged other than on the equator, characteristically all over the surface, as in Chenopodiaceae, but also included here are grains such as those of *Juglans*, in which there are a few off-equator pores, as well as a number arranged in the stephanoporate manner. *Carya* has three pores 120° apart. They are, however, slightly off the equator in one hemisphere. Nevertheless, we exercise some license and consider *Carya* as P03! (Fig. 5.8au).

4.2.21 Syncolpate, Syncolporate (Pas, Pbs, Pcs, Pxs)

Pollen with anastomosing colpi. In practice Pas and Pbs are not separable; one continuous colpus girdles the grain. The most common syncolpate is Pcs with a triangular polar colpal connection delimiting the polar area. Extant examples: *Nymphaea* (Pas or Pbs, also called zonisulculate), *Syzgium* and other Myrtaceae (Pcs). Note: In order to keep to the three-letter code designation, syncolpate and syncolporate are grouped together, so that both trisyncolpate and trisyncolporate are labeled Pcs. Fig. 5.8av illustrates a syncolporate form; see also Fig. 5.8bd.

4.2.22 Heterocolpate (Pf3, etc.)

Grains that are partly -colpate, partly -colporate; that is, only some of the colpi have pores. Extant examples: *Combretum, Lythrum* (Fig. 5.8as).

4.2.23 Fenestrate (P03-Fe, etc.)

The suffix in the code designation signifies that this is an exceptional case. The basic morphological type can be P03, Pc0 or Pc3, but this is so dominated by very large "windows" in the ektexine that the germinal apertures (which the windows are not) are often hard to observe. This morphological type is common in the tribe Cichorieae of the Asteraceae, e.g., *Sonchus*. Another example: *Passiflora* (Fig. 5.8ax-ay). In *Passiflora* the "windows" completely dominate, and there is no sign of other morphological features. The code designation therefore is only Pfe. It is interesting that in *Passiflora* the windows represent holes from which opercula have fallen out when the pollen is prepared by chemical treatment, such as acetylation, and these opercula are found abundantly in the preparations. Thus, the windows in this case are actually holes caused by loss of opercular pieces of the exine. In *Sonchus* and other typical fenestrate forms the windows are not caused by loss of such opercula.

4.2.24 Dyads (Pdy:___)

The double code designation means that the pollen grains are shed from the anthers as doubles, pairs of grains united. This represents presumably incomplete breakup into individual grains or monads. This is not a common condition. The code designation for dyads, Pdy, is followed by the code for the individual grains, e.g., Pdy:P00 for the extant genus *Scheuchzeria*.

4.2.25 Tetrads (Pte:___)

Grains shed in fours presumably are the unseparated product of meiosis. Although most pollen are shed as single grains ("monads"), tetrads are a common pollen type. The double code designation means that the code for the individual grain follows, e.g. Pte:Pc3 for many Ericaceae such as *Vaccinium*, Pte:P01 for *Typha*,

Pte:P03 for *Gardenia*. A further complication is that there are a number of types of tetrads (see Fig. 5.9). Only two types are common as fossils, tetragonal (e.g., *Typha*) and tetrahedral (e.g., *Vaccinium* and most other members of the family Ericaceae). Most tetrahedral tetrads have pairs of interradially placed apertures: "Fischer's rule"– six pairs of apertures are located as though halfway between the ends of an imaginary triradiate mark. However, radially placed apertures also occur, although not commonly: "Garside's rule"– four trios of apertures are located as though at the ends of radii of an imaginary triradiate mark (see the tetrads in Fig. 5.9). Although this is the conventional definition, it is easier to remember that Fischer's rule has pairs of apertures, and Garside's rule trios.

Obligate ("permanent") tetrads, those normally released from sporangia (anthers) in the tetrad condition, have a very long and interesting history. The cryptospores of latest Ordovician-early Silurian time are often such tetrads. Obligate tetrads reappear regularly throughout the subsequent history of land plants. Krutzsch (1970) has summarized some of the literature on the subject of fossil tetrads.

A curious sort of apparent single grain (monad) is represented by the pseudomonads formed in many members of the Cyperaceae, in which three of the four products of meiosis degenerate, and the one remaining microspore develops as a "pseudomonad," which contains the remnants of the rest of a tetrad, but to routine observation appears to be an ordinary single grain (cf. Simpson *et al.*, 2003).

4.2.26 Polyads (Ppd:___)

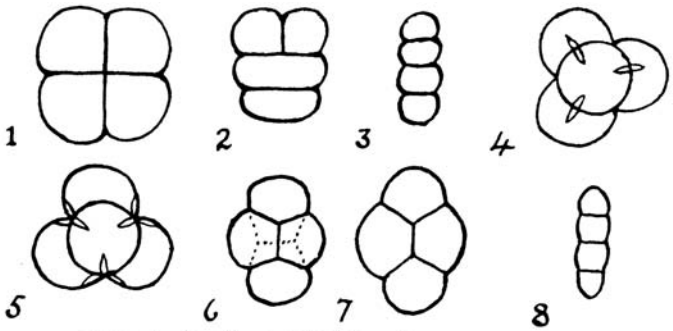
Grains shed in united groups in which the number of pollen grains usually is in multiples of four (16, 32, 64). Quite common in the mimusoid section of the legume family. The code designation for individual grains follows that for polyad, but often the individual grains are so small and so closely packed that this is very difficult to determine. Feuer *et al.* (1985) demonstrate that in some legume polyads the ektexines are fused so that individual grains are not separately discernible. Extant example: (Ppd: Pbs?) *Acacia* (Fig. 5.8bd).

Note that, in a broad sense, the polyad designation includes *massulae* consisting of an irregular, large number of grains, and *pollinia*, in which the whole contents of an anther or anther locule may be shed as one united mass of pollen. Extant example: *Asclepias* (Fig. 5.8aw,az).

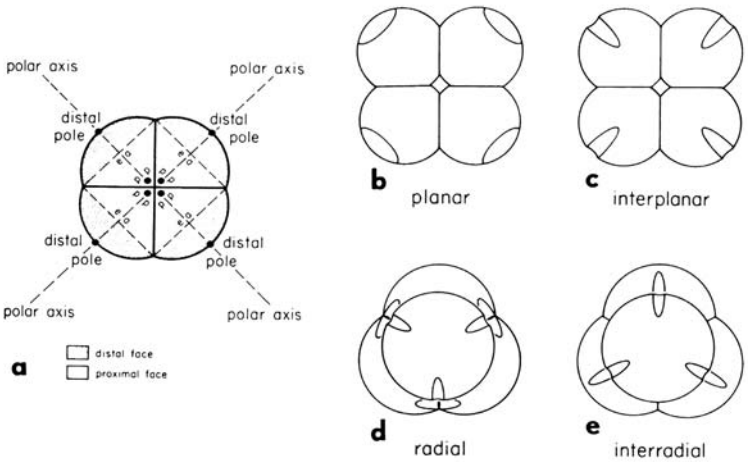
5 Supplemental Notes on Morphology

5.1 Colpus

This is really a furrow or "pleat" of the wall exine, part of which furrow may be membranous (thinned). The colpus thus serves as an accordion-pleat to accommodate swelling of the grain (a "harmomegathic" function). It may also serve as



Types of pollen tetrads. 1-3, Rigid uniplanar tetrads due to early wall formation. 1, tetragonal ; 2, T-shaped 3-linear ; 4-8, mobile tetrads determined by surface tension. 4, Tetrahedral tetrad with six pairs of inter-radial colpi according to Fischer's rule ; 5, Tetrahedral tetrad with four groups of three radial colpi according to Garside's rule. 6-8, Tetrad configurations determined by surface tension and increasing pressure. 6, Decussate ; 7, Rhomboidal ; 8, Linear.



Relationships of pollen tetrads and aperture positions.—a. Diagram of a tetragonal pollen tetrad showing the polar axis, one equatorial axis (e.a.) of the equatorial plane, the distal face, the proximal face, the distal pole, and the proximal pole (p.p.) of each pollen grain in the tetrad.—b–c. Tetragonal tetrads showing placement of distal-polar, furrow-like apertures in planar and interplanar positions.—d–e. Tetrahedral tetrads showing placement of equatorial, furrow-like apertures in radial and interradial positions; top pollen grain shown in polar view with its polar axis perpendicular to the plane of the figure.

Figure 5.9 Diagrammatic illustrations of kinds of pollen tetrad types (from Melville, 1981); (**a**)-(**e**) aperture positions in some tetrad types (from Walker and Doyle, 1975). Note that "d" below is equal to "5" above and "e" below to "4" above. That is to say, "Fischer's rule" refers to interradially and "Garside's rule" to radially arranged colpi in the tetrad. The total number of colpi per tetrad is twelve in both "rules".

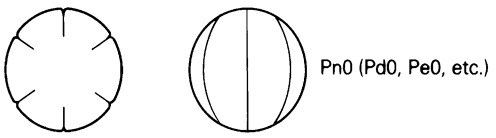
a site for germination of the grain. Technically, a colpus is supposed to be located on a line connecting the poles and to cross the equator of the grain (see sulcus), but most palynologists use the term more loosely than this. Erdtman would call many of the "colpi" of a pericolpate grain sulculi, as they are not meridional, do not cross the equator, but are more-or-less parallel to it, or colpoids, if otherwise located.

5.2 Sulcus

As colpus (see above), but distal and not crossing the equator of the grain. Typically one pole is located in the center of a sulcus. Most Pa0 grains are therefore technically monosulcate, not monocolpate, as the sulcus is a distal (polar) feature. However, colpus and sulcus, -colpate and -sulcate are really used more or less interchangeably in practical palynology.

5.3 Tricolpate (Pc0), Tricolporate (Pc3), Stephanocolpate (Pn0), Stephanocolporate (Pnn) vs. Pericolpate (Px_n0) and Pericolporate (Px_yn_y)

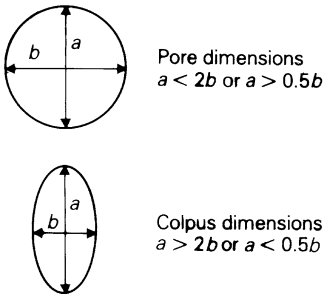
Tricolpate means, technically, having three colpi which must be separated in polar view by more or less 120°. Also, the colpi must be more or less on "meridians" of the grain, determined by theoretically projecting the surface of the grain onto a perfect sphere. The colpi must also be more or less bisected by the equator. If the colpi are not so arranged (are at angles to the equator other than 90°), or not bisected by the equator (are therefore mostly in one "hemisphere"), or are not separated as viewed from a "pole" by more or less 120°, the grains are pericolpate (Px_nO) or pericolporate (Px_yn_y). Stephanocolpate (Pn0), and stephanocolporate (Pnn) grains have colpi arranged regularly just as in tricolp(or)ate, but the number is four or more (which number is the "n" in the code formula). 6-stephanocolpate (see illustration) and 6-stephanocolporate grains, for example, have the colpi on meridians 60° apart.



5.4 -Colpate vs. -Colporate vs. -Colporoidate

-Colporate grains also have, in addition to the colpus, a further modification of the exine, usually a thinning, usually in the colpus, usually more or less in

the equatorial region. This modification is often an ulcus or pore, but may be an additional, transverse colpus. Sometimes the main colpus and the equatorial colpus form a cross, i.e., are cruciate. -Colporoidate grains have a modification of the colpus, usually more or less equatorial, which is not a true pore or transverse colpus. Sometimes it is an ulcus, or it may be just a roughening, wrinkling, thinning, or other modification of the colpal membrane. (The fossil record supports the idea that -colporoidate is transitional from -colpate to -colporate.) Rarely, some of the colpi of a pollen grain are -colporate and others are -colpate. This rather rare, mixed condition is *heterocolpate* (Pf3, etc.).



5.5 Ulcus (See Ulcerate–Pul.)

An irregularly thinned area of a pollen grain, apparently functioning as a pore. Cyperaceous pollen, for example, are characteristically ulcerate. There are often multiple ulci on ulcerate grains.

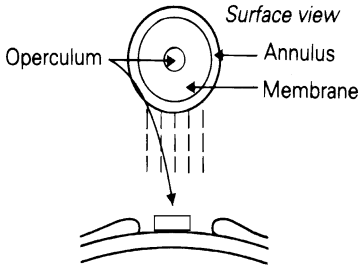
5.6 Pore

5.6.1 Pore vs. Ulcus and Colpus

The distinction between a pore and an ulcus is that pores are more or less uniform in size, shape and distribution, and have a membrane (usually thinner than the rest of the exine) that is a regular thickness. Ulci are irregular in size, shape and distribution, and they consist of irregular patchy thinnings rather than having membranes of uniform thickness. The dimensions of a pore are such that no axis is greater than twice that of another axis (see diagram above).

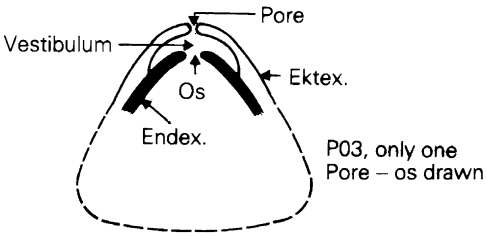
5.6.2 Annulus and Operculum

Pores may have a thickened rim, an annulus (= annular thickening). On the pore membrane may be a disk that thickens the membrane, called an operculum. The operculum is usually ektexinous, the rest of the membrane often endexinous.



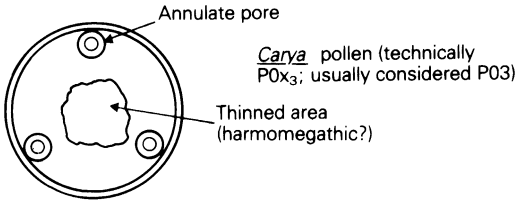
5.6.3 Vestibulum and Os (Plural, Ora, Adjectival Form, Orate.)

Sometimes an external, ektexinous pore (ectopore) is associated with an internal, sometimes complex structure involving the endexine. If the internal structure involves an additional opening, this is an os or endopore. The space between the (external) pore and the back of the internal structure is the vestibulum. A variant of the vestibulum in which the inner space is much larger than the outer pore is called an atrium. Some grains are therefore simply triporate (P03, e.g., *Celtis*), while others are tripor(or)ate (also P03, e.g., *Betula*, but in practical work one usually calls all such grains triporate).



5.7 Triporate (P03) and Stephanoporate (P0n) vs. Periporate (P0x)

Triporate grains are presumably homologous to tricolpate grains. Therefore, the pores must be 120° apart as viewed from a pole. Also, the pores must be bisected by, i.e., lie upon, or nearly on, the equator. Stephanoporate grains are multipored versions of the same plan. P06 (stephanoporate) grains therefore have the pores on the equator and more or less 60° apart. Arrangements of more than three pores off the equator are periporate (P0x). Characteristically, periporate grains have pores over much of the surface (example: Chenopodiaceae). However, *Juglans*, with only one or two pores off the equator, is technically P0x, as is even *Carya*, with three pores 120° apart but shifted into one hemisphere.



5.8 Margo

A modified exinal margin of pores or colpi, usually thinnings or thickenings, sometimes modified in sculpturing, are margos. Those associated with pores are usually called annuli. It is more erudite to use "margines" as the plural of margo, but I prefer margos.

5.9 Costa and Arcus

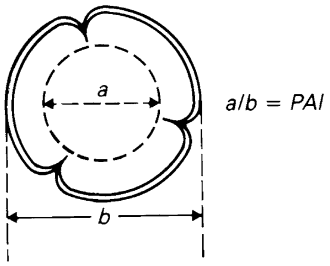
When there is a rib-like thickening in the exine (usually endexinous) underneath the edge of a colpus, this is called a costa. The thickening bands in the exine of *Alnus*, running from pore to pore, are not costae. They are arcs.

5.10 Fenestrate

This is a condition especially typical of certain Asteraceae pollen, e.g., *Sonchus*, in which there are large "windows" in the ektexine. The "windows" are neither a sculpturing type, nor a colpal type. Thus a fenestrate pollen grain can be Pc3 or P03, and echinate in sculpture, as well as fenestrate. See more complete explanation above, under Morphological Types in Detail.

5.11 Polar Area

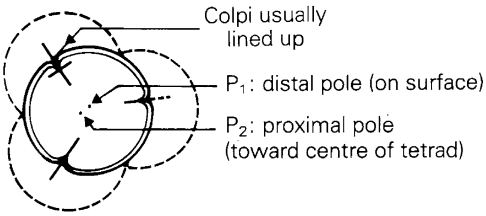
The degree to which the colpae of tricolp(or)ate or stephanocolp(or)ate grains encroach on the proximal or distal polar areas has diagnostic value. The size



of the non-encroached-upon polar area is sometimes measured by a polar area index (PAI).

5.12 Polar vs. Equatorial

You will find it helpful in understanding this to look at angiosperm pollen of forms that are shed as tetrads, e.g., *Rhododendron, Vaccinium* and *Gardenia*. P1 and P2 are poles. In the tetrad it is possible to tell for the individual grains that P1 on the outside, is the distal and P2 the proximal (= toward center) of the tetrad, but this is not possible as a rule when pollen occurs (as is usually the case) as monads. For this reason, "polar" and "equatorial" are used instead of distal-proximal and lateral for Pc0 and derived forms of dicot angiosperm pollen. With most spores and gymnosperm pollen the laesurae and other features usually permit identification of the distal and proximal poles, and these more accurate designations can be used for orientation.

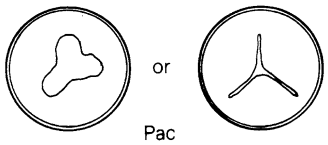


5.13 Tetrads and Polyads

Morphological analysis of these should wherever possible include analysis of the individual grains of the tetrad, e.g. Pte:Pc3, Ppd:Pc0. (See Fig. 5.9 for explanation of the various sorts of tetrads.)

5.14 Trichotomosulcate (loosely, "Trichotomocolpate") (Pac)

This is a variant of monosulcate in which the colpus (sulcus) is triangular instead of keel-shaped. It may even sometimes very closely approximate a trilete laesura in appearance.



Pac can usually be differentiated from Sc0, however, by the greater regularity of length and orientation of the radii of Sc0, and by the fact that the colpal margins of Pac are often more or less ragged or irregular compared to the edges of an open commissure of a spore's laesura.

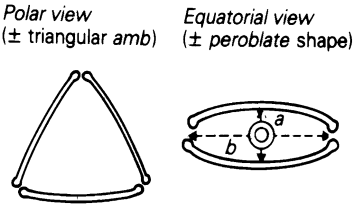
5.15 Perine (= Perispore)

This is a sporopolleninous envelope outside the exine, rather loosely organized compared to the exine, and therefore not usually persisting in fossil sporomorphs. Perines do occur on some gymnospermous pollen grains, e.g., *Taxodium*, but perines are much more common on spores. Often, acetolyzed preparations of perisporate spores show scraps of the perine still adhering to the exine, and these are easily misinterpretable as exinous sculpture. Some palynologists prefer to use perine for pollen and perispore for spores, but the terms are usually considered synonyms.

5.16 Amb (= "Limb")

It is often necessary to describe the "outline" of a spore or pollen grain. However, I see no reason to provide a chart of such terms, as triangular, oval, squarish, etc., all have well-understood meanings! You also should consult the shape-classes chart (see Fig. 5.18).

Of course, the "outline" can be the outline seen in either equatorial (or lateral) view, or in polar (or proximal-distal) view. The outline seen in equatorial view is the one used in determining whether a grain is more or less oblate, more or less prolate, etc. In other words, the shape-classes are of the shape around the polar axis. The outline seen in polar view is the amb (= outline of the equator) or "limb". For example, this P03 grain is of peroblate shape with a triangular amb. ($a/b = 0.3$; according to Erdtman, $a/b < 0.5$ is peroblate). When not otherwise specified, amb refers to what is seen from a pole.

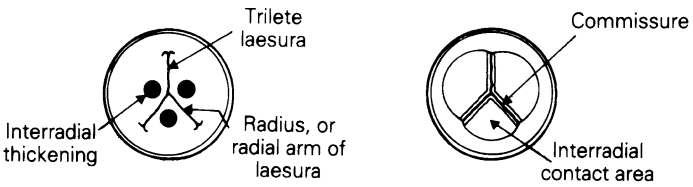


5.17 Laesura

This is the "scar" which shows the contact of spores (or of some, mostly fossil, pollen grains) with their neighbors in the original tetrad from which they have

separated. Laesurae can be: (most common) trilete (Sc0 = "Y-mark"); monolete (Sa0); dilete (Sb0; quite rare); or they can be absent (= alete, S00). Note that trilete and monolete are adjectives. It is never correct to speak of "the trilete" or "the monolete" when "the trilete laesura" or the "monolete laesura" is meant. Some palynologists use laesura to mean each arm or radius of a trilete laesura. They therefore use laesura for the single scar of a Sa0 spore, and laesurae (plural) for the branches of a single contact figure (= laesura in this book). To me it seems much clearer to regard spores as having a single laesura, which may be monolete or trilete in form, rather than to say that Sa0 has one laesura and Sc0 has three of them.

A laesura has a center suture or commissure, which usually serves the purpose of providing a zone of weakness for rupture upon germination of the spore. There may also be modifications of the spore wall adjacent to the laesura, such as thickenings, usually called lips (labiae). However, there are many terms for other marginal modifications next to the laesura, such as kyrtomes, interradial thickenings, etc. The separate arms of a trilete laesura are called radii. (Thus for those who regard a trilete spore as having three laesurae, radius and laesura are synonyms.). The terminal ends of radii may be forked; these extensions are called curvaturae. If these connect with neighboring curvaturae to surround contact areas, they are curvaturae perfectae. Otherwise, they are curvaturae imperfectae. Curvaturae are much more evident and prevalent in Paleozoic spores than in extant spores.



Sc0 with curvatura imperfecta *Sc0 with curvatura perfecta*

5.18 Saccate Pollen

Monosaccate (Pv1) and trisaccate (Pv3), as well as pseudosaccate and cavate or camerate grains simulating saccates are common as Mesozoic and Paleozoic fossils and they are not all coniferous pollen. However, all extant saccates are coniferous, and practically all are Pv2, e.g., *Pinus*. It is necessary to measure and describe the morphology and sculpture of the corpus (= "body") and sacci (= "vesicles" or "bladders") separately, as well as to measure the grains as a whole. (See Fig. 5.10 for further explanation.)

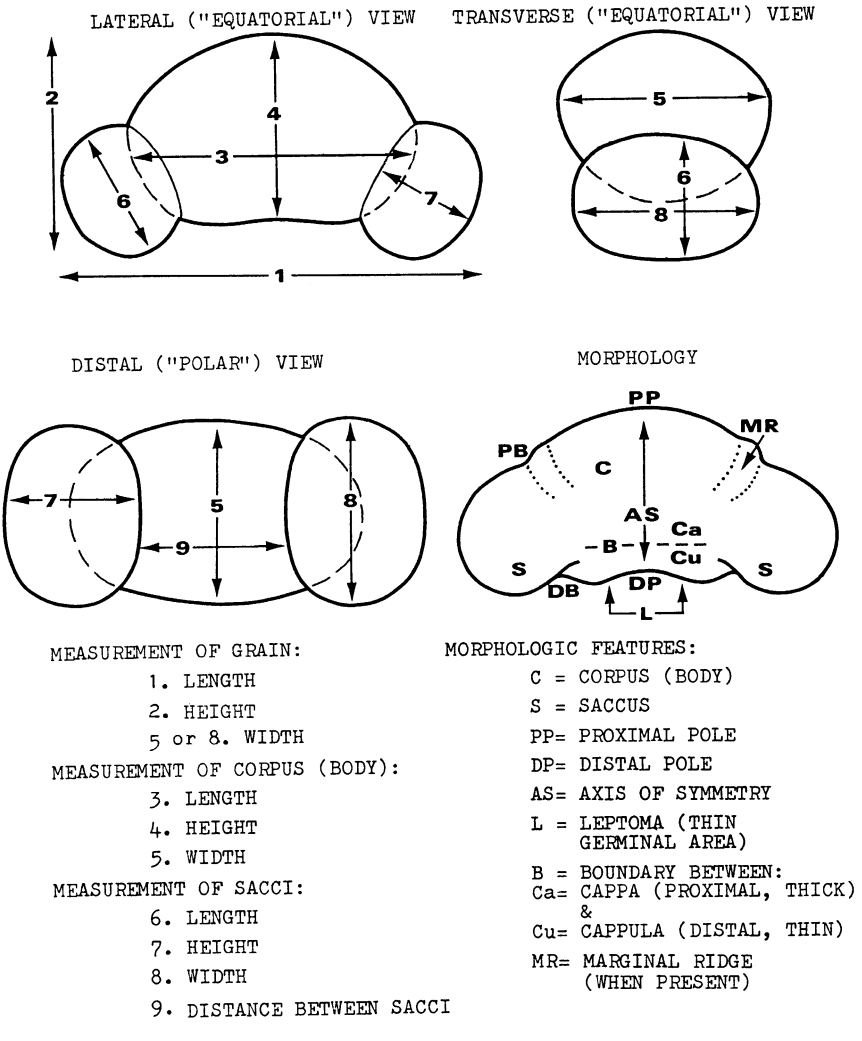


Figure 5.10 Bisaccate pollen present special problems in measurement because of their tri-partite structure. This figure presents the solution to the problems suggested by the Russian palynologist, Zauer (1977).

5.19 "Zono-"

Many palynologists use terms beginning with this expression, to indicate that the features are located on the equator of pollen grains. "Zonocolporate," for example, refers to colporate pollen with the colpi crossing the equator, with pores located

on the equator. The term is not different in practice from stephanocolporate, and I don't regard it necessary to complicate our task by use of such additional terms.

6 Exine Surface and Subsurface: Sculpture and Structure

Fig. 5.5 shows diagrammatically the major features of an average dicot angiosperm pollen grain (monocot pollen differs in morphological features but is similar in wall construction). Note that the intine (cellulosic-pectic) layer of the wall or integument of the pollen grain is not preserved in fossils and, along with the protoplasmic contents, is also completely removed by acetolysis or by boiling in solutions of KOH in the laboratory. The exine consists of a framework of sporopollenin (plus other compounds in the interstices and on the surface, which are also lost in fossilization) and constitutes the shell or exine that is found as a palynomorph. The exine is most complex in angiosperms, but gymnosperm pollen exines have a similar makeup. Because the pollen mother cells in an anther are sealed off with a layer of callose, and the microspores are sealed off further from the tapetum with more callose after microsporegenesis, it seems clear that formation of the exine is under control of the microspore genome. The tapetum, under sporophyte control, does play a role in late stage deposition of the surface sticky substance, pollenkitt. (M. Harley, personal communication, 2004; Takahashi and Skvarla, 1991; Cresti *et al.*, 1992.) The subject of the development of pollen and spore walls is beyond the scope of this book and it already has an enormous literature. A readily available paper on the subject, with a good bibliography, that I have found particularly enlightening for a grasp of the fundamental elements is El-Ghazaly *et al*. (2001), and a book packed with information about the subject is that of Harley *et al*. (2000).

Chunks of sporopollenin produced by the tapetum tissue of the anther or sporangium but not "used" in making exines often are shed as "ubisch bodies" or "orbicules" (Rowley, 1963), which may even occur as Paleozoic fossils (Taylor, 1976), showing that the basic mechanism of sporopollenin production and deposition in spores/pollen was well established over 300 million years ago. Ubisch bodies in modern cereal grasses have been shown by Wang *et al*. (2003) to be rich in tapetal genetic material important to the development of pollen exines, but that does not necessarily mean that the orbicules as such are agents of development. A genuine curiosity is the production of pseudopollen by members of the Theaceae, hollow sporopolleninous bodies about the same size as the regular pollen, but devoid of contents. These bodies could be regarded as a sort of giant ubisch body (cf. Tsou, 1997).

The exine of pollen usually has two layers. For the moment, we shall refer to these as ektexine and endexine, or sexine and nexine, without further comment, although we must deal with some complications later on. The inner layer (endexine or nexine) is relatively amorphous, and usually only its presence or

absence is noted. It is frequently missing, is very thin, granular or may be present only in the vicinity of the apertures. The outer layer (ektexine or sexine), however, may be complex either internally or externally or both. Surface complexity, such as verrucae (warts), spines, etc., is referred to as sculpture. This is sometimes called "ornamentation". I dislike this, as implying an esthetic value or purpose, but "sculpture" perhaps offends some also by suggesting a sculptor. There is further the problem that some see ontogenetic implications for both terms, sculpture being the result of removal, ornamentation the result of addition, of sporopollenin! I follow Faegri in distinguishing internal ektexine features as structure. With a light microscope, 100x objective (thus about 1,000x magnification), sculpture can be readily studied, but structure is hard to analyze in this manner and cannot be established or described with certainty without thin-sections and transmission electron microscopy.

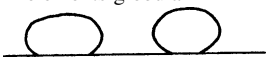
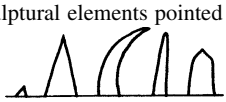
6.1 Sculpture: LO Analysis and Edge Analysis

Table 5.3 is the classification which I have used in our laboratory. It was modified and expanded from the 1975 edition of the Faegri and Iversen text (present, 4th, edition, 1989). It is far simpler than the sculpture classifications used by others, and yet has served us well, with few problems requiring other special terms. One major exception to this statement is that Faegri's classification apparently regards 1 μm as the practical limit of accurate observation of sculpture. Therefore, e.g., if the surface of a pollen grain or spore is more or less smooth, but has holes less than 1 μm, it is still regarded as psilate (= laevigate). I have no trouble recognizing holes of 0.5 μm diameter as holes, and therefore designate this kind of sculpture as micropitted. Similarly, Faegri's classification excludes sculpture from "reticulate" if the elements of the muri of the reticulum are less than 1 μm in length, and echinate is not so recognized if the spines are less than 1 μm in length. Sometimes I can recognize such features quite well under oil immersion with an objective of about 100x, and I get around the problem of the Faegri classification by calling these features microreticulate (this is a quite common type) and microechinate.

Erdtman, Faegri, and others have long ago described the possibilities of microscopic manipulation in understanding sculpture of exines. The problem is complicated, especially for beginners, by the fact that the sculpture is ordinarily present on a curved surface, whereas LM microscopy studies material in parallel flat planes, and there is a background created by the underlying internal ektexine structure, the endexine, and the entire exine of the opposite side of the grain as well, if the microscope can be focused that deeply. (For aerobiologists, who insist on studying whole pollen, including the protoplasm, surface lipids and oils, and pollenkitt, the situation is desperate.)

"LO analysis" (an erdtmanian term) refers to the possibility of distinguishing sculptural nuances by taking advantage of the fact that, as one focuses up and

Table 5.3 Principal sculpturing types for spores and pollen

A. Positive sculptural elements absent	
B. Surface smooth	*psilate*
BB. Diameter of pits $<1\,\mu m$	*micropitted*
BBB. Surface pitted, diameter of pits $\geq 1\,\mu m$	*foveolate*
BBBB. Surface with irregular grooves (includes negatively *reticulate*)	*fossulate*
AA. With positive sculptural elements	
B. Sculptural elements approximately isodiametric along the surface of the palynomorph (but may extend upward)	
C. No dimensions $\geq 1\,\mu m$	*scabrate*
CC. At least one dimension $\geq 1\,\mu m$	
D. Sculptural elements not pointed	
E. Lower part of element constricted	
F. Greatest diameter of element equal to or greater than its height: elements globular	*gemmate*
	
FF. Height of element greater than greatest diameter of projection: elements club-shaped	clavate
	
EE. Lower part of element not constricted	
F. Greatest diameter along the surface of palynomorph equal to or greater than height of element: elements wart-like	*verrucate*
	
FF. Height of element greater than greatest diameter Of projection: elements rod-shaped	*baculate*
	
DD. Sculptural elements pointed	*echinate*
	
BB. Sculptural elements elongated along the surface of the palynomorph (length at least twice the breadth)	
C. Elements irregularly distributed	*rugulate*
CC. Elements approximately parallel to each other	*striate (=ribbed)*
BBB. Sculptural elements forming a reticular (net-like) pattern (elements $<1\,\mu m$ but resolvable as reticulum: *microreticulate*)	*reticulate*

down in ordinary bright field microscopy (90x–100x objective, oil immersion) on an exine surface, the "brightness" or "darkness" of features varies. LO analysis was introduced by Erdtman and the initials are from the Latin words *lux* (light) and *obscurus* (dark). For example, as one focuses down on a spine, the first impression as one encounters the spine is a bright point, but it becomes broader and darker as one focuses down. By contrast, a hole in the surface is first encountered as a dark point (see Fig. 5.11). I also teach beginning students to exploit "edge analysis." If LO analysis and general impression indicate small spines, always carefully focus up and down on the outer edge of the grain. If one's interpretation of spines is correct, no matter if they're only .5 μm long, they'll show as tiny protrusions on the edge, as this is silhouetted in mid-focus. Similarly, if one has interpreted pits or micropits, they will not project in mid-focus on the edge, and careful focus will usually show them as tiny channels through the ektexine. (Reticulate sculpture causes beginners special difficulty, as the muri of the reticulum often simulate spines or baculae in mid-focus of the edge; but of course, LO analysis of the surface will not show spines!) However, the misinterpretation of reticulate as echinate or baculate, and the misinterpretation ("reversal") of LO analytical observations (that is, negative for positive, and vice-versa) are the most persistent problems I have had in teaching practical palynological microscopy to generations of Penn State students. Fig. 5.12 shows diagrammatically what can be done with LO and edge analysis.

SEM study of exine surfaces is the most sophisticated manner for sculpture study. As shown in Fig. 5.13, SEM micrographs even offer the possibility of separating species of genera and genera of difficult families such as Poaceae or Chenopodiaceae. The only drawback is that the method requires considerable additional pre-treatment of specimens and ready availability of a good scanning electron microscope. Relatively few palynologists really consider SEM as a routine matter.

TEM (transmission electron microscopy) offers additional possibilities for elucidating problems of sculpture and structure interpretation, because thin sections displaying internal features are studied, whereas SEM can elucidate only superficial features, except on edges of broken surfaces. As an illustration of the nuances of sculpture amenable to study with electron microscopy, Bolick *et al.* (1984) and Salgado-Labouriau (1984) debate the interpretation of tiny holes in the *spines* of composite pollen!

Interference contrast (Nomarski) LM microscopy requires special condensers and objectives for the bright-field light microscope and provides an SEM-like sort of contrast that is very useful for thin-walled palynomorphs that appear featureless in ordinary bright-field.

6.2 Structure

Angiosperm pollen exines apparently developed a separate ektexinous layer in the course of evolution, by the terminal fusion of granular and rod-like elements

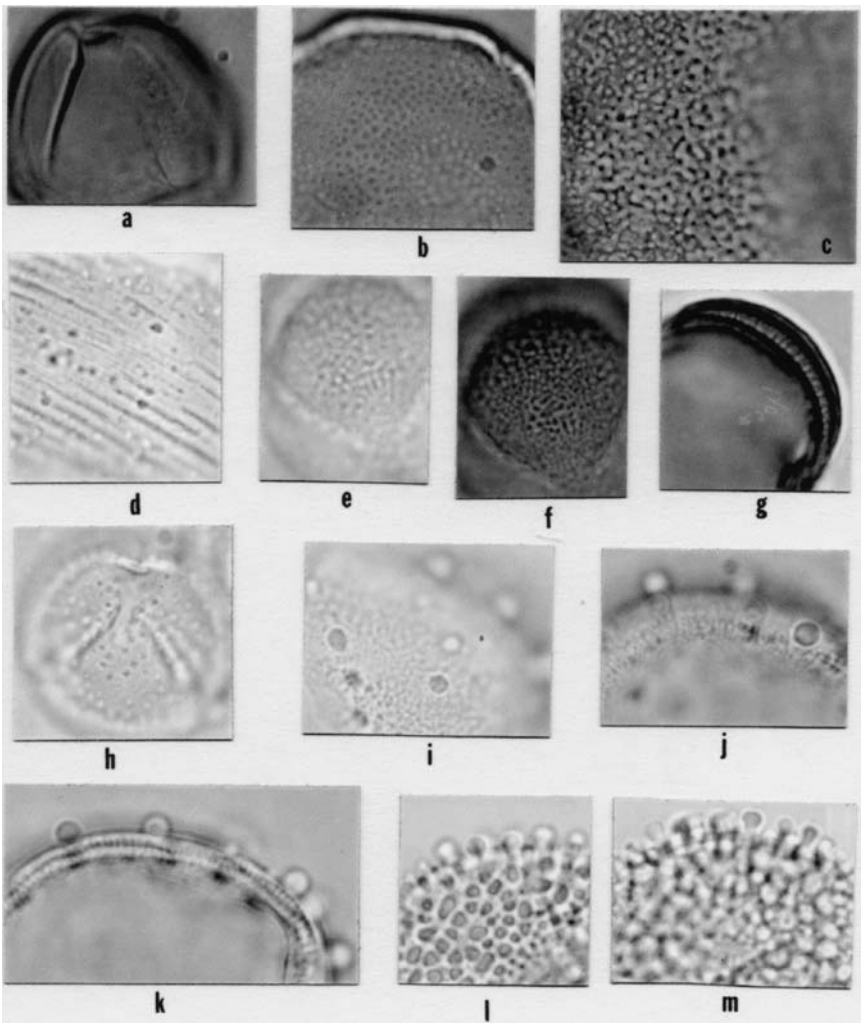


Figure 5.11

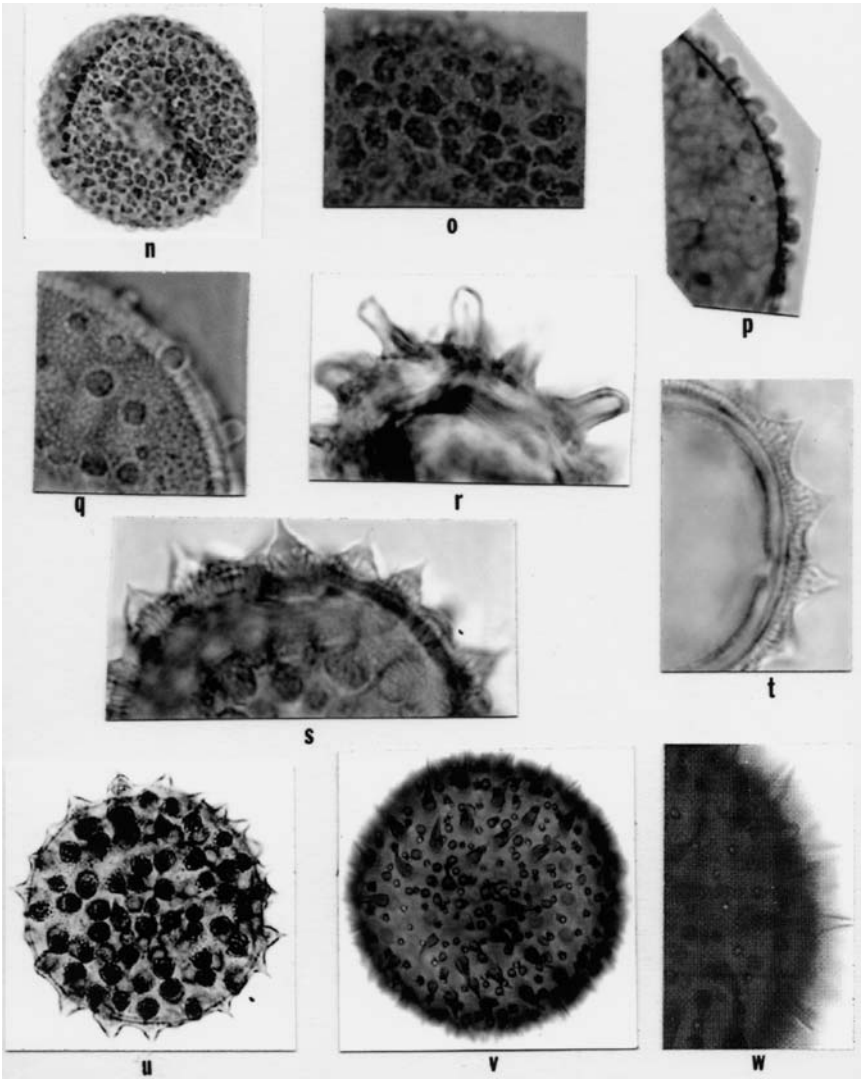


Figure 5.11 *(See caption on page 135)*

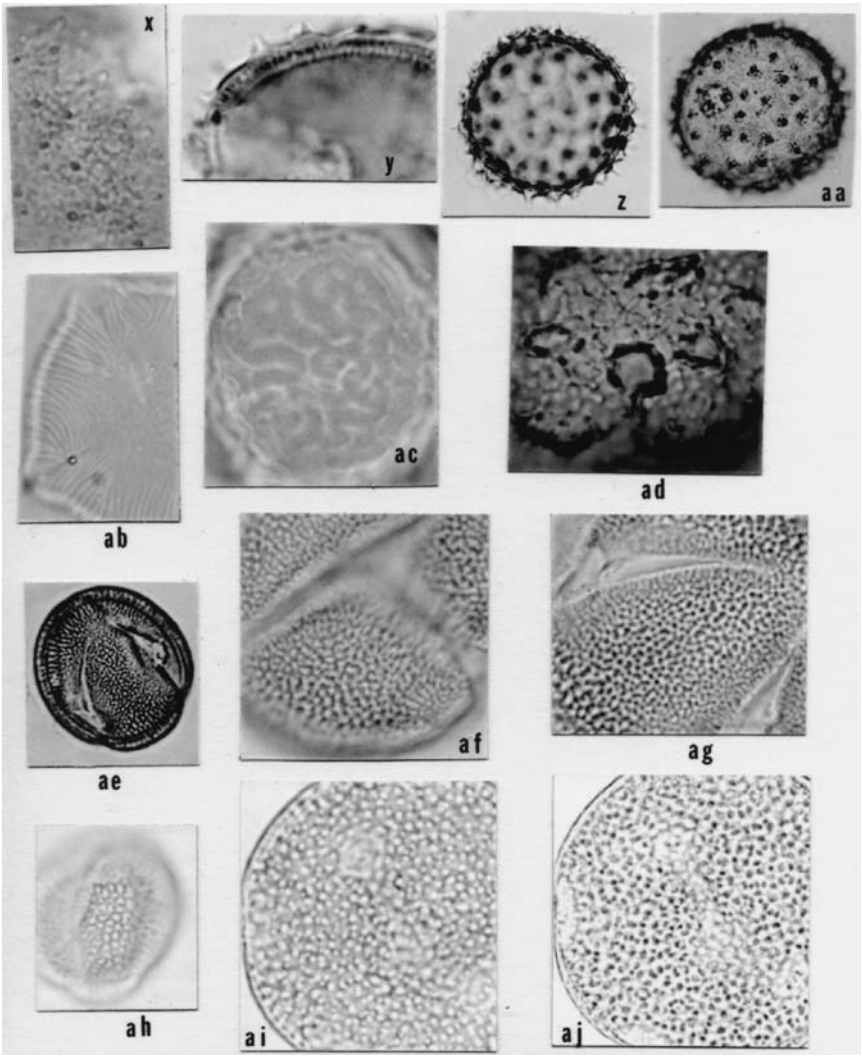


Figure 5.11

Figure 5.11 Photomicrographs (2,400x, oil immersion, except as noted) of extant plant principal spores/pollen sculptural types. Many of these types are easier to illustrate with SEM pictures, but as most users of this book will have access on a regular basis only to a light microscope, it is more useful to illustrate what they will see. Elements of structure are also illustrated. (**a**) Psilate (= laevigate): *Phoradendron serotinum* (Raf.) M.C. Johnston, Texas. High focus. Some texture is observable, as a truly smooth exine surface does not exist. (**b**) Psilate (!), internally reticulate (= intrareticulate): *Pterocarya stenoptera* DC., China. Low-focus of surface. (**c**) Foveolate (and rugulate!): *Alangium platanifolium* (S. & Z.) Hanus, China. High focus. The "holes" are observable as black spots. (**d**) Fossulate (see striate!): *Schizaea digitata* SW., Philippines. High focus. Fossulate sculpture refers to the grooves, i.e., negative sculpture. Obviously, striate sculpture, referring to the ridges, is a condition more or less indistinguishable from fossulate. (**e**) Scabrate: *Artemisia douglasiana* Bess., California. High focus. The bright spots are scabrae at high focus. (**f**) As (e). Low-focus. Some of the dark spots are scabrae that are bright in high focus. (LO analysis!). (**g**) As (e). Mid-focus. Shows columellae in side view, under the tectum. Hints of the scabrae are seen along the edge of the tectum ("edge analysis"). (**h**) Scabrate: *Cleome spinosa* Jacq., Venezuela. High focus. These scabrae are at the limit of resolution (1 μm). (**i**) Gemmate (plus micropitted): *Hyphaene crinita* Gaertn. (cult.), South Africa. High focus. (**j**) As (i). Lower focus, near edge. (**k**) As (i). Edge focus, showing gemmae and columellae of ektexine. (**l**) Clavate: *Ilex cassine* L., Florida. High focus. (**m**) As (l). Lower focus, showing several clavae on the edge and the dark appearance of claval stalk in low-focus. (**n**) Verrucate: *Sciadopitys verticillata* Sieb. & Zucc. (cult.). 1,000 x, high focus. (**o**) As (n). Slightly lower focus at 2,400 x. The verrucae are internally complex. (**p**) As (n). Low-focus of edge (edge analysis!), confirming that major sculpture type is verrucate. (**q**) Gemmate-baculate (plus pitted): *Hyphaene thebiaca* (L.) Del. (cult.), Curaçao. Mid-focus. Illustrates that distinction between sculpturing types may be blurred: some of the elements are gemmae, some bacula. (**r**) Baculate (perispore): *Cystopteris fragilis* (L.) Bernh., Mexico. Mid-focus. This sculpturing is perisporal, but as sculptural terms are purely descriptive of external texture, the same terms are used as for exine. (**s**) Echinate: *Sphaeralcea lindheimeri* Gray, Texas. Mid-focus. Note that echinae are biform (broad base narrowing abruptly to slender spine) and that the columellate underpinning of the spines is evident in edge analysis. (**t**) Echinate: *Senecio ampullacens* Hook., Texas. Mid-focus. See (s), an unrelated taxon. Echinae *Figure 5.11, continued.* not biform, but columellate ektexine under the spines is evident. (**u**) Echinate: *Abutilon incanum* (Link) Sweet, Texas. High focus, 1,000x. (**v**) Echinate (more or less biform and heteromorphic): *Althaea rosea* Cav. (cult.). High focus, 600x (!). As is common for malvaceous pollen, this is a huge form. See (w). (**w**) As (v). 1,000x. The exine is so thick that at higher magnifications it is hard to photograph. The picture demonstrates the several different sizes of spines and that a fine micro-sculpture exists between spines. (**x**) Figure Echinate: *Valeriana officinalis* L., Sweden. The echinae appear in mid-focus *Figure 5.11, concluded.* (of the surface) as dark blobs. The columellate structure of the ektexine shows through as a confused pattern. (**y**) As (x). Mid-focus of grain, showing biform echinae and columellate structure. (**z**) Echinate: *Sphaeralcea angustifolia* (Cav.) D.Don., Texas. Mid-focus, 1,000x. Note biform echinae and their appearance in mid-focus. See (aa). (**aa**) As (z). 1,000x, higher focus to show the surface appearance in optical section of the columellae of the echinae-bases (LO-analysis!). (**ab**) Striate (see fossulate!): *Cuphaea cordata* R.& P., Peru.

placed upon the endexine. These elements have variously fused in evolution, so that the outer surface of most angiosperm pollen is really a secondary surface. The pioneers of palynological microscopy long ago recognized this and called the new surface, where it really does comprise a cover, the tectum. (Erdtman's use of tegillum for one kind of such surface (< 80% coverage) and tectum for others (> 80% coverage) is not a helpful distinction and has not been much used.) When a tectum exists, the sculpture, of course, sits atop it or comprises the surface features of the ends of its elements. These elements are usually basically rod-like (columellae), but they may be broadened below the top or arranged in various complex patterns internally. The interstices between columellae are filled with various substances, such as recognition-signal compounds and lipids in the living pollen. Muller (1984) has observed that pollenkitt may be present on the surface of pollen and make it sticky, but if deposited in tectum cavities it makes the pollen powdery.

Thus, columellate reticulate pollen is usually (but not always) adapted to insect pollination. Summarized by Pacini and Hesse (2005) are the very complex set of pollenkitt's (the most common adhesive material on or in the outer exine) properties affecting the protection of pollen and its successful dissemination. Presumably, the sticky material reported by Kopp *et al.* (2002) as being a problem in the collection of *Salix* pollen for breeding purposes was pollenkitt.

Often the terms for structure are quite similar to those for sculpture, and the prefix "infra-" is added to the sculptural terms to make it clear that the terms refer to internal matters, e.g., infrareticulate. Truth to tell, structure is very difficult to study with light microscopy and most often all one can ascertain is that there is structure, that columellae exist (often visible in edge analysis), and perhaps that the pattern is infrareticulate, infrastriate or whatever.

Figure 5.11 High focus. As explained for (d), striate forms and fossulate forms are hard to distinguish from each other and really depend on whether the grooves (fossulate) or the ridges (striate) are emphasized. Striate as a morphological type has broader bands (taeniae) and should be called taeniate to limit confusion with striate sculpturing. (**ac**) Rugulate: *Ulmus scabra* Mill. (cult.). High focus. (**ad**) Rugulate (perispore): *Dryopteris cristata* (L.) A. Gray, Germany. High focus. Note variation in size of rugulae. (**ae**) Reticulate: *Gentianella amarella* L., Finland. High focus, 1,000x. Reticulate sculpture is often easier to recognize at lower power because at high magnification the structure underneath may confuse. See (af)-(ag). (**af**) As (ae). 2,400x, High focus. Reticulum consists of ektexinous blocks fastened together. (**ag**) As (af). Lower focus of surface showing the reticulum and (small dark points) columellae under it. (**ah**) Reticulate: *Sinapis nigra* L., Pennsylvania. High focus. Large pattern reticulum on small pollen grain. (**ai**) More or less psilate (!): *Saponaria officinalis* L., New York. High focus. See (aj). The bodies that appear to be gemmae are instead columellae, of which the "heads" appear as bright spots in high focus. (**aj**) As (ai). Lower focus of surface. The dark spots are not gemmae but columellae. Illustrates the importance of "edge-analysis": edge is entire or may have depressions.

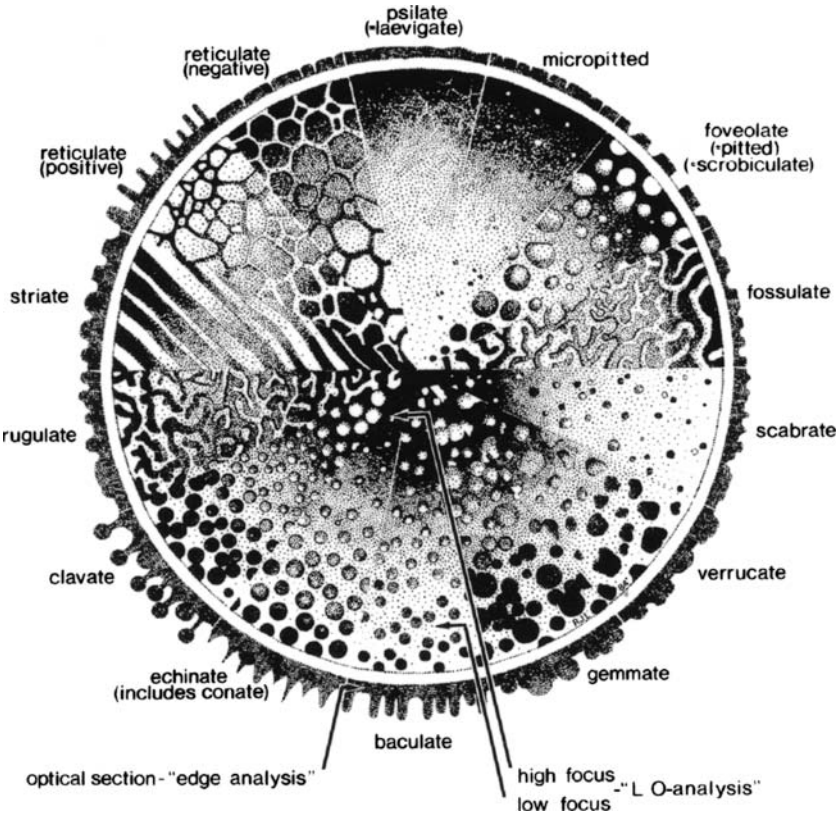


Figure 5.12 Sculpture types as seen at various levels of focus. Low focus is shown toward the outside of the grain, high focus toward the inside. Analysis of sculpture by comparing these levels is called "LO analysis," following Erdtman. For example, scabrae appear as bright spots at high level of focus and become dark as one focuses down through them. Pits appear dark in high focus and become brighter as one focuses down. Edge-analysis (focusing on the surface of the exine at the outer edge of the grain, in mid-focus) provides a check on conclusions drawn from LO analysis. Clavae, for example, will show up clearly. On the other hand, beginners will often identify the muri of reticulate sculpture seen in such side view as bacula or echinae. Edge-analysis should always be checked by LO analysis, and vice versa.

6.3 Additional Notes on Sculpture/Structure

6.3.1 Reticulate vs. Pitted (or Microreticulate vs. Micropitted!)

Students often have trouble differentiating these. In nature, there actually is a gradation. For convenience I consider porous sculpture with the area consisting mostly of holes (lumina) and less than half of solid walls (muri) as microreticulate

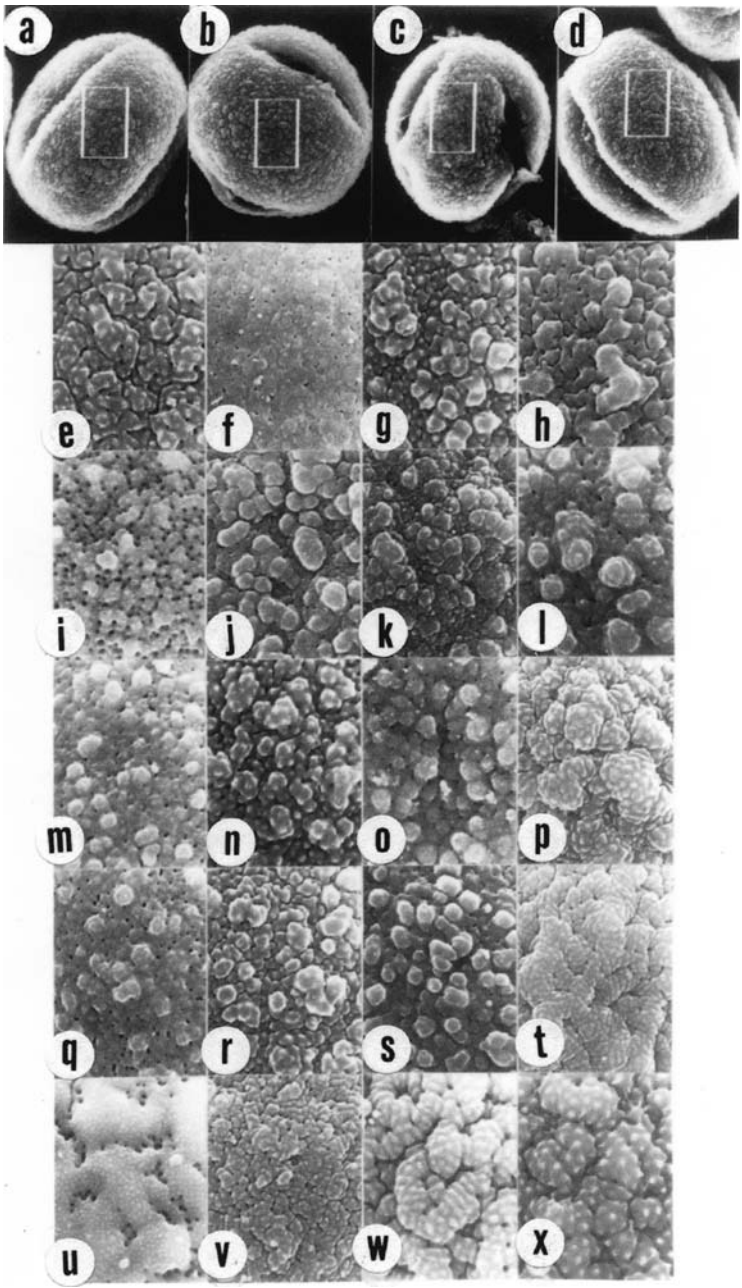


Figure 5.13 (a)-(d) Lower magnification (ca. 900x) SEM pictures of several species of oak pollen, with rectangles displayed to show the sizes of the blocks illustrated below.

or reticulate. Where there is more area of solid wall than of holes, we speak of micropitted or foveolate, depending on size of the openings. Some students have found it useful to compare the two situations with a sieve ("strainer"), which is reticulate (comprised mostly of holes), and a colander (comprised mostly of a solid surface, with more or less widely spaced holes), which is foveolate.

6.3.2 Mixed Sculpture

This is very common and often confusing, requiring careful microscopy to understand. In the Devonian, spores with biform appendages, e.g. sharp spines on the summits of mamillate protuberances, are common. In modern angiosperm pollen, it is common in Asteraceae for the pollen to have spines (echinae) on top of a reticulum. Clavae can also occur on top of a reticulum, e.g. in *Neobuchia*, in the Bombacaceae. It is common to have a mixture of different sorts of sculptural elements, e.g. gemmae and scabrae in *Grevillea banksii*, in the Proteaceae.

6.4 Additional Notes On Spores/Pollen Wall Morphology

6.4.1 Differences Between Groups of Embryophytes

Most of what has been presented so far about general wall morphology has to do with dicot angiosperm pollen. Monocot angiosperm pollen, though mostly based on a monosulcate pattern instead of a tricolpate pattern, does not differ enough in sculptural patterns to require separate treatment. Gymnosperm pollen is another story. Though some gymnosperm pollen approach a columellate condition (e.g., the Mesozoic fossil, *Classopollis),* the exine mostly lacks the angiosperm sculpture/structure difference that largely depends on columellate structure. Saccate gymnosperm pollen frequently has very different saccus sculpture from that of the corpus, and the corpus sculpture may differ markedly on proximal and distal surfaces of the grains. Pronounced positive sculpturing such as echinate or baculate is rare in gymnosperms but does occur.

Figure 5.13 (**a**) *Quercus incana*; (**b**) *Q. pumila*; (**c**) *Q. imbricaria*; (**d**) *Q. laurifolia*. (e)-(x) Surface features of pollen exines of a series of species of oak (*Quercus*, subgenus *Lepidobalanus*), as shown by SEM, magnification about 3,900x. Such sculptural differences of the exine in some instances permit identification of species or species groups in genera and of genera in families such as grasses, in which separation even of genera is difficult in light microscopy. In light microscopy the exines of oaks are usually too similar for routine separation. (**e**) *Quercus velutina*. (**f**) *Q. virginiana*. (**g**) *Q. velutina*. (**h**) *Q. palustris*. (**i**) *Q. georgiana*. (**j**) *Q. prinus*. (**k**) *Q. durandii*. (**l**) *Q. macrocarpa*. (**m**) *Q. lyrata*. (**n**) *Q. marilandica*. (**o**) *Q. bicolor*. (**p**) *Q. myrtifolia*. (**q**) *Q. ellipsoidalis*. (**r**) *Q. velutina*. (**s**) *Q. macrocarpa*. (**t**) *Q. virginiana* var. *minima*. (**u**) *Q. georgiana*. (**v**) *Q. virginiana* var. *minima*. (**w**) *Q. phellos*. (**x**) *Q. laurifolia*. Reproduced from Solomon (1983a and 1983b).

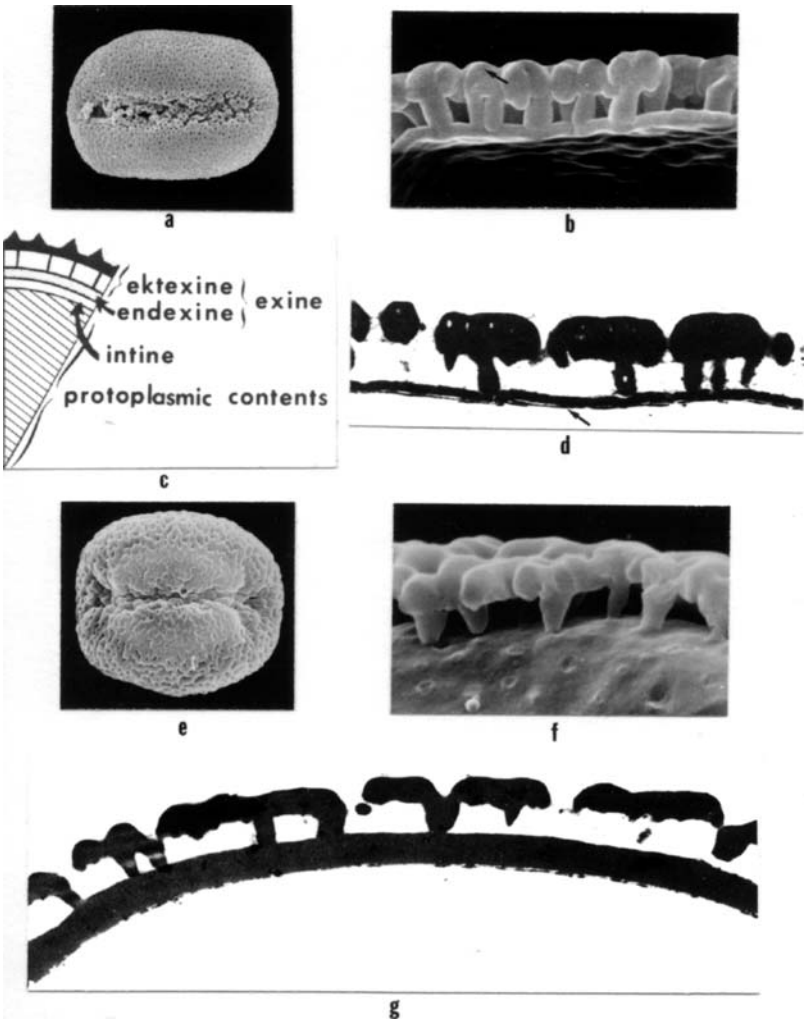


Figure 5.14 Exine structure of acetolyzed pollen, as revealed by scanning electron microscopy (SEM) and transmission electron microscopy (TEM) of two pollen grains of the Myristicaceae. (**a**) distal view SEM (2,500x) of pollen of *Virola elongata* (Benth.) Ward., showing sulcus and reticulate sculpture. (**b**) Same grain, SEM view of "cut face" of exine (16,000x), seen from the side. Compare with (c). The barrel-like columellae extend from the nexine to the outside, where the heads ("capitals") form a "roof" or, in Latin, tectum (arrow). (**c**) Diagram of section of whole pollen grain. Only the exine survives acetolysis or fossilization. (**d**) TEM of thin section of same grains as (a),(b). Arrow points to nexine (17,000x). (**e**) Distal view SEM (2,500x) of pollen of *Compsoneura capitellata* (A. Dc.) Warb., showing sulcus and rugulate-reticulate sculpture. (**f**) Same grain, "cut-face" SEM view of exine showing "piano-leg" columellae with "capitals" fused to form the

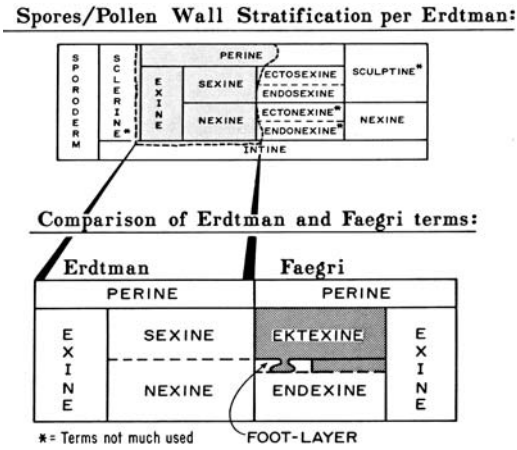


Figure 5.15 The Erdtman wall stratification classification with a comparison to the Erdtman and Faegri terms for wall stratification. In practice, only the terms in the lower diagram are much used. Note that as Erdtman's terms are purely locational, "foot layer" is only required in the Faegri classification, where the ektexine-endexine distinction is based on observed, e.g., by staining, chemically based differences. On the other hand, sexine-nexine terms do not imply that such a difference has been proven and are often therefore more in keeping with observation. The foot layer is a basal part of the ektexine, lying either on top of the endexine or interdigitating with it, as shown. If sexine-nexine terminology is used, the foot layer is best regarded as the top of the nexine. Some palynologists prefer to use "exospore" (= exosporium) and "perispore" (= Perispore) for the layers in spores similar to exine and perine for pollen. The term corresponding to intine would then be "endospore". (However this term is also used in another sense: see Glossary.)

Sacci are not hollow sacs, but have a lining consisting of a meshwork of strands; according to the definition, this is structure. In some gymnosperm pollen, e.g., commonly in the Taxodiaceae, a perine (= Perispore) occurs external to the exine, sloughing off rather easily and therefore not usually found on fossils. The perine is sporopolleninous, however.

Ferns and other non-seed-bearing embryophytes have relatively homogeneous exospores (= exines of pollen), not displaying the pronounced sculpture/structure distinction of angiosperms. However, the sculpture terms used for angiosperms can be applied without real difficulty. The most strikingly different feature of

Figure 5.14 tectum. The narrowed bases of columellae pull away from the endexine leaving depressions (16,000x). (**g**) TEM of thin section of same grain, showing same features as (f) (14,000x). (Electron micrographs courtesy of James W. and Audrey G. Walker.)

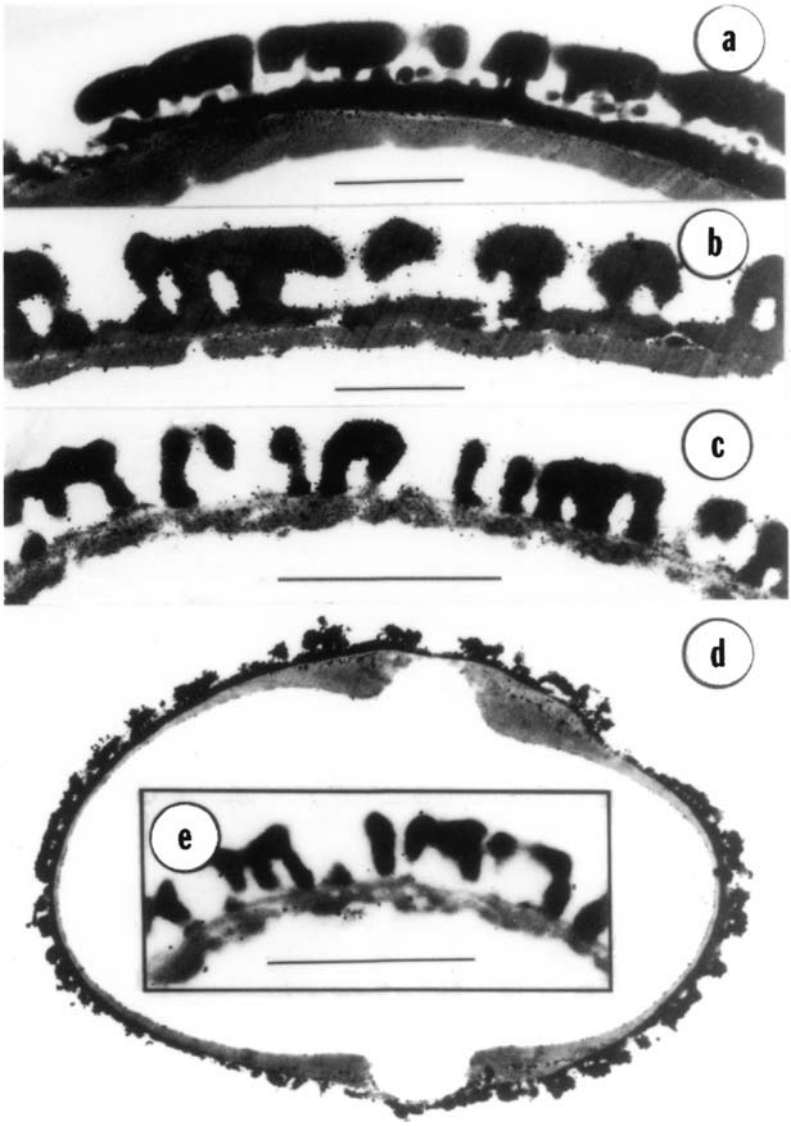


Figure 5.16 Transmission electron microscope (TEM) demonstration of structure of exine of pollen of extant Primulaceae. (**a**) *Naumbergia thyrsiflora*: thick tectum supported by reduced columellae. Note well-developed foot layer and prominent endexine (see Fig. 5.15). (**b**) *Omphalogramma vincaeflora*: columellae massive. (**c**) *Primula officinalis*: no foot layer. (**d**) *Stimpsonia chamaedryoides*: oblique section of whole grain. Note endexine thickening adjoining apertural areas. Some angiosperms have endexine only in these areas. (**e**) *Primula veris*: no foot layer. Scale lines = 1 μm. Photos courtesy of J. W. Nowicke, from Nowicke and Skvarla, 1977.

these spores is the prevalence of perispores (= perines of pollen), the outer wall layer just mentioned as present in some gymnosperm polle n. The perispore often sloughs off partially or entirely in acetolysis preparations and can be presumed to do the same during fossilization. On the other hand, some perispores are tough and adherent and survive acetolysis. The outer wall layer of some fossil spores may in fact be the perispore. The ektexine of angiosperm pollen could perhaps be regarded as a sort of perine, but this is very speculative.

6.4.2 Wall Stratification

As explained earlier, I routinely employ the terms used by Faegri in many publications (e.g., Faegri and Iversen, 1989) for the wall layers. This scheme of terminology was developed mostly for angiosperm pollen. Faegri's endexine is described as differing chemically from the ektexine, the latter containing more dense sporopollenin and staining more deeply. Stained angiosperm exines thick enough to permit observation of this feature show the two layers only at ca. 400x or more magnification. For that matter, the two layers can be seen also in unstained, acetolyzed preparations, because acetolysis affects the two layers differently. Erdtman used instead the terms sexine and nexine, purely "geographic" terms, with no clearly defined fixed boundary between them: the sexine is above and has sculptural elements, the nexine is beneath and does not. In practical palynology, it might have been better to use Erdtman's sexine and nexine because by so doing one is admitting that he/she has not necessarily observed the chemical difference between ektexine and endexine. As used by most people, the two sets of terms are more or less synonymous. A complication is that TEM work has substantiated early light microscopy suggestions that the ektexine may have "roots" that extend down into the endexine, or this lower ektexine may be a distinct layer below the columellae called the foot layer, and the Erdtman classification has no provision for this. The sexine in Erdtman's terminology cannot by definition occur below the arbitrary sexine/nexine boundary, i.e., below the structural elements. It should be noted, however, that some palynologists use "foot layer" as if it were the bottom layer of the sexine. Erdtman's terminology for wall layers also is handicapped by excess baggage. The sexine is further subdivided into a theoretical ectosexine and endosexine, and the nexine into ectonexine and endonexine, which terms are really not useful or necessary in practical palynology. As noted by Misset *et al*. (1982), the stratification in the area of apertures frequently is different from that away from them. The aperture membrane may have more of one layer than of the other, be lacking one layer entirely, or have one layer greatly modified. Erdtman's term "sporoderm" for the whole pollen wall, including perine, exine and intine, is useful. Some authors have also found it advantageous to speak of the sclerine, when they are sure a fossil wall is either exine or perine but not sure whether both are present. Fig. 5.15 shows the correspondence between the Erdtmanian terms in common usage and those of Faegri (see also Fig. 5.14).

Some palynologists carefully avoid using the "-ine" terms for spores. Instead, for spores the terms equivalent to exine and perine are exospore (= exosporium) and perispore (= perisporium). This makes some sense because it is really difficult to be sure which layer of a pollen wall is homologous to a fern spore perispore, for example. It should also be emphasized that studies of Paleozoic and Mesozoic spores, pollen, and prepollen show wall layers that are not readily homologized with extant pollen wall layers. Abadie *et al*. (1977), for example, studied exines of the medullosan prepollen *Schopfipollenites* by SEM, TEM, and light microscopy and showed the presence of four layers, which are difficult to assign to ektexine and endexine. Among modern polypodiaceous ferns it has been shown that the perispore is universally present, and this may even be true of ferns in general, including fossils, for which, however, the perispore is unlikely to be preserved (Van Uffelen, 1984; Tavera, 1982; Moy, 1986).

It has been suggested (Kress and Stone, 1982) that monocotyledonous angiosperms have no acetolysis-resistant endexine at all, or have it only in the apertural region. That is to say, monocot acetolysis-resistant exine is practically all ektexine. However (see Guedes, 1982), ektexine-endexine or sexine-nexine stratification seems general in the spores/pollen of vascular plants, based on ontogeny of the exine, and the absence of an ektexine-endexine separation where it occurs must be exceptional. The typical situation for angiosperms is for a columellate ektexine to support a superficial tectum, whereas in gymnosperms the outer exine is usually spongy (alveolar). The endexine of angiosperms is relatively homogeneous, whereas the inner exine of gymnosperms is typically laminate. A few gymnosperms and some angiosperms do not follow this pattern but have more or less granular exine structure. Taylor's (1982) study of Carboniferous medullosan seed fern prepollen (*Schopfipollenites* = the pollen of the pollen-bearing organs, *Potoniea*, and others), in comparison with extant cycad pollen, shows that the developmental stages by which the exine layers are formed are complex and can differ much from each other. Extant cycad pollen apparently produces an outer sexine layer first, and a lamellate nexine last, whereas *Potoniea* pollen apparently produced a lamellate nexine first, then a sculptured sexine. Zavada (1983) has shown that for *Zamia*, an extant cycad, sexine development begins in the tetrad phase and proceeds centripetally. This phase is followed by nexine development. All of this is quite in contrast to angiosperms, where a gametophytically controlled primexine is formed, perhaps providing a template for later sporopollenin deposition. Protosporopollenin is then deposited, a compound somewhat different from normal sporopollenin. Next, in angiosperms, the sporophytic tapetum of the anther can alter the protosporopollenin of the exine, depositing sporopollenin and depositing tapetally-derived compounds in the interstices of the exine. These compounds may be abundant and have to do with recognition and self-incompatibility. Thus, the sporophyte genome affect the function of angiosperm pollen to a greater extent than is true of gymnosperms, which at least typically lack recognition systems in the pollen exine. Mesozoic *Classopollis*

pollen was produced by coniferous plants, has complex columellate structure, may have had tapetal control as in angiosperms, and may have had recognition compounds in exine interstices, for reasons as yet not understood, as discussed by Taylor and Alvin (1984).

7 Spores/Pollen Orientation and Shape

Some special aspects of the shape and organization of spores/pollen of various groups will be dealt with later. The basic terms needed for written and oral description of spores/pollen shape and orientation are shown in Figs. 5.7, 5.10, 5.17 and 5.18. They apply only to embryophyte spores/pollen.

7.1 Spore Orientation and Polarity

Embryophyte spores are normally produced in tetrads, the end products of meiotic division. The spores normally separate, and the individual fossil spores occur in sediments as monads. The orientation of such spores is given with reference to the center of the (usually not observed) tetrad. The proximal surface of the spore is the surface that is or was toward the center of the tetrad, whereas the distal surface is away from the center. The haptotypic features, having to do with relicts of the contact between the members of the tetrad, are found on the proximal face and enable its recognition as proximal. The laesura is the main such feature. The basic laesura type is trilete, with three radii or arms. The monolete condition, which appeared much later in the fossil record and is still much less common, might be viewed as derived from the trilete condition by "loss" of radii, though such "loss" does not actually occur in ontogeny! The laesura may be complex, with thickened edges or other features such as raised lips, alongside the main ridges) of the radii. The laesura, because it is a zone of weakness, also usually subsumes the function of dehiscence of the spore for germination, and the auxiliary features of the laesura probably are mostly related to this function. The central line of a monolete laesura or of the radii of a trilete laesura is called the commisure. If a trilete spore is seen sideways, that is from a lateral view, the area including the laesura will, if ideally preserved, appear more or less tent-like, and the distal surface thus seen will be more or less rounded. In practice, fossil spores are usually collapsed and folded and are only with difficulty "restored" in one's mind to the ideal shown in Fig. 5.17. Monolete spores seen laterally are ideally the shape of a section of an orange. It is not best usage to refer to the proximal and distal surfaces of spores as "polar", because it is more precisely descriptive to speak of them as proximal or distal. It is best to reserve the adjectives "polar" and "equatorial" for tricolpate pollen and derivations thereof, where we must use these terms because it is not usually possible to determine what is proximal or distal.

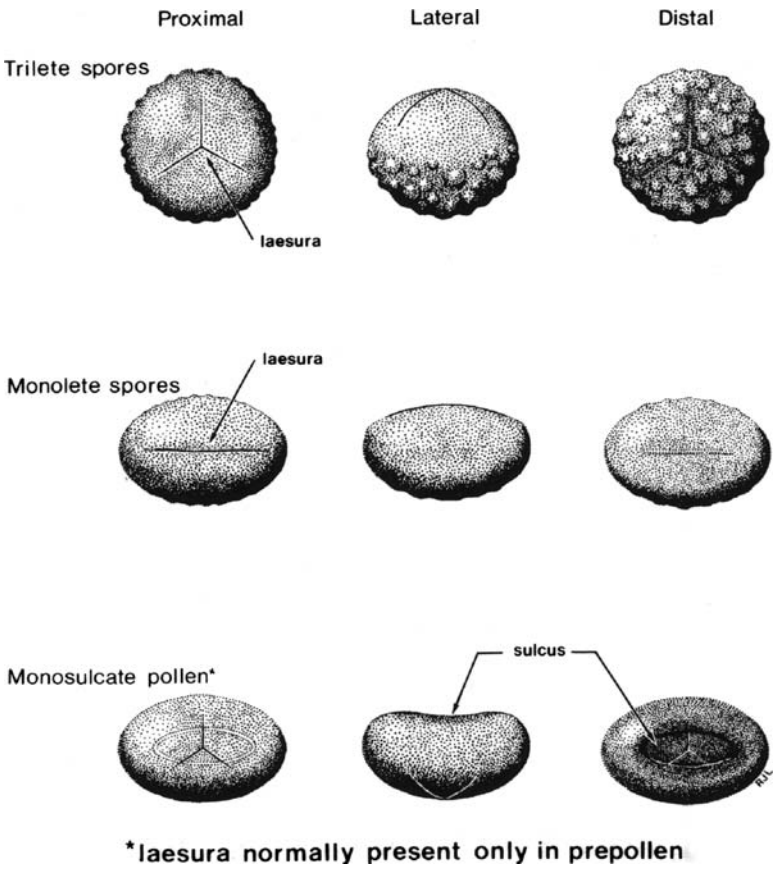


Figure 5.17 Orientation of spores and of monosulcate pollen (as well as forms obviously derived from monosulcates, such as monoporate and trichotomosulcate) is described in terms of the situation in the original tetrad. The side that was next to the center of the tetrad is the proximal side, the side away from it is the distal side. The scar on the proximal side of a spore, representing attachment to the other members of the tetrad, is the laesura, formed by intersection of the contact-faces of the spore where it was against the other three members of the tetrad. While it is accurate to call the center of the proximal and distal sides of such grains the "poles", the use of "polar view" should be reserved for angiosperm pollen, where proximal and distal cannot be determined. One should be more precise, in calling polar views either proximal or distal where that is possible (trilete spores, monosulcate pollen, etc.). Monosulcate pollen has the sulcus on the distal side. A laesura is not normally present on the proximal side of pollen except in the case of extinct, primitive fossil pollen (= "prepollen"). "Monocolpate" is often used as synonymous with monosulcate, but monocolpate is better reserved for instances where the aperture is not obviously distal. As defined by Chaloner (1970b), prepollen has *only* the proximal laesura and no other aperture, but others have shown that a laesura

7.2 Pollen Orientation

Primitive pollen from the Late Paleozoic ("prepollen") has haptotypic features like those of spores. For these prepollen grains the same observations as given under spore orientation apply. When the sulcus first appeared, it was always developed on the side away from the laesura, i.e., the distal surface, and had the function of permitting the development of a pollen tube whose function was presumably only haustorial. Germination to allow escape of the functional fecundating elements (spermatozoids) remained a function by dehiscence of the laesura on the proximal surface. With few exceptions, extant monosulcate pollen no longer bear a laesura, but the sulcus, from which the pollen tube emerges to serve both haustorial (see text associated with Fig. 8.10) and fecundative functions, remains always on the distal surface. As is true for all spores, it is also not good usage, though not incorrect, to refer to the proximal and distal faces of monosulcate pollen as "polar"–proximal and distal are more precise. Monosulcate pollen can be spoken of as heteropolar, and tricolpate pollen as typically isopolar, whereas inaperturate or multiaperturate pollen grains are usually apolar.

With the advent of the dicotyledonous angiosperms, and tricolp(or)ate and triporate pollen, a more complex situation developed. Some families, such as Ericaceae, release their pollen in tetrahedral tetrads, the typical dicot tetrad. In these instances the orientation can be observed. One pole of each grain is on the outside, directly opposite the center of the tetrad, and the other is toward the center, 180° from the other pole. These are therefore the distal and proximal poles. However, once the individual pollen grains are released from the tetrad, the typical situation at anthesis, it is no longer usually possible to tell which of the poles is proximal, which distal. Therefore, the grain is described with reference to what can be observed: the poles and the colpi and/or pores. Pollen is seldom if ever perfectly spherical, but is described as if it were (see Fig. 5.18). Views from either pole are polar. Views from the side are not usually spoken of as lateral (though this is not wrong) but equatorial. Thus "polar" can be either proximal or distal. An equatorial view is, of course, a kind of lateral view. But it is best to keep the terminology clear by using polar and equatorial only for tricolpate pollen and its derivatives. The polar amb or limb (= outline) is what is seen in an equatorial view, and an equatorial amb or limb is what is seen in a polar view! The latter is what is meant by "amb" unless otherwise specified.

Figure 5.17 and a sulcus can coexist, as would indeed be expected in the transition to distal germination. All of the forms illustrated here are models, not illustrations of actual specimens, and features shown are a combination of what would be seen by reflected and by transmitted light. However, the center of the proximal and distal surfaces can be and often are referred to as poles, and the term "equatorial" can in most cases be used without objection as synonymous with lateral.

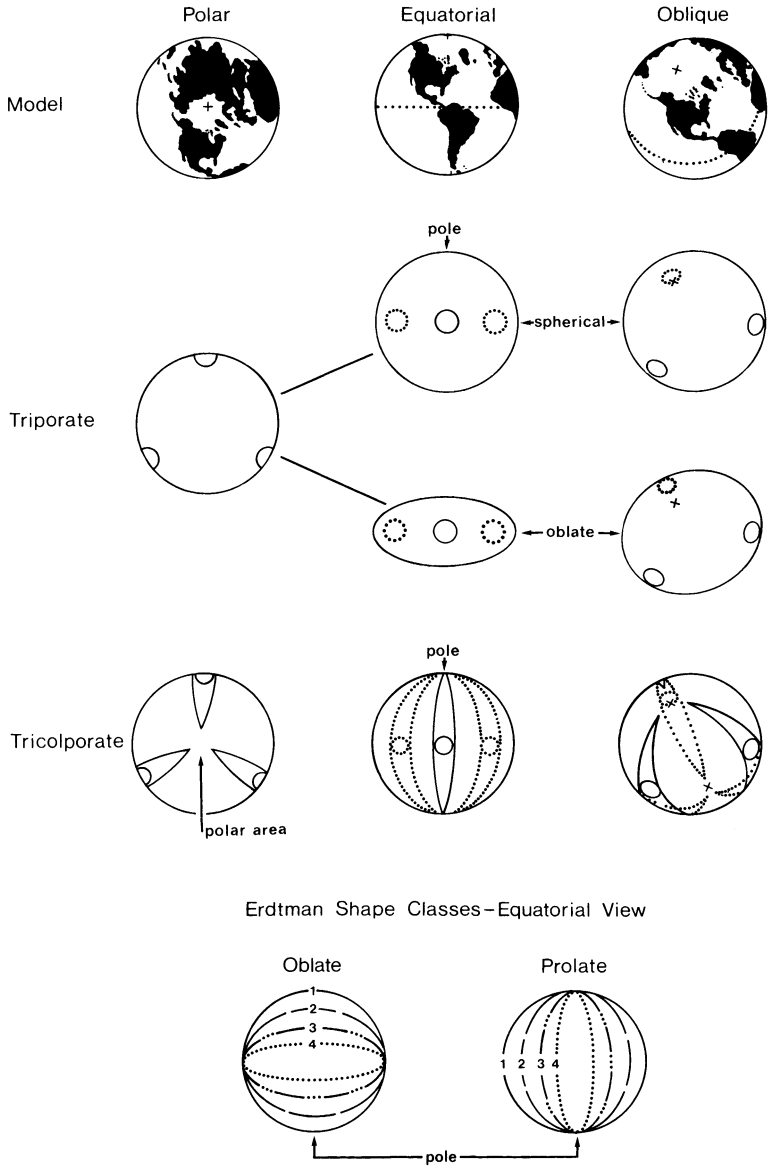


Figure 5.18 Description of the orientation of tricolporate and triporate pollen and multiaperturate forms of similar plan (4-stephanoporate, 4-stephanocolporate, for example) is a special problem because it is not usually possible to determine which part of the grain was proximal or distal with respect to the original tetrad. Instead, the proximal and distal sides are usually more or less identical. The centers of these two sides are termed "poles", and the other features are described in reference to them,

7.3 Orientation in Illustrations of Spores and Pollen

Although Erdtman tried to establish standards in orientation of illustrations he has been by no means universally followed. However, most of Erdtman's standards are sensible and should be followed for standardization. Specific comments are as follows:

7.3.1 Trilete Spores

In a proximal view, or a distal view if the laesura shows through, one radial arm of the laesura should according to Erdtman point up as shown:

In lateral views, the laesural prominence should logically (it is proximal) be down,

but few authors follow Erdtman on this. Fortunately, this is not often a problem, as proximal-distal views are overwhelmingly more often illustrated.

7.3.2 Monolete Spores

Erdtman illustrates the laesura as vertical in proximal-distal views,

Figure 5.18 e.g., an imaginary line equivalent to the Earth's equator is called the equator. The pores of a triporate (P03) grain and a tricolporate grain (Pc3), for example lie approximately on the equator by the definition used here. (If it can be shown that a three-pored grain has the pores elsewhere it is technically 3-periporate.) In a view from the pole, as of the triporate grain on the left of the figure, the equatorial rim is seen as the "amb" or "limb" outline of the grain. It is best to reserve "polar" and "equatorial" for such multiaperturate pollen, where proximal and distal cannot be determined, and to use proximal and distal wherever it is possible to know. In a monosulcate grain such as *Magnolia*, for example, the sulcus is distal. Many palynologists, however, call the center of the proximal and distal sides of such a grain "poles." In any case, the line around the grain equidistant from these "poles" *is* the equator. Erdtman's shape classes shown in the lower part of the figure are handy for describing the shape of pollen as seen in outline, when the axis of the poles is perpendicular to the line of sight. However, fossil grains are flattened like little pancakes, and oblate grains, which normally are flattened pole-to-pole can only be viewed from a pole, and strongly prolate grains can only be viewed in equatorial view, as of a tiny flattened American football. The shape classes therefore are best used only for relatively unflattened, non-fossil pollen.

and follows logic in having the laesura down (proximal!) in lateral views.

However, few authors follow Erdtman:

are much more common in the literature.

7.3.3 Monosulcate Pollen

According to Erdtman, as the sulcus is distal, one would expect that it should be up in a lateral view,

but he is very inconsistent in this. In distal views, the most common, Erdtman orients monosulcates with the sulcus vertical, as for laesurae of monolete spores.

But most authors illustrate monosulcates with sulcus parallel to top and bottom of page, whether lateral

or proximal-distal.

7.3.4 Bisaccates

As the cappula is distal it should be expected to be up

in lateral views, and it *is* in Erdtman's illustrations and in those of a few other authors, but most authors, for some reason always put the distal side (cappula) down.

In proximal-distal views, most authors show the long axis parallel to the bottom of the page.

7.3.5 Triporate, Tricolpate, Tricolporate, etc.

In polar views, Erdtman usually illustrates one pore or colpus down.

In equatorial views he shows the colpi vertical.

Without realizing it, the author of this book has always disobeyed Erdtman on polar views, showing one pore or colpus up.

I recall Erdtman berating me for publishing bisaccates "upside-down", but apparently his colpus-or pore-up dictum for P03-Pc0 didn't sink in.

It is certainly very disconcerting to illustrate spores and pollen randomly, and one should adopt a convention and stick to it. This includes drawings in laboratory notebooks of students!

7.4 Shape

The shape of angiosperm pollen is usually described with reference to the polar and equatorial dimensions. If the grain has a polar axis longer than the equatorial diameter, it is in the "prolate family," if the equatorial diameter exceeds the polar axis, the grain is in the "oblate family." In my laboratory we only use this to describe quite pronounced variants from spherical, such as prolate and perprolate. Erdtman, however, characteristically sought elegance in the matter, and his numbered shape classes are shown in Fig. 5.18.

8 Microscopic Methods and Sporomorph Morphology

Nehemiah Grew's 17th century observations of pollen morphology were made with a microscope that was hardly more than a hand lens on a small stand. The advances of spores/pollen studies have followed closely the technological advances of microscopy. Transmitted light microscopy (LM) has not changed markedly in optical characteristics for about a century (although the mechanical arrangements have become increasingly elegant), and the effective limit of magnification by this method, with a "medical style" binocular microscope, having an excellent oil immersion objective and good oculars, is about 1, 500x. At least 95% of practical palynological study is still made with such equipment. However, for study of the fine details of sculpture of palynomorphs in general and for the study of very thick-walled or otherwise more or less opaque palynomorphs, the scanning electron microscope (SEM) is a must. For the detailed study of ultrathin sections showing exine structure, the transmission electron microscope (TEM) is equally important. However, one should remember that day-to-day study is still done with the transmitted light microscope, and descriptions of palynomorphs only by SEM are not particularly helpful to the average palynologist who never, or only occasionally, uses the SEM. SEM pictures show almost exclusively the external aspects of the palynomorph (sometimes some internal structure shows on the edges of broken pieces). TEM pictures, plus SEM photos, tell one the same things that one sees with the light microscope, but more highly magnified, and with greater resolution of detail. It is possible to make preparations of fossil or recent palynomorphs for study by both electron and light microscopy. Photos of a single palynomorph from both sides using both light and SEM. microscopy can also be made. It is also possible to study palynomorphs by light, SEM and TEM, though to do so for a single specimen is something of a tour de force

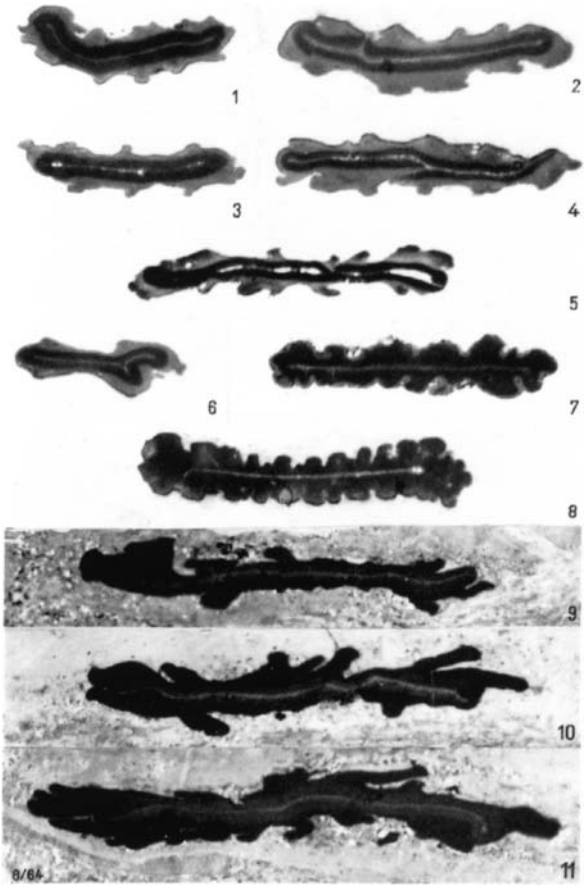


Figure 5.19 Spores in thin sections of bituminous coal, named as taxa by Stach (1964): (**1**)-(**6**) *Stratexinis ornatus*; (**7**),(**8**) *Thiessenexinis incisus*; (**9**)-(**11**) *Baculexinis raistrickii*. The two-layered nature of the exine is especially evident in (1)-(6). These taxa are undoubtedly synonyms of known dispersed spore forms. From Stach, 1964.

(Ferguson 1977; Walker and Walker, 1982)! Special light microscope attachments such as interference contrast ("Nomarski") allow detailed study, even of hyaline palynomorphs with very low contrast. An "SEM-like" effect is achieved. In some cases, fluorescence microscopy is also useful for palynomorphs of very low contrast and with very thin walls.

Although nearly all paleopalynology has been done with macerations of sediments, some studies have been done with rock thin sections, or even with polished surfaces studied by reflected light. The Green River Oil Shale (Eocene, western U.S.A.) defies ordinary maceration procedures. Thus, the famous studies

Figure 5.20 Sketch of himself playing the flute and sailing into the sunset aboard a triporate (P03) raft (betulaceous pollen), by Gunnar Erdtman, inscribed 19 Aug., 1967, on flyleaf of a book presented to John R. Rowley, by whose permission the drawing is published.

by Wodehouse (1932, 1933; see Fig. 5.1), among the earliest paleopalynological investigations, were made from thin sections. So were many of the early studies of fossil dinoflagellates by Eisenack, Deflandre and others. Dinoflagellate cysts were studied by them in thin sections of chert and flint. Many of the early investigations of spores in coal by Thiessen and others were made using coal thin sections (e.g., White and Thiessen, 1913). Thiessen, Stach, and others have even classified the spores observed in thin section and or in polished surfaces observed by reflected (incident) light. It is obviously difficult to do this, as the sectioned or polished spores are more or less two-dimensional, and one works only with an outline. Stach, a coal petrologist, specialized in the study of coal spores in thin-section and polished surfaces and even (Fig. 5.19) named species of spores based on such observations. As it is very difficult to compare these spore taxa with those based on whole, macerated spores, the use of such names is probably not desirable.

Chapter 6

Stratigraphic Palynology–Precambrian, Cambrian, Ordovician

1 Introduction

Other organizations of paleopalynological information could well be as good, but my practice in teaching the subject in stratigraphic sequence after introducing basic concepts will be followed here. The basic features of spores/pollen are included in Chapters 1–5. Beginning with this chapter we present the materials of paleopalynology systematically, including forays into the morphology, etc., of palynomorphs other than embryophyte spores and pollen, beginning with the oldest palyniferous rocks. This will be followed by chapters on biostratigraphic methods and other matters. One problem this plan presents is that we must frequently move from one aspect of palynology to another, sometimes dealing with spores/pollen matters and in the next breath switching to acritarchs, chitinozoans or dinoflagellates. However, that is the nature of the beast. As we have already noted, our subject of paleopalynology is held together not by DNA connections but by the robustness of our organic microfossils, the

nature of their occurrence in sedimentary rocks, and the mostly biostratigraphic problems they are uniquely suited to solve. The thread of continuity that links all palynomorphs is stratigraphic. A person who studies Jurassic palynology must perforce encounter not only spores and pollen, but also dinoflagellates, though the producing organisms are only slightly related. Similarly, a person who investigates Ordovician sediments will encounter scolecodonts, chitinozoans, and acritarchs in full bloom, but only the first hints of what will become later a flood of land plant spores and pollen. The oldest true palynomorphs (resistant-walled, right size-range) are acritarchs, remains of organisms we presume to have been algae, flagellate and/or protist-related, which first appear in the Late Precambrian.

2 Acritarchs and Other Phytoplankton of Precambrian–Ordovician

The first robust-walled acritarchs appear in late Proterozoic rocks about l.4 billion years old, although reports of forms more than 0.9 billion years old are rare (Vidal and Knoll, 1983; Martin, 1993). The early forms seem to be linked with the appearance of eucaryotic organisms, including probable green algae, and oxygen levels in the atmosphere sufficient to terminate the dominance of reducing environments. Although microfossils are reported from rocks as old as 3.4 billion years (see Fig. 6.1), these are moneran remains, representative of the only kingdom of organisms which does not produce true palynomorphs. The non-sporopolleninous spheres and filaments are not within the purview of paleopalynology, because the walls are not resistant enough to survive maceration.

Stromatolites also extend back in the fossil record about as far as the evidence for sedimentary rocks, but they were not abundant until about 2.5 billion years ago (Schopf, 1977). These stromatolitic rock structures were surely the product of mat-forming monerans, and they seem homologous with blue-green algal stromatolites of present-day Shark's Bay, Western Australia. Cyanobacteria-linked stromatolites thus range from the early Precambrian to the present, but their heyday was the late Precambrian and earliest Paleozoic, before O_2 levels in the atmosphere reached l0% of present levels ("PAL").

It is probable that most sporopolleninous acritarchs, beginning with the oldest occurrences, represent reproductive cysts of green algae, and that they establish a probable phylogenetic link between the green algae and other green plants. Some, however, may represent ancestral flagellate organisms. Actually, the definition of acritarch is so general that inevitably the total is something of a "grab bag," including, e.g., both marine and non-marine forms. Originally palynologists called all such things "hystrichosphaerids" (or even, informally, "hystrix"!). The name means "spiny spheres", but non-spiny bodies were always also included in the group. Evitt (1961, 1963) showed later from morphological studies, and Wall (1965) and Wall and Dale (1967) proved by culture of living forms, that many

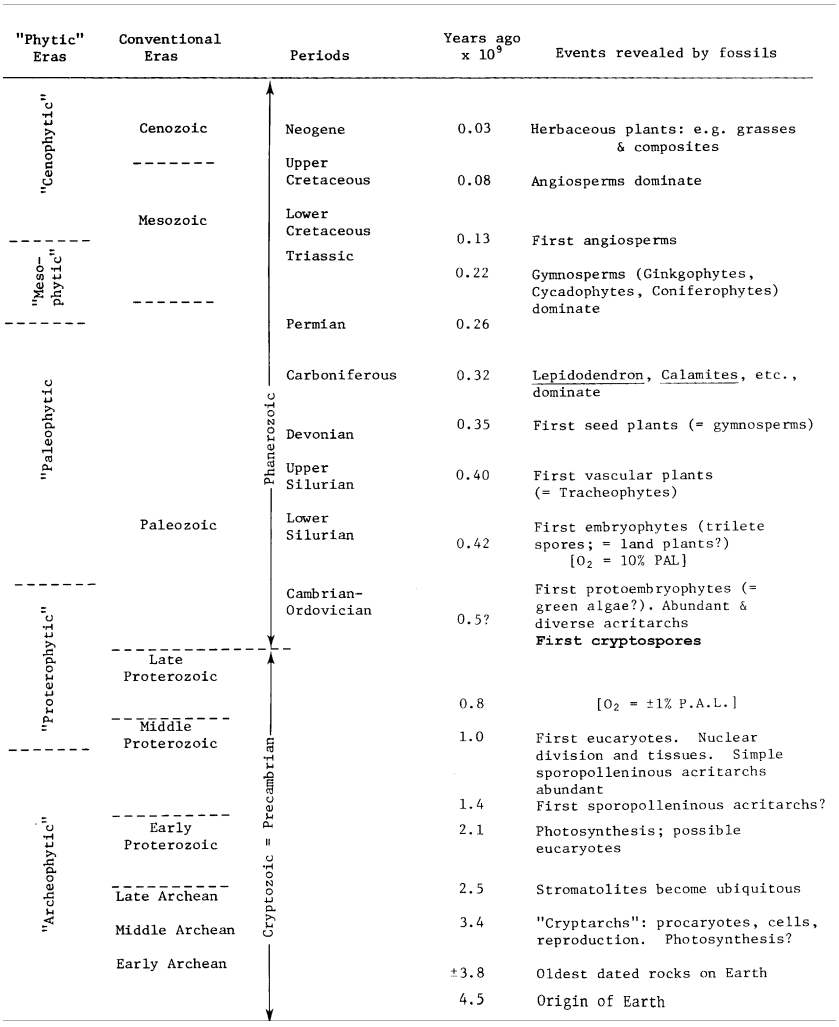


Figure 6.1 High points in plant evolution, as related to paleopalynology. Compiled from various sources. Compare with time chart, Fig. 2.1. Period and time information incomplete and not to scale here. The "phytic" eras, based on events in plant evolution, are discussed at various places in the text–see Index.

Mesozoic "hystrichosphaerids" were in fact dinoflagellate cysts. Evitt proposed "acritarch" (Greek *akritos* = undecided; *arche* = origin) for all of the hystrichosphaerids which could not be shown to be dinoflagellates. This was taken up, and "hystrichosphaerid" was dropped. As used by most palynologists, "acritarchs" are mostly marine green algal cysts, possessing extremely varied form. Some former

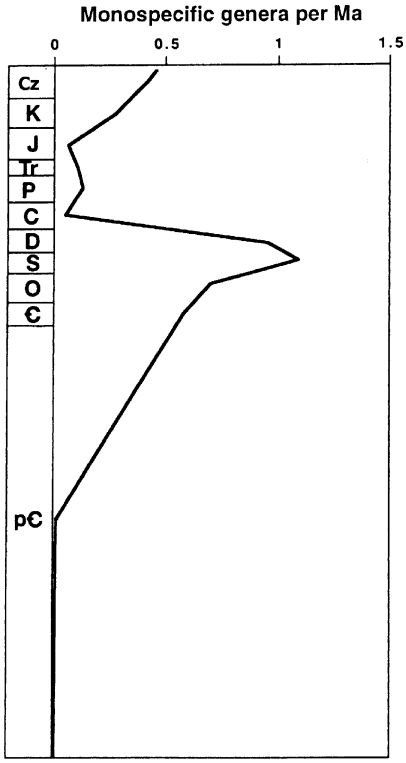


Figure 6.2 Acritarch species diversity from Proterozoic (Late Precambrian) to Cenozoic (Cz). Letters on the left refer to geologic eras and periods Precambrian through Cenozoic. The curve expresses species per Ma plotted per period of time. The latest Devonian acritarch crash is very obvious. Modified from Strother, 1996.

acritarchs have been removed from Acritarcha and referred to particular groups of algae.

Tasmanites, Tytthodiscus, various species of *Leiosphaeridia*, and other forms previously referred to the acritarchs, for example, have been referred to division Prasinophyta of the green algae (Tappan, 1980; Guy-Ohlson, 1996), and are thus no longer classifiable as acritarchs. Similarly, many items formerly called acritarchs are now known to belong to the Zygnemataceae of the green algae (cf. Grenfell, 1995; van Geel and Grenfell, 1996; Fig. 6.6 here). Some have suggested probable dinoflagellate relationships for other groups of Paleozoic acritarchs, based mostly on archeopyle-like openings (cf. Colbath and Grenfell, 1995, for treatment of this subject). However, all of these microfossils represent (mostly marine) algae or photosynthetic protists, and in my opinion it remains logical to think of these fossils as a unit: the term *phytoplankton* fits. In addition to

the treatments of acritarchs cited in the general bibliography in Chapter 1, q.v., persons interested in getting a grasp of this complex group of palynomorphs would also do well to consult the important summary articles of Martin (1993), Molyneux *et al.* (1996), and Strother (1996).

Sporopolleninous ("robust-walled") acritarchs did not become abundant until less than 1 billion (10^9) years ago (Horodyski, 1980). The oldest acritarchs are simple spheres, usually much folded and carbonized. The late Precambrian (= Proterozoic) acritarchs sometimes display a simple opening mechanism ("median split"), a linear rupture, and some of them are enclosed in sheaths. Low diversity assemblages of these Proterozoic acritarchs seem to indicate coastal environments, whereas higher diversity floras indicate more open-shelf situations (Vidal and Knoll, 1983). In the Lower Vendian (latest Proterozoic), acritarchs with processes became common, polygonomorphic forms and double-walled forms appear, but mid-Vendian glaciations are correlated with a depauperation of this flora, and the terminal Precambrian flora is dominated again by simple sphaeromorphs, evidence of the earliest known episode of large-scale extinction (Vidal and Knoll, l983).

Acritarchs were much diversified by the earliest Paleozoic (post-Precambrian = Phanerozoic). A great variety of sculptural and structural complexity of acritarchs comes in during Cambrian time and reaches especially diverse development in the Ordovician. Fig. 6.3 illustrates a variety of Precambrian and early Paleozoic acritarch and prasinophyte algal forms. Plates 6.1 and 6.2 show many Cambrian-Ordovician and Ordovician species of acritarchs.

The usefulness of acritarchs in practical stratigraphy is now well established. Moczydlowska and Stockfors (2004), for example, demonstrate the applicability of acritarch stratigraphy to establishing the Cambrian/Ordovician system boundary in Arctic Russia. As pointed out by Servais *et al.* (2004), the group has a very promising future in biostratigraphic work in the early Paleozoic, even though there is pronounced provincialism in the acritarch palynofloras. Recent studies include the profusely illustrated work of Parsons and Anderson (2000), which provides a Cambrian/Ordovician stratigraphic succession for a part of eastern Canada, and compares it to coeval sequences from eastern Europe, and the research of Vanguestaine *et al.* (2002), which does a similar job in Ireland. It is evident from the bibliographies in these and other similar recent studies, how extensive the reach of such work is becoming.

Provincialism in geographic distribution of acritarchs also bespeaks ecological sensitivity that also suggests potential usefulness for sequence stratigraphic studies and basin analysis in general, as well as in palynofacies research. Staplin (cf. Staplin, 1961) was a pioneer in demonstrating the existence of what I call palynobiofacies for Devonian acritarchs of Alberta–certain acritarch forms are associated with sediments away from reefs, others are more typical of sediments occurring near reefs. This was of economic importance because of the role of Devonian reefs

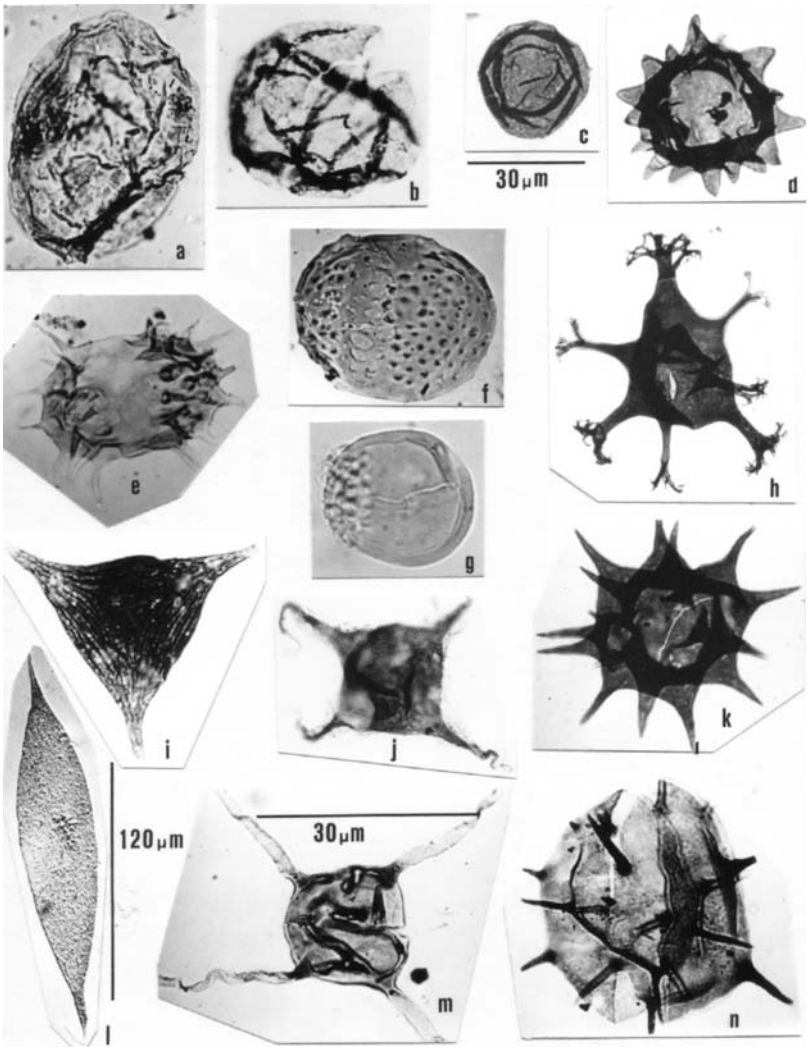


Figure 6.3 Precambrian and early Paleozoic acritarchs/prasinophyte algal phycomata of various forms. Those in (a-c) and (g) are sphaeromorphs, (f) is a diacrodioid, and (g) is an oömorph. All others, in a broad sense, are acanthomorphs. (R. Wicander, pers. comm. 2005, a leading acritarch authority, regards (a-c) as prasinophyte algae phycomata and hence not acritarchs *sensu stricto.*) Bars below (c) and next to (l) indicate approximate magnification for those individual photomicrographs. Bar above (m) indicates approximate magnification for all other photos. (**a**) *Protoleiosphaeridium* sp. (= *Leiosphaeridia* sp.), late Precambrian, former USSR. (**b**) *Trachysphaeridium* sp., late Precambrian (0.8 billion years), Greenland. (**c**) *Kildinella* sp. (= *Leiosphaeridia* sp.), late Precambrian, former USSR. (**d**) *Micrhystridium* sp., Lower Ordovician (Arenig), Morocco

as petroleum reservoirs. Montenari and Leppig (2003) have made some important analytical comments and illustrations on Paleozoic acritarch paleoecology.

The diversity crash at the end of the Devonian (see Fig. 6.2) unfortunately means that the group is only modestly useful in studies of Carboniferous and Permian rocks. Post-Devonian acritarchs are well known and occasionally are abundant in marine rocks. However, they are not any longer a diverse group. The Permian and Triassic were barren times for acritarchs, and in the Jurassic they are replaced ecologically by the dinoflagellates. It is not surprising that systematic schemes for classifying acritarchs were mostly developed from studies of Paleozoic forms.

The "purpose" of the sporopollenin-like shell of acritarchs is intriguing. It may have been an ultraviolet light shield for the reproductive contents, which are less resistant to ultraviolet light than the rest of the life cycle. On the other hand, this would be a little strange, as sporopolleninous acritarchs became abundant just as the O_2 level of the atmosphere became high enough to screen out ultraviolet. More likely, these outer shells developed to protect the contents from oxidation, and from the ravages of oxygen-using bacteria and fungi, which became abundant about the same time.

The "sporopollenin" of the wall is very likely a member of the same family of substances as in the walls of spores, pollen, and dinoflagellate cysts, but this has not really been proven. (cf. Colbath and Grenfell, 1995, for a discussion of this matter.) In any event, acritarch sporopollenin seems in some of the forms to have been very tough: Montenari and Servais (2000) found some that were identifiable, albeit in very battered condition, in metamorphosed sedimentary rock of Late Cambrian or Early Ordovician age.

2.1 Morphology of Acritarchs

Plates 6.1 and 6.2 and Figs. 6.3, 6.8 and 6.9 illustrate various basic Paleozoic acritarch forms. The wall may be simple or complex. The shape of acritarchs is very diverse, and there are a great variety of appendages and sculpturing features. (See Fig. 6.5)

Figure 6.3 (**e**) *Acanthodiacrodium* sp., lowest Ordovician (Tremadoc), former USSR. (**f**) *Lophodiacrodium* sp., lowest Ordovician (Tremadoc), former USSR (**g**) *Ooidium* sp., lowest Ordovician (Tremadoc), former USSR. (**h**) *Vogtlandia* sp., Lower Ordovician (Arenig), Morocco. (**i**) *Arkonia* sp., Lower Ordovician (Arenig), Morocco. (**j**) *Aureotesta* sp., Lower Ordovician (Arenig), Morocco. (**k**) *Polygonium* sp., Lower Ordovician (Arenig), Morocco. (**l**) *Cleithronetrum* sp., Bromide Fm., Middle Ordovician, Oklahoma. (**m**) *Orthosphaeridium* sp., Upper Ordovician (Caradoc), England. (**n**)*Gorgonisphaeridium* sp., Maquoketa Fm., Upper Ordovician, Missouri. Photomicrograph (b) courtesy of Paul K. Strother, all others courtesy of Charles Downie.

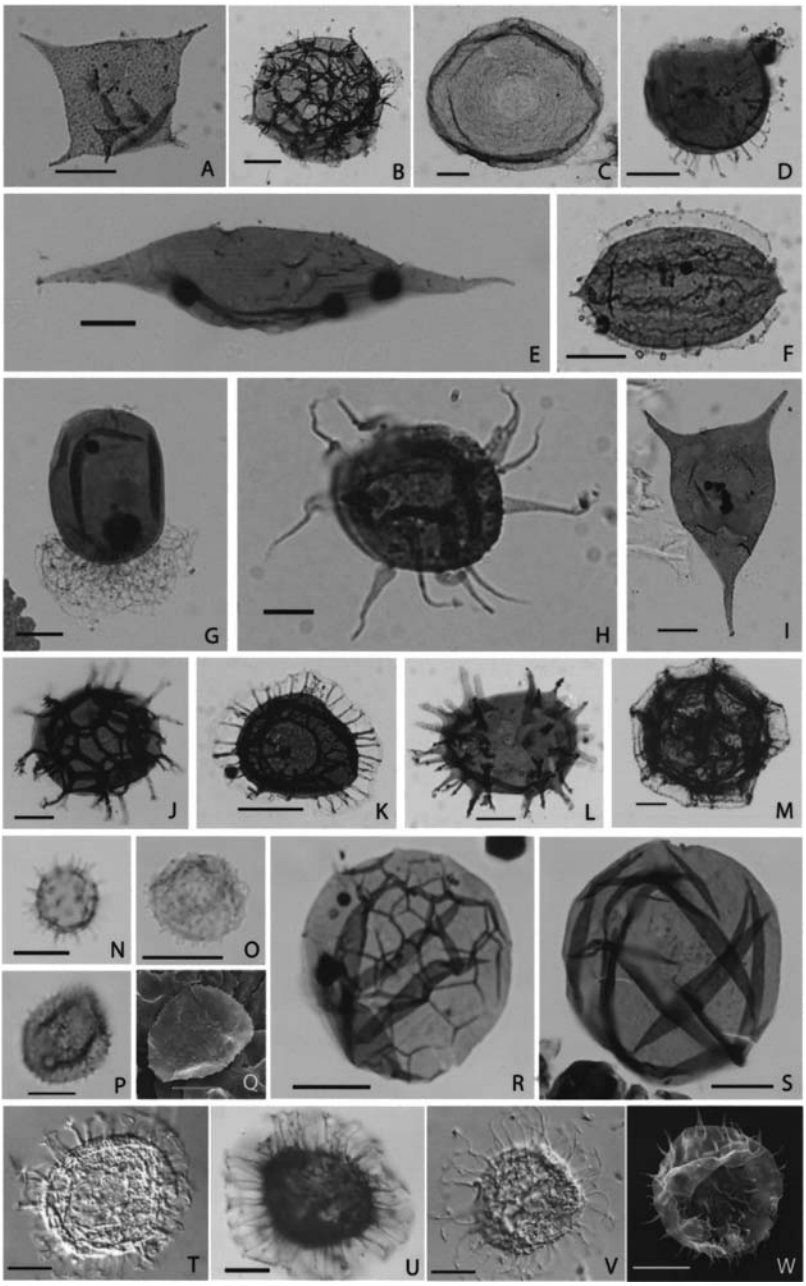


Plate 6.1

Based on the shape and the appendage/sculpturing style, a number of artificial morphological categories have been suggested for classification. Some of the more important of these groupings are described below (cf. Cramer and Diez, 1979; Downie, 1979; Martin, 1993; Molyneux *et al.*, 1996; Strother, 1996).

2.1.1 Sphaeromorphs (Sphaeromorphitae)

(See Figs. 6.3 and 6.8) As the name implies, these are mostly more or less spherical. Often, if the walls are thin, these are collapsed and folded, the folds simulating morphological features (which even have been interpreted by the unwary as laesurae). The walls may be psilate, scabrate, verrucate, rugulate, fossulate, but not truly spinous (echinate). *Leiosphaeridia* and relatives (Precambrian to present), *Tasmanites* and relatives, early Paleozoic to present, would have been listed under this heading until it became certain that they are remains of prasinophyte algae, and thus not acritarchs. (cf. Fig. 13.19 and associated text.) According to Guy-Ohlson (1996), the former acritarch genera illustrated in

Plate 6.1 Cambrian/Ordovician acritarchs from various locations. The scale bar for all images represents 10 μm, except for Q, in which case the bar is 5 μm. **A**. *Villosacapsula foraminifera* (Pittau) Tongiorgi *et al.*, Lower Ordovician, Oman; **B**. *Vulcanisphaera africana* Deunff, Lower Ordovician, Oman; **C**. *Saharidia fragilis* (Downie) Combaz, Lower Ordovician, Oman; **D**. *Cymatiogalea cristata* (Downie) Rauscher, Lower Ordovician, Oman; **E**. *Eupoikilofusa squama* (Deunff) Eisenack *et al.*, Lower Ordovician, Oman **F**. *Dactylofusa velifera* Cocchio, Lower Ordovician, Oman; **G**. *Ooidium*? *clavigerum* Parsons & Anderson, Upper Cambrian, Oman; **H**. Ferromia cf. *pellita* (Martin) Martin, Lower Ordovician, Oman; **I**. *Veryhachium dumontii* Vanguestaine, Upper Cambrian, Oman; **J**. *Timofeevia phosphoritica*Vanguestaine , Upper Cambrian, Oman; **K**. *Cymatiogalea velifera* (Downie) Martin, Lower Ordovician, Oman; **L**. *Acanthodiacrodium*? aff. *dilatum* Molyneux, Lower Ordovician, Oman; **M**. *Cymatiosphaera* sp., Lower Ordovician, Oman; **N**. *Celtiberium*?, Middle Cambrian (*Ehmaniella* zone), eastern Tennessee, USA; **O**. *Asteridium pallidum* (Volkova) Moczylowska, Upper Cambrian, Nolichucky Shale (*Crepicephalus-Cedaria* zone), eastern Tennessee, USA; **P**. *Asteridium*?, Middle Cambrian (*Ehmaniella* zone), eastern Tennessee, USA; **Q**. *Revinotesta microspinosa* Vanguestaine, Rogersville Shale, Middle Cambrian (*Ehmaniella* zone) eastern Tennessee, USA; **R**. *Retisphaeridium dichamerum* Staplin *et al.,* Middle Cambrian, Rutledge Limestone (*Glossopleura* zone), eastern Tennessee, USA; **S**. *Leiosphaeridia* sp., Middle Cambrian, Rogersville Shale (*Ehmaniella* zone), eastern Tennessee, USA; **T**. *Skiagia pura* Moczydlowska, Lower Cambrian, Estonia; **U**. *Skiagia scottica* Downie, Lower Cambrian, Poland; **V**. *Skiagia ornata* (Volkova) Downie, Lower Cambrian, Estonia; **W**. *Globosphaeridium cerinum*(Volkova) Moczydlowska , Lower Cambrian, Estonia. Plate prepared for the author by Paul K. Strother. A-M provided by S. G. Molyneux, N-S from Strother, T-V courtesy of M. Moczydlowska-Vidal. C and J previously published in Molyneux *et al.*, 2006, and appear here by courtesy of *GeoArabia*.

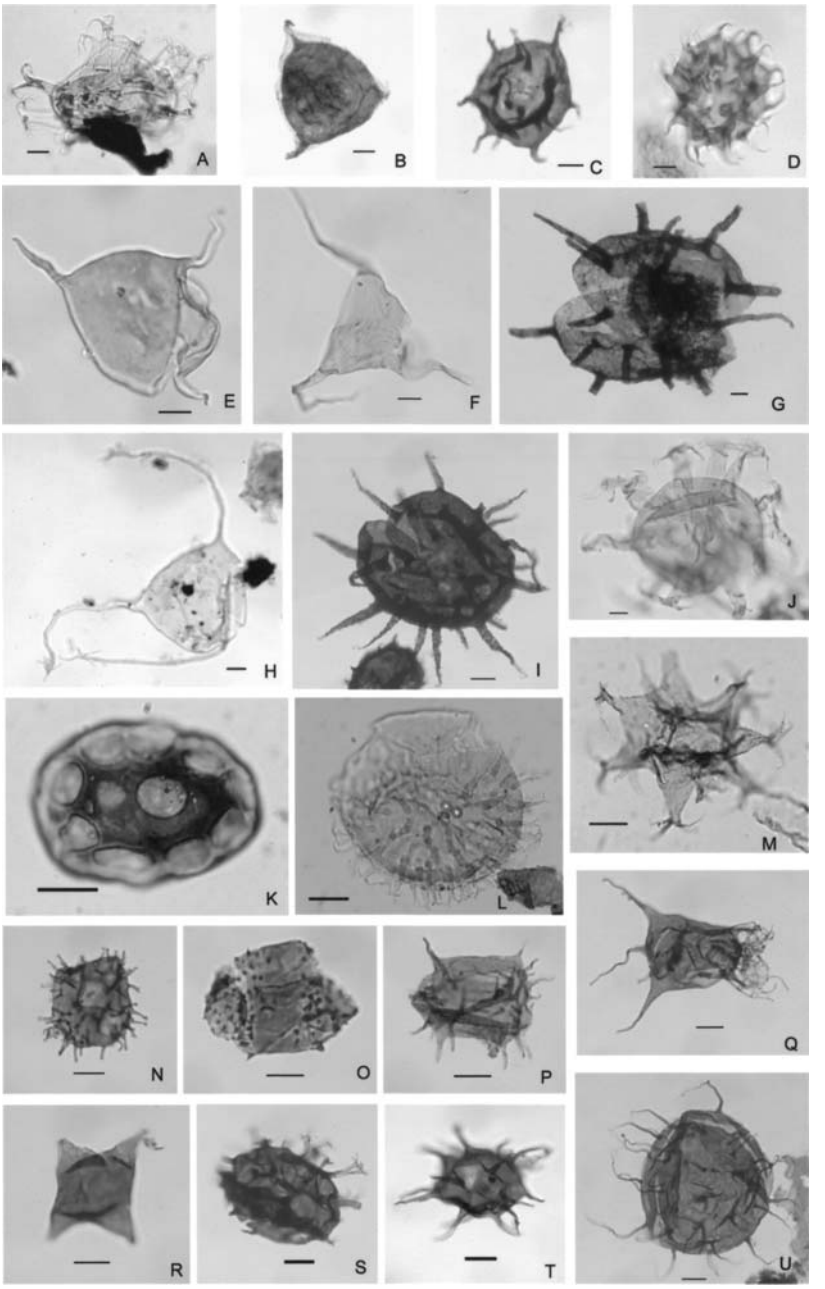


Plate 6.2

this book that belong to the Prasinophyceae are *Cymatiosphaera, Leiospheridia (sensu lato), Pterospermella, Tasmanites.*

Pictured below in Fig. 6.4 are palynologists who have made landmark contributions to the practical use of (mostly Paleozoic) acritarchs for palynostratigraphy.

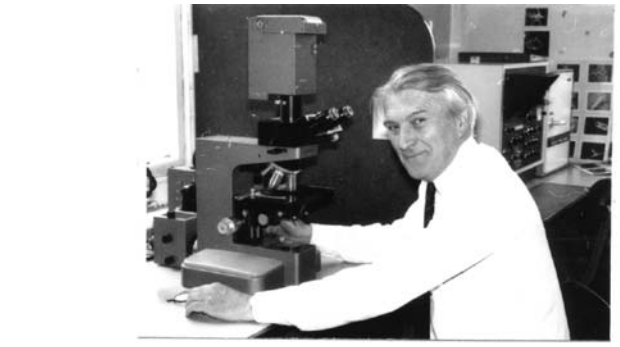
2.1.2 Acanthomorphs (Acanthomorphitae)

(See Fig. 6.8) Main body is essentially spherical, with processes, from simple spines and baculae to complex branched processes. Some acritarch palynologists use the term "sculpture" for elements less than 5 μm long, "processes" for larger elements. Inner central body may be present. Possible germinal openings (not accidental slits) may be present. Sub-units (per Cramer and Diez, 1979) are as follows:

2.1.2.1 Acanthomorphs-proper. Outline regular. Process distribution (symmetry) regular. Examples: *Baltisphaeridium, Micrhystridium, Multiplicisphaeridium.*

◄

Plate 6.2 Ordovician acritarchs from various locations. The scale bar for all of the photomicrographs is 10 μm. **A**. *Ordovicidium elegantulum* Tappan & Loeblich, Upper Ordovican, Oman; **B**. *Villosacapsula* sp., Kosov Fm., Ashgillian, Upper Ordovician, Prague Basin, Czech Republic; **C**. *Timofeevia* sp., Kosov Fm., Ashgillian, Upper Ordovician, Prague Basin, Czech Republic; **D**. *Gorgonisphaeridium* sp., Harnage Shales, Caradocian, England; **E**. *Veryhachium* sp., Harnage Shales, Caradocian, England; **F**. *Arkonia tenuata* Burmann, Harnage Shales, Caradocian, England; **G**. *Baltisphaeridium* sp. Kosov Fm., Ashgillian, Prague Basin, Czech Republic; **H**. *Frankea longiuscula* Burmann, Hanadir Formation, Middle Ordovician, Saudi Arabia; **I**. *Baltisphaeridium klabavense* (Vavrdová) Kjellström , Klabava Fm., Lower Ordovician, Prague Basin, Czech Republic; **J**. *Ordovicidium* sp., Harnage Shales, Caradocian, England; **K** . *Clypeolus*? sp., Middle Ordovician, Oman; **L**. *Stelliferidium* sp., Middle Ordovician, Oman; **M**. *Vogtlandia flosmaris* (Deunff) Molyneux, Middle Ordovician, Oman; **N**. *Coryphidium bohemicum* Vavrdová, Klabava Fm., Lower Ordovician, Prague Basin, Czech Republic; **O**. *Lophodiacrodium* sp., Klabava Fm., Lower Ordovician, Prague Basin, Czech Republic; **P**. *Timofeevia martae* (Cramer & Diez) Fensome *et al.,* Klabava Fm., Lower Ordovician, Prague Basin, Czech Republic; **Q**. *Arbusculidium filamentosum* (Vavrdová) Vavrdová, Klabava Fm., Lower Ordovician, Prague Basin, Czech Republic; **R**. *Striatotheca quieta* (Martin) Rauscher, Klabava Fm., Lower Ordovician, Prague Basin, Czech Republic; **S**. *Vogtlandia flosmaris* (Deunff) Molyneux, Middle Ordovician, Oman; **T**. *Polygonium gracile* Vavrdová, Klabava Fm., Lower Ordovician, Prague Basin, Czech Republic; **U**. *Solisphaeridium* sp., Klabava Fm., Lower Ordovician, Prague Basin, Czech Republic.Plate prepared for the author by P. K. Strother. A, K-M, and S courtresy of S. G. Molyneux; B-G, I, J, N-R are photomicrographs taken by Strother from samples provided by M. Vavrdová and processed by J. H. Beck. H is a photomicrograph by Strother of a microslide from S. Al-Hajri. K and L were previously published by Molyneux *et al.*, 2006, and appear here by permission of *GeoArabia*.



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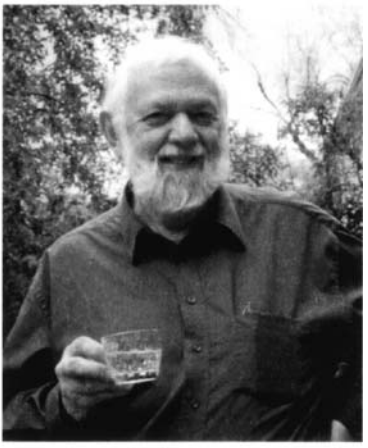

c

Figure 6.4 Pioneers in the study of paleostratigraphic applications of acritarchs. (**a**) Charles Downie, (1923–1999) Sheffield, England. Downie's publications have demonstrated the utility of acritarch studies in unraveling the stratigraphy of otherwise difficult sequences (see Downie, 1979). He also has contributed greatly to the systematics of these microfossils (see biographical notes in Sarjeant 1984). (**b**) Fritz H. Cramer and Maria del Carmen R. ("Carmina") Diez. This husband (more or less Dutch) and wife (Spanish) paleopalynological team comprise one of the more fascinating stories in the field. It is difficult to be sure where legend ends and biography begins, and nobody as yet has attempted to do so in print. However, the Cramer-Diez team has, despite many vicissitudes, made great contributions to various aspects of paleopalynology, especially to acritarch studies. Their descriptive and cataloging work has been especially valuable (see Cramer and Diez, 1979; Eisenack *et al.*, 1973–). (**c**) William A. S. Sarjeant, 1935–2002, originally British, long associated with the University of Saskatchewan, Canada. He made many original contributions to various aspects of palynology, but was especially prominent in acritarch studies. Also known as an expert on animal ichnofossils and an author of fiction! The photo is from the service card at his funeral, courtesy of Jan Jansonius.

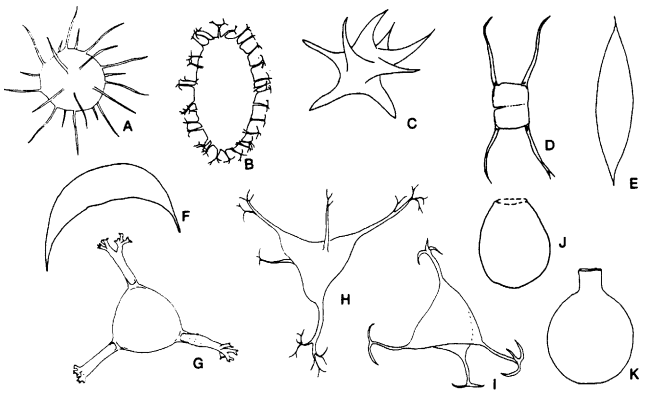

Figure 6.5 Basic acritarch shapes. **A**. Spheroidal; **B**. Ellipsoidal; **C**. Stellate; **D**. Rectangular; **E**. Fusiform; **F**. Crescentic; **G**. Triapsidate; **H**. Triquitrate; **I**. Tetrahedral; **J**. Ovoid; **K**. Flask-shaped. From Strother, 1996.

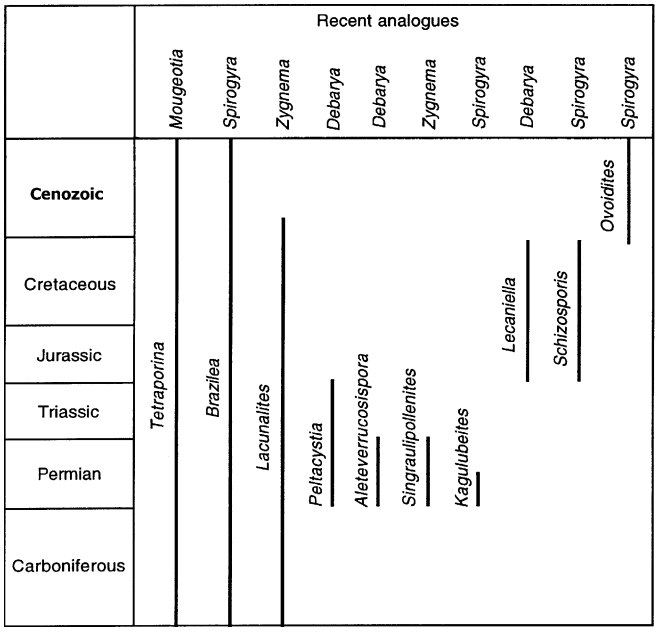

Figure 6.6 Approximate stratigraphic ranges of zygnematacean fossil genera. Modified from van Geel and Grenfell, 1996.

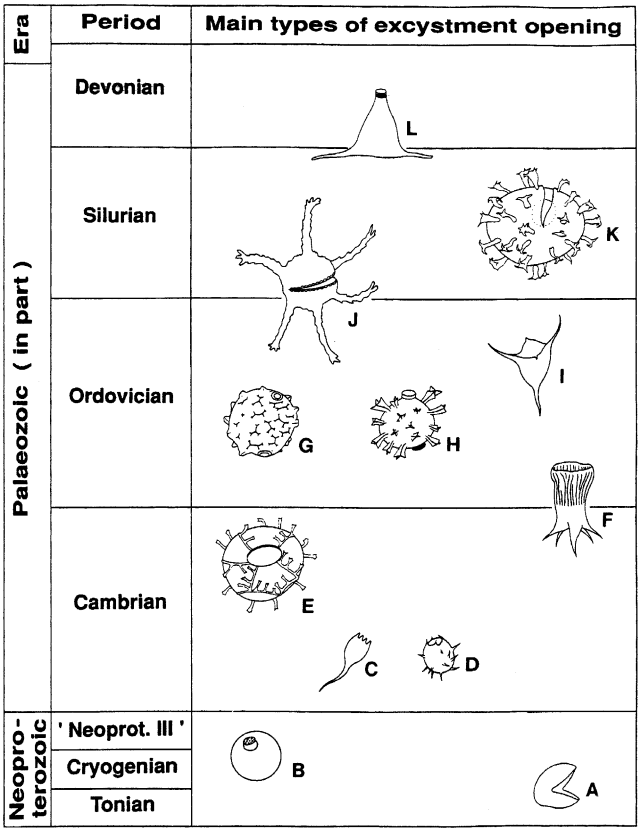

Figure 6.7 Main types of excystment structures shown in order of stratigraphic appearance. **A**. Sphaeromorph with median split. **B**. Sphaeromorph with pylome and operculum-like structure. **C**. *Volkovia* with a munium. **D**. *Revinotesta* with munitium. **E**. *Cymatiogalea* with pylome and operculum. **F**. *Corallasphaeridium* with flared circular opening. **G**. *Asketopalla* with two pylomes. **H**. *Polyancistrodorus* with pylome and pseudopylome. **I**. *Veryhachium* with epityche. **J**. *Diexallophasis* with lateral rupture that has ornamented borders. **K**. *Visbysphaera* with simple lateral rupture. **L**. *Onondagaella* with epibystra. From Playford, 2003, modified from Martin, 1993.

2.1.2.2 Netromorphs Outline fusiform. Example: *Leiofusa*.

2.1.2.3 Diacromorphs (Diacromorphitae) Outline bipolar. Processes may be distributed similarly or dissimilarly on the two poles. Example: *Acanthodiacrodium*.

Zygnemataceae forms such as *Mougeotia (*=fossil genus *Tetraporina*), illustrated in Fig. 1.1, would have been called sphaeromorph acritarchs until

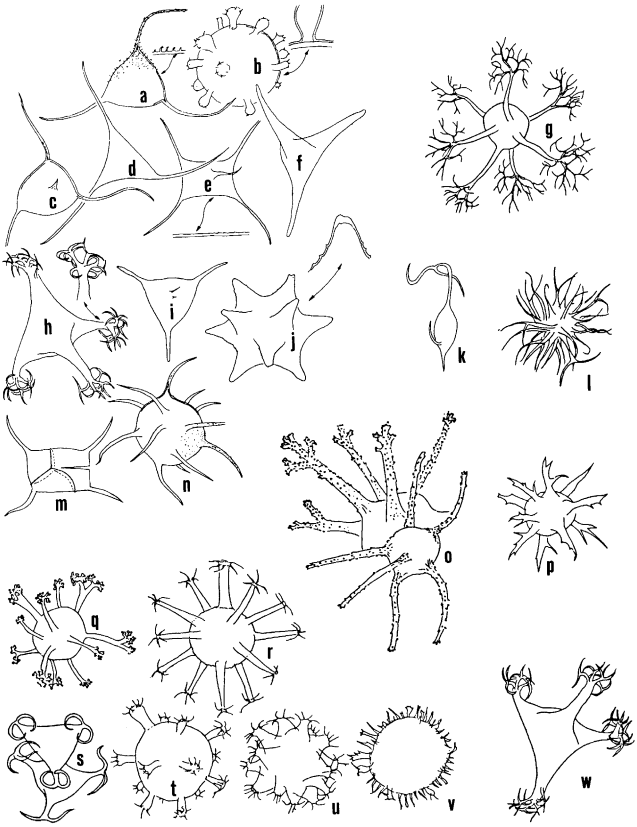

Figure 6.8 Diagrams of various acanthomorphic (in a broad sense) form-genera of Lower Paleozoic acritarchs. Magnifications vary greatly. Compare with Fig. 6.3 for approximate scale. (**a**) *Villosacapsula*. (**b**) *Visbysphaera*. (**c**)-(**f**) *Veryhachium*. (**g**) *Multiplicisphaeridium* (see (o)-(w). (**h**) *Vogtlandia*. (**i**) *Wilsonastrum*. (**j**) *Cordobesia*. (**k**) *Downiea*. (**l**) *Multiplicisphaeridium* (see (o)-(w). (**m**) *Winwaloeusia*. (**n**) *Crassisphaeridium*. (**o**)-(**w**) *Multiplicisphaeridium* (see also (g) and (l)). All drawings are from Cramer and Diez, 1979.

recognized as belonging to the extant family. Zygnemataceae microfossil forms range from Carboniferous to Holocene. (See Fig. 6.6)

2.1.3 Various Other Acritarchs (Neither Acanthomorphs Nor Sphaeromorphs)

(See Fig. 6.9) A wide variety of unusually constructed or ornamented forms, such as the "fenestrate" *Cymatiosphaera*, the double-sleeved *Riculasphaera*, Herkomorphs (Herkomorphitae)–more or less spherical bodies with surface divided into

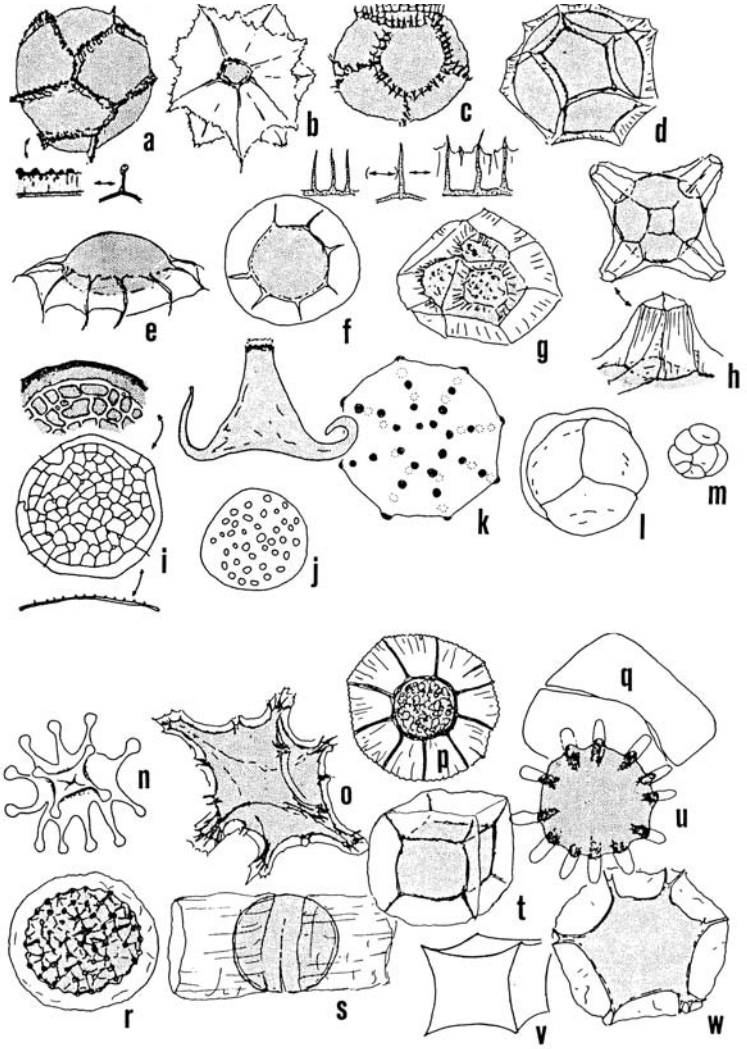

Figure 6.9 Diagrams of various form-genera of Lower Paleozoic acritarchs/prasinophyte phycomata, other than sphaeromorphs or acanthomorphs. Magnifications vary greatly–for approximate scale, compare with Figs. 6.4 and 6.7. (R. Wicander, personal communication, 2005, a leading authority on acritarchs, regards (d)-(g), (o)-(p) and (w) as prasinophyte algal phycomata, and hence not acritarchs, *sensu stricto*.) (**a**) *Cristallinium*. (**b**) *Conradidium*. (**c**) *Cymatiogalea*. (**d**) *Cymatiosphaera*. (**e**), (**f**) *Duvernaysphaera*. (**g**) *Muraticarea*. (**h**) *Daillydium*. (**i**) *Ovnia*. (**j**) *Perforella*. (**k**) *Pardaminella*. (**l**), (**m**) *Polyedrosphaeridium*. (**n**) *Polyplanifer*. (**o**) *Polyedryxium*. (**p**) *Pterospermella*. (**q**) *Pulvinomorpha*. (**r**) *Pterotosphaerula*. (**s**) *Riculasphaera*. (**t**) *Senzeillea*. (**u**) *Tornacia*. (**v**) *Staplinium*. (**w**) *Veliferites*. All drawings are from Cramer and Diez, 1979.

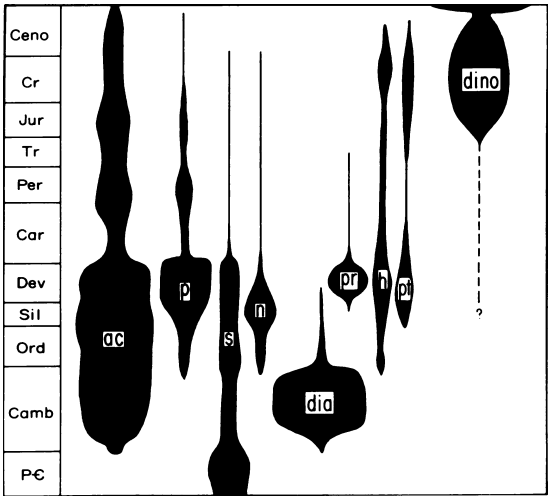

Figure 6.10 Geological range of principal acritarch groups, and dinoflagellate cysts. **ac**, Acanthomorphitae; **p**, Polygonomorphitae; **s**, Sphaeromorphitae; **n**, Netromorphitae; **dia**, Diacromorphitae; **pr**, Prismatomorphitae; **h**, Herkomorphitae; **pt**, Ptermorphitae; **dino**, dinoflagellates. Abridged and modified from Downie, 1967.

polygonal fields, Tasmanitomorphs (Tasmanititae)–*Tasmanites*, etc. (see Fig 6.9). However, tasmanitids can also be grouped with sphaeromorphs, and are not now regarded as acritarchs.

More complex classifications are available. There are less than 500 described genera of acritarchs and several thousand species, but their study is still young enough that the number of genera and species used depends to some extent on the acritarch palynologist. Cramer and Diez (1979) stated that they could greatly reduce the number of generic units by severe application of the procedures for synonymy.

Downie (1973) has shown that acritarchs can be separated also on the basis of wall structure, as follows:

2.1.3.1 Tasmanitid Wall uniform, laminated, with narrow radial pores. Wall thickness often variable in a species, probably because of growth. Present in *Tasmanites, Baltisphaeridium*, and others. Because the tasmanitids are now known to belong to the prasinophyte algae, they are no longer regarded as acritarchs, though they remain part of the phytoplanktonic fossil palynoflora.

2.1.3.2 Micrhystridian Wall homogeneous, simple, usually thin. Examples: *Veryhachium, Micrhystridium*.

2.1.3.3 Diacrodian Wall thin, simple, homogenous. Tends to split into angular planes. Examples: all diacrodians (= diacromorphs).

2.1.3.4 Visbysphaerid Wall thin, homogeneous. Has capacity to develop an inner body closely attached to outer wall, forming a double wall. Example: *Visbysphaera*.

2.1.4 Classification According to Excystment Style

Shape and style of excystment opening in acritarchs can also be used to classify acritarchs. See Fig. 6.7 for a presentation of most of the opening types, plotted against their time of appearance in the record. A simple such classification per excystment type is as follows:

2.1.4.1 Archeopyle Should be reserved for dinoflagellate cysts. A few acritarch excystment openings are similar.

2.1.4.2 Cyclopyle Opening circular in outline, sometimes elongated. This is really synonymous with pylome, which is sometimes used in a general sense for acritarch excystment openings.

2.1.4.3 Epityche Excystment by a curving split allowing a flap to open (see *Veryhachium*).

2.1.4.4 Median Split Splits into two more or less equal halves. Examples: many leiospheres, e.g., *Hemisphaeridium*. For more details on excystment openings of acritarchs, see Playford (2003) and Strother (1996). More complex classifications for the acritarchs are available. There are somewhat fewer than 500 described genera of acritarchs and several thousand species, but their study is still young enough that the number of genera and species used depends to some extent on the acritarch palynologist. Cramer and Diez (1979) stated that they could greatly reduce the number of generic units by severe application of the procedures for synonymy.

2.2 Stratigraphic Occurrence of Early and Mid-Paleozoic Acritarchs

As already noted, sporopolleninous or "true" robust-walled acritarchs first occur in shales about 1.4 billion years old (Mesoproterozoic), and rather abundantly from a bit less than 1 billion years ago to the end of the Proterozoic. (Indeed, there is a well recognized extinction at the end of the Ediacaran, the last stage of the Precambrian.)

These are mostly simple, more or less psilate sphaeromorphs, mostly in the 20–40 μm size range. Despite the similarity of the forms, enough size and sculpturing difference exists for palynostratigraphic applicability of their study. For example,

the range of size increases somewhat in the later Proterozoic (= late Precambrian). According to Grey (2005) there are more than 50 species of acanthomorph acritarchs alone at the end of the Ediacaran. Earliest Phanerozoic (i.e., Cambrian) acritarch floras continue the trend to more diversity in size ($25-200\,\mu$m–with some giant forms that even exceed our accepted upper limit for palynomorphs of 500 μm), but the most striking feature of early Cambrian acritarch floras is the advent of prominent and diverse sculpture: granulae, very short spines and baculae.

In the Ordovician the sculpture of many forms becomes much more pronounced (though low-sculptured and psilate sphaeromorphs continue to be present), with many sorts of spines and other processes, including some that are branched, and some that are nearly as long as the diameter of the body of the acritarch. In other words, the Ordovician is the heyday of the acanthomorphs of all sorts, such as diacromorphs and acanthomorphs proper. Acritarchs' origination rates trend downwards from the Cambrian to their major extinction episode in the Famennian (Late Devonian) to their near disappearance in the Carboniferous. However, their diversity increased from Cambrian into the Middle Ordovician (Mullins *et al.*, 2005).

The study of acritarchs has been applied to the solution of practical stratigraphic problems, and more progress can be expected in this direction. Cramer and Diez showed that studies of acritarch distribution can also be used for study of problems such as probable paleo-position of continental plates in the early Paleozoic and they (1974b) suggested two contrasting acritarch provinces in the Early Ordovician. Vavrdova (1974) also described two similar acritarch provinces for the Ordovician, a Baltic province and a Mediterranean province, but by the time of Servais *et al.* (2004) knowledge of worldwide acritarch provinces for the Ordovician had exploded from that simple base, even though the field is still expanding. Acritarchs have been especially useful also in Devonian studies. Playford and Dring (1981) have described a very diverse acritarch palynoflora from the marine Devonian of the Carnarvon Basin of Western Australia. Wicander (1983, 1984) and Wicander and Wood (1997) have demonstrated the usefulness of acritarch studies in the Devonian of North America.

Fig. 6.10 shows the stratigraphic range of acritarchs in general, showing that they are largely a Paleozoic group. The dramatic decline of the acritarchs at the end of Devonian is easily perceived in this diagram.

3 Cambrian/Ordovician Cryptospores

Beginning with about Middle Cambrian time, and ending in Early Devonian, there occur in a variety of non-marine shales from many parts of the world sporopolleninous sporelike bodies that lack evidence such as haptotypic marks

that they were produced as by-products of normal sporogenesis in a sporangium. The term cryptospore was introduced by Richardson *et al.* (1984) for some Devonian forms and has since been widely applied to tetrads, dyads and monads of various sorts. The tetrads are unlike "normal" tetrads of higher plants in that they lack evidence of separability and sometimes have an enclosing membrane that probably establishes that separation into monads was not a part of their program. Dyads automatically qualify as cryptospores, because such forms are practically non-existent in sporangia of extant and fossil plants.

Some cryptospores even occur in triads, which are difficult to explain as products of meiosis. The monad cryptospores lack laesurae or other regularly occurring evidences of association with other members of a tetrad. As noted by Richardson (1996), some cryptospore features that are atypical for spores in general compare closely with characters of some modern bryophyte spores, suggesting possibly some sort of affinity such as common ancestry. There have been no finds of *in situ* cryptospores from megafossil plants, probably indicating that the producing plants were embryophytic-type, perhaps semi-aquatic, plants that had not developed robust enough tissues to be preserved–only the sporopollenin of the cryptospores themselves provide a record of the existence of such plants (cf. Strother, 2000). Strother and Beck (2000) have pointed out that dyads and other irregular forms such as triads among the cryptospores suggest that the producing organisms of such forms may have been at the algal level of evolution, and they propose that formal definition of cryptospores should not limit them to the embryophytes-proper. Dyads in particular are so odd and have such a rich early record that they make assignment of botanical relationship difficult. A classificatory scheme for cryptospores has been proposed by Strother (1991), and Richardson (1996) has summarized their stratigraphic distribution and changes over their more than 120 million years of known occurrence. Examples are illustrated in Fig. 1.2; Plate 6.3 is devoted entirely to cryptospores. If cryptospores are regarded as true spores of embryophytic plants, as proposed by Steemans and Wellman (2004), they are, of course, miospores, inasmuch as that term is purely a size classification for undoubted spores and pollen. Strother (cf. Strother and Beck, 2000), on the other hand, advocates a more liberal definition of cryptospores, to include sporopolleninous spore-like bodies of non-marine origin that may represent an interface in evolution between algae and organisms at the bryophyte level. Inasmuch as the exact nature of cryptospores has not been determined, it does not seem to me that they qualify as miospores, and thus a broad definition seems more logical than a narrow one. Furthermore, I think that it would clearly be better to avoid using the term miospore for cryptospores altogether, because it is not proven that any of them is strictly speaking a spore.

The situation may well be analogous to that of acritarchs, with various forms being removed from the cryptospore category when it is proven that they are,

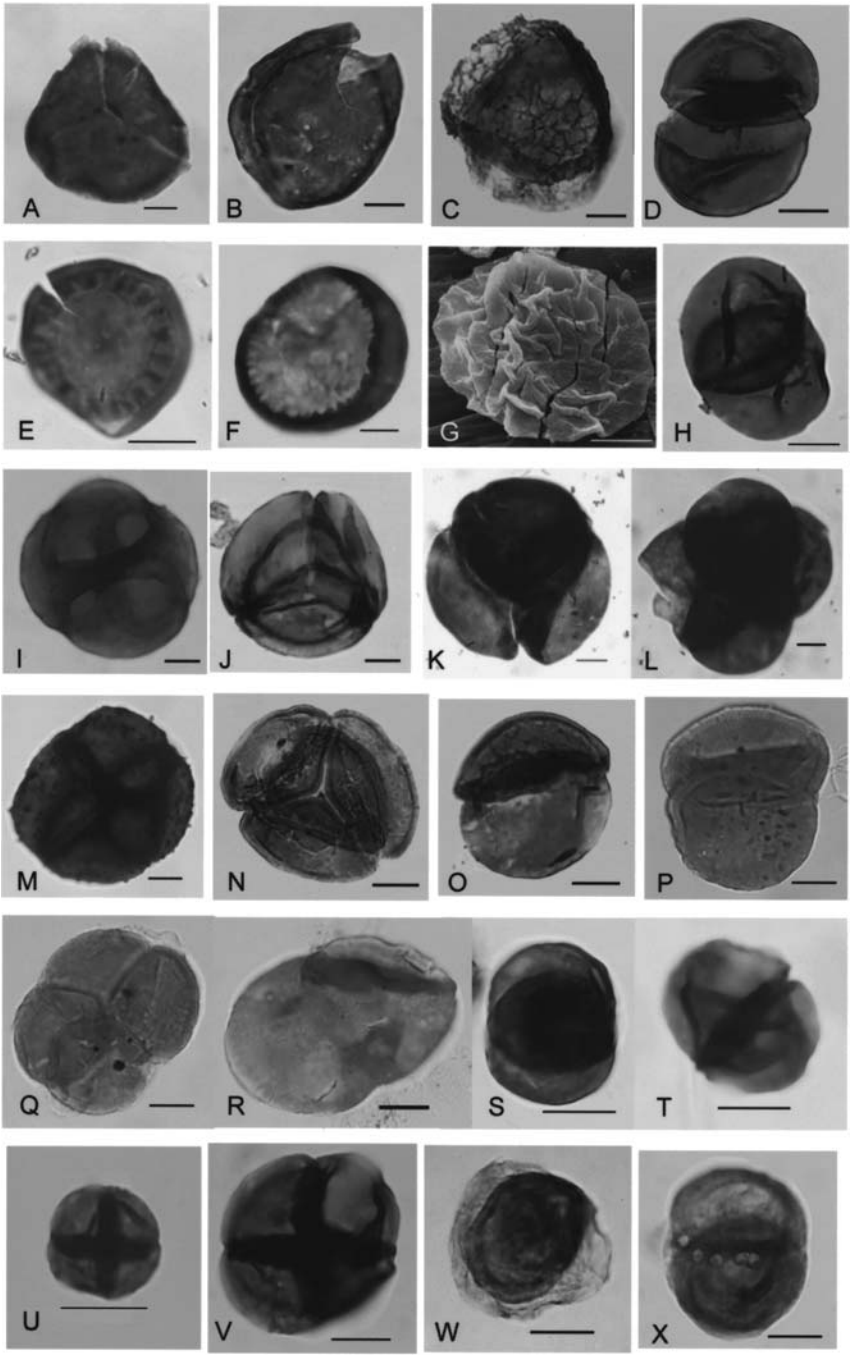

Plate 6.3 *(See caption on page 176)*

Plate 6.3 Cambrian–Ordovician–Silurian-Lower Devonian cryptospores. **A**. *Imperfectotriletes vavrdovae* Steemans, Higgs & Wellman. Wenlock (Lower Silurian), Mifflintown Fm., Fort Robinson, PA, USA, sample S97-2. **B**. *Laevolancis* sp., Wenlock (Lower Silurian), Mifflintown Fm., loc. as A, sample S97-2. **C**. *Abditusdyadus histosus* Wellman & Richardson, Lochkovian (Lower Devonian), Arbuthnott Group, Scotland, sample CB1A. **D**. *Dyadospora murusdensa* Strother & Traverse, Lochkovian (Lower Devonian), Arbuthnott Group, sample CB1A.. **E**. *Drycryptorites radiatus* Strother, Wenlock (Lower Silurian), Bloomsburg Fm., near Snyders, PA, USA, sample S-05-77. **F**. *Artemopyra brevicosta* Burgess & Richardson, Wenlock (Lower Silurian), Mifflintown Fm., near Bluegrass, VA, USA, sample BSK97-113A. **G**. *Rugosphaera* sp., Wenlock (Lower Silurian), Wills Creek Fm., along Juniata River, near Allenport, PA, USA, sample BSK97-67. **H**. *Dyadospora murusattenuata* Strother & Traverse, Wenlock (Lower Silurian), from the type sample, S-05-77, Bloomsburg Fm., near Snyders, PA, USA . **I**. *Tetrahedraletes medinensis* Strother & Traverse, Llandovery (Lower Silurian), Power Glen Fm., Niagara Gorge, NY, USA. **J**. *Tetrahedraletes medinensis* Strother & Traverse, Ashgill (Upper Ordovician), Prague Basin, Czech Republic, Kozov Fm., sample BHT92-5. **K**. *Rimosotetras prolematica* Burgess, Llandovery (Lower Silurian), Tuscarora Fm., near Mill Hall, PA, USA. **L**. Loose tetrad of spherical cells, Llandovery (Lower Silurian), Tuscarora Fm., near Mill Hall, PA, USA.. **M**. *Nodospora oyleri* Strother & Traverse, Llandovery (Lower Silurian), from type locality near Poe Paddy, PA, USA. **N**. Tetrahedral tetrad, similar to *Rimosotetras*, Caradoc (Upper Ordovician), Oman. **O.** Permanent dyad, similar to *Dyadospora murusdensa*, Caradoc (Upper Ordovician), Oman. **P**. Dyad, similar to *Dyadospora murusdensa*, Llanvirn (Middle Ordovician) Hanadir Shale, sample RA3-2, Saudi Arabia. **Q**. Tetrad, similar to *Velatitetras*, Llanvirn (Middle Ordovician), Hanadir Shale, sample RA4-1, Saudi Arabia. **R**. Dyad similar to *Pseudodyadospora laevigata*, Llanvirn (Middle Ordovician), Hanadir Shale, Tayma-4, Saudi Arabia. **S**. *Pseudodyadospora petasus* Wellman & Richardson, Middle Cambrian, Rogersville Shale, ORNL Joy-2 core (1578′), eastern TN, USA. **T**. Dyad similar to *Dyadospora murusattenuata*, Middle Cambrian, Rogersville Shale, ORNL Joy-2 core (1518′), eastern TN, USA. Size smaller than *D. murusattenuata* from younger rocks, otherwise indistinguishable. **U**. Planar tetrad, Middle Cambrian, Rogersville Shale, ORNL Joy-2 core, eastern TN, USA. **V**. Planar tetrad, Middle Cambrian, Rogersville Shale, ORNL Joy-2 core (1518′), eastern TN, USA. **W**. *Sphaerasaccus glabellus* Steeman, Higgs & Wellman, Middle Cambrian, Pumpkin Valley Shale, ORNL Joy-2 core (1803′), eastern TN, USA. **X**. Dyad. Middle Cambrian, Rogersville Shale, ORNL Joy-2 core (1518′), eastern TN, USA. The hemispherical outline of the individual spores is reminiscent of *Dyadospora murusdensa*, but the wall texture of this Cambrian form is distinct from the thick, smooth character of the Silurian species. Plate prepared for the author by Paul K. Strother. Photographs in C, D, N, and O are courtesy of Charles Wellman. Samples in C and D are cited in Lavender and Wellman, 2002. Samples represented by specimens in F and G were collected by John Beck and Deborah Skilliter. The sample represented by I was provided by Merrell A. Miller. The sample represented by J was provided by M. Vavrdova and J. H. Beck. Specimens illustrated in K and L were from samples collected by Leslie Desimone The samples from which the specimens in P, Q and R were obtained were provided by Said Al-Hajri of Saudi Aramco. All samples not otherwise identified were collected by Paul K. Strother and/ or the author.

in fact, spores produced in a sporangium on the one hand, or part of the life cycle of an undoubted alga on the other. Strother (personal communication, 2005) estimates that there are at least 30 genera and 75 species of cryptospores, based on a survey of 374 published records, dating from Cambrian to Early Devonian (Lochkovian). It should be noted that authorities on the cryptospores give different times of origin for them, depending on what is accepted as a cryptospore. Steemans (1999), for example, says that the oldest cryptospores are from the Llanvirn, but if some of Strother's recent finds are accepted as cryptospores, they go back into the Cambrian.

4 Cambrian/Ordovician Chitinozoans

Acritarchs were joined in Cambrian time by other organic resistant-walled palynomorphs, parts of, or elements of, various animals. The most important are chitinozoans (range: Cambrian to latest Devonian) and scoledoconts (range: Ordovician to present). Chitinozoans are composed of "pseudochitin," a C-H-O-N compound of uncertain structural formula which behaves much like chitin and sporopollenin (appearance and resistance to decay and to laboratory maceration of the enclosing rock). Always found in marine rock, chitinozoans occur much less abundantly per gram of sediment than do acritarchs and sporomorphs. Some special processing techniques need to be applied, and larger samples must be used. Paris (1984) reported a maximum of about 100/g being common. This is approximately an order of magnitude less abundant than sporomorphs in palyniferous samples containing them. Lithology is not as controlling a factor as it is for sporomorphs. Limestones, for example, are often productive, but so are marine shales. Unfortunately for us, chitinozoans are thick-walled, and as a result are often opaque or nearly so and difficult to investigate with the light microscope. They mostly range in size from 50 to 250 μm, though there are some smaller than 50 μm, and a few "monsters" up to 600 μm or more. SEM studies are best for elucidation of morphology but are not usually practical for routine work such as counting. The biological affinities of chitinozoans are still not known, and various investigators have suggested as diverse provenance as graptolites (Jenkins, 1970) and fungi (Loquin, 1981). Fungal origin seems very unlikely if for no other reason than that resistant-walled fungal spores, and hyphae universally recognized as such, do not appear regularly until late Jurassic, although non-robust walled fungi range to the Precambrian. An anomalous, saltating record would exist if chitinozoans were fungal. Also suggested have been Tintinnids and eggs of various unknown animals. An interesting circumstantial case (chemistry, common range, frequent association) can be made for derivation of chitinozoans from graptolites (Jenkins, 1970), which would make chitinozoans probable chordate remains.

Since the publication of the first edition of this book, many estimable contributions have made to the chitinozoan literature. Examples are Grahn (2005), Paris *et al.* (2000), Miller (1996), and Paris (1996). The latter two publications are packed with valuable general information about chitinozoans.

4.1 Morphology of Chitinozoans

Fig. 6.11 shows the basic morphology of typical chitinozoans (see also Fig. 1.2a,b). Chitinozoans are often referred to as "flask-shaped," but this, and the term "mouth" (= oral) imply that we know more than we do about which end is "up." Specimens are sometimes encountered that consist of two or more units joined together, collar and mouth to base. Fig. 6.11 shows several modes of joining of chitinozoan units. Chitinozoans may be psilate or highly sculptured, with simple or complex processes, as is seen in Fig. 6.11. Fig. 6.12 presents photomicrographs and SEM micrographs of various characteristic forms.

4.2 Stratigraphic Occurrence of Chitinozoans

Chitinozoans first occur in Cambrian rocks but are most abundant in Ordovician and Silurian. They continue to be modestly abundant in the Devonian but are rare by Carboniferous and gone by late Carboniferous time. Fig. 6.13 shows the stratigraphic range of the more important chitinozoans.

5 Cambrian/Ordovician Scolecodonts

Associated with acritarchs and chitinozoans in early Paleozoic marine sediments are often found the chitinous mouthparts (= "jaw apparatuses") of marine annelid worms (polychaetes). These mouthparts are called scolecodonts. Colbath and Larson (1980) showed that the chitinous layer of scolecodonts covers an inner $CaCO_3$ layer. Palynological maceration presumably destroys the $CaCO_3$, just as it does in foraminifera, though Colbath and Larson believe the organic layer may protect the carbonate from acid digestion. Identification of the organic matter as chitin depends on appearance and behavior. Germeraad (1980) has noted the occurrence of scolecodont-like fossils in possibly non-marine sediment of Cenozoic age, but this is very exceptional.

Scolecodonts first occur in the Ordovician. They, like chitinozoans, vary a great deal; in size, they vary from around 100 to well over 200 μm, even to over 3000 μm in some examples, which are thus easily visible to the naked eye. Also like chitinozoans, they are not particularly abundant in absolute terms in the marine shales in which they occur; they are found in the l00/g range, instead of l00-l0,000/g, as is typical of acritarchs or spores/pollen in a moderately productive

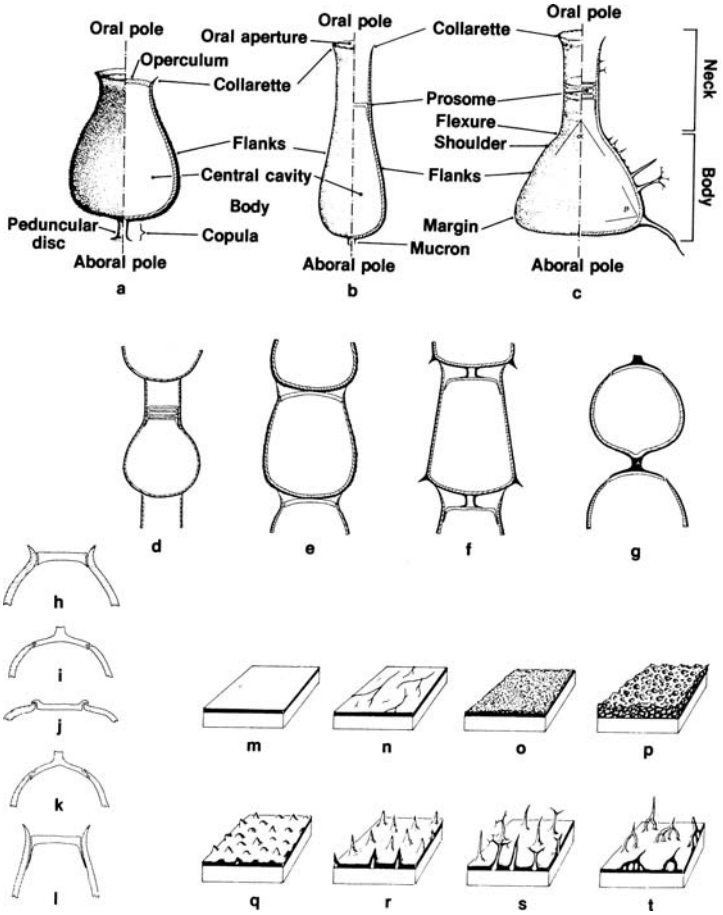

Figure 6.11 Morphology of chitinozoans. (a)-(c) General morphological features: (**a**) Desmochitinidae, (**b**) Conochitinidae, (**c**) Lagenochitinidae. (**d**)-(**g**) Different types of linear "colonies": (**d**) junction by simple juxtaposition; (**e**)-(**f**) junction by double adherence; (**g**) reinforced junction (black = periderm; hachured = ectoderm; stippled = endoderm). (**h**)-(**l**) Different types of fastening of operculum in the oral aperture: (**h**)-(**k**) mechanical assembly; (**l**) adherence (stippled = operculum; hachured = external and internal membranes). (**m**)-(**t**) Sculpturing types for chitinozoans: (**m**) psilate, (**n**) chagrenate, (**o**) tomentose ("felty"), (**p**) spongy, (**q**) conic verrucate, (**r**) echinate, (**s**) filiform, simple, and branched, (**t**) filiform, bi- or miltipodal. The black layer represents the periderm and the white layer the ectoderm. Tests with (m)-(p) texture are regarded as glabrous, those with (r)-(t) texture as ornamented. Modified from Paris, 1981.

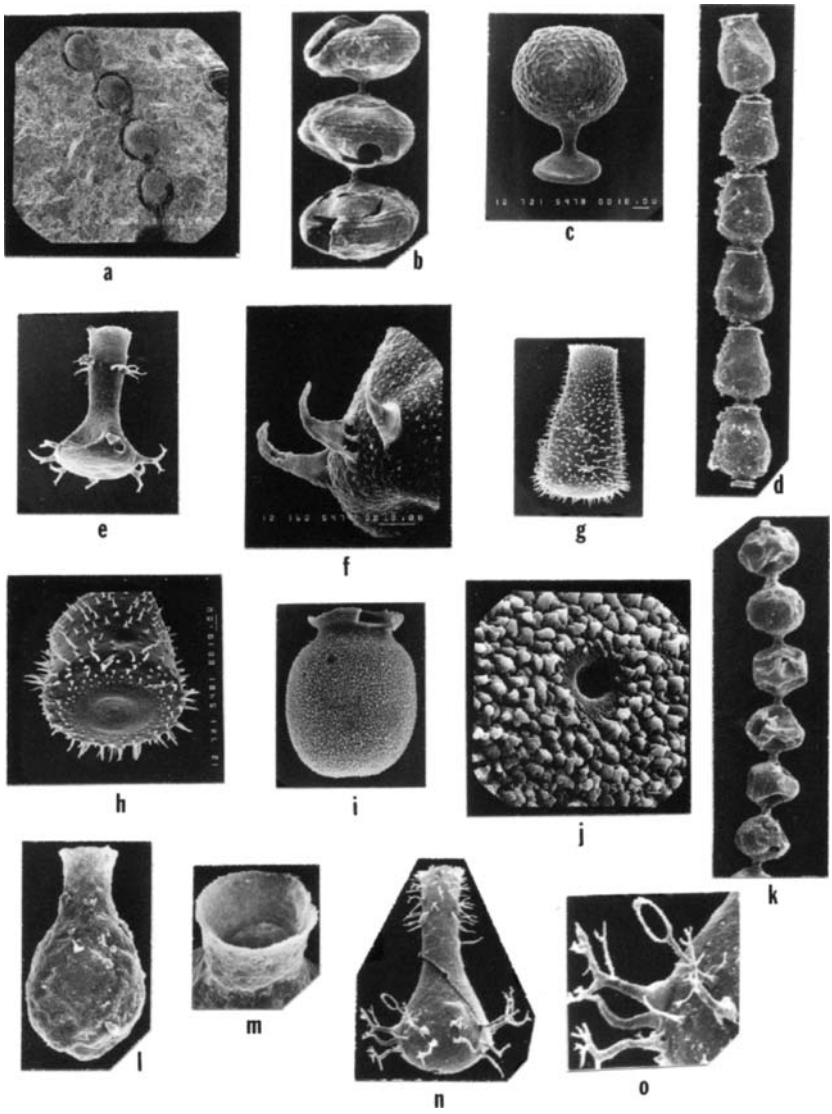

Figure 6.12

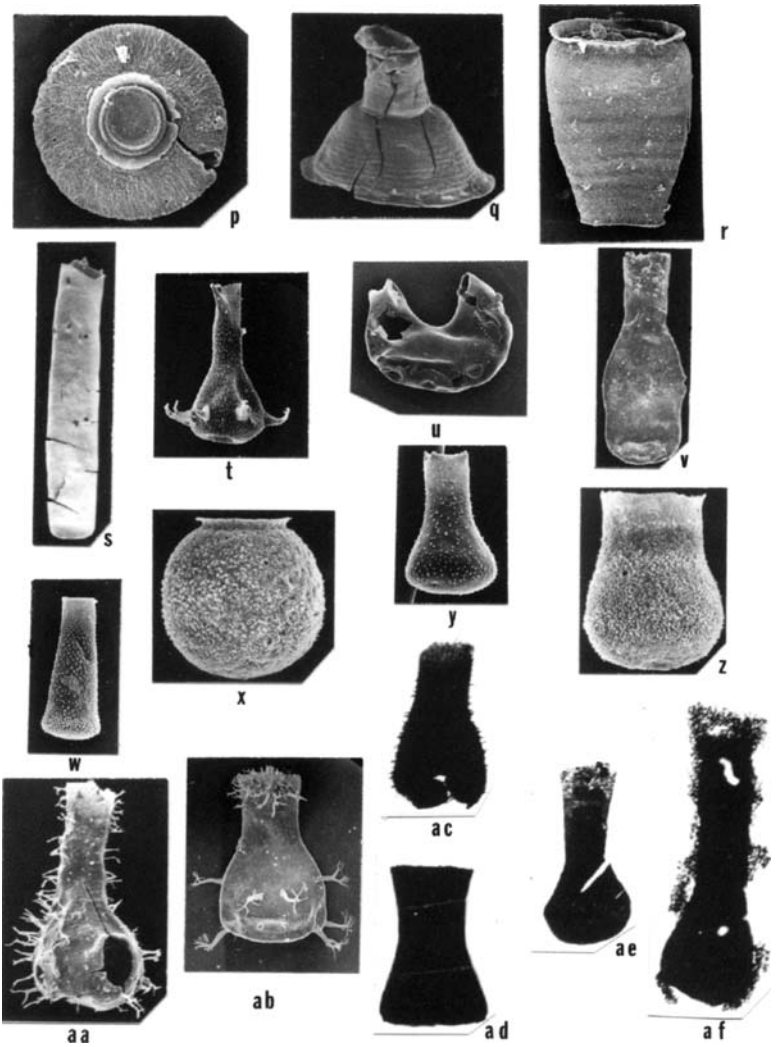

Figure 6.12

Figure 6.12 Representative chitinozoans as observed by photomicrography (ac)-(af) and scanning electron microscopy (all others). Compare with diagrams in Fig. 6.11. Obviously, chitinozoans are an outstanding example of the advantages of SEM for thick-walled palynomorphs, although some chitinozoans are more translucent than the specimens illustrated here. All specimens except (a) were obtained by rock maceration. (**a**) Chain of connected individuals of *Desmochitina* (*Desmochitina*) *bulla* Taugourdeau & Jekhowsky, SEM of uncoated rock surface. Each unit about 230 μm long. Lower Ordovician, Czechoslovakia. (**b**)*Margachitina catenaria tenuipes* Paris, chain of three units. Note connecting "necks". Each unit about 75 μm long. Lower Devonian, France. (**c**) *Margachitina margaritana* (Eisenack), individual unit in orientation as in (b), showing that the copula is linked to an operculum from both an aboral and an oral end of a chitinozoan-unit. Fossil is about 95 μm long as shown. Silurian (Wenlockian), Sweden. (**d**) *Urnochitina urna* (Eisenack), chain of chitinozoan units linked by double adherence. Each unit about 100 μm long. Silurian (Pridolian), Czechoslovakia. (**e**) *Ancyrochitina gutnica* Laufeld, with filiform sculpture. Fossil is about 130 μm long. Silurian (Wenlockian), Sweden. (**f**) *Ancyrochitina* sp., two sizes of echinate sculpture. Large spines extend about 25 μm from surface. Silurian (Wenlockian), Sweden. (**g**) *Belonechitina wesenbergensis brevis* (Eisenack), with profuse echinate sculpture. Fossil about 150 μm long. Upper Ordovician glacial erratic, Baltic area. (**h**) Same species as (g), showing difference of sculpturing on aboral pole: echinate on flanks, verrucate toward pole. Larger spines about 12 μm long. Upper Ordovician glacial erratic, Baltic area. (**i**) *Desmochitina* (*Pseudodesmochitina*) *minor* Eisenack, closely packed verrucate sculpture. Fossil about 90 μm long. Upper Ordovician glacial erratic, Baltic area. (**j**) Same specimen as (i), aboral area, enlarged to show densely packed verrucate sculpture. Perforation shown about 5 μm in diameter. Upper Ordovician glacial erratic, Baltic area. (**k**) *Margachitina* sp., example of chain of units coupled by reinforced junction. Each unit about 70 μm long. Lowermost Devonian (Borshow), former USSR (**l**) *Lagenochitina deunffi* Paris, illustrating a form with large body, long neck and tomentose sculpture. Specimen about 100 μm long. Ordovician (Caradocian), Portugal. (**m**) Same species and source as (l), specimen showing interior of neck with operculum at junction of neck and body. (**n**) *Gotlandochitina racheboeufi* Paris, a narrow flask-shaped form with branched filiform sculpture. Specimen about 165 μm long. Devonian (Emsian), France. (**o**) Detail of lower left side of (n), enlarged. (**p**) *Calpichitina lenticularis* (Bouché), oral view of specimen with highly developed collarette and operculum *in situ*. Specimen about 160 μm in diameter. Upper Ordovician, Libya. (**q**) *Cyathochitina* sp., specimen compressed dorsoventrally, presenting concentric structures on the body. Specimen about 200 μm long. Upper Ordovician, Portugal. (**r**) *Armoricochitina nigerica* Bouché, showing a carina and granulous sculpture. Specimen about 200 μm long. Upper Ordovician, Libya. (**s**) *Rhabdochitina magna* Eisenack, an elongated tubular form. Specimen about 600 μm long. Late Ordovician, Portugal. (**t**) *Ancyrochitina* sp., with narrow flask shape and two sorts of spines–detail of same shown in (f). Specimen about 140 μm long. Silurian (Wenlockian), Sweden. (**u**)*Parachitina curvata* Eisenack, possible chitinozoan (not yet so classified), with psilate sculpture. Specimen about 280 μm from left to right. Upper Ordovician glacial erratic, Baltic area. (**v**) Angochitininae group, specimen showing a constriction, possibly an abnormality (technical term: "teratoid"). Specimen about 220 μm long. Lowermost Devonian, France. (**w**) *Belonechitina robusta* (Eisenack), tubular form with short, scattered, complex, multipodal sculpture. Specimen

sediment. Because of this, and the size of scolecodonts, special processing, including larger original sample size and less or no pulverizing, is recommended. Specimens may be hand-picked from the residues and mounted dry, as foraminifera, or mounted in a mountant on strew slides as other palynomorphs. Scolecodonts are not quite as likely to be opaque as chitinozoans, but they frequently are thick-walled, and SEM. studies are a useful supplement to light microscopy. In Ordovician to Permian marine shales scolecodonts are especially prominent. These marine worm fossils persist in the modern oceans. They occur but are uncommon in Mesozoic and Cenozoic sediments (Jansonius and Craig, 1971; Schäfer, 1972; Germeraad, 1980).

Complications of processing and microscopy are not the only reason that scolecodont studies are difficult. These "worm jaws" are not jaws but the chitinous mouth linings of the worms producing them. Unfortunately, one worm has more than one kind of mouth lining (see Fig. 6.14).

Scolecodonts are also quite variable in morphology, making their systematics even more difficult. Edgar (1984) points out that the jaw apparatuses consist of three element groups: the anterior maxillae, the posterior maxillae, and

Figure 6.12 about 275 μm long. Upper Ordovician glacial erratic, Baltic area. (**x**) *Desmochitina* (*Pseudodesmochitina*)*minor* Eisenack, unusually broad vase-formed. Ornate tomentose-spongy sculpture. Specimen about 80μm long. Ordovician (Lower Caradocian), Portugal. (**y**) *Fungochitin fungiformis* (Eisenack), flask-shaped form with scattered, mostly echinate sculpture. Specimen about 140 μm long. Upper Ordovician glacial erratic, Baltic area. (**z**) *Eisenackitina rhenana* (Eisenack), broad form with tomentose sculpture. Specimen about 90 μm long. Upper Ordovician (Caradocian), Portugal. (**aa**) *Gotlandochitina marettensis* Paris, showing filiform sculpture. Specimen about 190 μm long. Devonian (Emsian), France. (**ab**) *Alpenachitina eisenacki* Dunn & Miller, specimen with long branching processes on the chamber and echinate sculpture on the upper neck. Specimen about 150 μm long. Middle Devonian, Libya. (**ac**) *Belonechitina* sp., abnormally large body (split and flattened). Specimen about 130 μm long, P.M. Lower Ordovician, France. (**ad**) *Cyathochitina varennensis* Paris. Specimen about 120 μm long, P.M. Lower Ordovician (Llanvirnian), France. (**ae**) *Sphaerochitina lycoperdoides* Laufeld, flattened specimen showing disorganized prosome. Specimen about 150 μm long, P.M. Silurian, Portugal. (**af**) *Muscochitina muscosa* Paris. The shaggy excrescences are indeed the loosely tomentose sculpture. Specimen about 260 μm long, P.M. Lowermost Devonian, France. Note that chitinozoans are governed by the zoological rules of nomenclature, which accounts for some differences from spores/pollen names, which are controlled by the botanical code. For example, *Eisenackitina rhenana* (Eisenack) means that Eisenack first named *rhenana*, in another genus, but the name of the transferring author does not appear after "(Eisenack)", as is required under botanical rules. Names in parentheses after the generic name are subgeneric names, as in (a) and (i). In trinominal names, as in (g), the second epithet (*brevis*) is the subspecific name (in botany, it would have to be labeled subspecies, variety, etc.). All illustrations courtesy of Florentin Paris.

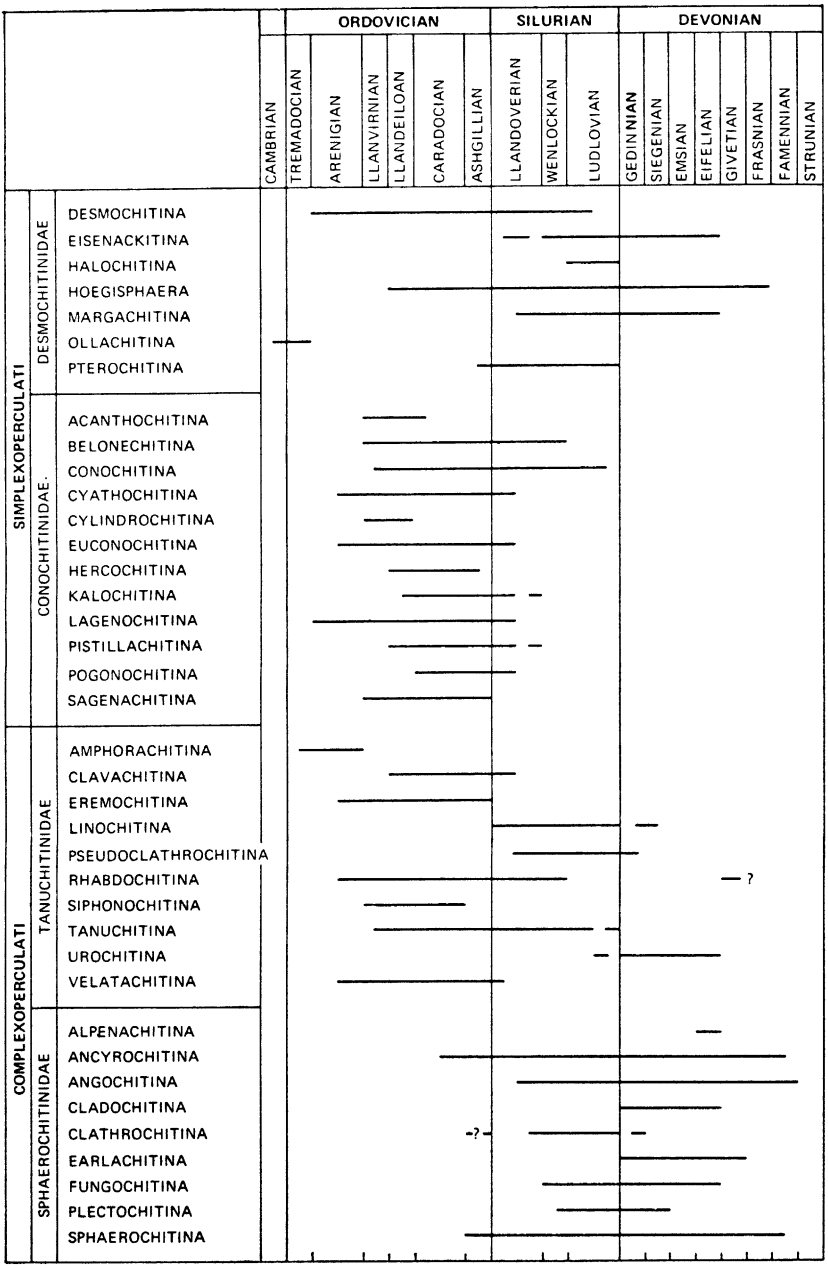

Figure 6.13 Approximate ranges of the most important chitinozoan genera. The family groupings of the genera are quite different from those in Fig. 6.8, q. v. Illustrations from Jansonius, 1970.

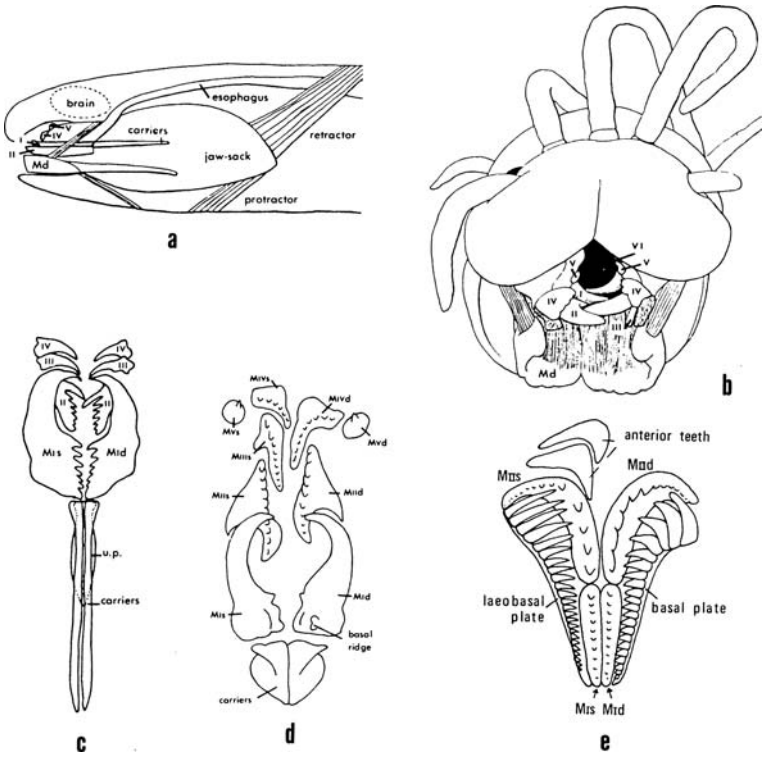

Figure 6.14 Scolecodont morphology. Scolecodonts are various parts of the chitinous "jaw" apparatus of the mouth-proboscis of a number of sorts of polychaete annelid worms. These worms range from early Paleozoic to the present, but were most abundant in the Paleozoic. The various "teeth" and "jaw" parts are found as strengthened ridges and folds from a chitinous mouth-proboscis lining. Thus, the whole apparatus is hollow, filled in life with soft tissues. The various complex parts of an apparatus are connected in life by a thin lining of the proboscis, but the parts are easily disarticulated and thus quite different scolecodonts can and do represent the same species of animal. Under zoological rules, the correct name for a dozen different named scolecodonts is the first published of any of these, if they are shown to belong together. Form-taxa, for such items occurring dispersed, are not recognized in zoology. (**a**) *Eunice siciliensis* Grube, sagittal section of anterior portion, showing relationship of mandible (Md) and the maxillary apparatus (carriers plus maxillae I, II, III and IV). The mandible is located ventrally and often has a calcareous cap. (**b**) Same species, frontal view, mandibles pulled down, showing maxillary apparatus behind. Parts of maxillae are numbered from posterior to anterior. (**c**) Diagram of maxillary arrangement of a prionognathid "jaw", viewed dorsally, showing long narrow carriers: u.p. = unpaired piece, MIs = first maxilla left (sinistral), MId = first maxilla right (dextral). (**d**) *Diopatria neapolitana* Ehlers, exploded diagram of labidognathid jaw arrangement: MIs = left first maxilla, MId = right first maxilla, etc., as explained for (c) and (d). Note the extra units: basal plate and its paired mate, the laeobasal plate, and anterior teeth (see Fig. 6.15). Illustrations from Jansonius and Craig, 1974.

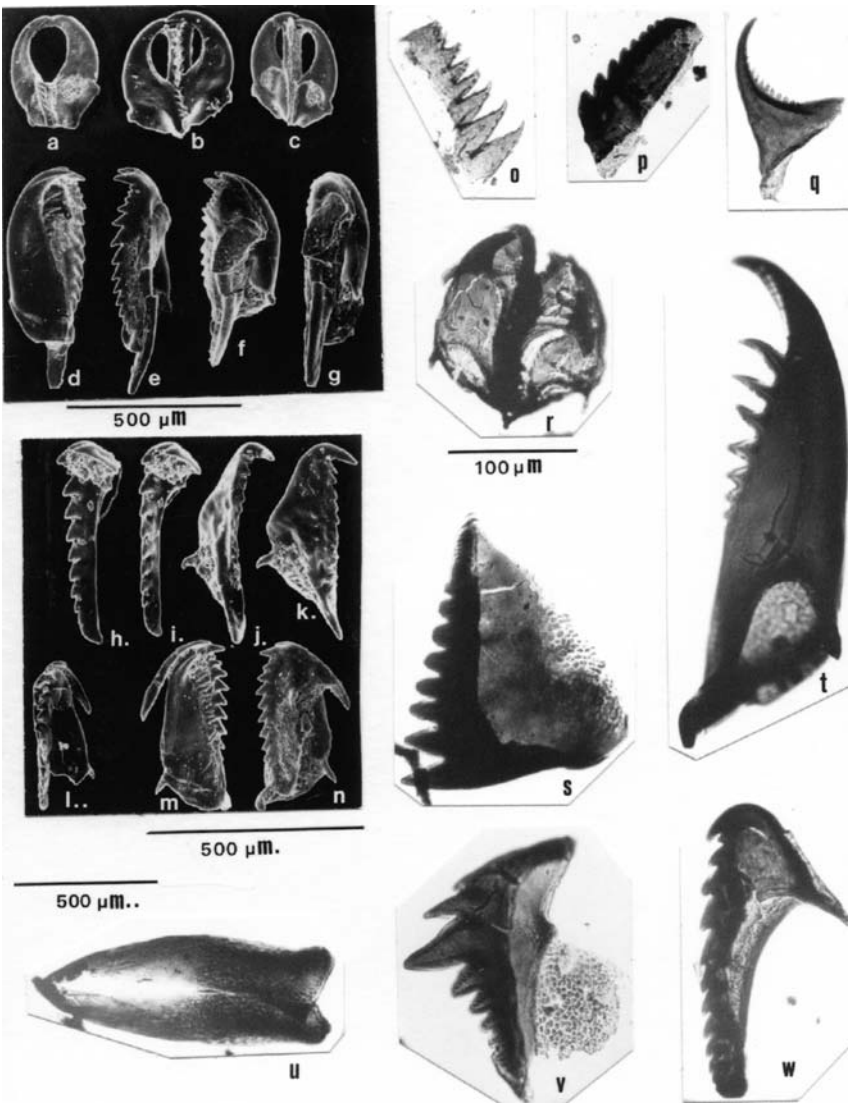

Figure 6.15

carriers (see Fig. 6.14). The MI elements of the posterior maxillae are the most useful for diagnostic purposes. Note that scolecodonts are chitinous and produced by worms. Conodonts (range lowest Cambrian to Upper Triassic) which are sometimes confused with scolecodonts, are phosphatic, and never occur in palynological preparations, as they are dissolved by strong acids in our procedures; they are derived from extinct animals. Some conodonts and some scolecodonts resemble each other a bit. Conodonts tend to be larger– over 300 μm, though this is well within the limits of scolecodont size. Morphological terms for fossil scolecodonts are based on the presumed position in the annelid mouth, and on anatomical terms used by zoologists. See Fig. 6.15 for illustrations of a variety of scolecodonts.

5.1 Scolecodont Stratigraphy

First found in the Ordovician, scolecodonts range to present, but their greatest abundance is from Ordovician to Permian. More concerted work would doubtless

Figure 6.15 Scolecodonts, the chitinous "jaws" (= mouthpart elements) of marine polychaetous annelid worms. These fossils are usually found as isolated parts of the complex mouth lining of the worms, because they easily disarticulate; however, articulated or partially articulated apparatuses commonly occur. See Fig. 6.13 for diagrams of the anatomical situation in the living worm. The maxillary jaws are usually numbered from the rear, the posteriormost maxillary elements being MI and MII. MIII is usually not paired. Other parts are named: basal tooth, mandibles, carriers, etc. (a)-(n) S.E.M. pictures of elements from Upper Devonian (Frasnian) of Northern Alberta; (r)-(w) photomicrographs of scolecodonts of same origin as (a)-(n); (o)-(q) scolecodonts from Ordovician, Anticosti Island, Quebec. Magnification for (a)-(g) and (m),(n) indicated by bar under (d) and (e); magnification for (h)-(k) indicated by bar under (m) and (n) (bar and fossils set off by use of single dot with letters (h)-(k); magnification for (l) (two dots) shown by bar under (l); magnification for (r)-(w) indicated by bar under (r); magnification for (o)-(q) is approximately the same as that for (a)-(g). (**a**)-(**c**) *Xanthoprion albertensis* Jansonius & Craig, pair of MI, dorsal and ventral views. (**d**)-(**g**) *Elleriprion*? sp., MI and MII, left mandible: (**d**),(**e**) are dorsal views of assembled jaws with shaft of mandible below, (**f**) is oblique frontal view, (**g**) a full ventral view. (**h**)-(**k**) *Albertaprion* sp.: (**h**),(**i**) is a MIId, (**j**),(**k**) is an MId; (h)-(k) were articulated but separated in processing; (h),(i) would be put in genus *Leodicites*, (j),(k) in *Delosites* if found dispersed! (**l**) *Albertaprion*?, MId (posterior damaged) and MIId, dorsal view. (**m**)-(**n**) *Albertaprion* sp. MIs and MIIs, oblique view of outer face, full lateral view of inner face. (**o**) *Mochtyella cristata* Kielan-Jaworowska. (**p**) *Marlenites millerae* Eller. (**q**) *Ungulites* sp. (**r**) *Albertaprion comis* (Eller), more or less complete maxillary apparatus: MId, MIId, MIs, MIIs. (**s**) *Paleoenonites triangularis*, showing squamate connecting tissue. (**t**) *Nereigenys* sp., MI. (**u**) A pair of carriers (see Fig. 6.14). (**v**) *Anisocerasites guttulatus* Taugourdeau. (**w**) *Leodicites divexus* Eller. All photos courtesy of J. Jansonius; (a)-(j) appeared in Jansonius and Craig, 1974.

improve their utility for practical palynostratigraphy but only a handful of specialists work on them. The fact that one species of worm may produce several "genera" of mouth-linings is an annoyance but not a serious barrier to application, as the several "taxa" from one worm species will obviously have the same range!

Chapter 7

Cambrian to Silurian Non-Marine Palynology

1 General Discussion

In marine shales of earliest Silurian age, acritarchs, scolecodonts and chitinozoans continue to provide the palynomorph assemblages encountered. (It is possible that some of the acritarchs were actually forms ancestral to dinoflagellates.) However, well preserved and fairly abundant non-marine microfossils are found world-wide in sediments from deltaic and other non-marine environments of Lowest Silurian (Llandovery) age (Pratt *et al.*, 1978; Strother and Traverse, 1979; see Figs. 7.1 and 7.2 here; Steemans *et al.*, 2000), indicating the first experiments of plants with the sub-aerial milieu. Indeed, researchers (Gray *et al.*, 1982; Richardson, 1988; Strother *et al.*, 1996; Wellman, 1996) have now found these harbingers–cryptospores–in many rocks from various parts of the world, dated as Late and Middle Ordovician (Caradoc-Ashgill–Llanvirn–cf. Wellman *et al.*, 2003), and even down to Middle Cambrian (Strother *et al.*, 2004). The suites of microfossils reported by Gray *et al.* (1982) and Richardson (1988) from late Ordovician of Libya seem essentially identical to those of the early Silurian. Steemans (1999) notes that the cryptospores seem to have hit an important extinction event in the Llandovery. However, this sort of palynoflora persisted for as much as 40 million years before the appearance of true spores with haptotypic features such as *Ambitisporites*. This is a remarkable example of stasis, and the reign of cryptospore-producing plants in general is even more impressive. It is now known to have lasted well over 100 million years, from at least Middle Cambrian to Early Silurian. As of 2004, Strother (personal communication) estimates that about 30 genera with about 75 species of cryptospores have been published for Cambrian to Lower Devonian rocks.

As Wellman and Gray (2000) have pointed out, the appearance of true embryophyte spores with haptotypic marks in the Early Silurian could represent the arrival of vascular embryophytes, or of plants transitional to them. As can

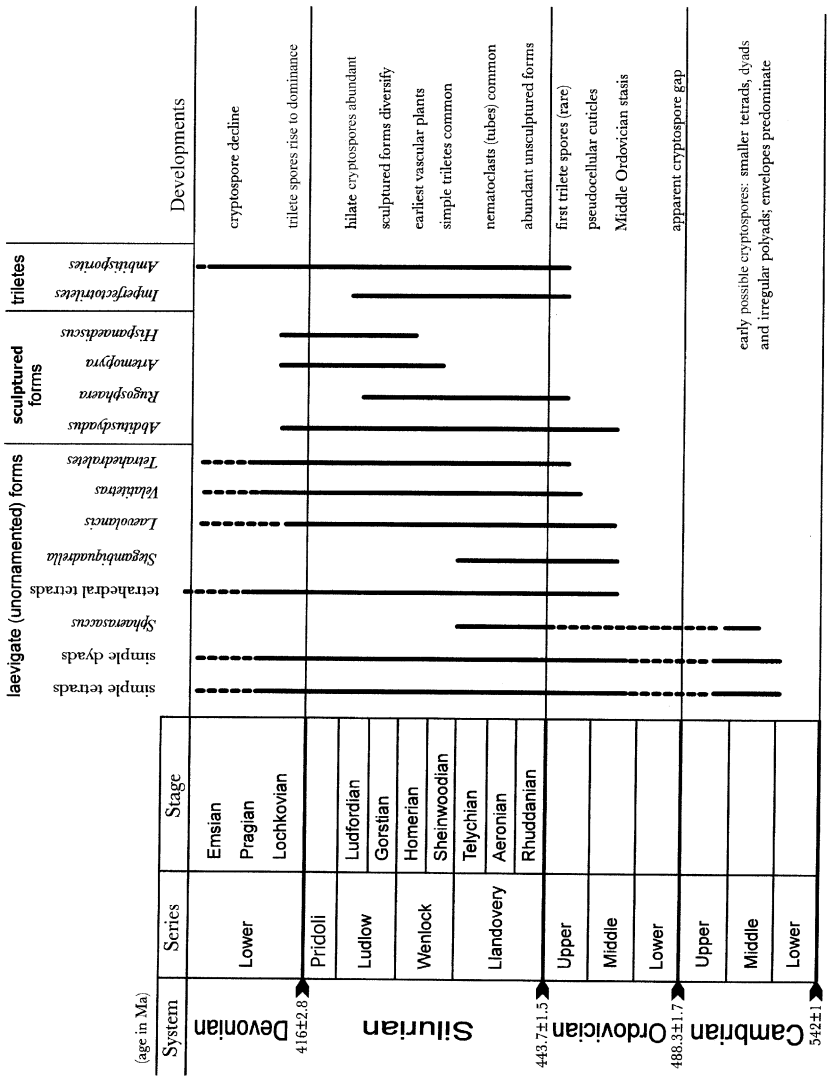

Figure 7.1 Cambrian to Devonian history of cryptospore, spore and plant maceral evolution. "Hilate" refers to J. B. Richardson's use of that term for Silurian cryptospores, as in Burgess and Richardson (1995). "Apparent cryptospore gap" refers to the lack of cryptospore record for the Early Ordovician, despite the fact that there are probable cryptospores in the Late Cambrian. Fig. prepared for the author by P. K. Strother (personal communication, 2005).

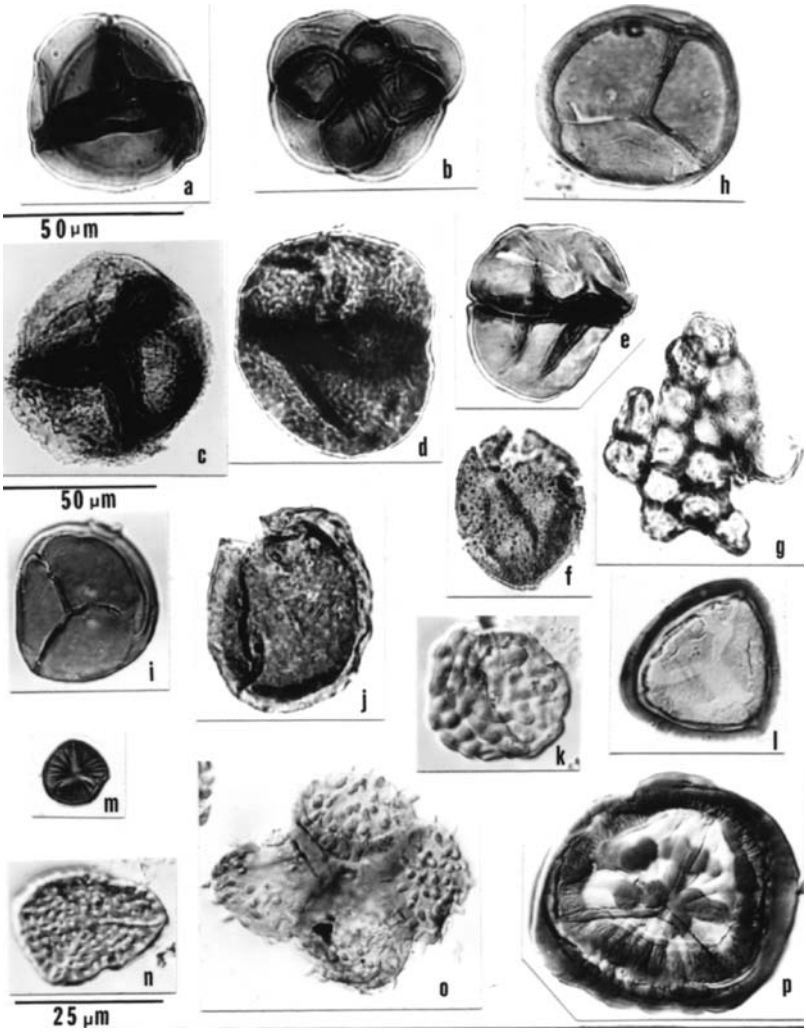

Figure 7.2 Silurian palynomorphs of non-marine origin, including cryptospores [(a)-(f), (j) and (o)]. Illustrated are: obligate tetrads (a)-(c), (o), dyads and pseudodyads (d),(e), leiospheres (f), resistant-walled tissue fragments (g), double-walled monads (j) and true trilete spores (h),(i, (k)-(n), (p). The 50 μm bar for (a) indicates magnification for all specimens except (c) and (n), which have their own bars. FM numbers in parentheses refer to specimen numbers of the British Museum (Natural History). (**a**) *Tetrahedraletes medinensis* Strother & Traverse, an obligate tetrad, Tuscarora Fm., Lower Silurian (Llandovery), Pennsylvania. (**b**) Same as (a), different view. Thickenings at contacts between individual spores or spore-like bodies produce the characteristic "pretzel" figures. (**c**) *Velatitetras retimembrana* (Miller & Eames) Wellman & Richardson, an obligate tetrad with conspicuously double-wall construction. Same source

be seen in Fig. 7.2, cryptospores (a term suggested by Richardson *et al.*, 1984) consist of monads (these would be classified as acritarchs if found associated with more "normal" marine Silurian acritarchs), dyads, triads, and tetrads, some with thicker exines than is normal for acritarchs. Wellman *et al.* (2003) have described Ordovician cryptospores from sporangia and have suggested that they may well represent liverwort-level bryophytes.

Forms such as *Tetrahedraletes* show peculiar thickenings along the contacts between members of the tetrad: a "contact ring." As pointed out by Johnson (1985), many of the dyads to tetrads have a membrane or extra wall enclosing the whole unit, perhaps suggesting algal origin. In rocks of Llandovery age, monads with conspicuous, well defined trilete laesurae are found: *Ambitisporites* sp., which was originally described by Hoffmeister (1959) from the Silurian of Libya, in rocks also more recent than Llandovery. *Ambitisporites* is surely a true embryophytic plant spore and indeed resembles some modern liverwort spores. In the Tuscarora Fm., along with abundant monad cryptospores lacking laesurae, and the cryptospore tetrads of *Tetrahedraletes*, etc., are also found puzzling pieces of cells and tissues: tubes of various kinds and sheets of cellular (pseudocellular?) material (Fig. 7.2). It is tempting to speculate that some of these represent other parts of the first sub-aerial plants. As is well known, bona fide fossils of the first vascular plants do not occur until the very tiny upright plant, *Cooksonia*, of later Silurian time. *Ambitisporites* was soon joined by *Punctatisporites* and,

Figure 7.2 as (a). (**d**) *Pseudodyadospora rugosa* Johnson, an incompletely divided dyad-like form. Same source as (a). (**e**) *Dyadospora murusdensa* Strother & Traverse, a true dyad with complete cross-walls. Same origin as (a). (**f**) *Lophosphaeridium sp.*, a sac-like leiosphere. Same origin as (a). (**g**) Sheet of cells with resistant walls. Same origin as (a). (**h**) *Ambitisporites avitus* Hoffmeister, Lower Silurian (Llandovery), Libya, zonate trilete spore. (FM1). (**i**) *Retusotriletes warringtonii* Richardson & Lister, a non-zonate trilete spore with conspicuous curvaturae perfectae, but obviously not greatly different from *Ambitisporites*. Same origin as (h). (FM3). (**j**) *Sphaerosaccus glabellus* Steemans, Higgs & Wellman, a membrane-enclosed (= two-walled) monad. Same origin as (a). (**k**) cf. *Synorisporites verrucatus* Richardson & Ioannides, trilete (not demonstrated in this view) spore with verrucae, Silurian (Wenlock/Ludlow), Libya. (FM12). (**l**) *Archaeozonotriletes chulus* (Cramer) Richardson & Lister, trilete zonate spore with widely gaping laesura. Same origin as (h). (FM5). (**m**) *Emphanisporites neglectus* Vigran, trilete spore with radiating exinal thickenings. Same origin as (k). (FM19). (**n**) cf. *Brochotriletes* sp., trilete spore with foveolate sculpture. Same origin as (k). (FM22). (**o**) *Quadrisporites sp.*, an obligate tetrad. Same origin as (k). (FM23). (I consider this a cryptospore, but some would regard it as of algal origin.) (**p**) *Emphanisporites splendens* Richardson & Ioannides, trilete spore with both radiating and circumpolar exinal thickenings. Same origin as (k). (FM30). (a)-(e), (f), (g) and (j) are from Johnson (1984); (h), (i) and (k)-(p) are from Richardson and McGregor (1986), per permission in first edition of this book. The latter pictures are by interference contrast microscopy.

soon after *Cooksonia*'s fairly common appearance in late Silurian time, about a dozen genera of land plant spores were occurring. Some of these, for example the zonate *Ambitisporites*, do somewhat resemble certain liverwort spores. They might represent plants which, if they still occurred today, would be classified as bryophytes. However, there is no certain evidence as yet that these spores are referable to that group of extant plants, which includes mosses, liverworts, and hornworts. They could have come from some sort of transition from bryophyte body plan to tracheophyte (vascular plant). Richardson and Ioannides (1973) recorded a rich palynoflora of spore forms referred to 10 genera in Ludlow-Downton (Late Silurian to Early Devonian) sediments of Libya, North Africa. Wood (1978) notes that the Ludlow of Indiana also has a considerable variety of spore types, reflecting the rapid evolution of the land flora.

A very important aspect of the study of all fossil sporomorphs is to determine the exact taxa of plants from which the spores or pollen originated. This is accomplished by the study of *in situ* sporomorphs from sporangia of fossil plants. Such work has been carried to a remarkable degree of success with Devonian and younger rocks, but even in the Silurian, much has been done with the spores of relatively simple rhyniophyte plants such as *Cooksonia* (cf. Fanning *et al.*, 1991).

2 "Non-Spore" Palynology

The relative abundance of acritarchs and other marine palynomorphs vis-à-vis spores is a useful indicator of marine influence, beginning with the Wenlock stage of the Early Silurian. For example, McGregor and Sarbonne (1978) are able to hypothesize a sheltered nearshore marine environment for Ludlow beds of the Canadian Arctic, based on the mix of spores, acritarchs, chitinozoans, and scolecodonts. Richardson *et al.* (1981) emphasize that late Silurian spores are sensitive stratigraphic markers, as might be expected from the rapidly evolving plants which produced them. According to Richardson *et al.*, acritarchs of late Silurian time are more influenced by provinciality and local ecological factors. The early spores are more cosmopolitan and hence, when available, are theoretically better for stratigraphy. However, despite this fact, in the Silurian, the "norm" for palynology remains marine acritarchs (plus chitinozoans and scolecodonts). Fig.7.3 illustrates some of the characteristic Silurian acritarch forms. Sherwood-Pike and Gray (1985) have described probable ascomycete fungal remains from the Silurian, strongly suggesting the existence of land vegetation to provide sustenance for the ascomycetes. However, chitinous, robust-walled fungal spores do not occur in paleopalynological macerations of rocks until some hundreds of millions of years later.

Many acritarch specialists have demonstrated that acritarchs permit stratigraphic zonation of marine sediments throughout the Silurian, as they do in the

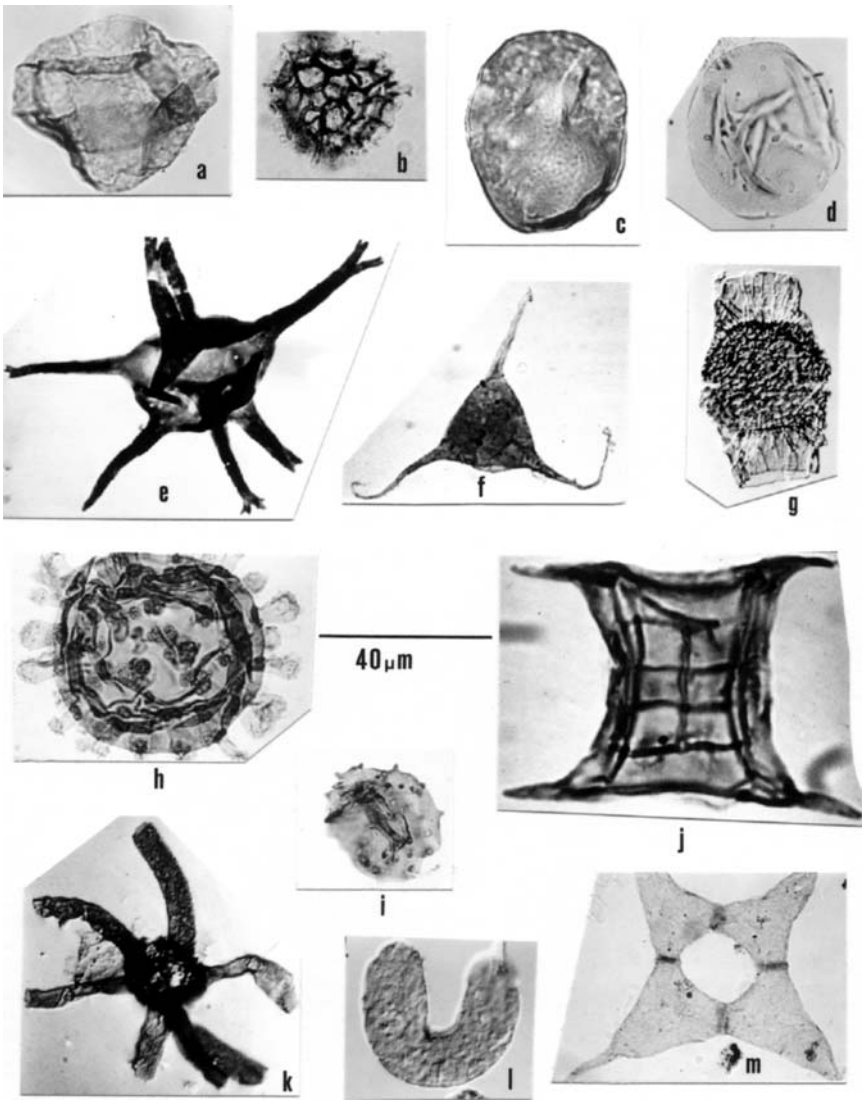

Figure 7.3

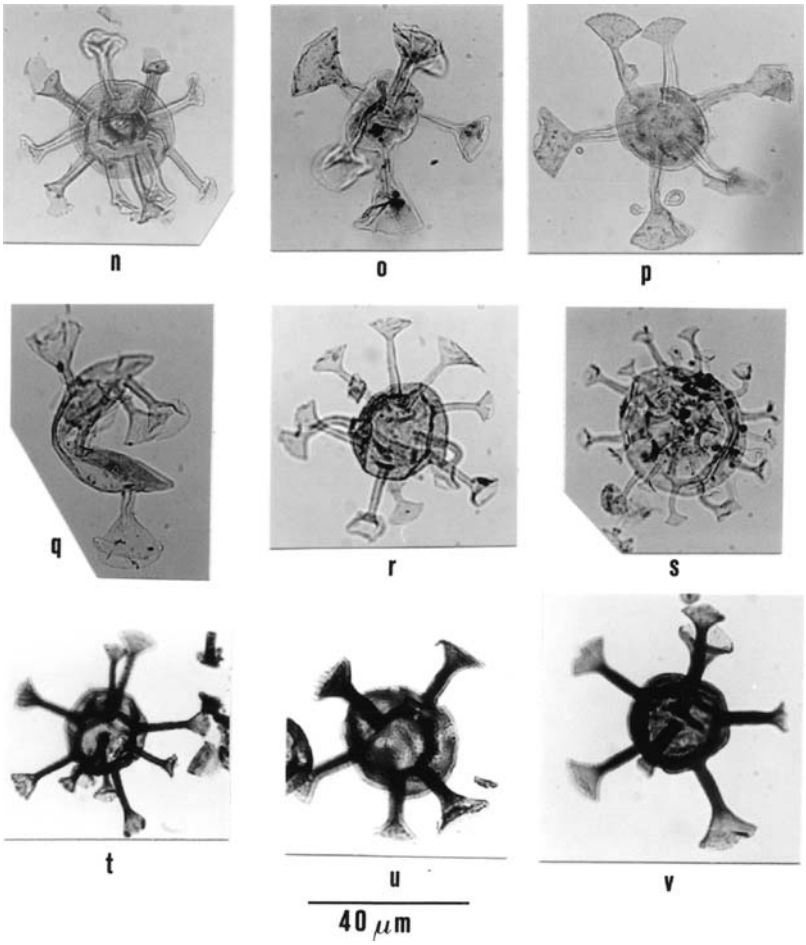

Figure 7.3 *(See caption on page 196)*

Ordovician.. Dorning (1985), for example, has shown that acritarch assemblage zones can be established for the Ordovician and Silurian of eastern North America and northwest Europe with an average duration of about a million years–about 55 zones for the two periods combined. On the other hand, as noted earlier, Silurian acritarchs were provincial and sensitive to local environments, so that Thusu (1973) could use *Deunffia* and *Domasia* complexes to suggest paleogeographical relationships of the source rocks, as Cramer (1969) had noted for Lower Silurian rocks of Pennsylvania. Acritarchs are so numerous and well preserved in continuous sequences of marine sediments from Anticosti Island, Canada, that it has been proposed (Duffield and Legault, 1982) to use stratigraphy based on them for standard general reference sections at the Ordovician/Silurian boundary and for the lower Silurian.

Cramer (1970a) and Cramer and Diez (1972, 1974b) have described a series of acritarch-based belts for the Silurian of eastern North America, northwest Africa and Europe. They suggested that these belts are parallel to paleolatitudes because they are determined by climates. Cramer (1970b) was even able to suggest a northwest movement of Pangea of 2-3 cm/yr.

In late Silurian time, more or less at the Ludlow/Downton (or Pridoli) boundary, about 405 million years ago (Gensel, 1977), after the arrival of the tiny vascular plant, *Cooksonia*, vascular vegetation developed on land. Non-marine shales of

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Figure 7.3 Silurian (mostly) and Devonian acritarchs of various morphological groups. R. Wicander (personal communication, 2005) regards (a) through (d) and possibly (l) as prasinophyte phycomata. All of these are therefore not acritarchs, *sensu stricto*. Approximate magnification for most of the photos indicated by bars next to (h) and under (u). However, for (g) and (m) the bar should be read as = 80 μm, and for (j) it should be read as = 20 μm. (**a**) *Leiosphaeridia* sp., lowest Silurian, Pennsylvania. (**b**) *Cymatiosphaera densisepta* Miller & Eames, lowest Silurian, Pennsylvania. (**c**) *Leiosphaeridia* sp., lowest Silurian, Pennsylvania. (**d**) *Leiosphaeridia* sp., Lower Silurian, Missouri. **e**) *Diexallophasis* (*Continued*) sp., Silurian, Libya. (**f**) *Veryhachium*, Silurian, Libya. (**g**) *Carminella maplewoodensis* Cramer, Lower Silurian, New York. (**h**) *Visbysphaera* sp., Silurian, England. (**i**) *Buedingisphaeridium* sp., Silurian, Libya. (**j**) *Neoveryhachium* sp., Silurian, New York. (**k**) *Dilatisphaera laevigata* Lister, Silurian, England. (**l**) *Quisquilites buckhornensis* Wilson & Urban, Upper Devonian, Oklahoma (this form is referred, e.g., by Tappan (1980), to the Tasmanitaceae, but G. D. Wood (pers. comm.) points out that few if any specimens display the characteristic perforate structure of that group; he would keep the taxon in the acritarchs. (**m**) *Deflandrastrum* sp., Devonian, Libya (a coenobial form). (**n**)-(**v**) Various forms of the genus *Umbellasphaeridium*: (n)-(s) from the Bedford Shale, Upper Devonian, Ohio, (t)-(v) from the subsurface of Peru. (s) is a specimen of *U. deflandrei*) (Moreau-Benoit) Jardiné *et al.*, and all others are representative of *U. saharicum* Jardiné *et al.* Part (q) shows equatorial (medial) excystment structure. Photos (a)-(c) are from Norma G. Johnson, (d)-(m) are from Charles Downie; (n)-(v) are courtesy of Gordon D. Wood, some of which were published in Wood, 1984.

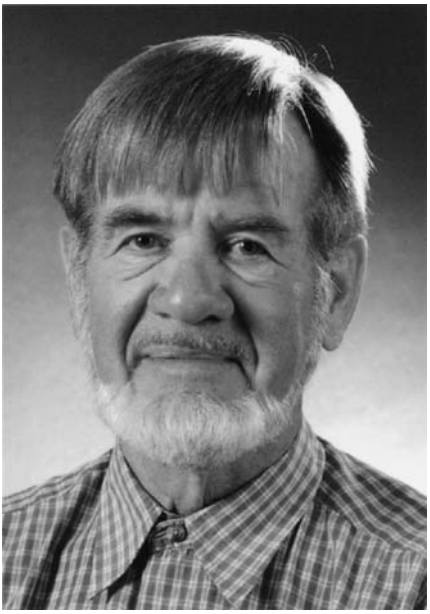

Figure 7.4 Jan Jansonius, Visiting Scientist, Geological Survey of Canada, Calgary, Alberta. Born and trained originally in the Netherlands, Jansonius has worked for many years for the Canadian branch of what is now the Exxon-Mobil Oil Company, and then in retirement as a special research scientist at the GSC. It is hard to decide where to put this incredibly productive man's picture in this book. He is well known for his work with Paleozoic scolecodonts and chitinozoans, as well as with mostly Cenozoic fungal spores, but he surely is best known for his creation of and tireless labor with the *Genera File of Fossil Spores*, an indispensable tool for the study of all fossil embryophyte spores and cryptospores, and, curiously, for the totally unrelated fungal spores. (See Traverse, 2004, for further information.) So, JJ belongs naturally in this stratigraphically intermediate point in our story.

that age and younger contain abundant land plant spores. The sporopolleninous exines "pioneered" by acritarchs and later by bryophyte-like green plants served presumably to protect the protoplasts of the haploid spores from desiccation, oxygen, ultraviolet light, and/or predation, mostly by arthropods.

There is a rich literature of Silurian chitinozoan studies, and it is unfortunate that space does not permit illustration of the often beautifully preserved chitinozoan faunas that have been published. One such paper with spectacular SEM illustrations is that of Ghavidel-Syooki and Winchester-Seeto (2004).

Scolecodonts continue to be important marine microfossils in the Silurian. One of the authorities on them is Jan Jansonius (see Figs. 6.14, 6.15, and 7.4).

Chapter 8

Devonian Palynology

1 Introduction

The approximately 45 million years long Devonian period was probably the finest hour of the embryophytic plants (see Fig. 8.1a). Represented in the Gedinnian stage at the beginning of the period by only *Cooksonia*, the parade was soon joined in that stage by *Zosterophyllum*, a member of a primitive line probably related to the lycophytes, then in the Siegenian by the trimerophytes (*Psilophyton et al.*), many more lycophytes (*Baragwanathia, Drepanophycus*), and possible arthrophytes (= sphenopsids) such as *Protohyenia*. In the Emsian all of these lines continued, joined by cladoxylaleans (*Cladoxylon*) and progymnosperms (*Aneurophyton*). By the Givetian the protopterids were around (see Fig. 8.1b). By latest Famennian time the progymnosperms had even produced true seeds. When this occurred, by definition, the microspore exine, plus the microgametophyte developed inside it, was a pollen grain. These primitive pollen grains, which morphologically were indistinguishable from microspores or isospores, are called prepollen. Hughes (1994) makes the interesting and defensible point that the critical thing about seed plants is actually the pollen and pollination, not the seed and whether it is "naked" (gymnosperms), or enclosed within a carpel (angiosperms). He thus introduced the concept of the "Pollenifera" for all Paleozoic and Mesozoic plants that produced seeds. So far, the concept has not been widely accepted.

All of the names mentioned in the preceding paragraph are for megafossil plants. The dispersed spores are separately named, and only relatively rarely do we find spores *in situ* in sporangia, giving us an idea of which *Sporae dispersae*

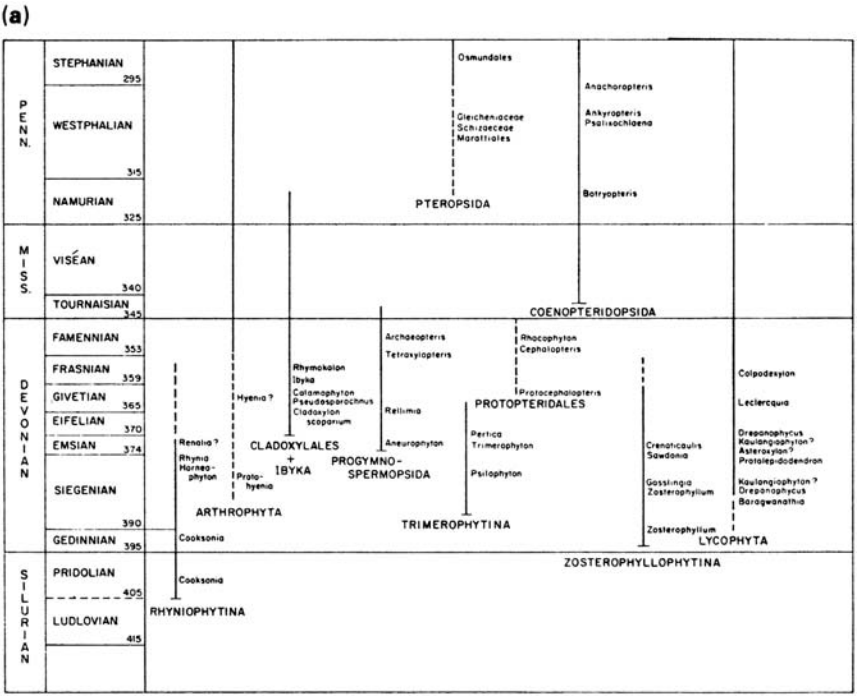

Figure 8.1a Ranges of early vascular land plant groups, stressing their rapid evolutionary expansion in the Devonian, reflected also in the spore record, as shown in *Fig. 8.1b*. From Gensel, 1977.

go with which megafossil plants. A list of such correlations is provided in the next chapter. From what we know of modern plants, it is not surprising that one sort of megafossil plant may produce more than one sort of dispersed spore, and that one sort of spore may occur in several different megafossil taxa!

As can be seen in Figs. 8.1b and 8.2, the numbers of kinds of embryophytic spores increase steadily during the Devonian. More generic names could now be added to Fig. 8.2, and the ranges extended somewhat, but the overall picture is unchanged. Not surprisingly, this is in line with the increase in diversity of kinds of vascular plants, and with increasing variety and complexity of vascular plant organs. Fig. 8.3 shows the concomitant diversification of spore features, both of general morphological characteristics and of exine construction. Chaloner (1970a) and others have said that steady increase in complexity and introduction of new forms of embryophytic plants from Lower Silurian through Devonian time, as reflected for example by spore morphology, bespeak a strong likelihood of monophyletic origin.

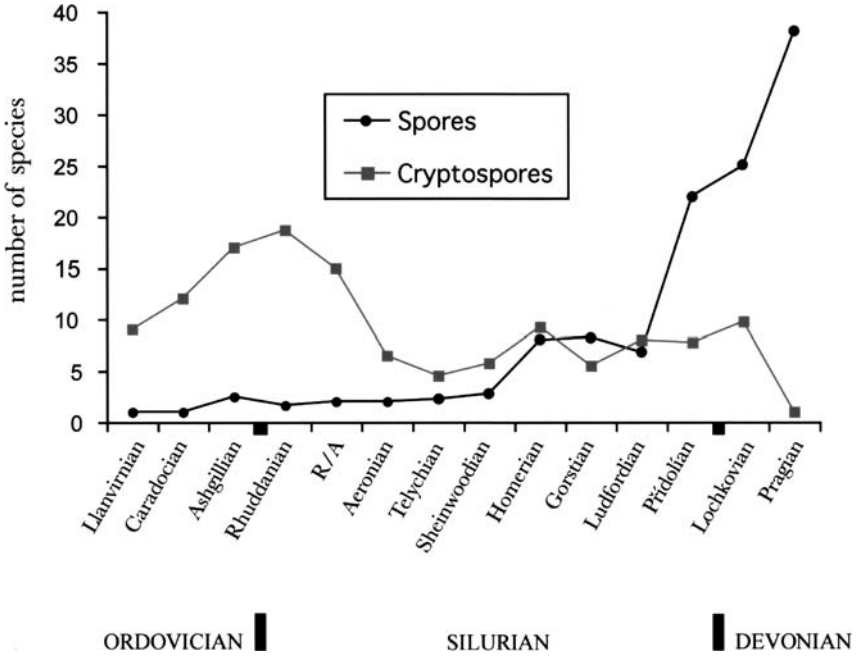

Figure 8.1b Spore and cryptospore species plotted as average species diversity per geologic stage. Stage R/A is from a deposit that has an age corresponding to the Rhuddanian/Aeronian (Lower Silurian) boundary. Data are based on 20 deposits for which new systematic studies or revisions have been published. The diagram was produced for the author by P. K. Strother (personal communication, 2005).

Regarding the developing provincialism of vegetation during the Devonian, studies of both spore and megafossil floras have demonstrated that detailed investigation reveals regional diversification, as would have been expected from great latitudinal spread of Devonian land masses (Raymond *et al.*, 1985a). Use of multivariate techniques such as cluster analysis promises to elucidate much more about phytogeography from abundant Devonian spore data. In the later part of the early Devonian, evidence has already been summarized by Raymond *et al.* (1985a) for an equatorial-low latitude unit (North America-Eurasia), an Australian unit, and a south Gondwana unit. The reservation expressed by Raymond *et al.* (1985b) that palynofloral and megafossil plant data may not correspond phytogeographically does not agree with either modern or sufficiently studied fossil models. Indeed, fossil spores/pollen from sediments other than peat and/or coal, because of their wide dispersal, generally do present, however, a more regionally representative picture than do megafossil floras.

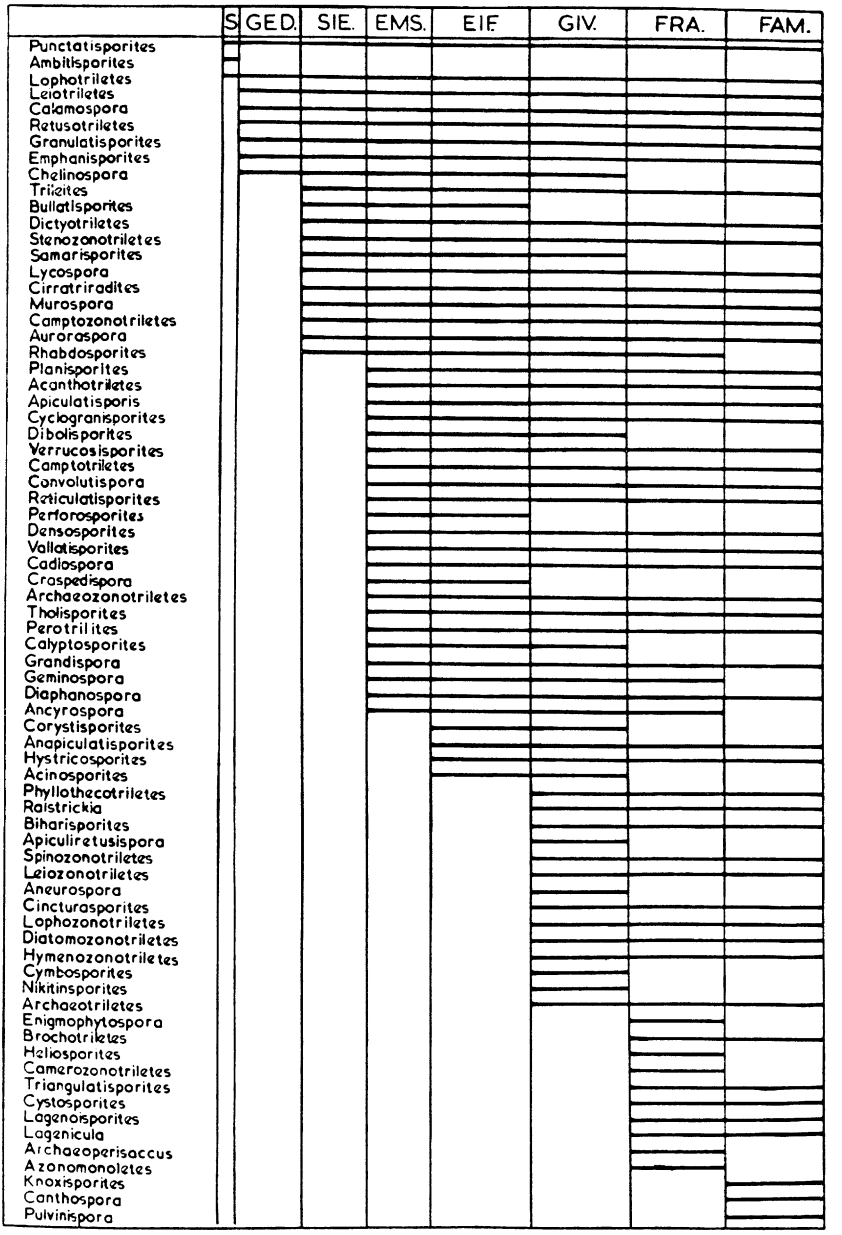

Figure 8.2 Devonian spore ranges. (S = Silurian; other abbreviations at top refer to Devonian stages; see Fig. 8.1). Most forms occurring at the end of the Famennian also occur in the Carboniferous. Chaloner (1967) in publishing this chart noted that it is a fair indication of diversification of land plants in the Devonian, and this remains true despite the fact that some of the ranges have been extended by more recent information.

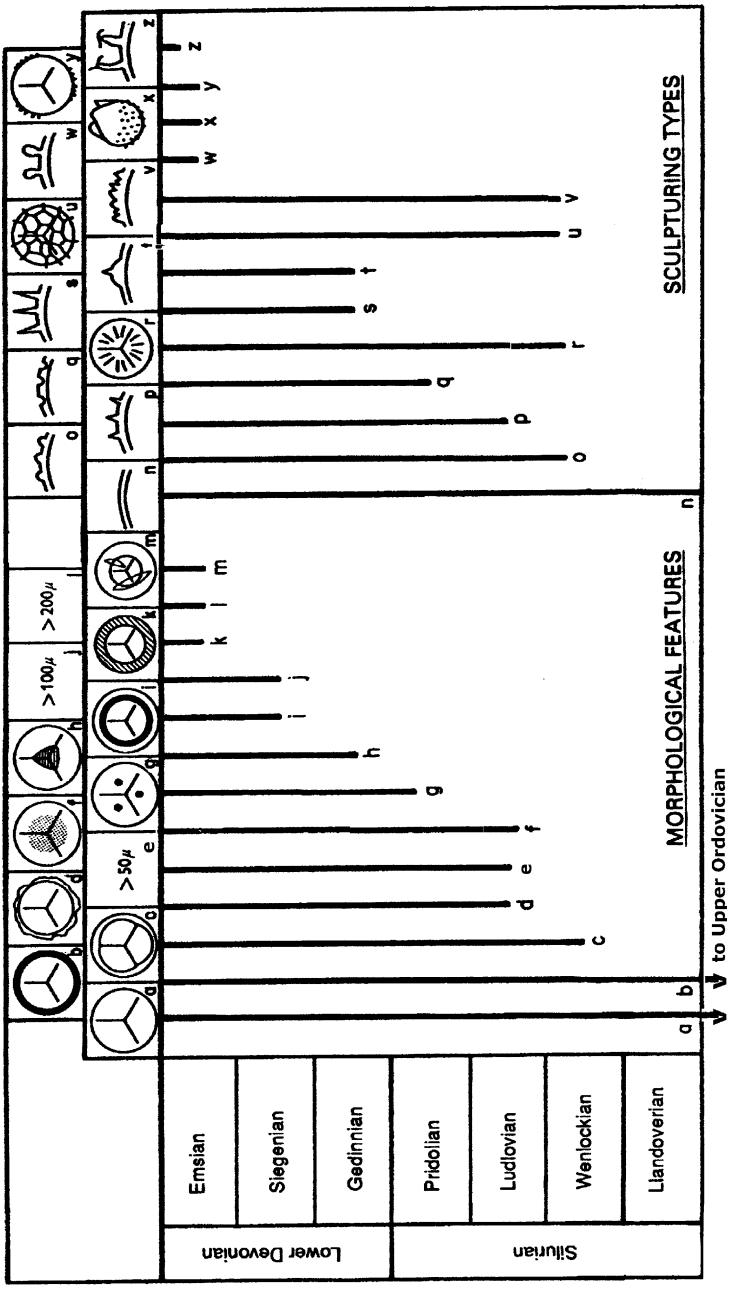

Figure 8.3 *(See caption on page 204)*

In the late Devonian, despite the near cosmopolitanism of some forms, particularly of the important latest Devonian marker, *Retispora lepidophyta* (Kedo) Playford, various taxa had restricted distribution, e.g., the early monolete form, *Archaeoperisaccus*, confined to a zone north of the presumed Devonian equator, Hudson Bay to Scandinavia (McGregor, 1979a).

2 Paleozoic Spore Morphology and Pertinence to the Devonian

In order to explain the course of Devonian spore developments, it is necessary to present some simple concepts about Paleozoic embryophytic spore morphology (see Fig. 8.4 for clarification). The fundamental type of embryophytic spore is trilete, as we have previously seen. When embryophyte spores first appear (excluding cryptospore forms such as the obligate tetrad form *Tetrahedraletes*, and monads which could be alete spores) in the Late Ordovician, they are small (about 20-30 μm range), trilete (with a raised laesura), relatively psilate in sculpture, simple. Some forms soon developed equatorial exinal thickenings (see Fig. 8.3). This makes the spores zonate. If the zona is thick, it is spoken of as a cingulum (Fig. 8.4). The contact areas between four distinct members of the original tetrad are the explanation for the trilete laesura's existence. These contact areas may be bounded on their outer sides by arcuate ridges (Figs. 5.6 and 8.4). This sort of feature is called a curvatura. If bounding the entire contact area, it is a curvatura perfecta; if fading out between ends of the radii, it is a curvatura imperfecta. Curvaturae are very important features of Devonian spore morphology. The zona and arcuate ridges were very early developments. Spores also quite soon began to include forms with an increase in size from the original 20-30 μm which still characterizes many homospores (= isospores). The 50 μm limit was reached in mid-Silurian time (Fig.8.3). Increase in size of disseminules

Figure 8.3 (**a**) simple triradiate sutures. (**b**) an equatorial thickening. (**c**) arcuate ridges. (**d**) a perisporal membrane. (**e**) diameter greater than 50 μm. (**f**) diffuse apical darkening. (**g**) interradial (proximal) papillae. (**h**) triangular apical darkening. (**i**) bizonal equatorial feature. (**j**) diameter greater than 100 μm. (**k**) a cingulum. (**l**) diameter greater than 200 μm. (**m**) spore with saccus. (**n**) exine smooth. (**o**) exine papillate. (**p**) exine with cones. (**q**) exine with punctae. (**r**) radial ribs (muri) on the proximal face. (**s**) exine with spines. (**t**) exine with biform processes. (**u**) exine reticulate. (**v**) exine verrucose. (**w**) exine with clavate processes. (**x**) strong differentiation of prominent proximal unornamented face and distal, ornamented, hemisphere. (**y**) ornament concentrated interradially. (**z**) exine with grapnel-ended processes. Modified from Chaloner (1970a) for the first edition; modernized here, per suggestions of J. H. Beck and P. K. Strother (personal communication, 2005), based on Burgess and Richardson, 1995; Dufka, 1995; Beck and Strother, 2001; Rubinstein and Steemans, 2002.

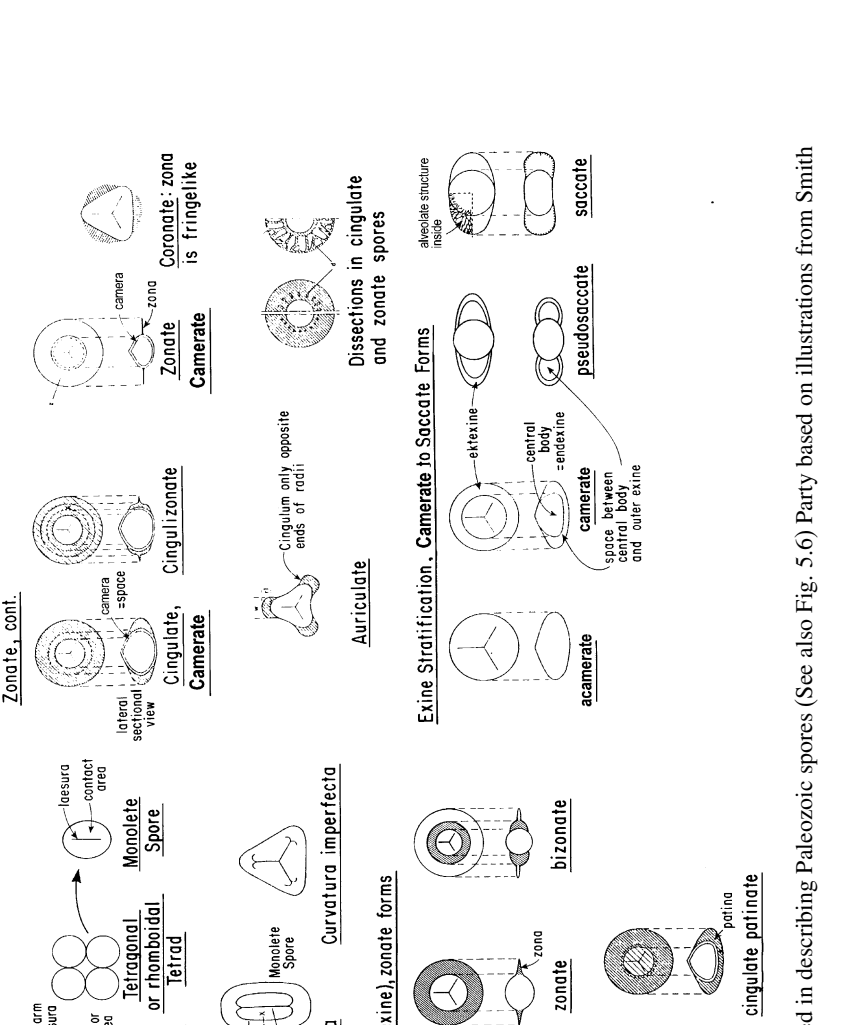

Figure 8.4 Salient features used in describing Paleozoic spores (See also Fig. 5.6) Party based on illustrations from Smith and Butterworth, 1967.

is a competitive advantage where environmental circumstances of dispersal favor greater investment in certain survival of a few disseminules, as opposed to random survival of a small percentage of many smaller ones, and may reflect dispersal other than by wind. At the end of the Silurian and early Devonian, exine modifications appear in greater diversity, presumably also reflecting dissemination requirements of some sort. For example, as reported by Labandeira (1998, 2002), insect and other arthropod coprolites from Silurian and Devonian rocks show that hexapod feeding on spores was well established that time. Thickenings ("darkenings") of interradial areas of the proximal face of the spore (Fig. 8.3) came in, soon followed by interradial spot thickenings or papillae and triangular thickenings in the area of the intersection of the laesurae arms.

In the Siegenian stage of the Devonian, there appears a further modification of the zonal equatorial feature that will continue to be important through the Paleophytic: bizonal, resulting from an equatorial extension that has two different thicknesses (see Figs. 8.3 and 8.4). In the Emsian, true cingula appear (like zonae, but thick), and spores with a saccus (or more exactly, pseudosaccus, because they lack internal structure of the "sacci"). Monolete spores are, from a phylogenetic point of view, derived from the basic trilete spore form, and they typically result from the spores being arranged in the original tetrad, not like a heaped up tetrahedron, but with the centers of the spores more or less in one plane, like the sections of an orange (see Figs. 5.3 and 5.8). (Intermediate, dilete forms exist but are rare.) Monolete spores sometimes occur in modern ferns in the same sori as trilete spores. They have never been as important a spore type as trilete. They first occur in the Emsian.

Other important features of Paleozoic spore morphology not already mentioned in connection with the first appearance of morphological types are illustrated in Fig. 8.4. The curvatura, already mentioned, is an important feature in Devonian spores, characterizing, for example, the genus *Retusotriletes*. Beginning already in the Devonian, Paleozoic spores show all sorts of changes on the equatorial extension or zonate theme, from simple zona or cingulum to bi- and trizonate and patinate (where a patina, or cingulum-like thickening covers the distal surface of the spore). If the cingulum is confined to the ends of the laesura radii, the form is called valvate or auriculate, and if fringe-like zona is seen (as in *Reinschospora*), the term coronate is employed to describe it (see Figs. 1.2 o-p and 8.4).

It is common, beginning with late Devonian spores, for the exine to have layers which separate from one another. If the separation is relatively small, the condition is called camerate (cavate). If the camera (separation space) is relatively large and becomes vesicle- or blister-like, the spore or pollen grain is called pseudosaccate. If the vesicle or saccus is partially filled with alveolar or webby contents instead of being empty, the spore or pollen grain is saccate. (As far as is known, truly saccate forms are always pollen.) Intermediate forms occur which are hard to "shoehorn" into camerate, pseudosaccate or saccate.

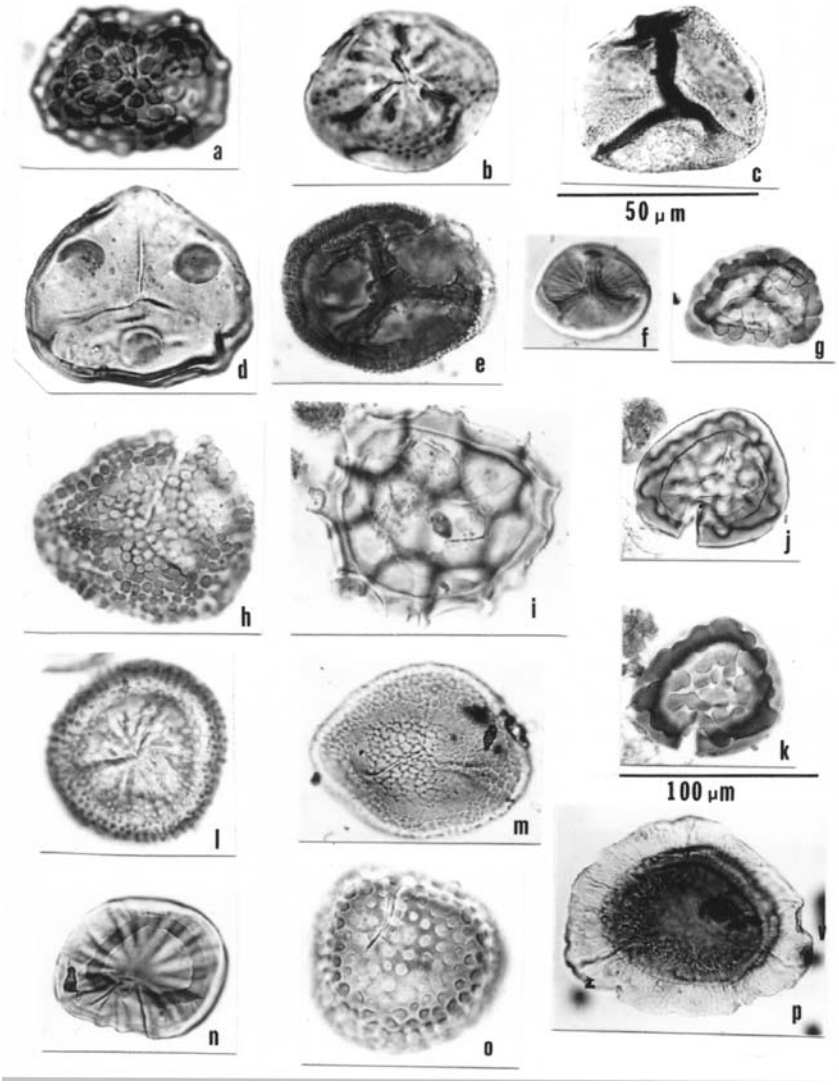

Figure 8.5 *(See caption on page 209)*

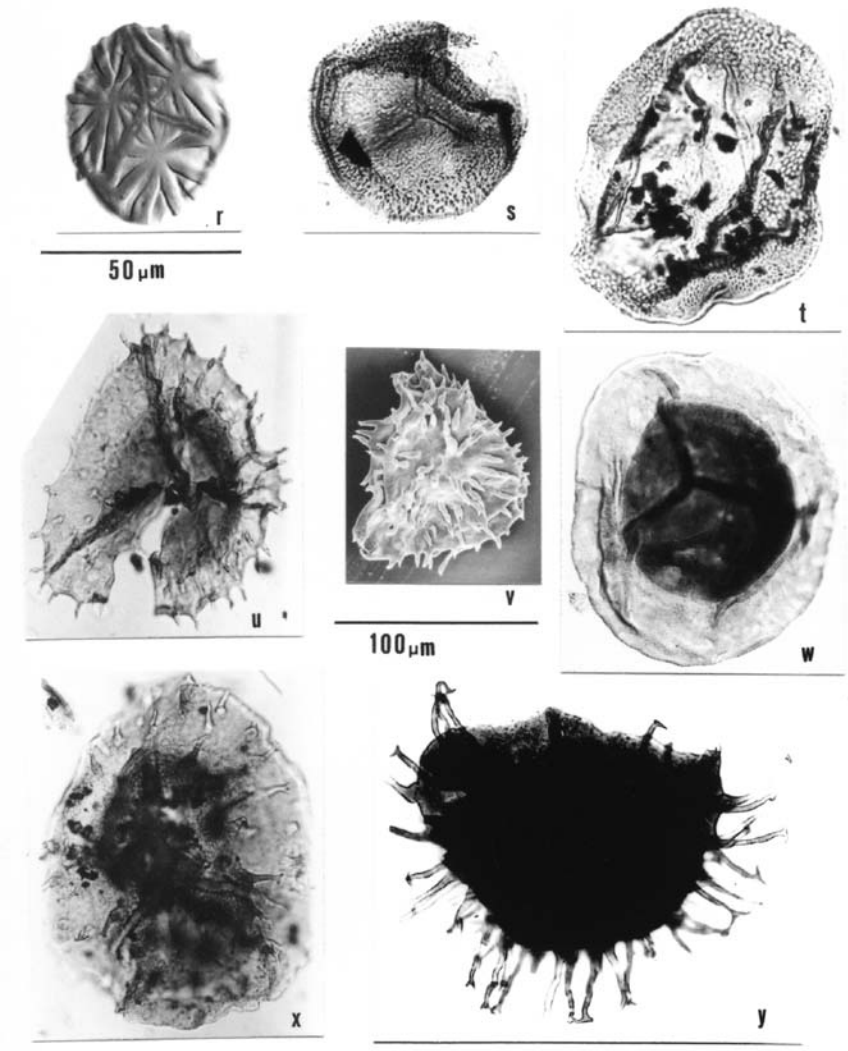

Figure 8.5

Along with the constructional changes noted during the Devonian, Chaloner (1970a) also pointed out (see Fig. 8.3) that exine sculpture changed in a regular progression. *Ambitisporites* of the Llandovery-Wenlock stages of the Silurian was smooth (psilate). Scabrate and slightly echinate (with coni) forms appeared soon after. Foveolate pitted exines appeared in latest Silurian time, as did radial ribbing (as in *Emphanisporites*) on the proximal surface. Truly spiny (echinate) sculpture began in the Gedinnian, along with biform appendages, e.g., spines on top of small mammae, and reticulate sculpture. Verrucose exines appeared in the Siegenian. Clavate sculpture is first encountered in the Emsian, along with spores with a bipolar difference in sculpture between proximal and distal faces. Sculpture confined to limited interradial areas also comes in during the Emsian, as well as exinal processes with curious "grapnel" hooks. Similar hooks are fairly common in both acritarchs and dinoflagellate cysts, but are very rare

Figure 8.5 Photomicrographs of Lower and Middle Devonian spores. Magnification for (a)-(f), (h),(i),(l), and (n) indicated by bar under (c), except that for (b) the same line represents 25 μm. A separate line is provided under (k) for (g),(j),(k),(m),(o) and (p). Magnification for (r)-(y) indicated by bar under (v), except for (r) which has its own bar. (**a**) *Cymbosporites verrucosus* Richardson & Lister, Gedinnian, U.K. (FM29). (**b**) *Emphanisporites microornatus* Richardson & Lister, Siegenian, U.K. (FM35). (**c**) *Apiculiretusispora plicata* (Allen) Streel, Emsian, Quebec (GSC-15153). (**d**) *Retusotriletes maculatus* McGregor & Camfield, Siegenian, Ontario (GSC-41706). Note interradial thickenings. (**e**) *Perotrilites microbaculatus* Richardson & Lister, Gedinnian, U.K. (FM38).(**f**) *Emphanisporites epicautus* Richardson & Lister, Gedinnian, U.K. (FM37). (**g**) *Clivosispora verrucata* McGregor var. *verrucata*, Emsian, Quebec (GSC-15179). (**h**) *Verrucosisporites polygonalis* Lanninger, Emsian, Quebec (GSC-31989). (**i**) *Dictyotriletes emsiensis* (Allen) McGregor, Siegenian, Ontario (GSCD-41734). (**j**),(**k**) Two focal levels of *Clivosispora verrucata* McGregor var. *convoluta* McGregor & Camfield, Siegenian, Ontario (GSC-27081). (**l**) *Emphanisporites decoratus* Allen, Siegenian, Ontario (GSC-27076). (**m**) *Dictyotriletes favosus* McGregor & Camfield, Emsian, Quebec (GSC-15181). (**n**) *Emphanisporites annulatus* McGregor, Emsian, Quebec (GSC- 32002). (**o**) *Brochotriletes hudsonii* McGregor & Camfield, Siegenian, Ontario (GSC-41729). (**p**) *Camptozonotriletes caperatus* McGregor, Emsian, Quebec (GSC-15197). Note filmy zona, approaching saccus structure. (**r**) *Emphanisporites schultzii* McGregor, Emsian, Quebec (GSC-32008). (**s**) *Dibolisporites echinaceus* (Eisenack) Richardson, Eifelian, Quebec (GSC-31972). (**t**) *Dictyotriletes canadensis* McGregor, Emsian, Quebec (GSC-32001). (**u**) *Grandispora douglastownense* McGregor, Emsian, Quebec (GHSC-32034). (**v**) *Hystricosporites microancyreus* Riegel, Emsian, Germany. (**w**) *Rhabdosporites langii* (Eisenack) Richardson, Eifelian/Givetian boundary, Scotland (FM46). (**x**) *Ancyrospora loganii* McGregor, Emsian, Quebec (GSC-15282). (**y**) *Hystricosporites* cf. *corystus* Richardson, Emsian, Germany. Numbers in parentheses are Geological Survey of Canada (GSC) or British Museum (FM) specimen numbers. Most of photomicrographs are courtesy of D. C. McGregor, except (a), (b), (e), (f) and (w) courtesy of J. B. Richardson, and (v) and (y) courtesy of W. Riegel.

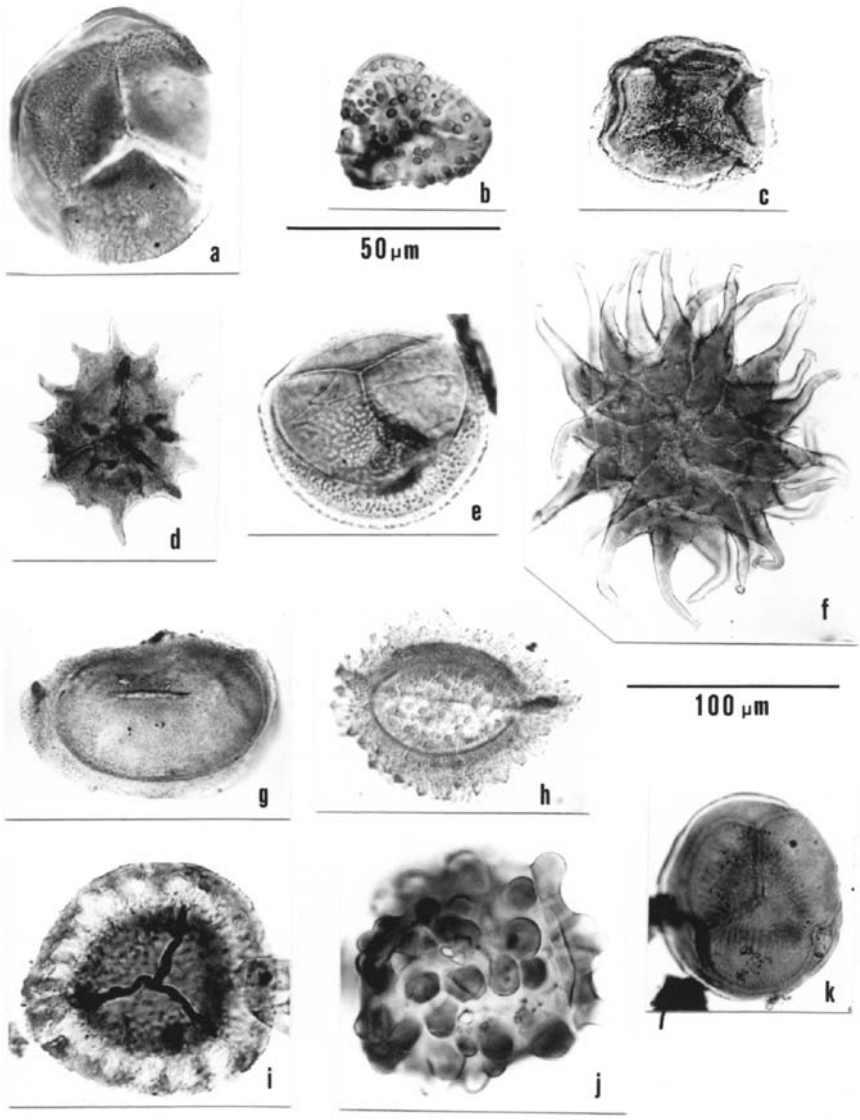

Figure 8.6

in spores, as far as I know. Turnau (2000) makes an interesting and important contribution to understanding some peculiarities of fossil palynomorph sculpturing by suggesting that it can actually be pseudosculpture caused by deposition of pyrite crystals in interstices of the wall. Turnau observed this phenomenon in probable Devonian prasinophyte phycomata, but I have observed similar pyritization effects producing "pseudosculpture" very often in palynomorphs of different ages, including the exines of land-derived pollen grains deposited in marine sediment.

A rather complex terminology has grown up to describe Paleophytic spore morphology. A compendium of such terminology, mostly from Smith and Butterworth (1967), is presented in Fig. 8.4. See also, if possible, the very useful summary of Grebe (1971). Figs. 8.5 and 8.6 present illustrations of the more prominent genera of Lower, Middle, and Upper Devonian spores. Note that, in the next chapter, a listing of "Paleophytic" (see Fig. 2.1) spores per their "turmal" classification and as to their relationship to producing plants is given. This list also includes Devonian spores.

3 Megaspores, Seeds, and Pollen

We have already noted that certain spores reached the 50 μm size range in mid-Silurian time (see Fig. 8.3). This already probably represents a trend because the size for average modern isospores is around 30-40 μm. A much clearer indication

Figure 8.6 Middle and Upper Devonian spores. Magnification for (a),(b),(e),(g),(i) and (k) indicated by bar under (b). Magnification for (c),(d),(f), and (h) indicated by bar under (f). Devonian stage name for source immediately follows name of spore. (**a**) *Retusotriletes rugulatus* Riegel, Givetian, Melville Island, Arctic Canada (GSC-66379). (**b**) *Lophotriletes devonicus* (Naumova ex Chibrikova) McGregor & Camfield, Upper Eifelian-Lower Givetian, Melville Island, Arctic Canada (GSC66356). (**c**) *Perotrilites conatus* Richardson, Eifelian/Givetian boundary, Scotland (FM57). (**d**) *Ancyrospora melvillensis* Owens, Frasnian, Ellesmere Island, Arctic Canada (GSC73295). (**e**) *Geminospora lemurata* Balme, Givetian, Melville Island, Arctic Canada (GSC66296). (**f**) *Hystricosporites gravis* Owens, Givetian, Melville Island, Arctic Canada (GSC15550). (**g**) and (**h**) represent very early monolete spores: (**g**) *Archaeoperisaccus ovalis* Naumova, Frasnian, Melville Island, Arctic Canada (GSC-73296). (**h**) *Archaeoperisaccus opiparus* Owens, Frasnian, Melville Island, Arctic Canada (GSC73298). (**i**) (?)"*Hymenozonotriletes denticulatus* Naumova" McGregor 1967 (GSC49850). (**j**) *Lophozonotriletes lebedianensis* Naumova, Famennian, Bathurst Island, Arctic Canada (GSC 15422). (**k**) *Retusotriletes phillipsii* Clendening *et al*., Famennian, New York (FM64). Numbers in parentheses are Geological Survey of Canada (GSC) type specimen numbers, except for (c) and (k), for which British Museum (FM) specimen numbers are given. Photomicrographs courtesy of D. C. McGregor, except (c) and (k) courtesy of J. B. Richardson.

of trend is shown by the first 100 μm spores in Siegenian (Lower Devonian) time, and the first 200 μm spores in the Emsian. I have already stated that 200 μm is the arbitrary limit between the artificial categories "miospore" and "macrospore" of Guennel, but it works pretty well also as the size limit between the functional biological categories of megaspore and microspore (see Fig. 8.7). In other words, the 200 μm spores of late Devonian time were almost certainly true, functional megaspores. Hemsley *et al.* (1999) suggest that 115 μm may well have been close to the actual dividing line, and Marshall (1996) in a very interesting study showed that the transition to functional megaspore/microspore differentiation can possibly be traced in the British middle Devonian to the evolution from aneurophytalean progymnosperms, represented by *Rhabdosporites* homospores, to archaeopteridalean progymnosperms, represented by *Geminospora* microspores and *Contagnisporites* megaspores. Chaloner and Hemsley (1991) present evidence that while heterospory developed independently in various vascular plant lineages, the ultrastructure of megaspore exines provides strong indications that the evolution leading to the seed-habit was in all cases from homospore through megaspore, and never directly from homospore to seed-habit. Kar and Dilcher (2002) suggest that at least in some lines of plant evolution the development of megaspores was initially an adaptation to dispersal by floating of the spores in aquatic environments.

To illustrate the difficulty of making definitions fit all cases, some genera of fossil spores, such as *Hystrichosporites*, range well below and well above the 200 μm limit and thus, in the "Guennel sense," include both "macrospores" and miospores! Furthermore, a Devonian megaspore form, *Cystosporites*, can be over a centimeter (!) in largest dimension, consisting of one very large functional spore and three aborted spores closely adhering to it. It is natural to speculate that, though this spore was produced by a lycopsid and was biologically a megaspore, it functioned from a practical point of view almost as a seed, hence the term for it: "seed-megaspore." Such enormous free-sporing megaspores were also made by sphenopsids and progymnosperms.

The trend toward existence of some much larger spores was a big feature of the Devonian. This increase in disseminule size certainly represented a stage in the move toward the seed-habit. The large investment in a limited number of megaspores was perhaps an advantage for establishing a plantlet in a hostile environment. After late Devonian-Carboniferous time, functional, free megaspores were never again so important, though a few heterosporous non-seed plants, e.g., *Selaginella, Marsilea*, and *Azolla*, continue to produce them still. The study of megaspores is therefore especially rewarding in the Devonian and Carboniferous, although important studies have also been made of Mesozoic megaspores. Their potential stratigraphic and paleoecological usefulness has been amply demonstrated in such works as Chi and Hills (1976) for Arctic Canada, Scott and King (1981) in England, Higgs and Scott (1982) in Ireland, and Candilier *et al.* (1982) in North Africa. Stolar (1978) has shown that the Devonian/Carboniferous

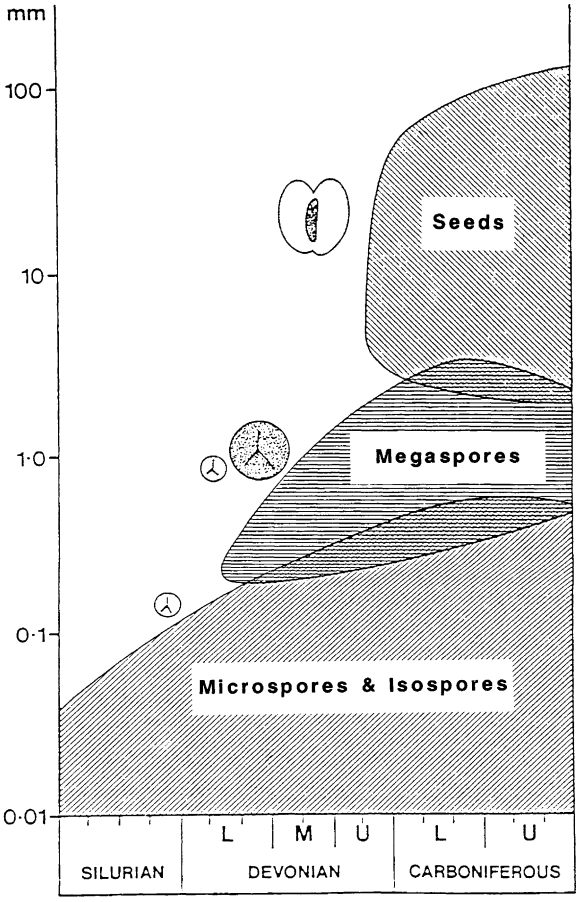

Figure 8.7 The transition from plants producing only isospores, to heterosporous plants with two kinds of spores, microspores and megaspores, came about in the Lower Devonian. It is probable that when the 100 μm (.1 mm) size-limit was crossed in the Lower Devonian, at least some of the 100 μm spores were functional megaspores. When the 200 μm boundary was crossed just a little later, most of the spores greater than 200 μm were surely functional megaspores. Free-sporing megaspores range up to about 5, 000 μm(5 mm). Hence, in size, megaspores overlap with large isospores-microspores, and with small seeds. Seeds first appeared in uppermost Devonian and range in maximum size to about 100 mm (10 cm) by Upper Carboniferous. (Modified from Scott, 1984, originally based on a figure in Chaloner and Sheerin, 1981.)

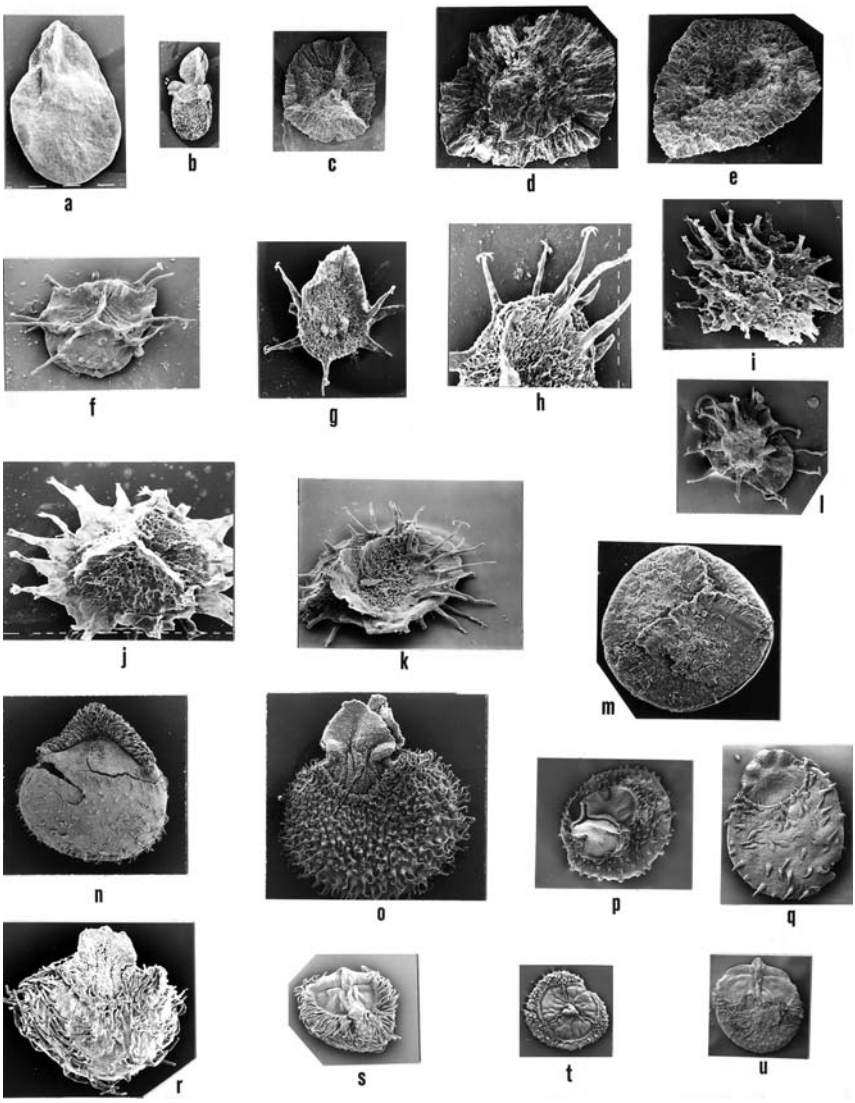

Figure 8.8

Figure 8.8 Latest Devonian and Carboniferous megaspores. Late Devonian to mid-Carboniferous was the heyday of sporopolleninous free-sporing megaspores. All of the pictures shown are SEM micrographs, but megaspores can also be photographed with appropriate lenses by reflected light, as microphotographs. Transmitted light study is not so satisfactory, because of the thickness of the specimens, but can be useful for demonstration of a central body. All of these SEM micrographs are at much smaller magnification than is true for photomicrographs of miospores elsewhere in this book. Magnification varies considerably and size is given with each caption. (a)-(l) are from latest Devonian, Ireland; (n)-(o) and (r) are from the Lower Carboniferous of Scotland; and (m),(p),(q) and (s)-(u) are Carboniferous megaspores reworked into Tertiary, southern England. (**a**) *Sublagenicula* cf. *nuda* (Nowak & Zerndt) Dybova-Jackowicz *et al.* Lateral view, length 830 μm. The upper section is the contact area with a three-cornered "hat" appearance. This is termed the gula, but it is only modestly developed here. (**b**) *Auritolagenicula rugulata* Higgs & Scott. Lateral view, length 1, 100 μm (photo is at low magnification!). The gula is here very fully developed, with auriculate extensions of the trilete rays. (**c**) *Triangulatisporites*(?) *leinsterensis* Higgs & Scott. Proximal view, diameter 1, 120 μm. (**d**) Same species as (c). Specimen 1, 000 μm in diameter but more magnified than (c). Proximal view. (**e**) Same species as (c),(d). Distal view, showing well developed zona, length 920 μm. (**f**) *Hystricosporites delectabilis* (McGregor) McGregor. Lateral view, length 600 μm. Note "grapnel hooks" on ends of processes, characteristic for the genus. Fragments of these processes are frequently found in miospore preparations. (**g**) *Hystricosporites* cf. *multifurcatus* (Winslow) Mortimer & Chaloner. Length 460 μm. (**h**) Same species as (g), detail. (**i**) *Ancyrospora furcula* Owens. A genus quite similar to *Hystricosporites*, with specimens sometimes well below the 200 μm usual cutoff for megaspores. Length of this specimen 380 μm. (**j**) Same species as (i). Proximal surface, demonstrating the zonate nature of Ancyrospora, a feature helping to distinguish it from *Hystricosporites*. (**k**) *Hystricosporites winslovae* Higgs & Socott. Proximal view, length 300 μm. A somewhat flattened specimen showing from the one complete process what has happened to the others. *Hystricosporites* process tips tend to be broken off. (**l**) *Hystricosporites winslovae* Higgs & Scott. Distal view, length 500 μm. (**m**) *Zonalessporites brassertii* (Stach & Zerndt) Potonié & Kremp. Proximal view, diameter 1, 000 μm. (**n**) *Setispora subpaleocristatus* (Alvin) Spinner. Lateral view showing an erect laesura with anastomosed hairs along the radii, and scattered echinate sculpture on the distal side. Maximum dimension 1, 430 μm. (**o**) *Lagenicula crassiaculeata* Zerndt. Lateral view showing apical prominence or gula, being the ruffled" contact area. Maximum dimension 1, 830 μm. (**p**) *Lagenicula horrida* Zerndt. Proximal view showing the contact area and modest gula. Diameter 800 μm (see (q)). (**q**) Same species as (p). Lateral view. Maximum dimension 960 μm. (**r**) *Lagenicula subpilosa* (Ibrahim) Potonié & Kremp forma *major* Chaloner ex Dijkstra. Lateral view showing the apical prominence or gula and the pilose sculpture. Diameter 1, 200 μm. (**s**) *Setosisporites* cf. *hirsutus* (Loose) Ibrahim. Obliquely proximal view showing the contact area, "ruffled" laesural radii and strands of exine sculpture. Maximum dimension 580 μm. (**t**) *Setosisporites hirsutus* (Loose) Ibrahim. A different variety from that in (s). Proximal view showing contact area and small gula. Diameter 560 μm. (**u**) Same species as (t). Further illustrating sculptural variability of this species. Maximum dimension 600 μm. (a)-(k) courtesy of A. C. Scott, originally appeared in Higgs and Scott, 1982. (n)-(o) courtesy of A. C. Scott, originally appeared in Scott and Meyer-Berthaud, 1985. (m), (p), (q), and (s)-(u), courtesy of M.E. Collinson, originally appeared in Collinson *et al.*, 1985.

boundary in central Pennsylvania can be demonstrated with megaspores as well as with miospores.

The techniques for processing and study of megaspores are different from those for miospores, because of their size and abundance (see Appendix). Whereas Paleophytic miospores commonly have a concentration of 5,000 to 10,000 per gram of sediment, megaspores are always much (several orders of magnitude) less abundant. Hills (1984) describes Devonian-Carboniferous megaspores with a concentration of 100/g as "extremely common"! For miospores, a sample with such a concentration would be reported as "yield poor." Fig. 8.8 shows some typical Paleozoic megaspores.

4 Pollen vs. Spore Morphology, Polarity, and Germination

It is necessary at this point to digress somewhat to review and expand what we have learned earlier of basic spores/pollen morphology, in order to have a clear grasp of what the morphology of Paleozoic spores/pollen means. Figs. 8.9 and 8.10 help review the facts. Basic homosporous spores are what existed in

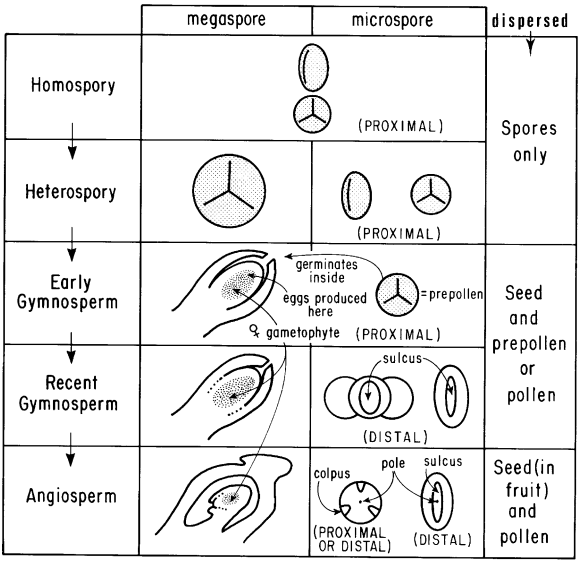

Figure 8.9 Spore evolution. Note that early gymnosperm prepollen germinated proximally, as do pteridophyte spores. Recent gymnosperm pollen germinates distally at the sulcus, and angiosperm pollen germinates either distally (sulcus) or laterally (colpus), or otherwise. (Modified from Chaloner, 1970b).

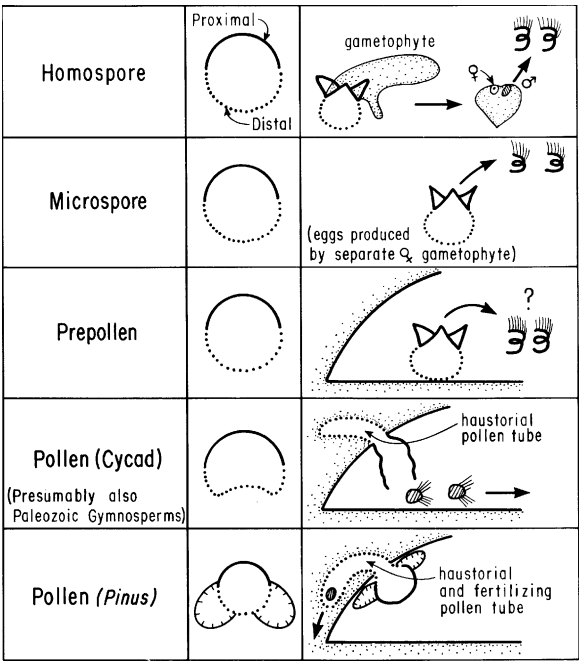

Figure 8.10 Diagram of evolutionary change in polarity of spore germination. Homospores germinate proximally by dehiscence along the laesura. The usually bisexual gametophyte produces eggs and sperm. Microspores germinate proximally just as homospores, but the male gametophyte is very reduced, producing practically nothing but sperm. Prepollen germinated in a pollen chamber of the female, seed-producing organ. Primitive gymnosperm pollen presumably germinated as modern cycad pollen–distally to produce a haustorial pollen tube but proximally to release sperm. In modern conifers, the pollen germinates distally to produce a pollen tube, but this acts both haustorially and to convey the gamete nuclei, the method also used by angiosperms. Modified from Chaloner, 1970b.

Silurian and Lower Devonian time. The laesura is a scar representing the place of the spore in its original tetrad–in other words, it is a haptotypic feature. It also serves as a zone of weakness for the opening of the spore for the germination of the contents. As seen in Fig. 8.10, the spore thus opens proximally for the gametophyte to begin to grow.

Spermatozoids and eggs are produced by this bisexual gametophyte. Heterospory probably was under way when spores larger than 100 μm appeared in the Siegenian, but certainly was present when spores larger than 200 μm appeared in Emsian time. As can be seen from Fig. 8.10, microspores germinate in the same manner as homospores, along the laesura on the proximal side of

the spore. It is not shown in the diagram, but the megaspores also germinate the same way.

Seed plants appeared in the Famennian. The term "seed" means that a single megaspore germinates in the megasporangium to produce a megagametophyte, the egg of which is fertilized in situ. The associated microspores in the Famennian were by definition pollen grains (prepollen = pollen with morphological features of spores) which germinated on or very near the opening to the megasporangium, producing male gametophytes, the spermatozoids of which fertilized the egg of the female gametophyte yielding a seed. Note in Figs. 8.9 and 8.10 that a prepollen grain behaved just as the microspore it is; it germinated proximally and presumably produced motile spermatozoids. This kind of fertilization is called zoidogamy, and it still occurs in cycads and *Ginkgo*, as was discovered more than a century ago (see historical discussion by Poort *et al.*, 1996). Prepollen can

Figure 8.11 Nobody has had more impact on the basic concepts of the pollen and spore parts of paleopalynology than William G. Chaloner (see Figs. 8.9 and 8.10). Emeritus Professor of Botany, Royal Holloway, University of London, UK, "Bill" is shown here in front of Royal Holloway's main building. I have eulogized this outstanding figure in print (Traverse, 1993), at which time I felt especially grateful to him for his help and encouragement in the production of the first edition of this book. He is also an important figure in paleobotany generally.

develop pollen tubes which emerge distally, but their function is haustorial, not the delivery of sperm nuclei to the megagametophyte, as in typical pollen.

A little later, presumably in the Pennsylvanian, gymnospermous fossil evidence and observations of some present-day cycads show that the pollen tube's function was originally haustorial, i.e., it acted as a "root" for the pollen, to absorb nutrients to support its life processes. The grain continued to open proximally for the generative purpose. Only later did more advanced gymnosperms abandon proximal germination of the pollen and used the pollen tube, produced distally from a germinal furrow (colpus), for both haustorial action, and to conduct sperm nuclei to the megagametophyte for generative purposes (a very clear explanation of prepollen is to be found in Poort *et al*, 1996, and in Visscher, 1997). Angiosperms, of course, do basically the same thing–the pollen tube of *Zea mays*, for example, comes out of the (distal) pore of the pollen grain, and then traverses up to a half-meter of style ("silk"), "living off the land" haustorially and carrying its important message of sperm nuclei to the ovule (=megagametophyte). A major player in the development of this subject has been William G. Chaloner. (Fig. 8.11).

5 Non-Spore Palynomorphs in the Devonian

Acritarchs in marine Devonian rocks are important and useful in palynostratigraphy. They have also been used in paleoecological reconstruction of paleoenvironments. Their undoubted stratigraphic and paleoecological potential still is only partly realized. Staplin (1961), working when acritarchs were still called hystrichosphaerids, clearly showed their importance in interpreting current patterns and other marine sedimentation factors. Riegel (1974), has shown that Devonian neritic (shallow water) facies of Europe have relatively depauperate acritarch assemblages compared with associated pelagic (open ocean) facies.

Paleographic studies of Devonian acritarchs are still needed, although Nautiyal (1977) some time ago identified acritarch facies areas that may be climatically controlled. Playford and Dring (1981) have demonstrated the usefulness of Devonian acritarch studies in Australia, and Playford (1977), Wicander and Wood (1981), and Wicander (1983, 1984) have put Devonian acritarchs on the map in North America and have summarized the considerable potential stratigraphic use of acritarch studies in the North American Devonian. Wicander and Wood (1997) have done innovative work in the Middle Devonian of Iowa in which phytoplankton, chitinozoans and spores are all used in relation to each other, to get a grasp of the sedimentary and general environment indicated for transgressive and regressive cycles. This utilizes a concept that I describe later in this book as palynobiofacies.

The worldwide biological crisis near the end of the Devonian (known, especially in Europe, as the Kellwasser Event) at or near the Frasnian/Famennian boundary had very obvious effects in the paleopalynological record. As has been seen in Chapter 6 (see especially Fig. 6.10), acritarchs, certainly the major phytoplanktonic element of early Paleozoic seas, are reduced to a relatively few forms at the end of the Devonian, one of the great palynological mass extinctions of the geological record. What is just as curious as the decimation of the acritarchs at that time is, that for the Carboniferous, Permian and most of the Triassic periods–about 140 million years–they are not replaced by ecologically equivalent microscopic forms with a sporopolleninous wall, until robust-walled dinoflagellate cysts appear in the Late Triassic. See Fig. 8.17 at the end of this chapter, which highlights the fact that the acritarchs remained a diverse, abundant and important group in marine environments right up to their end-Devonian near-demise.

Chitinozoans are another apparent casualty of the Kellwasser Event. At least, they continue to occur in marine sedimentary rocks right up to the end of the Devonian and are then gone. Scolecodonts continued to occur in marine rocks

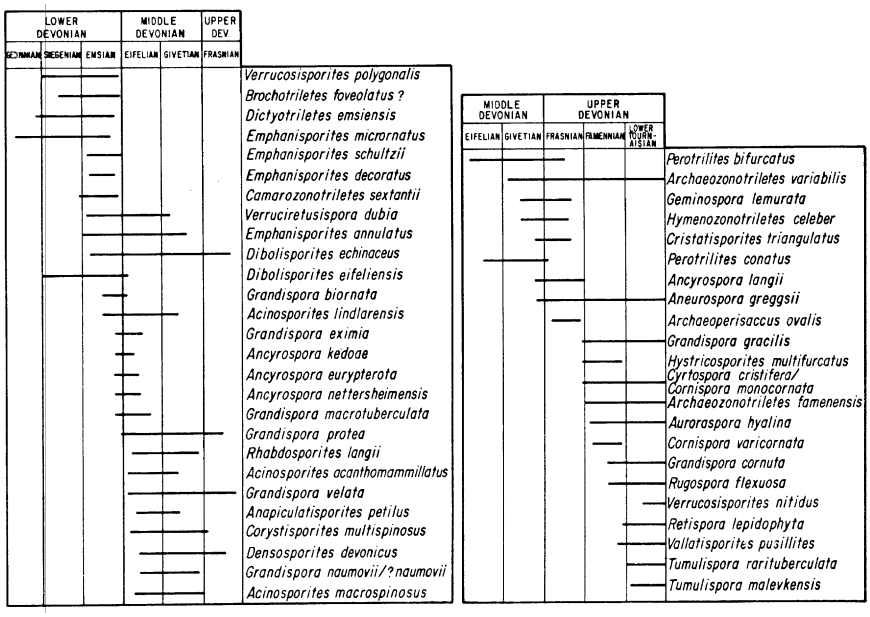

Figure 8.12 Stratigraphic ranges of Devonian spores useful for zonation, for which age ranges have marine faunal control: Lower and Middle Devonian at left, late Middle and Upper Devonian at right. Information from D. C. McGregor. Previous version published in McGregor, 1970b.

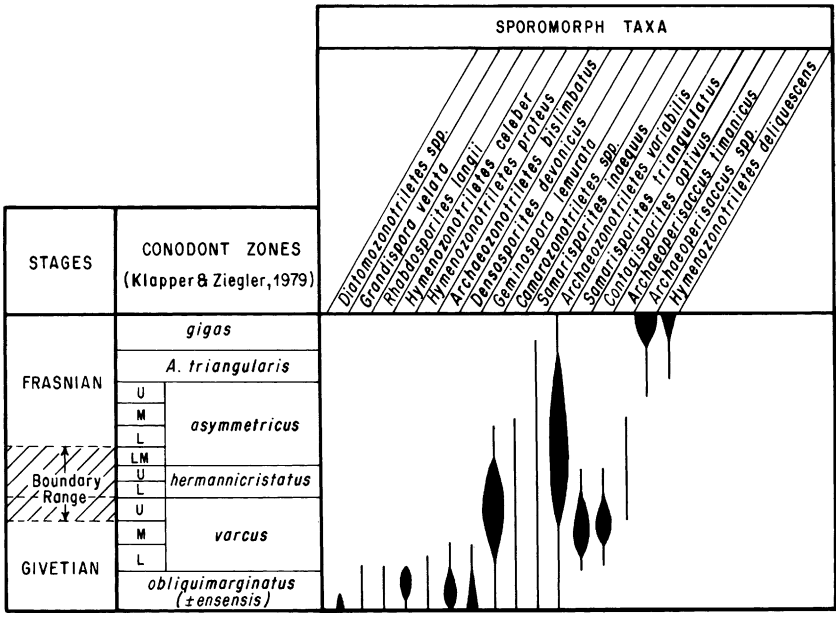

Figure 8.13 Graphical summary of palynological contributions to stratigraphy of the Middle vs. Upper Devonian. The internationally recognized standard is based on conodont zonation in Europe. The Givetian/Frasnian boundary is now established by international agreement at the base of the *asymmetricus* conodont zone. The spores/pollen ranges correlated with the conodont zones can be extended over wide areas and into non-marine sections such as the Catskill Magnafacies of New York-Pennsylvania, USA. (Modified from McGregor, 1981.)

across the Devonian/Carboniferous boundary and for that matter do so to the present, though they are not as abundant or diverse in Mesozoic and Cenozoic rocks as they were in the Paleozoic (cf. Jansonius and Craig, 1971). As we shall see in the next section, the end-Devonian event apparently had some effect in the non-marine parts of the plant kingdom. There were some extinctions, but it is clear that whatever happened in the oceans had a much more muted effect on land.

6 Devonian Palynostratigraphy

Paleopalynology, especially spores/pollen-based, has been much used in connection with various Devonian biostratigraphic problems. McGregor in North America (Figs. 8.12 – 8.14), Streel, Richardson, and Clayton in northwest Europe, and Kedo in the former USSR have been particularly active in establishing

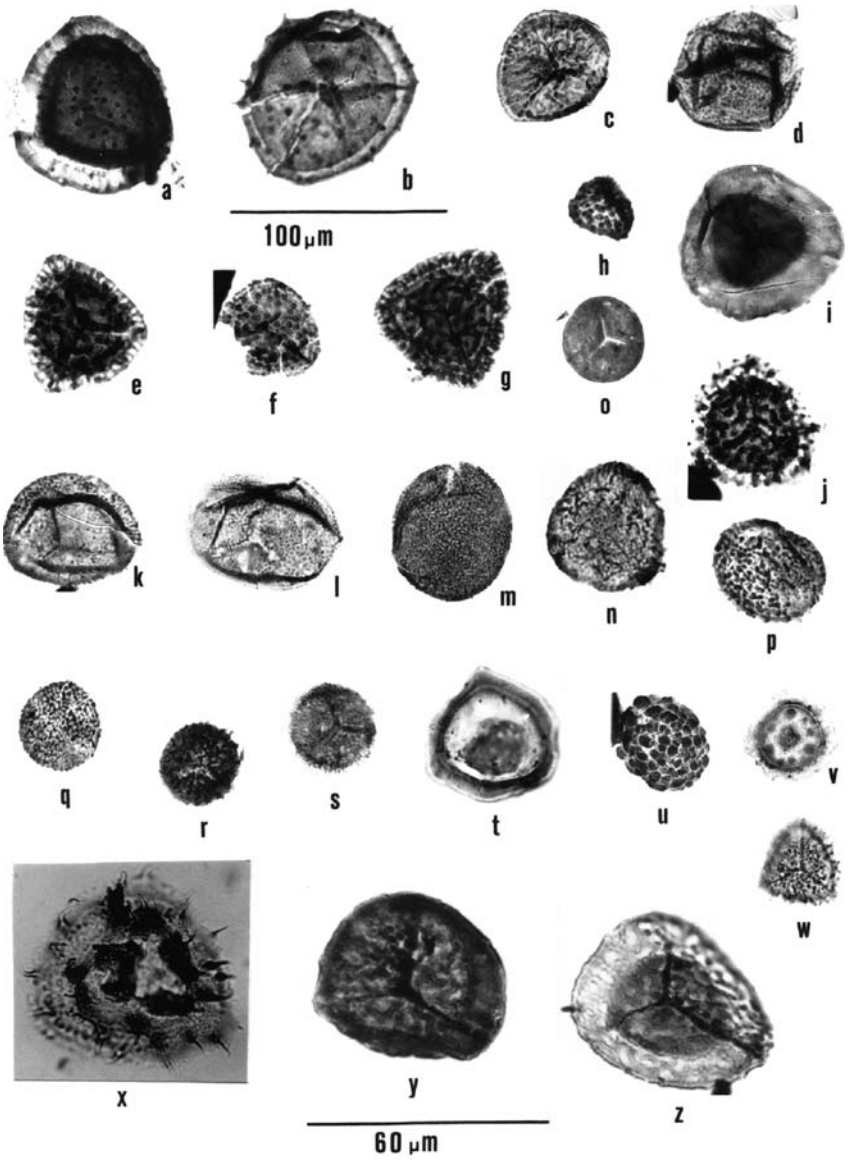

Figure 8.14

palynostratigraphic frameworks for the Devonian. Fig. 8.13 shows a summary of the application of palynostratigraphic methods to establishing the boundary between Middle and Upper Devonian. Fig. 8.14 displays some of the prominent spore types employed in Upper Devonian to Lower Carboniferous palynostratigraphy. (See Fig. 9.1: Mississippian in North America is equivalent to Lower Carboniferous in some classifications but includes some of the lower part of the Upper Carboniferous in others.)

The Kellwasser event mentioned above as related to decimation in diversity and abundance of acritarchs and the extinction of chitinozoans also affected land vegetation and therefore the miospore palynoflora, as has been summarized by Streel *et al.* (2000). Various authors have noted that, in addition to extinction of some forms and a decline in miospore diversity near the Frasnian/Famennian boundary, there even was a marked decrease in the size of miospores of some species that persisted, as if the spore-producing plants were stressed. I have observed in the modern vegetation that pollen from plants collected near the distribution limit of a species are often smaller than those from the species main center of distribution.

One especially interesting palynostratigraphic problem has been that of the Devonian/Carboniferous (Mississippian) boundary. Since publication of the first

Figure 8.14 Characteristic spores of the Devonian/Carboniferous (Mississippian) boundary. Magnification for (a)-(w) indicated by bar under (b). Magnification for (x)-(z) indicated by bar under (y). Spores (a)-(w) are from the uppermost Devonian of the Schiefergebirge of the Rhine area, Germany: (a)-(j) are from LE Biozone in the Riescheid section; (k)-(w) are from LN Biozone in Seiler trench B. Spores (x)-(z) are from the uppermost Devonian of Centre County, Pennsylvania. (**a**) *Hymenozonotriletes explanatus* (Luber) Kedo. (**b**) *Grandisporea echinata* Hacquebard. (**c**) *Rugospora flexuosa* (Jushko) Streel. (**d**) *Cyclogranisporites* sp. (**e**) *Vallatisporites verrucosus* Hacquebard. (**f**) Same as (e), to show variability. (**g**) *Vallatisporites pusillites* (Kedo) Dolby & Neves. (**h**) *Archaeozonotriletes minutus* Kedo. (**i**) *Diducites mucoronatus* (Kedo) Van Veen. (**j**) *Vallatisporites pusillites* (Kedo) Dolby & Neves; compare with (g). (**k**) *Apiculiretusispora verrucosa* (Caro-Moniez) Streel. (**l**) *Cyclogranisporites* sp.; compare with (d). (**m**) *Convolutispora ampla* Hoffmeister, Staplin & Malloy. (**n**) *Pulvinispora scolephora* Neves & Ioannides. (**o**) *Punctatisporites planus* Hacquebard. (**p**) *Pustulatisporites* sp. (**q**) *Camptotriletes paprothii* Higgs & Streel. (**r**) *Raistrickia* sp. (**s**) *Rugospora* sp. (**t**) *Tumulispora ordinaria* Staplin & Jansonius. (**u**) *Verrucosisporites nitidus* (Naumova) Playford. (**v**) *Lophozonotriletes triangulatus* (Ischenko) Hughes & Playford. (**w**) *Vallatisporites vallatus* Hacquebard. (**x**) *Cirratriradites hystricosus* Winslow–some regard this as part of a complex of "palynodeme" with (g),(j) and (w). (**y**) *Rugospora flexuosa* (Jushko) Streel; compare with (c). (**z**) *Retispora lepidophyta* (Kedo) Playford. (Photomicrographs (a)-(w) are courtesy of M. Streel and K. Higgs; most of them were published in Higgs and Streel, 1984.)

edition of this book there have been many conferences and publications dealing with this problem. Particularly significant have been Streel and associates' investigations on stage type sections in Belgium. Streel has shown that this boundary can be well established palynologically in Belgium on the basis of the last appearance en masse of *Retispora lepidophyta* (alias *Hymenozonotriletes lepidophytus* or *Spelaeotriletes lepidophytus* of various authors) in the uppermost Devonian, along with other forms such as *Cirratriradites hystricosus* and *Rugospora flexuosa* (= "*Hymenozonotriletes famennensis*").These spore-based levels in Belgium can be keyed to the critical conodont levels because there are strata in which the land-based spores and the marine conodonts both occur. Maziane, Higgs and Streel (1999) have published the detailed spore sequence for the uppermost Devonian stage, the Famennian, keyed to the conodont zonation. An interesting example of the applicability of Devonian palynology

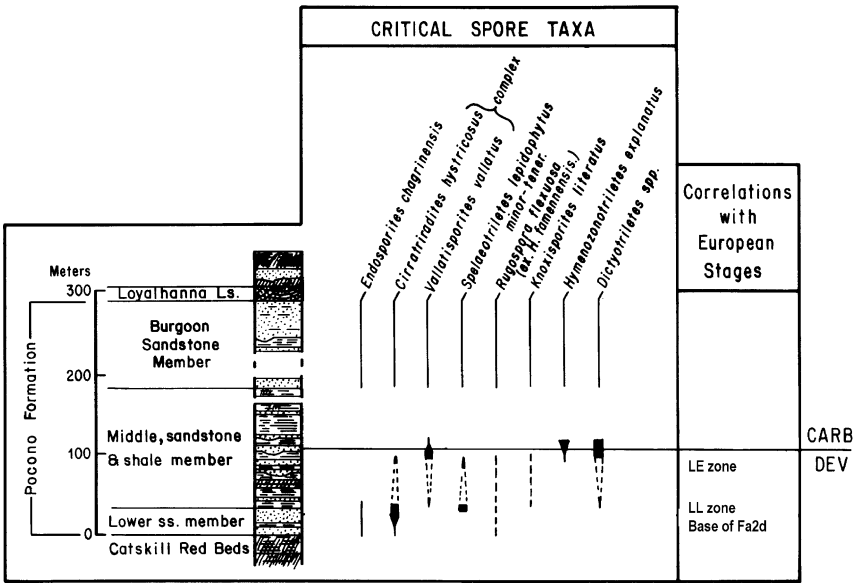

Figure 8.15 Horseshoe Curve, near Altoona, Pennsylvania: placement of Devonian/Mississippian (= Lower Carboniferous) boundary in the Pocono Formation, Horseshoe Curve, PA (at the top of the Famennian Stage) by palynology. (N.B. *Spelaeotriletes lepidophytus* is the same taxon as *Retispora lepidophyta* and *Hymenozonotriletes lepidophytus*.) LE and LL zones are the designations for divisions of the uppermost Famennian Substage Fa2d, per Maziane, Higgs and Streel, 1999. (Modified from Streel and Traverse, 1978; updating from first edition of this book per M. Streel, personal communication.)

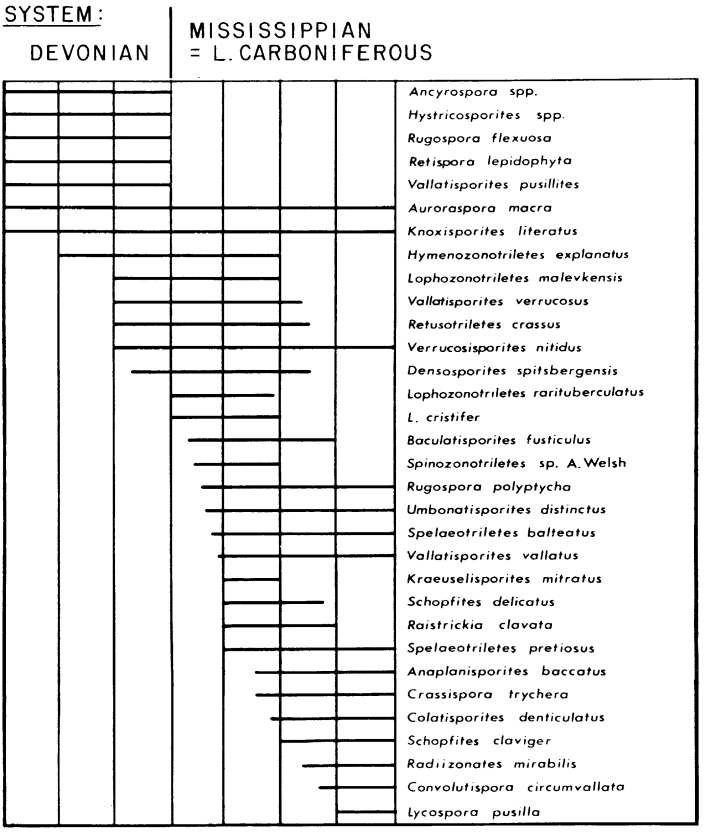

Figure 8.16 Stratigraphic ranges of important miospore taxa in Tournaisian and earliest Visean of central Ireland. The vertical lines represent palynologically based zones. Modified from Keegan, 1981.

to general paleontology is the dating of the earliest tetrapods. Marshall *et al.* (1999) demonstrated this for Greenland and Traverse (2003) for central Pennsylvania. In both cases the early tetrapods were dated as very late Devonian: Famennian Stage.

Streel and I long ago examined the classic American section at Horseshoe Curve, Pennsylvania, and other related sections in central Pennsylvania. Assuming that the European and American palynofloral zones are comparable, as would be expected from paleogeography, the Devonian/Mississippian boundary in central Pennsylvania (the top of Maziane *et al.*'s LN zone at the end of Famennian substage Fa2d) occurs well up in the Pocono Formation (Middle Sandstone unit), a rock unit traditionally regarded as Mississippian (see Fig. 8.15). In Pennsylvania

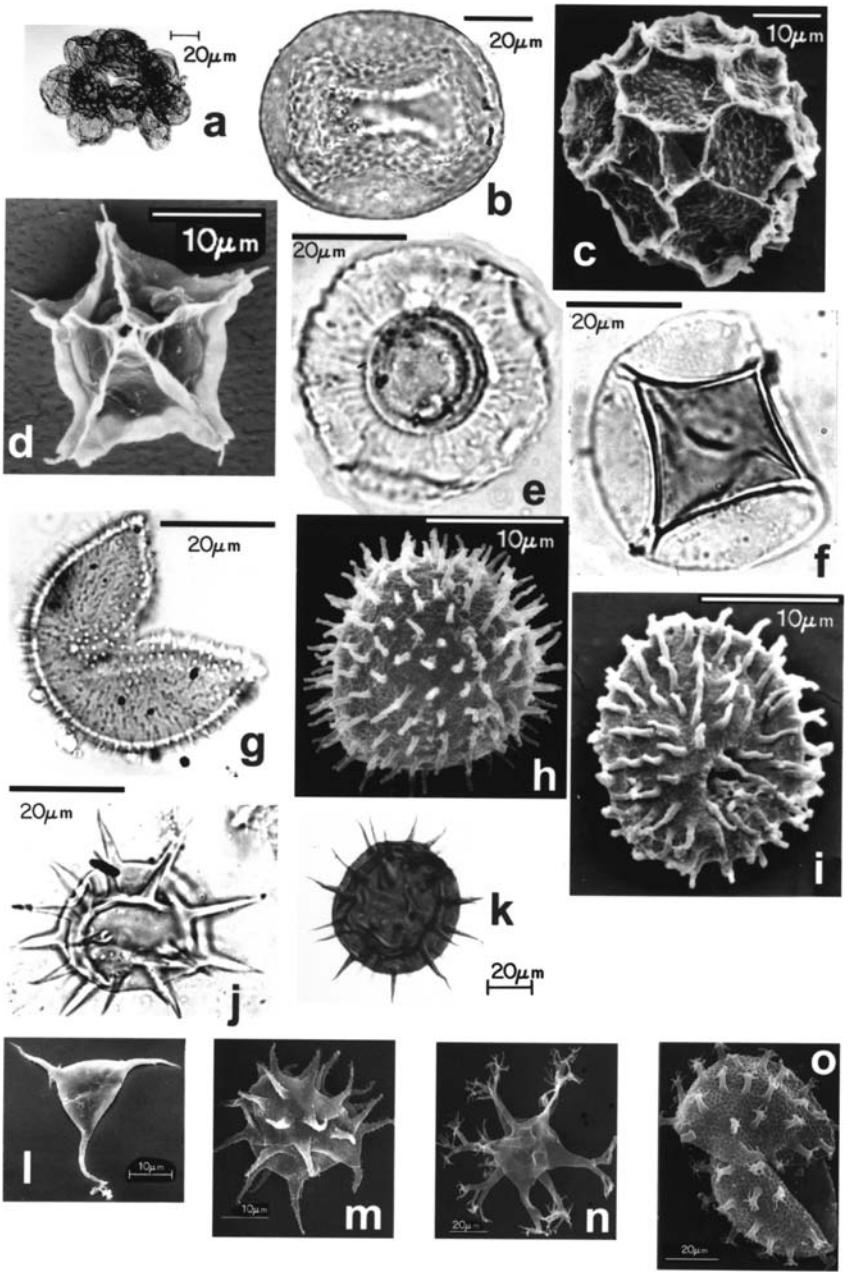
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Figure 8.17

we have not yet found strata containing both spores and conodonts, so the correlation depends on the spores, and their known relation to conodont levels in Europe. The top of the *Retispora lepidophyta* horizon has been used for palynological location of the Devonian/Carboniferous system boundary in other places as well (see Fig. 8.16).

The figures labeled Gneudna Fm. are of specimens from the western Carnarvon Basin, Western Australia. They appeared in Playford (1981), and the photos were provided by Playford. The Gneudna Fm. is Frasnian in age. The figures labeled Chagrin Shale and Cleveland Shale are of specimens from those two closely related units from Ohio, USA, both of which are usually regarded as Famennian in age. The photos were published in Wicander (1974) and were made available by Wicander. All of the specimens in this figure came from rocks deposited near the time of the Kellwasser Event that decimated much of the Late Devonian biosphere.

Figure 8.17 Late Devonian (Frasnian/Famennian) acritarchs from North America and Australia. (**a**) *Leiosphaeridia* sp., Chagrin Shale. (**b**) *Dictyotidium torosum*, Gneudna Fm. (**c**) *Dictyotidium granulatum*, SEM, Gneudna Fm. (**d**) *Daillydium pentaster*, SEM, Gneudna Fm. (**e**) *Pterospermella tenellula*, Gneudna Fm. (**f**) *Duvernaysphaera tessella*, Gneudna Fm. (**g**) *Helosphaeridium microclavatum*, Gneudna Fm. (**h**) *Elektoriskos villosa*, SEM, Gneudna Fm. (**i**) *Gorgonisphaeridium condensum*, SEM, Gneudna Fm. (**j**) *Solisphaeridium spinoglobosum*, Gneudna Fm. (**k**) *Gorgonisphaeridium ohioense*, Chagrin Shale. (**l**) *Veryhachium trispinosum*, SEM, Chagrin Shale. (**m**) *Uncinisphaera lappa*, SEM, Cleveland Shale. (**n**) *Multiplicisphaeridium anastomosis*, SEM, Chagrin Shale. (**o**) *Acriora petala*, SEM, Chagrin Shale.

Chapter 9

Carboniferous/Permian Palynology to the End of the "Paleophytic"

1 Introduction

Carboniferous spore/pollen paleopalynology is, in one sense, where pre-Pleistocene palynology all began. To be sure, Ehrenberg, Goeppert and others had looked at palynomorphs of other pre-Pleistocene ages, but this is of little more than historical interest, as was Dawson's study of probably Carboniferous megaspores, which led ultimately to publication of the genus *Sporites* by H. Potonié in 1883. Reinsch in 1884 published the first photomicrograph of a fossil sporomorph, a Carboniferous form later named "*Reinschospora*" in his honor by Schopf *et al.* (1944). Bennie and Kidston (1886) described Carboniferous megaspores.

Thiessen in the early 1900s described spores in Carboniferous coal thin sections and noted that they might be used stratigraphically. Fortunately, very few spores have been formally described and named from rock thin sections, as the slices of spores so prepared are devilishly difficult to study. The best

known examples of genera of fossil spores that were so described are various genera of Wodehouse (1932, 1933), such as *Momipites*, described from thin sections of Eocene Green River Oil Shale, and various genera such as *Baculexinis*, described by Stach (1957) from Carboniferous coal thin sections. The latter are actually sections that cut through the sporomorphs, whereas Wodehouse's specimens are whole spores/pollen that he examined in the rock thin sections. The British "protopalynologist," Raistrick, made a concerted effort in the 1920s to employ fossil spores/pollen for the correlation of British Carboniferous Coal Measures.

Several factors have conspired to keep from Raistrick as much credit as he clearly deserves for his pioneer work. First, he did not name his groups of spores with formal, binomial Latin nomenclature, using instead code designations of letters and numbers. Many would feel he used uncommonly good sense, but the fact is that the people whose names pop up constantly in the paleopalynological literature, and are hence remembered, are mostly those who, rightly or wrongly, have named many taxa. Secondly, coal beds are notoriously difficult to correlate palynologically, mostly because coal beds are a very atypical biofacies, in which the palynoflora is nearly 100% autochthonously derived, not representing the regional flora. Thirdly, as has been emphasized by Marshall (in press) in a fine study of the pioneer's life, Raistrick had many other interests inside and outside of science, was regarded for his political views and actions as "odd," and published relatively little in what we now call palynology. Nevertheless, in some sense Raistrick must be recognized as a founder, if not the father, of stratigraphic palynology. Similarly, much important work in this field was done by Soviet, mostly Russian, palynologists whose work did not get as much attention in the rest of the world as it should have, because their publications were not readily available, and the scientists themselves were isolated by political circumstances over which they had no control (cf. Fig. 9.1).

When Robert Potonié began in the late 1920s and early 1930s to study fossil spores/pollen in detail, he worked on both Cenozoic and Carboniferous coals, at first mostly the palynofloras of Paleogene brown coals (lignites) of central Europe, but a little later Carboniferous coals as well. At this point, World War II played an important role in developments. Potonié served in the German army on the Eastern Front and was a prisoner of war. While a prisoner, he developed his turmal system for artificial classification of sporomorphs. (Germs of the ideas were already present in his earlier publications and came in part from his students and associates, such as Ibrahim-Okay.) The system is especially useful for Paleozoic, notably Carboniferous, spores. Meanwhile, in North America in the 1930s, James M. Schopf and others had begun studying the spores/pollen of Pennsylvanian (see Fig. 9.2) coals. Schopf was very interested in taxonomy and nomenclature, and was always convinced that fossil sporomorphs should be described and named formally as paleobotanical entities representing fossil genera and species of plants

Figure 9.1 Sofiya N. Naumova, 1902-1974. It is unfortunate that many very talented and productive, mostly Russian, paleopalynologists had to be cut off to a large degree for most of the 20th century from much of the rest of the world, because they worked in the Soviet Union. One of the most prominent of these scientists was S. N. Naumova. Her scientific history, published in *Review of Palaeobotany and Palynology*, 21:135-139 (1976), bespeaks a woman of enormous energy who headed important geoscience laboratories in both Moscow and Leningrad and also taught paleopalynology for a quarter-century at a geological institute in Moscow. I have placed her photo here at the beginning of the Carboniferous and just after the Devonian chapters of this book because those two periods are the ones for which her spore/pollen work had the most impact. Although she worked on rocks of many different parts of the geological column, Naumova's classification system for Devonian/Carboniferous spores and pollen published in 1937 was totally independent of other schemes such as the much later one of Potonié, and many names from it still must be reckoned with today. Had she been able to share ideas freely with researchers outside of the USSR, I am certain that the interplay so created would have had even greater impact on our field. Photo was published in the *In Memoriam* article cited above, by permission from Elsevier.

that happened to be known provisionally from the spores/pollen they produced. The first really comprehensive taxonomic treatment of Carboniferous spores was that of Schopf *et al.* (1944). This was also the first important comprehensive

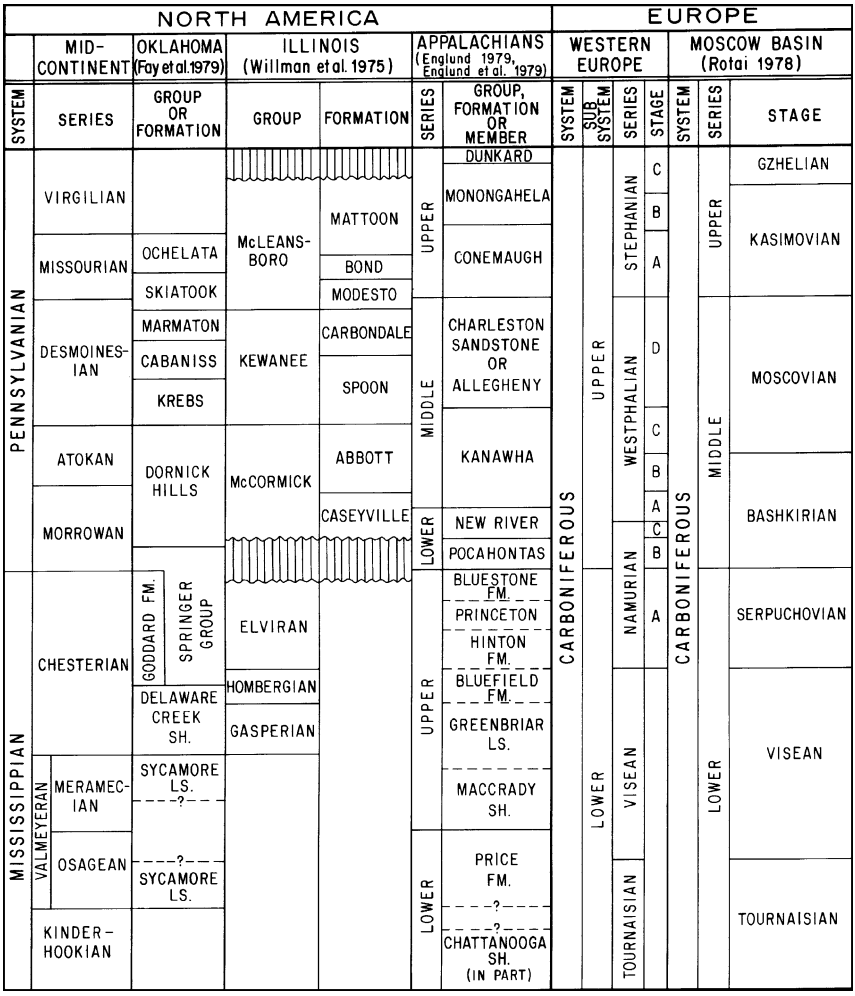

Figure 9.2 Comparison of Carboniferous stratigraphy of Europe and North America. Courtesy of R. A. Peppers, Illinois Geological Survey.

taxonomic treatment of fossil palynomorphs generally. Potonié's efforts in the 1930s with the Paleogene brown coal pollen/spores of Germany were somewhat confused by the problem that such pollen/spores represent largely plants with extant relatives. It is interesting that Potonié's turmal system is least useful for the sporomorphs he knew in most detail, those of the Cenozoic! In any event, we must now present the system because it is in well-nigh universal use for Carboniferous spores.

2 Potonié's Turmal System and Modifications of It

Perhaps because of the military setting in which the turmal system was developed, Potonié used terms from the Roman army for the categories in the system. The largest unit is the Anteturma, more or less like an army. In botanical terms, it is comparable to Class. Potonié set up an Anteturma Sporites for spores and an Anteturma Pollenites for pollen. Already he was in trouble, for the distinction between spores and pollen, as we have seen in Chapter 8, is functional, not morphological. Under the Anteturmas, the next smaller group is the Turma (= military division), dependent on major morphological features and more or less equivalent to Order in conventional taxonomy. Under Sporites are two large Turmas, Triletes and Monoletes, and two very small Turmas, Hilates (see Fig. 9.3) and Aletes. Under Anteturma Pollenites are Turmas Saccites (saccate) and Plicates (with colpi or colpi-like structures). The next smaller unit is the Subturma, taxonomically more or less equivalent to Family, based on smaller morphological differences, e.g., within Triletes whether member spores are zonate (Cingulati) or not (Azonotriletes). Note that some authors interpolate another category, Suprasubturma, between Turma and Subturma (see Fig. 9.3). Below the Subturma is the Infraturma, more or less equivalent to Subfamily, which in Sporites is based on major sculptural differences, e.g., Infraturma Apiculati (positive sculpturing consisting of projections) in the Subturma Azonotriletes. Under Infraturma is Subinfraturma, based on smaller sculptural differences, e.g., Subinfraturma Verrucati (verrucose) under Infraturma Apiculati. Under Anteturma Pollenites, however, Subturmas are based on how many sacci (in Saccites) or colpi (in Plicates) are present. Infraturmas under Saccites are based on haptotypic features–whether laesurae are present or not, etc. Infraturmas under Plicates are not much used.

First of all, it must be made clear that, while the turmal system is much used in paleopalynological systematics and is rather helpful for Carboniferous and Permian palynofloras, it is in my opinion much less useful for Mesophytic palynofloras, and is no use at all in the Cenophytic. Secondly, and very important to stress, is that the various turmal categories are completely informal and do not enjoy the protection of the *International Code of Botanical Nomenclature* (Greuter *et al.*, 2000), or any other code. It is absolutely "dealer's choice" which version of Potonié's system one employs, or one can make up one's own; that is, indeed, one of the problems with use of the system. The individual units in the system are not subject to rules of priority, and one should *not* use author citations and dates for the units (except possibly in parentheses?), which imply that they are validly published names subject to priority. Potonié in his own Synopsis volumes, the main source for the system, does this. For example, he uses "Subinfraturma Nodati Dybova & Jachowicz 1957. . . .," and so forth. Authors also should not publish new turmal terms as if they were new taxa, e.g. "Turma Hilates turma nov." A curious side issue here is that some of Potonié's

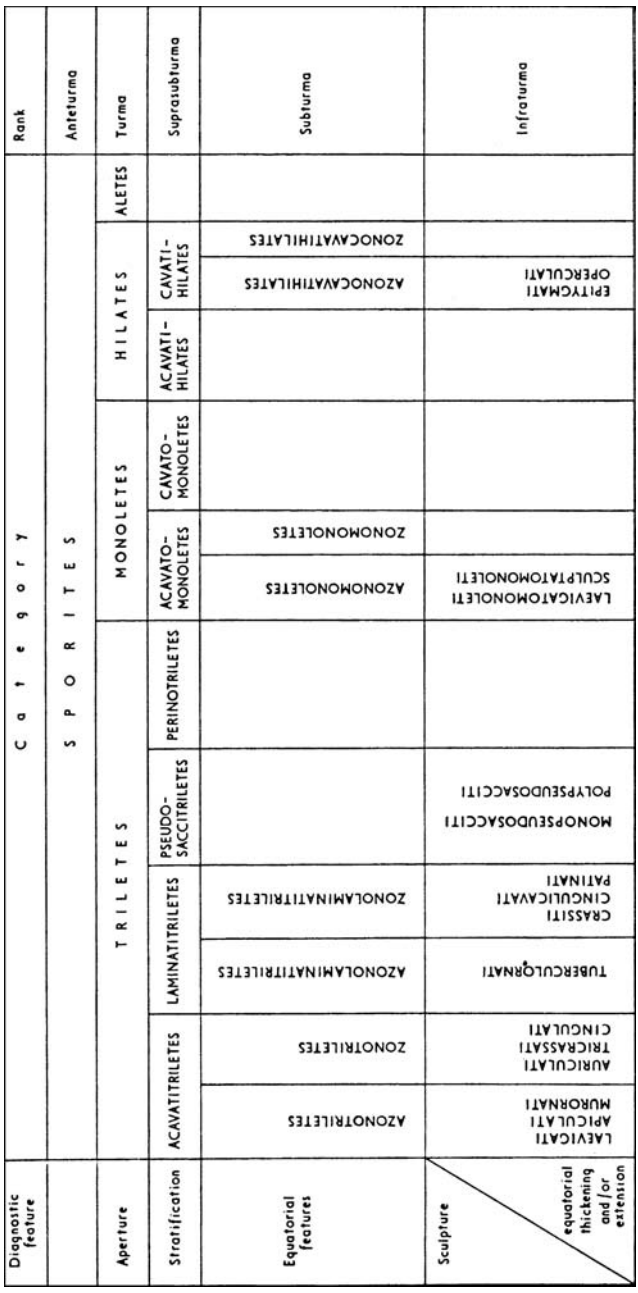

Figure 9.3 The Potonié Anteturma Sporites, as revised by Dettmann (1963) and Smith and Butterworth (1967). Note that Dettmann used the turmal classification for Cretaceous, and Smith and Butterworth for Carboniferous spores. Best usage is probably to restrict this classification to pre-Triassic material.

turmal terms also exist as validly published generic names, e.g. Sporites and Monoletes. Potonié incorrectly thought the use of these names as generic names could simply be suppressed. It is quite clear that Potonié and many who have followed him at least *appear* to have operated on the assumption that the turmal system is a formal classification with formally published names for the various categories.

Fig. 9.3 shows in tabular form one noteworthy summary of the Potonié system for the Anteturma Sporites. All one need do is to reproduce such a table, or refer to it, or make up a modified one and present it, when explaining in a systematic presentation that one is using a turmal classification. Hardly any two palynologists use exactly the same version. I am presenting here my version of the turmal classification for late Paleophytic spores/pollen. Once again, note that the names in italics are validly published formal generic names. The turmal terms (Azonotriletes, etc.) are not validly published names and are absolutely informal! Illustrations of representative species of many of the genera appear in Figs. 8.5, 8.6, 8.14, 9.4, 9.5 and 9.7.

3 "Turmal" Classification of Paleophytic (Silurian to About Mid-Permian) Spores and Pollen

This classification has been simplified from Smith and Butterworth (1967), and the five volumes of *Synopsis der Gattungen der Sporae dispersae*, by R. Potonié (1956,1958,1960,1966,1970). *Synopsis V* (1970), Potonié's last revision, was given special weight. The symbols are as follows: * = megaspore genus (at least in part); + = also appears in the other Anteturma; ++ = a one-letter difference occurs between these names and those of certain other genera.

I. Anteturma SPORITES

A. Turma TRILETES

1. Subturma AZONOTRILETES (no zone, cingulum, or auricle)
   a. Infraturma LAEVIGATI (more or less psilate)
      Calamospora
      *Enigmophytospora**
      Laevigatisporites++
      Leiotriletes
      Phyllothecotriletes
      Punctatisporites++
      Retusotriletes
      *Trileites**
      *Triletes**

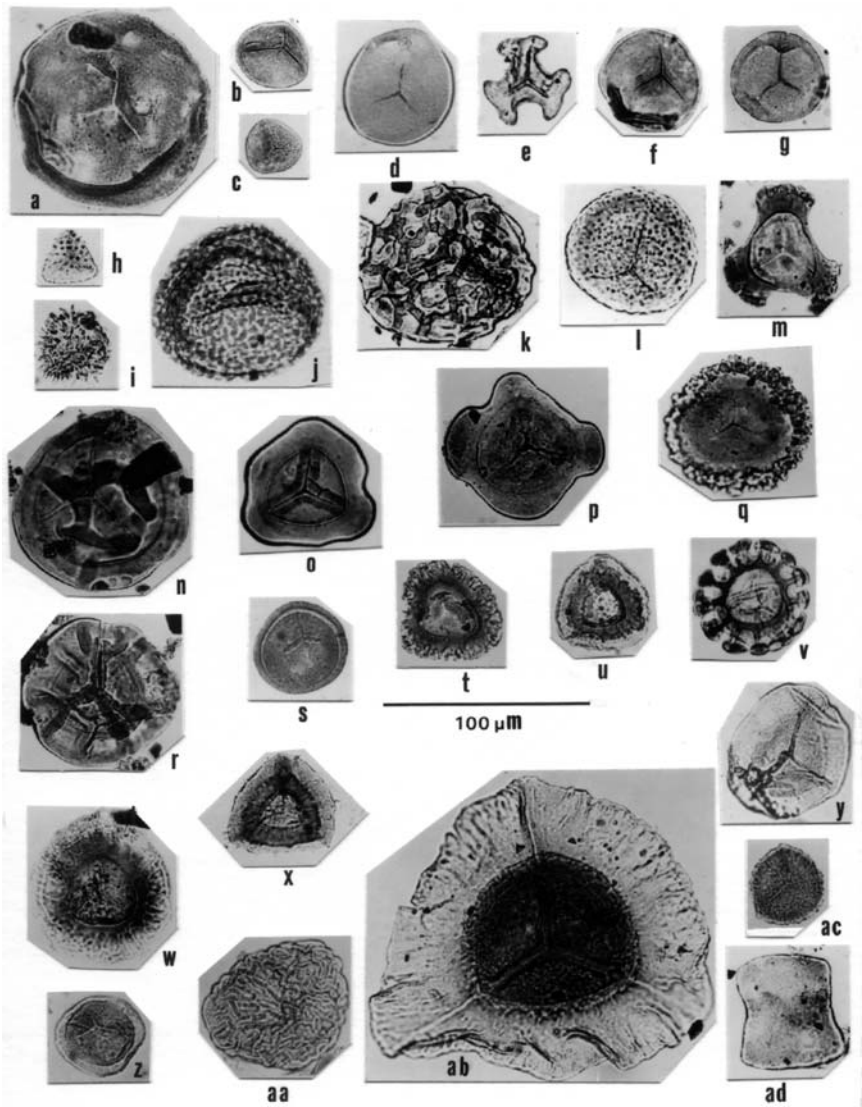

Figure 9.4 Mississippian (Visean stage) palynomorphs, Maritime Provinces (MP) and Northwest Territories (NT), Canada, arranged according to the Potonié turmal system. Note that, according to some usage (Geological Society of America), Mississippian is essentially equivalent to Lower Carboniferous, and Pennsylvanian to Upper Carboniferous. Others regard part of the Upper Mississippian as Namurian and place that in the Upper Carboniferous (see Fig. 9.2). Note that (ad) is probably a zygnematacean algal spore (cf. Grenfell, 1995). Magnification shown by bar below (t)-(v). (**a**) *Calamospora microrugosa* (Ibrahim) S.W. & B. (MP). (**b**) *Leiotriletes ornatus* Ishchenko (NT). (**c**) *Leiotriletes inflatus*

b. Infraturma APICULATI
  i. Subinfraturma GRANULATI (scabrate)
    Cyclogranisporites
    Geminospora
    Granisporites
    Granulatisporites
  ii. Subinfraturma VERRUCATI (verrucate)
    Cyclobaculisporites
    Kewaneesporites
    Schopfites
    Verrucosisporites
  iii. Subinfraturma NODATI (more or less echinate)
    Acanthotriletes
    Anapiculatisporites
    Anaplanisporites
    Aneurospora
    Apiculatisporis
    Apiculiretusispora
    *Biharisporites**
    Grandispora
    Lophotriletes
    Planisporites
    Procoronaspora
    Spinosisporites

Figure 9.4 (Schemel) P.& K. (MP). (**d**) *Punctatisporites* cf. *platirugosus* (Valts) Sullivan (MP). (**e**) *Waltzispora albertensis* Staplin (NT). (**f**) *Punctatisporites glaber* (Naumova) Playford (NT). (**g**) *Retusotriletes incohatus* Sullivan (MP). (**h**) *Anapiculatisporites minor* Butterworth & Williams (NT). (**i**) *Acanthotriletes castanea* Butterworth & Williams (NT). (**j**) *Convolutispora ampla* Hoffmeister, Staplin & Malloy (NT). (**k**) *Reticulatisporites cancellatus* (Valts) Playford (NT). (**l**) *Foveosporites insculptus* Playford (NT). (**m**) *Tripartites incisotrilobus* (Naumova) P.& K. (NT). (**n**) *Knoxisporites hederatus* (Ishchenko) Playford (NT). (**o**) *Murospora aurita* (Valts) Playford (NT). (**p**) *Murospora friendii* Playford (NT). (**q**) *Monilospora moniliformis* Hacquebard & Barss (NT). (**r**) *Camptozonotriletes velatus* (Valts) Playford (NT). (**s**) *Stenozonotriletes facilis* Ishchenko (MP). (**t**) *Densosporites subserratus* Hacquebard & Barss (NT). (**u**) *Densosporites bialatus* (Valts) P.& K. (NT). (**v**) *Densosporites duplicatus* (Naumova) P.& K. (NT). (**w**) *Densosporites* sp. (NT). (**x**) *Densosporites* cf. *landesii* Staplin (NT). (**y**) *Endosporites micromanifestus* Hacquebard (NT). (**z**) *Endosporites minutus* Hoffmeister, Staplin & Malloy (MP). (**aa**) *Rugospora* sp. (MP). (**ab**) *Cirratriradites solaris* Hacquebard & Barss (NT). (**ac**) *Perotriletes* sp. (MP). (**ad**) *Tetraporina horologia* (Staplin) Playford. Photomicrographs courtesy of M. S. Barss, also published in Barss, 1967.

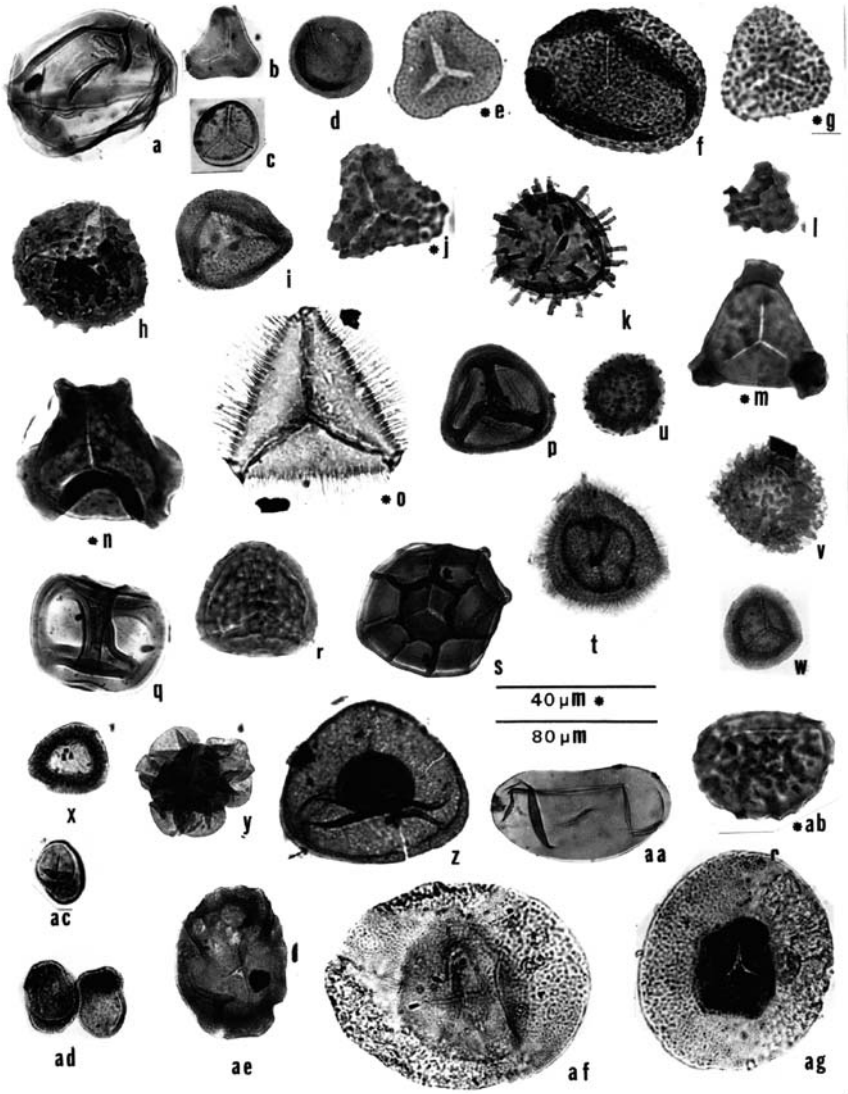

Figure 9.5 Upper Carboniferous (= Pennsylvanian) spores and pollen, arranged according to the Potonié turmal system. Specimens (b),(c),(ac),(ad),(af) and (ag) are referable to the Westphalian stage, Maritime Provinces, Canada. All other photos are of specimens from Illinois, and also are Westphalian. The magnification for items with an asterisk is indicated by the bar under (t) marked with an asterisk. Magnification for all other specimens is indicated by the other bar. (**a**) *Calamospora hartungiana* Schopf in S.W.& B. (**b**) *Leiotriletes adnatus* (Kos.) P.& K. (**c**) *Punctatisporites* sp. (**d**) *Cyclogranisporites orbicularis* (Kos.) P.& K. (**e**) *Granulatisporites granularis* Kosanke. (**f**) *Verrucosisporites sifati* (Ibr.) Smith & Butterworth. (**g**) *Acanthotriletes aculeolatus* (Kos.) P.& K.

Trimontisporites
*Tuberculatisporites**

iv. Subinfraturma BACULATI (baculate)
Ancyrospora
Dibolisporites
*Hystrichosporites** (in part)
*Nikitinisporites**
Raistrickia

I. A. 1. c. Infraturma MURORNATI (more or less reticulate)
Camptotriletes
Convolutispora
Dictyotriletes
Emphanisporites
Microreticulatisporites

2. Subturma ZONOTRILETES (zone or cingulum, etc., present)
a. Infraturma AURICULATI (auriculate)
Ahrensisporites
Mooreisporites
Trilobozonotriletes
Tripartites
Triquitrites
*Valvisporites**

Figure 9.5 (**h**)*Apiculatisporis abditus* (Loose) P.& K. (**i**) *Crassispora kosankei* (P.& K.) Smith & Butterworth. (**j**) *Lophotriletes mosaicus* P.& K. (**k**) *Raistrickia crocea* Kosanke. (**l**) *Triquitrites sculptilis* Balme. (**m**) *Triquitrites* sp. Note that magnification is 1,000x; this specimen is really about the same size as (l). (**n**) *Ahrensisporites querickei* (Horst) P.& K. (**o**) *Reinschospora triangularis* Kosanke. (**p**) *Cadiospora* sp. (**q**) *Knoxisporites triradiatus* Hoffmeister, Staplin & Malloy. (**r**) *Savitrisporites nux* (Butt. & Will.) Smith & Butterworth. (**s**) *Reticulatisporites reticulatus* (Ibr.) Ibrahim. (**t**) *Cirratriradites annulatus* Kosanke. (**u**) *Densosporites lobatus* Kosanke. (**v**) *Cristatisporites indignabundus* (Loose) P.& K. (**w**) *Lycospora pellucida* (Wicher) S.W.& B. (**x**) *Radiizonates striatus* (Knox) Staplin & Jansonius. (**y**) *Alatisporites hexalatus* Kosanke. (**z**) *Endosporites globiformis* (Ibr.) S.W.& B. (**aa**) *Laevigatosporites vulgaris* (Ibr.) Ibrahim. (**ab**) *Thymospora pseudothiessenii* (Kos.) Wilson & Venkatachala. (**ac**) *Torispora laevigata* Bhardwaj. (**ad**) *Torispora securis* (Balme) Alpern *et al*. (Note that whether all of even any species of *Torispora* are monolete spores or some other sort of sporopolleninous-walled call is still debated.) (**ae**) *Schulzospora rara* Kosanke. (**af**) *Florinites similis* Kosanke. (**ag**) *Guthoerlisporites magnificus* Bharadwaj. (Photos (b), (c), (ac), (af), and (ag) courtesy of M. S. Barss and the Geological Survey of Canada; all the other photos are courtesy of R. A. Peppers and the Illinois Geological Survey.)

SYSTEM	SERIES	STAGE	(FREQUENTLY USED GERMAN TERMS)
TRIASSIC	UPPER	RHAETIAN* NORIAN KARNIAN	KEUPER
	MIDDLE	LADINIAN ANISIAN	MUSCHELKALK
	LOWER	SCYTHIAN	BUNTSANDSTEIN
PERMIAN	UPPER	TATARIAN KAZANIAN	ZECHSTEIN
	MIDDLE	KUNGURIAN	ROTLIEGENDES
	LOWER	ARTINSKIAN SAKMARIAN	

Figure 9.6 International Permian and Triassic subdivisions. *The status of the Rhaetian is disputed, with majority opinion of stratigraphers tending toward eliminating it or regarding it as merely a terminal substage of the Norian. Palynostratigraphers, however, have found it definable (see Visscher, 1980).

b. Infraturma TRICRASSATI

Diatomozonotriletes
Reinschospora
*Triangulatisporites**
*Zonalessporites**

c. Infraturma CINGULATI (cingulate)

Ambitisporites
Archaeozonotriletes
Cadiospora
Contagisporites
Knoxisporites
Leiozonotriletes
Lophozonotriletes
Reticulatisporites
Rotaspora
Samarisporites
Savitrisporites
Stenozonotriletes
Vallatisporites

d. Infraturma APPENDICIFERI (with appendages)

Appendicisporites
Elaterites

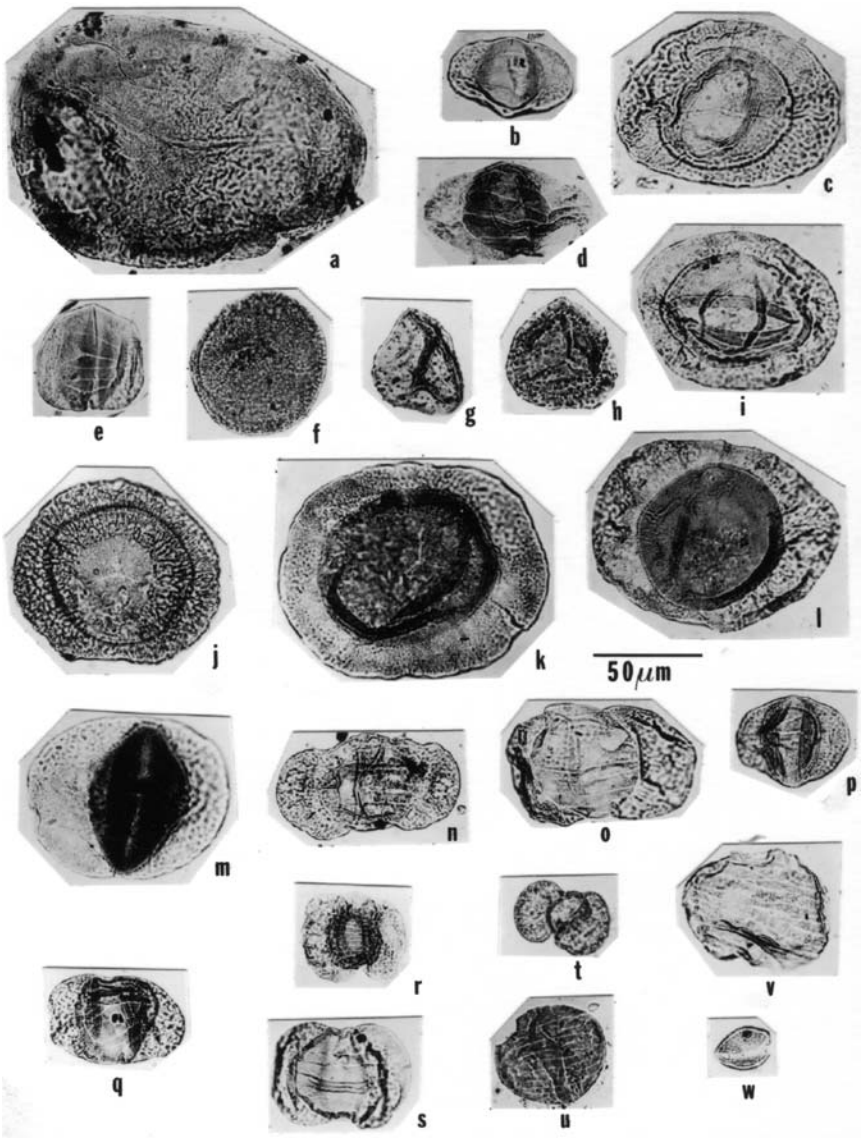

Figure 9.7 Uppermost Carboniferous (= Pennsylvanian, Stephanian Series) pollen (a)-(e) and lowermost Permian (Sakmarian Stage) spores (f)-(h) and pollen (i)-(w) of Canada. Items (g) and (w) are from Yukon Territory, all others from the Maritime Provinces. Nomenclature provided by H. Visscher and W. A. Brugman. Magnification shown by bar under (l). (**a**) *Schopfipollenites ellipsoides* Potonié & Kremp. (**b**) *Illinites unicus* Kosanke; see (e),(p),and (q). This is a very variable taxon, of which *Complexisporites polymorphus* Jizba is a synonym. (**c**) *Potonieisporites novicus* Bhardwaj.

3. Subturma ZONOLAMINATITRILETES (cavate, zonate)
   a. Infraturmae CRASSITI and CINGULICAVATI
      Cingulizonates
      Cirratriradites
      Crassispora
      Cristatisporites
      Densosporites
      Gondisporites
      Hymenozonotriletes
      Lycospora
      Radiizonates
      Samarisporites
      Simozonotriletes
   b. Infraturma PATINATI (patinate)
      Camarozonosporites
      Camarozonotriletes
      Cappasporites
      Tholisporites

I. A. 4. Supersubturma PSEUDOSACCITRILETES (pseudosaccate, trilete)
   a. Infraturma MONOPSEUDOSACCITI
      Endosporites
      Remysporites
      Schulzospora+
      Spencerisporites+
   b. Infraturma POLYPSEUDOSACCITI
      Alatisporites+

I. A. 5. Subturma PERINOTRILETES
   Perotrilites
   Vestispora

Figure 9.7 (**d**) *Protohaploxypinus* sp. (**e**) *Illinites unicus* Kosanke; see (b). (**f**) *Cyclogranisporites vagus* (Kosanke) Potonié & Kremp. (**g**) *Lophotriletes commissuralis* (Kosanke) Potonié & Kremp. (**h**) *Lundbladispora* sp. (**i**) *Potonieisporites grandis* Tschudy & Kosanke. (**j**) *Luberisaccites subrotatus* Dibner. (**k**) *Plicatipollenites indicus* Lele. (**l**) *Potonieisporites bhardwajii* Remy & Remy. (**m**) *Vestigisporites* sp. (= *Jugasporites omai* Helby). (**n**) *Protohaploxypinus* sp. (**q**) *Illinites unicus* Kosanke; see (b). (**r**) *Striatopodocarpites* sp. (**s**) *Protohaploxypinus* sp. (**t**) *Platysaccus* sp. (**u**) *Vittatina vittifer* (Luber) Samoilovich. (**v**) *Vittatina costabilis* Wilson. (**w**) *Cycadopites* sp. Photos courtesy of M. S. Barss and the Geological Survey of Canada; they were also published in Barss, 1967.

I. A. 6. Subturma LAGENOTRILETES
*Lagenicula**
*Setosisporites**

B. Turma MONOLETES

1. Subturma AZONOMONOLETES
a. Infraturma LAEVIGATOMONOLETI
Laevigatosporites++
Latosporites
b. Infraturma SCULPTATOMONOLETI
Columinisporites
Punctatosporites++
Spinosporites
Thymospora
Torispora
Verrucososporites

2. Subturma ZONOMONOLETES (zonate monolete spores are very uncommon)
Speciososporites

C. Turma HILATES (with hilum–a very small group)

D. Turma ALETES

1. Subturma AZONALETES
Fabasporites

E. Turma CYSTITES
*Cystosporites**

II. Anteturma POLLENITES

A. Turma SACCITES (one or more vesicles = sacci)

1. Subturma MONOSACCITES
a. Infraturma TRILETESACCITI
Endosporites+
Felixipollenites
Guthoerlisporites
Nuskoisporites
Rhabdosporites

Schulzospora+
Spencerisporites+
Sullisaccites
Wilsonites

b. Infraturma ALETESACCITI
Archaeoperisaccus (see VESICULOMONORADITI)
Cladaitina
Florinites (sometimes has a vestigial trilete laesura)
Perisaccus

c. Infraturma VESICULOMONORADITI (saccate, monolete)
Archaeoperisaccus
Potonieisporites

d. Infraturma SACCIZONATI
Zonalasporites

2. Subturma DISACCITES
   a. Infraturma DISACCITRILETI (bisaccates with trilete laesurae)
   Illinites
   b. Infraturma DISACCIATRILETI (bisaccates without trilete laesurae)
   Parasporites
   Pityosporites
   Vesicaspora
3. Subturma STRIATITES (striate saccates)
   Lueckisporites
   Striatites
4. Subturma POLYSACCITES
   Alatisporites+

B. Turma PLICATES (pollen with one or more colpi, with or without pores)

1. Subturma PRAECOLPATES (with several parallel folds, one being a true colpus)
   Marsupipollenites
   Schopfipollenites (= *Monoletes*)
2. Subturma POLYPLICATES
   Vittatina
3. Subturma MONOCOLPATES
   Entylissa

4 Paleobotanical Matters Regarding the Late "Paleophytic"

During the Carboniferous, trends in plant evolution already established in the Devonian were expanded, with the establishment of widespread forests consisting of lycopsids such as *Lepidodendron* and *Sigillaria*, seed-fern trees and shrubs such

as *Medullosa*, sphenopsid trees and shrubs such as *Calamites*, ferns including both herbaceous forms and tree ferns such as *Psaronius*, tree and shrub cordaitaleans such as *Cordaites*, and primitive conifers presumably derived from them. The seed plus pollen habit was by now dominant, and free-sporing megaspores began to assume a lesser importance. About Carboniferous and early Permian plants we know a great deal, partly from very widespread occurrence of compressed plant parts, but more especially from the fact that, as the name implies, the Carboniferous was a time of vast extent of coal-forming swamps. From studies of petrified peat (coal balls) containing exquisitely preserved fossil plants found in many Carboniferous coals, we know more about both anatomy-morphology and ecology of some Carboniferous plants than we do about many of their extant descendants. See, for example, current texts of paleobotany such as Stewart and Rothwell (1993) and Taylor and Taylor (1993) for more information about coal-ball studies of Carboniferous plants. Various papers by Phillips *et al.* have contributed greatly to understanding of Carboniferous plant ecology (Phillips and DiMichele 1981; Phillips *et al.*, 1974, 1985). Scheihing and Pfefferkorn (1984) have shown that study of modern plant taphonomy in a tropical delta can provide a model for the fossil plant association found in Carboniferous rocks.

One fallout effect of the relatively great amount of effort spent studying Devonian and Carboniferous petrified and compressed plant remains is that we know a considerable amount about what plants produced many of the taxa of dispersed spores ("*Sporae dispersae*"). Indeed, it is curious that we have far more such information than we do for Cenozoic dispersed spores/pollen! At least in part this is a product of the relatively poorer chances of fossilization of comparatively delicate angiosperm inflorescences and flowers than of gymnosperm and "pteridophytic" fructifications.

5 "Paleophytic" Spores/Pollen: The Plants Which Produced Them

The following data are, with few exceptions, for spores/pollen that have been removed directly from fructifications–that is, the information is from *in situ* spores. Relationships of dispersed sporomorphs to megafossil plant taxa are ideally based on study of such *in situ* spores, but close and regular association of dispersed sporomorphs with particular megafossils is sometimes persuasive. The botanical relationships of the dispersed spores/pollen are organized below according to the "turmal" classification presented earlier in this chapter, to which the reader is referred for more information on the various categories and for the meaning of symbols. (Remy and Remy, 1955, make the important point that because of different stages of development and different states of preservation, different specimens of the same of fructification taxon may contain what appear to be quite different sorts of spores.) Note that Edwards and Richardson (1996), in the Jansonius and McGregor three-volume treatise on paleopalynology, present

very complete tables for the relationship between dispersed spore taxa and the plants in which they have been found *in situ*, for the Silurian and Devonian systems, with much detailed and useful information about each taxon. That sort of information extended through the whole geological column would be a substantial and very useful publication. An existing publication that is a big stride in that direction is the catalog of *in situ* fossil spores by Balme (1995). An important publication for *in situ* spore studies in the Carboniferous is that of Bek and Opuštil (1998), perusal of which will astonish the reader with the clear and carefully documented evidence that one and the same cone can produce several different morphospecies and even morphogenera! The treatment of the subject by the present book for the various time periods is comparatively simple and discursive.

I. Anteturma SPORITES

A. Turma TRILETES

1. Subturma AZONOTRILETES

a. Infraturma LAEVIGATI

Calamospora

Calamospora is the spore of *Calamites*, and other sphenopsids such as *Sphenophyllum* (Good, 1978), *Paleostachya* (Gastaldo, 1981a), *Calamostachys, Macrostachya*, and *Palaeostachya* (Bek and Opluštil, 1998),*Protocalamostachys* (Hemsley *et al.*, 1994). However, spores referable to the morphogenus are also found in ferns (Pfefferkorn *et al.*, 1971), such as *Scolecopteris* (Millay, 1979). Also it comes from *Sawdonia*, a mid-Devonian zosterophylloid (Gensel *et al.*, 1975), but the same plant also apparently produced spores referable to *Retusotriletes*. It is produced also by the Devonian trimerophytes, *Dawsonites* and *Psilophyton* (Allen, 1980; Gensel, 1980b; see also *Retusispora* and *Apiculiretusispora*). The heterosporous Devonian plant *Enigmophyton*, referred by Gensel and Andrews (1984) to the "Barinophytaceae," produced some microspores referable here (others are *Retusotriletes*; Allen, 1980). Spores comparable to *Calamospora* were also produced by *Orcilla*, a Devonian zosterophyll (Gensel, 1982b); cf. *Retusotriletes*), and by *Hostinella*, a Devonian rhyniophyte (Allen, 1980). *Protobarinophyton* and *Barinophyton*, Devonian plants of uncertain affinity ("Barinophytaceae", according to Gensel and Andrews, 1984), were said to produce *C*. spores by Gensel (1980b), and by Taylor and Brauer (1983).

*Enigmophytospora**

This megaspore was obtained from the Devonian plant, *Enigmophyton* (Allen, 1980; see also *Phyllothecotriletes*), referred to "Barinophytaceae" by Gensel and Andrews (1984).

**Laevigatisporites* ++*

Laevigatisporites megaspores have been found in the sigillarian cones, *Mazocarpon* and *Sigillariostrobus* (see Scott and King, 1981), but see also *Tuberculatisporites*.

Leiotriletes

Leiotriletes is, in part, a bryophytic spore (Potonié and Kremp, 1956a). This spore can also belong to the ferns, *Sermaya* (Eggert and Delevoryas, 1967), *Pecopteris* sp. (Laveine, 1969), *Botryopteris* (Good, 1979), *Donneggia* (Permian; Rothwell, 1978), and other ferns (Bharadwaj and Venkatachala, 1968), and probably to the lycopsids. Allen (1980) suggests that some late Silurian *Cooksonia* made spores referable here, as well as others identified as *Ambitisporites*.

Phyllothecotriletes

Phyllothecotriletes is produced by calamarians. Banks (1968, information from Vigran) says that the Devonian plant, *Enigmophyton* made *P*. spores (as well as *Enigmophytospora*).

Punctatisporites++

Punctatisporites is the homospore of *Pecopteris* sp. (Laveine, 1969), *Scolecopteris* (Millay, 1979, 1982a), *Botryopteris* (Millay and Taylor, 1982, but compare *Verrucosisporites*), the zygopteridalean fern, *Biscalitheca* (Millay and Rothwell, 1983), the Pennsylvanian marattialean, *Araiangium* (Millay 1982b) and of other Filicineae (Pfefferkorn *et al.*, 1971). It also occurs in certain Cycadofilicales (in which case, it would by definition be a pollen grain–or "prepollen", pollen that has laesurae and other evidence of spore-like habit), for example, *Telangium*, according to Eggert and Taylor (1968), and *Potoniea illinoensis* (*Punctatisporites kankakeensis* Peppers) according to Stidd (1978). It is also produced by certain of the Psilopsida, according to Gothan and Weyland (1964), and by Devonian *Zosterophyllum* (cf. Gensel, 1982a). It also occurs in certain Cycadofilicales (in which case, it would by definition be a pollen grain–or "prepollen", pollen that has laesurae and other evidence of spore-like habit), for example, *Telangium*, according to Eggert and Taylor (1968), and *Potoniea illinoensis* (*Punctatisporites kankakeensis* Peppers) according to Stidd (1978). A similar case is that of *Punctatisporites* found in *Potoniea* pteridosperm synangia by Rothwell and Mapes (1988a) As *Punctatisporites* is a morphotaxon, it is perfectly legitimate for the taxon to include items that come from totally unrelated plants. Note that this is not the same morphogenus as *Punctatosporites*. There is unfortunately a whole series of such one-letter differences between spore generic names. The "o" ones are monolete, the "i" ones trilete, an idea , I believe, of Ibrahim-Okay. Even palynologists can get confused by these orthographic variants, but they are perfectly legal.

Retusotriletes

Retusotriletes spores were produced by a variety of plants of various geological ages and botanical relationship, for example, by *Renalia*, a Devonian plant close to rhyniophytes and zosterophylls (Gensel, 1976). Edwards and Richardson (1996), in their table of spore relationships show *Retusotriletes* in a number of rhyniophytes, as well as in zosterophylls and trimerophytes Gensel (1980a) says that *Psilophyton* produced these spores (inter alia). Banks (1968, data from Hueber) notes that the Devonian trimerophyte, *Dawsonites*, made *R*. spores and it was also produced (along with *Apiculiretusispora*) by *Trimerophyton* (Allen, 1980). This spore type was also produced by *Zosterophyllum* (Gensel, 1980b; Allen, 1980), and by the Devonian zosterophyll, *Orcilla* (cf. *Calamospora*). Another zosterophyll, *Sawdonia*, was reported by Gensel *et al.*(1975) to produce both *Retusotriletes* and *Calamospora*. Some of the microspores of *Enigmophyton*, a Devonian plant of doubtful relationship, are referable here (Allen, 1980, but see *Calamospora, Enigmophytospora*, and *Phyllothecotriletes*). This sort of spore was also produced by Lower Carboniferous sphenopsids, according to Scott *et al.* (1985b). Allen (1980) even refers the ca. 200 μm spores of the Upper Devonian non-vascular plant, *Foerstia*, to *Retusotriletes*.

*Triletes**

The megaspore *Triletes* (not to be confused with Turma Triletes!) was produced by heterosporous lepidodendrids, per Brack-Hanes (1978), and by herbaceous lycopods as well (Chaloner, 1954; Schlanker and Leisman, 1969). Fortunately, the name is not much used now as a megaspore generic name, the genus having been subdivided. As a genus, *Triletes* can be confused not only with the Turma Triletes but also with the genera *Trilites* (echinate miospore, Triassic) and *Trileites* (psilate, retusoid megaspore, Devonian-Carboniferous).

b. Infraturma APICULATI

i. Subinfraturma GRANULATI

Cyclogranisporites

Cyclogranisporites is the isospore of *Pecopteris* spp. (Laveine, 1969; Millay, 1979), and of other Filicineae (Potonié and Kremp, 1956a; Bharadwaj and Venkatachala, 1968; Pfefferkorn *et al.*, 1971), the marattialeans, *Acitheca* (*Pecopteris* foliage, Mapes and Schabilion, 1979a), and *Scolecopteris* (Millay and Taylor, 1984), and of *Noeggerathiostrobus*, a problematic pteridophyte perhaps related to *Archaeopteris* (Beck, 1981). *C*.was also found in the psaronian fern leaf fronds, *Acitheca*, by Bek and Oplušti (1998). Millay and Taylor (1977) say that *C*. occurs as the prepollen of the lyginopterid, *Feraxotheca*, Millay *et al.* (1978) say the

same of the lyginopterid, *Crossotheca*, and Stidd *et al.* (1985) of the lyginopterid, *Schopfiangium* (but see *Verrucosisporites*). Various authors (Banks, 1968; Gensel, 1980b) mention that *C*. was produced as a microspore by *Archaeopteris*. Allen (1980) refers some *Rhynia* (early Devonian) spores here (but see also *Granulatisporites* and *Apiculiretusispora*).

Geminospora

Geminospora may be the spore of *Rhynia* (see Gensel, 1980b). *G*. spores have been mentioned as a microspore type of various species of the Devonian progymnosperms, *Archaeopteris* (Gensel, 1980b; Allen, 1980) and *Svalbardia* (Allen, 1980). (cf. *Aneurospora* under Subinfraturma Nodata, below.)

Granulatisporites

Granulatisporites is the spore of certain Filicineae, such as *Botryopteris* (Good, 1979) and *Renaultia* (Scott, 1978), but it also can be the pollen (=prepollen) of some Cycadofilicales (Potonié and Kremp, 1956a) such as the lyginopterid, *Feraxotheca* (Millay and Taylor, 1977) and *Crossotheca* (Millay *et al.*, 1978). Also it may be the spore of certain sphenopsids (Schopf *et al.*, 1944), and of the early Devonian rhyniophyte, *Rhynia* (Allen, 1980; Bhutta, 1987; spores of *Rhynia* spp. are also referred to *Apiculiretusispora*, *Granulatisporites*, and *Cyclogranisporites*).

ii. Subinfraturma VERRUCATI

Cyclobaculisporites

Cyclobaculisporites was produced by ferns such as Lower Gondwana *Dichotomopteris* (Lele *et al.*, 1981).

Kewaneesporites

Kewaneesporites, a spore with odd, hollow verrucae, occurs in the sporangia of the fern *Cyathotheca* (Taylor, 1972; Mickle and Rothwell, 1986), a Carboniferous plant of uncertain affinity.

Verrucosisporites

Verrucosisporites is a fern spore, for example, of *Biscalitheca* (Courvoisier and Phillips, 1975; Bharadwaj and Venkatachala, 1968), of the marattialean ferns, *Scolecopteris* (Jennings and Millay, 1978), *Eoangiopteris* (Millay, 1978), and *Millaya* (Mapes and Schabilion, 1979b), of botryopterids (Millay and Taylor, 1980, 1982, but compare also *Punctatisporites*), and can also be a seed-fern prepollen (Bharadwaj and Venkatachala, 1968), e.g. of the lyginopterid, *Schopfiangium* (Stidd *et al.*, 1985).

iii. Subinfraturma NODATI

Acanthotriletes

Acanthotriletes spores (among others) have been found on *Botryopteris* fern foliage (Good, 1979; Millay and Taylor, 1982). Also it is said (see Gensel, 1980b) to be made by the Devonian plant, *Eviostachya*. Species of the Lower Gondwana ferns, *Dichotomopteris* and *Neomariopteris*, produced *A*. spores, as well as other forms, according to Lele *et al.* (1981). Scott *et al.* (1985b) reported spores referable here or to *Apiculatisporis* from Carboniferous zygopterid ferns.

Anapiculatisporites

According to Ravn (1983, pers. comm.) , spores illustrated by Baxter (1971) from the lycopsid fructification, *Carionstrobus foresmanii*, are referable to *A. spinosus* (Kosanke) Potonié & Kremp.

Aneurospora

Aneurospora is said to have been produced by the Devonian progymnosperms, *Aneurophyton* (Gensel, 1980b) and *Archaeopteris* (Allen, 1980; see *Geminospora*), and has been mentioned also as produced by the Devonian lycophyte, *Leclercqia* (Streel, 1972). (*Streelispora* is a similar spore taxon, which Edwards *et al.*, 1986, and Fanning *et al.*, 1988, say was found in sporangia of the rhyniophyte, *Cooksonia*; *Synorisporites* is also somewhat similar to *Streelispora* and *Aneurospora* and is reported by Fanning *et al.*, 1991, as coming from *Cooksonia* sporangia.) Edwards and Richardson (1996) report that the rhyniophyte *Salopella* produces *A*. spores.

Apiculatisporis

Apiculatisporis (= Apiculatisporites) spores were produced by the fern, *Corynepteris*, according to Galtier and Scott (1979) and Hemsley *et al.* (1994), and by other Filicineae (Pfefferkorn *et al.*, 1971), also as one kind of "large" spore by *Chaleuria*, a Devonian possible progymnosperm. Another kind of *Chaleuria* large spore is referable to *Apiculiretusispora*. The small spores are *Camarozonotriletes* (Gensel, 1980b). Lele *et al.* (1981) note that a Lower Gondwana fern, *Dizeugotheca*, produced spores similar to *Apiculatisporis*, but also made spores referable to *Punctatosporites* (monolete!).

Apiculiretusispora

This spore type was produced by *Pertica*, a Devonian trimerophyte progymnosperm ancestor (Granoff *et al.*, 1976; Doran *et al.*, 1978). *Psilophyton* produced

A. spores (and other kinds) according to Gensel (1980a). The spores of the Devonian rhyniophyte, *Horneophyton lignieri*, have also been referred here, as have those of *Cooksonia*, the earliest vascular plant (Gensel, 1980b; Allen, 1980; but see *Leiotriletes* and *Ambitisporites). A*. has also been mentioned by Gensel (1980b) as produced by the Devonian plants, *Krithodeophyton* and *Chaleuria* (as one kind of "large" spore; see *Apiculatisporis*). Spores referable to *A*. were produced by *Renalia* (but see *Retusotriletes*) and *Rhynia*, early Devonian rhyniophytes (Allen, 1980; but see *Granulatisporites* and *Cyclogranisporites*). *A*. spores were produced by the zosterophyll, *Nothia* (Allen, 1980), and by the Devonian *Trimerophyton robustius* (Allen, 1980; see also *Retusotriletes*).

*Biharisporites**

This megaspore was produced by various species of the Devonian progymnosperm, *Archaeopteris* (Gensel, 1980b; Allen, 1980; some of these plants also made megaspores referable to *Contagisporites*, or only made these, according to Allen).

Grandispora

Grandispora (and *Samarisporites*) was produced by *Oocampsa*, trimerophyte-progymnosperm, according to Andrews *et al.* (1975).

Lophotriletes

Lophotriletes (and others) have been found on *Botryopteris* fern foliage (Good, 1979), and were produced by species of the Lower Gondwana ferns, *Dichotomopteris* and *Neomariopteris*, according to Lele *et al.* (1981).

Planisporites

Planisporites has been described from sigillarian (lycopsid) cones such as *Sigillariostrobus* by Chaloner (1953b), but is also said to be a cycadofilicalean prepollen (Bharadwaj and Venkatachala, 1968).

Trimontisporites

Trimontisporites is a spore of the fern, *Scolecopteris* (Millay 1979).

*Tuberculatisporites**

This megaspore is produced by the lycopsid cones, *Sigillariostrobus* and *Mazocarpon* (see Scott and King, 1981), but see also *Laevigatisporites*.

iv. Subinfraturma BACULATI

Dibolisporites

Dibolisporites was produced by the Devonian plant, *Calamophyton*, according to Bonamo and Banks (1966a).

*Nikitinisporites**

This megaspore was probably produced by the late Devonian lycopod *Kryshtofovichia* (Allen, 1980; see *Archaeoperisaccus*).

Raistrickia

Raistrickia is the spore of *Pecopteris* sp. (Laveine, 1969), *Ankyropteris* sp. (Mickle, 1980) and of other Filicineae (Schopf *et al.*, 1944; Bharadwaj and Venkatachala, 1968). Remy and Remy (1957) illustrate *R.* from *Senftenbergia*, a schizaeaceous Carboniferous fern, though they do not specifically make this identification (see *Convolutispora* below).

c. Infraturma MURORNATI

Camptotriletes

Camptotriletes is the spore of *Pecopteris* sp. (Laveine, 1969) and of other Filicineae (Schopf *et al.*, 1944; Pfefferkorn *et al.*, 1971).

Convolutispora

Convolutispora is the spore of *Pecopteris* sp. (Laveine, 1969) and of the zygopterid fern, *Biscalitheca* (Cridland, 1966; but see *Verrucosisporites*). It is clear from the illustrations that Remy and Remy (1955) also found *C.* in *Senftenbergia*, a Carboniferous schizaeaceous fern, though the identification is not specifically made (see *Raistrickia*).

It is significant as a matter of concern for *in situ* studies, that Smith (1962) notes that aborted spores of the Lower Carboniferous pteridosperm, *Staphylotheca*, could be referred to *C.*, but the mature spores are larger and have different conformation.

Dictyotriletes

Hamer and Rothwell (1983) found spores of this genus in *Phillipopteris*, a Pennsylvanian fern-like fructification. Scott *et al.* (1985b) illustrate beautifully preserved examples from Carboniferous botryopterid ferns. Ravn (1983, personal communication) states that the type species, *D. reticulatus*, is probably a lycopsid spore, but that other species are from ferns.

Emphanisporites

Emphanisporites spores may be produced by *Horneophyton* (Gensel, 1980b).

2. Subturma ZONOTRILETES

a. Infraturma AURICULATI

Tripartites and *Triquitrites*

Tripartites and *Triquitrites* are spores of *Phlebopteris*, Matoniaceae, according to Potonié (1962). *Triquitrites* spores were also obtained from Permian gleicheniaceous ferns by Yao and Taylor (1988).

*Valvisporites**

Valvisporites was produced by *Polysporia*, a herbaceous lycopod (Chaloner, 1958a; DiMichele *et al.*, 1979), and by the closely related lycophyte, *Chaloneria* (Pigg and Rothwell, 1983). Gastaldo (1981b) noted that this spore type occurs in *Lepidocystis*, a lycopsid reproductive organ (see *Endosporites*).

b. Infraturma TRICRASSATI

Reinschospora

Reinschospora is probably derived from certain Filicineae, according to Schopf *et al.* (1944).

*Triangulatisporites**

This megaspore is found in *Selaginellites* cones (see Scott and King, 1981).

*Zonalessporites**

Zonalessporites is found as a megaspore in the heterosporous lycopod cone, *Sporangiostrobus* (microspores are *Densosporites*; see Chaloner, 1962; Leisman, 1970; and summary in Scott and King, 1981).

c. Infraturma CINGULATI

Ambitisporites

This spore, along with *Punctatisporites*, ranges to earliest Silurian or latest Ordovician and the two are thus the earliest trilete spores in the fossil record. Allen (1980) says that *in situ* spores of some *Cooksonia* sp., the earliest vascular plant, and possibly of some *Rhynia* spp. (early Devonian) are referable to this genus (but see also *Leiotriletes*, *Cyclogranisporites, Granulatisporites*, *Streelispora, Aneurospora, Synorisporites* and *Apiculiretusispora*, which are have been obtained from Cooksonia spp., according to various authors–see Fanning *et al.*, 1991 and Edwards and Richardson, 1996).

*Contagisporites**

These spores, certainly megaspores, though often well below 200 μm in size, were produced by various species of the Devonian progymnosperm, *Archaeopteris*, some of which also produce megaspores referable to *Biharisporites* (Allen, 1980).

Knoxisporites

Knoxisporites specimens were found by Scott *et al.* (1985b) in sporangia of uncertain relationship but possibly filicilean. It had been earlier suggested that they are possibly the spores of certain Selaginellales.

Reticulatisporites

Reticulatisporites is possibly the spore of certain *Sphenophyllum* species (Schopf *et al.*, 1944). Other species of *Sphenophyllum* have *Calamospora* spores.

Vallatisporites

Vallatisporites is said by Bharadwaj and Venkatachala (1968) to be a spore of lepidophyte cones.

Reticulatisporites

Reticulatisporites is possibly the spore of certain *Sphenophyllum* species (Schopf *et al.*, 1944). Other species of *Sphenophyllum* have *Calamospora* spores.

Vallatisporites

Vallatisporites is said by Bharadwaj and Venkatachala (1968) to be a spore of lepidophyte cones.

d. Infraturma APPENDICIFERI

Elaterites

Elaterites is the spore of certain calamarians–found in *Calamostachys* by Baxter and Leisman (1967) and by Good and Taylor (1975).

3. Subturma ZONOLAMINATITRILETES

a. Infraturmae CRASSITI and CINGULICAVATI

Cirratriradites

Cirratriradites was produced as a microspore by fossil *Selaginella*, according to Schlanker and Leisman (1969), and by *Selaginellites*, per Chaloner (1954) and Taylor and Taylor (1990).

Crassispora

Crassispora is the microspore of *Mazocarpon* and other sigillarian cones (Courvoisier and Phillips, 1975; Bharadwj and Venkatachala, 1968; Feng and Rothwell, 1989).

Cristatisporites

Cristatisporites (if separated from *Densosporites*) was found as a microspore in *Sporangiostrobus*, a lycopod cone, by Chaloner (1962) and Leisman (1970). A number of the *in situ* spores removed from *Sporangiostrobus* sporangia by Bek and Opluštil (1998) are referred to this morphogenus.

Densosporites

Densosporites is the microspore of certain lycopsids (Chaloner 1958b, 1962). Potonié (1967) and Chaloner (1962) associate this genus with the lycopsid genus *Porostrobus*. Chaloner (1962) and Leisman (1970) found *Densosporites* (or *Cristatisporites*, if that taxon is maintained) as a microspore in *Sporangiostrobus*, a heterosporous lycopsid cone. The Devonian possible lycopod, *Barrandeina*, produced spores referable here (Allen, 1980; see *Samarisporites)*. Bek and Opluštil (1998) found spores referable to various *Densosporites* and *Cristatisporites* species in sporangia of the same species of the lycophyte, *Sporangiostrobus*.

Gondisporites

Gondisporites is the spore of certain lycopod cones (Bharadwaj and Venkatachala, 1968).

Lycospora

Lycospora was unquestionably produced by a variety of lycopsids (see Balbach, 1967; Courvoisier and Phillips, 1975). Heterosporous lepidodendrids made *L*. as microspores, according to Brack-Hanes (1978). On the other hand, some apparently homosporous *Lepidostrobus* cones also produced *Lycospora* (see Thomas, 1970). The Devonian plant, *Svalbardia*, has been mentioned as a producer of *L*. spores (see Gensel, 1980b). Willard (1989), in a detailed study of *Lepidostrobus*, was able to assign various *Lycospora* species to particular species of the cone genus. Bek and Opluštil (1998) also got various *Lycospora* spp. from different *Lepidostrobus* sporangia.

Radiizonates

Radiizonates (Courvoisier and Phillips, 1975) was produced by *Sporangiostrobus*, a lycopod.

Samarisporites

Samarisporites (and *Grandispora*) were produced by *Oocampsa*, a trimerophyte-progymnosperm, according to Andrews *et al.* (1975). *S*. (and *Densosporites*) were made by the Devonian possible lycopod, *Barrandeina*, according to Allen (1980).

b. Infraturma PATINATI

Camarozonotriletes

Camarozonotriletes is mentioned as a "small" spore of the Devonian plant, *Chaleuria* (Gensel, 1980b; see also *Apiculatisporis*).

Cappasporites

According to Courvoisier and Phillips (1975), *Cappasporites* was produced as a microspore by *Achlamydocarpon*, an arborescent lycopod. Chadwick (1983) also shows that these spores, seldom showing a trilete laesura, were produced in arborescent lycopods.

4. Suprasubturma PSEUDOSACCITRILETES

a. Infraturma MONOPSEUDOSACCITI

Endosporites+

Potonié and Kremp (1956a) put this in the Subturma Monosaccites as a pollen grain. Clearly this is because originally the genus was very loosely used, including forms now referred to *Florinites*, and other monosaccate genera. However, Chaloner (1953a, 1958a) has found spores referable to this genus as microspores in lycopsid fructifications, and Chaloner (1953a), Brack-Hanes and Taylor (1972) and DiMichele *et al.* (1979) have shown that *Polysporia*, a herbaceous lycopod, produced *Endosporites* microspores. Pigg and Rothwell (1983) note that the lycophyte, *Chaloneria*, produces this type of microspore. See *Valvisporites**.

Remysporites

Smith (1962) suggests that spores of *Protopitys*, a Carboniferous progymnosperm, could be referred here (or to "*Glomospora* Butterworth & Williams," which is an illegitimate synonym for *Vestispora*). However, if the perine is removed, which happens even in preparations of the strobili, the spores would be referred to *Calamospora.*

Schulzospora+

Schulzospora is a seed-fern prepollen (Potonié, 1962).

Spencerisporites+

Spencerisporites (= Microsporites) is the spore of the arborescent lycopsid fructification, *Spencerites* (Potonié and Kremp, 1956a; Potonié, 1962). Leisman and Stidd (1967) found, in addition to "normal" trilete spores, some monolete spores.b.

Infraturma POLYPSEUDOSACCITI

Alatisporites^{+}

Potonié and Kremp (1956a) put this in the Subturma Polysaccites as a pollen grain and suggest cordaitean affinity. Schopf *et al.* (1944) suggested sphenopsid relationship. Note, therefore, that this form appears also as a pollen grain (Infraturma Triletesacciti).

5. Subturma PERINOTRILETES

Perotrilites

Perotrilites was produced by species of the Devonian fern *Rhacophyton* (Andrews and Phillips, 1968) and possibly by *Rhynia* (Gensel, 1980b).

Vestispora

Vestispora is a spore of sphenopsids, found as a developmental stage of the same cones that produced *Calamospora*, according to Good (1977). However, this idea is disputed by Ravn (1983), who says *V*. was produced as a mature spore by the Sphenophyllales and other sphenopsids. Taylor (1986) reports *V*. from the sphenophyllaleans, *Sphenostrobus* and *Koinostachys*. Bek and Opluštil obtained *Vestispora* spores in the sphenophyllean, *Bowmanites*.

6. Subturma LAGENOTRILETES

Lagenicula*

Lagenicula is the megaspore of heterosporous lycopods, such as the late Devonian *Cyclostigma* (Chaloner, 1968c), and of the Carboniferous cone, *Lepidostrobus* (Brack-Hanes, 1981; Scott and King, 1981). Note that Brack-Hanes and Thomas (1983) have shown that *Lepidostrobus* should be subdivided, and the bisporangiate cones, such as those producing *Lagenicula*, would go into *Flemingites*.

Setosisporites*

Megaspore of lycopsid cone, *Porostrobus* (see Scott and King, 1981; Leary and Mickle, 1989).

B. Turma MONOLETES

1. Subturma AZONOMONOLETES

a. Infraturma LAEVIGATOMONOLETI

Laevigatosporites++

Laevigatosporites is in part derived from sphenopsids such as *Bowmanites* (Courvoisier and Phillips, 1975; Potonié and Kremp, 1956a), and *Sphenophyllum* (Bek and Opluštil, 1998, who obtained *Latosporites* from the same cones), and from lycopsids (Potonié, 1967). Good (1978) notes that *Columinisporites* spores of certain sphenophyllaleans "become" *Laevigatosporites* if the perine is lost! Others are the spores of ferns such as *Pecopteris* sp. (Laveine, 1969; Pfefferkorn *et al.*, 1971), and *Scolecopteris* (Millay, 1979, 1982c; Millay and Taylor, 1984; Bek and Opluštil, 1998, who also found *Latosporites* in the same leaf specimens) The often very abundant *L. minimus* was shown to be produced by the fern, *Zeilleria* (Thomas and Crampton, 1971).

Latosporites

This kind of psilate monolete spores was found in the same *Sphenophyllum* cones as *Laevigatosporites*, and in the same *Scolecopteris* fronds as that morphogenus by Bek and Opluštil, 1998.

b. Infraturma SCULPTATOMONOLETI

Columinisporites

Columinisporites is the spore of *Peltastrobus*, a sphenophyllalean cone (Taylor, 1986) and of other sphenophyllaleans, per Good (1978), but the same things are said to "become" *Laevigatosporites* if the perispore is lost. Riggs and Rothwell (1985) found *C*. spores in the sphenophyllalean, *Sentistrobus*.

Punctatosporites++

Punctatosporites is the spore of *Pecopteris* spp. (Laveine, 1969) and *Scolecopteris* (Lesnikowska and Millay, 1985), but this is a rather generalized monolete spore, being produced (Lele *et al.* 1981) by the Lower Gondwana fern, *Dizeugotheca*, along with trilete spores. (*Scolecopteris* also makes *Punctatisporites*, a trilete spore.)

Spinosporites

According to Ravn (1983, personal communication), *S. exiguus* Upshaw & Hedlund 1967, apparently corresponds to a monolete spore illustrated by Millay

(1979) for *Scolecopteris*. Millay and Taylor (1984) show that *S*. is also produced by *Scolecopteris*, a marattialean fern also making other trilete and monolete spores.

Thymospora

Thymospora (a synonym for *Verrucososporites*) was produced by the ferns, *Scolecopteris* and *Asterotheca*, according to Wilson and Venkatachala (1963). Millay and Taylor (1984) found *T*. spores *in situ* in *Scolecopteris*, as did Lesnikowska and Willard (1997). Doubinger and Grauvogel-Stamm (1971) reported *T*. from *Pecopteris* fronds.

Torispora

Torispora was produced by sporangia of *Pecopteris* spp. (Laveine, 1969). Some have doubted that all *T*. species are actually spores, but Lesnikowska and Willard (1997) showed that they are a peripheral spore type in *Scolecopteris* fructifications that also produced *Laevigatosporites* spores centrally. (*Crassosporites* is synonymous with *Torispora* according to Potonié, 1960, p. 145).

2. Subturma ZONOMONOLETES

Speciososporites

Speciososporites is the spore of *Pecopteris* spp. (Laveine, 1969). (*Archaeoperisaccus*, cf. Vesiculomonoraditi under Pollenites, probably belongs here.)

C. Turma HILATES

A very small group, with hilum.

D. Turma ALETES

1. Subturma AZONALETES

Fabasporites

Fabasporites was produced by the marattialean fern, *Acaulangium*, according to Millay (1977). Potonié includes *F*. under monocolpate pollen, and the original author intended to describe *F*. as a monocolpate pollen grain. Others have considered it monolete, but the current consensus seems to be that it is alete. (Millay, quoted above, thought his *F*. spores might be immature trilete forms!)

E. Turma CYSTITES

*Cystosporites**

Cystosporites, a large "seed megaspore", was produced by *Achlamydocarpon*, an arborescent lycopod (Leisman and Phillips, 1979). Balbach (1966) had noted that *C*. megaspores were produced in *Lepidostrobus* cones. (See summary in Scott and King, 1981. Compare *Lagenicula*.)

II. Anteturma POLLENITES

A. Turma SACCITES

1. Subturma MONOSACCITES

a. Infraturma TRILETESACCITI

Endosporites+

This has been included above under Monopseudosacciti.

Felixipollenites

Felixipollenites is prepollen of the cordaitean cone *Gothania* (Taylor and Daghlian, 1980), that is, of the *Mesoxylon* type of cordaitean (Trivett and Rothwell, 1985). (See *Florinites*, IIAlb).

Guthoerlisporites

Guthoerlisporites is a cycadofilicalean pollen grain (Bharadwaj and Venkatachala, 1968).

Nuskoisporites

Nuskoisporites has been presumed to be a seed-fern pollen grain, but has been found in Permian conifer cones by Clement-Westerhof (1974).

Rhabdosporites

Rhabdosporites, a trilete monosaccate, is the microspore (or prepollen) of such Devonian progymnosperms as *Tetraxylopteris* and *Rellimia* (Bonamo and Banks, 1966a, 1967; Bonamo, 1977; Taylor and Scheckler, 1996), and *Cathaiopteridium* (Allen, 1980). Beck and Wight (1988) state that Smith's (1962) Carboniferous *Protopitys* spores, referred by Smith to *Remysporites* resembles *Rhabdosporites*, but this observation does not seem to be correct. Millay and Taylor (1974) suggest that saccate cordaite pollen evolved from this pseudosaccate type.

Schulzospora+

Schulzospora is said to be a seed fern prepollen. (See listing above under Monopseudosacciti.)

Spencerisporites+

This is included in Monopseudosacciti.

Sullisaccites

Trivett (1983) reports this sort of prepollen from the cordaitean pollen cone, *Gothania*, but see also *Felixipollenites*.

Wilsonites

Wilsonites was produced by the Cycadofilicales (Potonié and Kremp, 1956a; Bharadwaj and Venkatachala, 1968).

b. Infraturma ALETESACCITI

Cladaitina

Cladaitina is the pollen of *Cladostrobus*, a probable cordaitalean (Maheshwari and Meyen, 1975).

Florinites

Florinites, in a restricted sense, is the pollen grain of primitive conifers such as *Ernestiodendron, Lebachia*, and *Walchiostrobus* (Potonié and Kremp, 1956a; Bharadwaj and Venkatachala, 1968; Rothwell, 1982), and of cordaiteans with *Cordaianthus* cones and endarch xylem (Trivett and Rothwell, 1985). *Florinites* in this sense is alete. The name *Florinites* has also been used in a broad sense for monosaccate pollen, even of seed ferns, with or without laesurae (Bharadwaj and Venkatachala, 1968) When further "split", *Florinites*-type pollen of *Lebachia* is *Potoniesporites*, that of cordaiteans with mesarch xylem and *Gothania* cones is *Felixipollenites* according to Daghlian and Taylor, 1979, but *Mesoxylon* wood has also been associated with *Sullisaccites* pollen-bearing material (Trivett and Rothwell, 1985).

Perisaccus

Perisaccus is the pollen grain of cordaitaleans, according to Naumova (1953).

c. Infraturma VESICULOMONORADITI

Archaeoperisaccus

Archaeoperisaccus is a cycadofilicalean pollen grain, according to Naumova (1953). However, the microspore of the late Devonian lycopod, *Kryshtofovichia*,

belongs here according to Allen (1980; see *Nikitinisporites*). As emended by McGregor (1969), *A*. is a monolete, camerate miospore (presumably microspore). Many have noted its close resemblance to *Aratrisporites*, a lycopod microspore. Note that Potonié regarded this form as alete and therefore listed it under ALETESACCITI. As now understood, *A*. should probably be listed under ZONOMONOLETES (Sporites). (See Braman and Hills, 1985.)

Potonieisporites

Potonieisporites is the pollen of the coniferalean, *Lebachia* (Rothwell, 1982; Mapes, 1983; Rothwell and Mapes, 1988b), the coniferophyte, *Barthelia* (Rothwell and Mapes, 2001) and also of the conifer pollen cones, *Walchianthus*, and (those of) the coniferophyte, *Lebachia* (Rothwell and Mapes, 1988b). Hernandez-Castillo, et al. (2001) found this morphogenus of pollen in the walchian conifer, *Thucydia.* Bharadwaj (1964) concluded that *Sahnites* and *Vestigisporites* are synonyms of *Potonieisporites*.

2. Subturma DISACCITES

a. Infraturma DISACCITRILETI

Illinites

Illinites (Potonié and Kremp, 1956a) was produced by coniferalean species (see *Florinites*, above) according to Bharadwaj and Venkatachala (1968).

b. Infraturma DISACCIASTRILETI

Parasporites

Parasporites is pollen of the medullosan, *Parasporotheca* (Dennis and Eggert, 1978; Millay *et al.*, 1978).

Pityosporites

Pityosporites is the pollen of conifers (see *Florinites*, *Illinites*, above) according to Potonié and Kremp (1956a).

Vesicaspora

Vesicaspora was thought to be the pollen of Caytoniales by Potonie and Kremp (1956a), but more recently it is referred to the pteridosperms, *Callistophyton* (Hall and Stidd, 1971; Rothwell, 1972–who describes pollen tubes of *Vesicaspora*!) and *Idanothekion* (Millay and Taylor, 1970). Rothwell and Mapes (1988a) found this morphogenus of pollen in *Idanothekion* synangia.

3. Subturma STRIATITES

Lueckisporites

Lueckisporites is the pollen grain of certain early conifers, for example of *Sashina*, a Permian conifer (Clement-Westerhof, 1974), Caytoniales(?), Gnetales(?) (the latter seems doubtful), and other gymnosperms, according to suggestions of various authors.

Striatites

Striatites is the pollen grain of glossopterid plants (Potonié, 1967) in part, but is thought by many also to be associated with various members of the gnetalean alliance.

II.B. Turma PLICATES

1. Subturma PRAECOLPATES

Monoletes (= Schopfipollenites)

Monoletes (= Schopfipollenites) pollen (prepollen) has been found in a variety of medullosan seed fern "anthers" or synangia (Bharadwaj and Venkatachala, 1968; Leisman and Peters, 1970; Millay *et al.*, 1978). Examples are *Dolorotheca* (Dennis and Eggert, 1978; Drinnan and Crane, 1994), *Sullitheca* (Stidd *et al.*, 1977), *Stewartiotheca* (Eggert and Rothwell, 1979; Millay *et al.*, 1980), *Aulacotheca* (Eggert and Kryder, 1969), *Rhetinotheca* (Rothwell and Mickle, 1982), *Boulaya* (Kurmann, 1983), *Codonotheca* and, *Schopfitheca* (Drinnan and Crane, 1994), *Codonotheca* (Rothwell and Mapes, 1988a). Taylor (1988) notes that *Monoletes* ranges from less than 80 μm to more than 500 μm. Although they are pollen grains, the ones larger than 200 μm would not qualify as miospores in Guennel's definition, but would be "macrospores" (not megaspores!). That is confusing, as is the fact that Monoletes is also a Turma for monolete spores!

2. Subturma POLYPLICATES

Vittatina

According to Potonié (1967), this pollen grain has been referred to the Gnetales by some authors and to the conifers by others.

3. Subturma MONOCOLPATES

Entylissa

Entylissa is widely recognized as the monocolpate pollen grain of various members of the ginkgoaelean and cycad alliances (Potonié and Kremp, 1956a).

6 Paleoecology of Late Paleozoic Spores

Most consideration of this subject has grown out of palynological studies of Carboniferous coals and their associated sediments. In a pioneer work in England, Smith (1962) showed a strong relationship between Carboniferous coal lithotypes and spore composition, finding four miospore assemblages, each assemblage being more or less associated with a distinctive coal petrographic type. In the initial phase of formation of a peat, *Lycospora* and associated forms dominate. In the terminal phases, *Densosporites* and associated forms prevail. The intermediate levels are dominated by "transition" palynofloras of *Laevigatosporites*, *Densosporites*, and others, and "incursion" floras dominated by *Crassispora* and *Punctatosporites*. Butterworth (1966) has summarized the distribution of "densospores" (*Densosporites, Cingulatizonates, Cristatisporites*, *et al.*), trilete spores with a thick cingulum which is typically differentiated into thicker and thinner parts, giving the spore in proximo-distal view by transmitted light a "tire-within-a-tire" appearance. Most if not all are apparently spores of lycopods. They frequently occur in large numbers in coal seams and range stratigraphically from Devonian to Permian. They first occur abundantly in more northerly regions, but their distribution is displaced southward during the Carboniferous. They are most abundant and diverse in areas of slow subsidence. Coals formed under drier conditions are usually devoid of densospores. They are, for example, missing from the Carbondale Formation, a Pennsylvanian coal-bearing formation in Illinois with coals to 15 ft (4.5 m) thick. A decrease in humidity is thought responsible. Densospores disappear in the Upper Westphalian C in parts of Europe, also probably because of drop in humidity. On the other hand, in cyclothem situations, densospores often increase toward the top of coal seams, where the coal swamp was in the process of being transgressed (Habib, 1966). Densospore production by lycopods requiring much moisture is the obvious explanation. Scott and King (1981), studying lycopod megaspores in relation to coal lithotypes in the Upper Carboniferous of England, showed that these spores also have relationship to level in the coal beds, with *Zonalessporites*, for example, relatively abundant in the upper part of the seams.

Phillips and DiMichele (1981), and Phillips *et al.* (1974, 1985) have studied the palynomorph content of shales and coals of Illinois Basin coal-bearing cyclothems. *Florinites* (from *Cordaites* trees and shrubs and similar forms) occurs in the lowest and highest parts of some coal seams, apparently coming from areas marginal to the swamp. *Lycospora* (mostly from *Lepidophloios*) tends to dominate (up to 80%), but decreases upward, being replaced by *Thymospora* (*Psaronius* fern), and, at the top, by *Laevigatosporites* (ferns) (see Fig. 2.2). *Cappasporites* (arborescent lycopods, cf. *Lepidodendron*) is never a dominant but increases upward. *Calamospora (Calamites)* and *Vesicaspora* (seed ferns) are always minor constituents, interpreted by various authors as meaning that the producing plants lived outside the swamp on levees or point bars.

Obviously, much of the underlying information depends on the vast array of data on Carboniferous megafossil plants. However, a succession in time is also at work, so that lycopod-dominated floras gave way to floras dominated by tree ferns (especially, *Psaronius* spp.) at the Westphalian/Stephanian boundary. Then *Lycospora* and *Densosporites* yield to *Laevigatosporites, Punctatisporites*, and other fern spores. This trend is apparently widespread in the late Carboniferous of Euramerica. Chaloner (1961, 1968a, b) and others have noted that *Florinites*, a monosaccate pollen form, is more abundant in deeper-water sediments, indicating upland origin for this buoyant pollen. (*Pinus* pollen sedimentation in the modern Great Bahama Bank shows somewhat similar distributions.) Others (Scott, 1979) have pointed out that some *Cordaites* were perhaps mangrove-like, so the situation is probably not ecologically simple. However, *Florinites* is never a dominant in coal palynofloras, though *Cordaites* was a heavy pollen producer, indicating that *Cordaites* was not a dominant plant in the swamps. Chaloner's work with Jurassic sediments showed that there is a regular relationship between general spores/pollen type and sediment type, with conifer pollen more abundant in marine sediments. Peppers and Pfefferkorn (1970) showed that the sedimentation of spores/pollen in Carboniferous coals and other sediments is really a complex of plant autecology (lycopods preferred swampy environments) and such factors as sporomorph preservation (thin-walled spores such as *Calamospora* do not preserve as readily as *Densosporites*). Overrepresentation of plants that produced many spores, and even the differentiated destruction effects of different maceration techniques, must be considered.

Spores/pollen studies of Carboniferous sediments have contributed considerably to phytogeography and may be expected to make bigger contributions in the future because of the massive amount of spores/pollen data compared with those from megafossil studies. As noted earlier, palynological data tend to be more regionally representative than those from megafossil floras (Raymond *et al.*, 1985b; Sullivan, 1967; Van der Zwan, 1981). Through the early Carboniferous (Mississippian), phytogeographic diversity decreased and this trend continued into the later Carboniferous, probably as a result of moves toward assembly of Pangea II and warmer and/or moister conditions that resulted over large areas (Raymond, 1985). Van der Zwan *et al.* (1985) used multivariate statistical methods (principal components) to link palynological assemblages of the Lower Carboniferous of Euramerica with climatic indications such as prevalence of evaporites or coal in the source rocks. In this way they were able to show a shifting southward of climatic zones, related to northward drift of Euramerica in the Lower Carboniferous.

As noted above, very detailed studies of the American late Carboniferous (= Pennsylvanian) coal swamps have shown similarly detailed local plant successions and migrations (Phillips *et al.*, 1985). In the early middle Pennsylvanian, lycopod (*Cappasporites, Lycospora*) decrease was accompanied by cordaite

(*Florinites*) and tree fern (*Punctatisporites*, *Laevigatosporites, Punctatosporites*) increase. Between middle and late Pennsylvanian, extinctions of coal-swamp lycopods permitted tree-fern dominance. However, Phillips *et al.* note that corrective factors need to be carefully considered because of over- and under-representation of certain spores/pollen taxa. (The same is undoubtedly true for megafossil floras, but spores/pollen are orders of magnitude more numerous, making the statistics more obvious!) Tree fern spores and *Lycospora*-producing lycopods tend to be overrepresented in the coal-swamp sediments, whereas seed plants, particularly medullosan seed ferns, are underrepresented. *Florinites*, pollen of cordaiteans, is underrepresented in coal-swamp flora, on a percentage basis, because of lycopsid dominance.

In Gondwanaland, various studies have shown that the late Carboniferous glaciation in that area marked the beginning of provincialism in the floras, although the palynological data are as yet confined to Australia and southern South America (Truswell, 1981) because of non-deposition, probably related to the glaciation. Azcuy (1975a,b) in Argentina noted that, although the South American palynofloras were of cosmopolitan aspect in the mid- to late Carboniferous, by early Permian they were distinctly related to other Gondwana palynofloras.

7 Comments on Trends in the "Paleophytic" and the "Paleophytic"/ "Mesophytic" Boundary

During the Lower Permian, most of the same sorts of plants persisted as dominated the Carboniferous. (See Fig. 9.6 for Permian and Triassic subdivisions.) However, provincialism, already marked in the Carboniferous, becomes more noticeable in the Permian, and the correspondence between spore assemblages and megafossil floras is clearer (Truswell, 1981).

Especially obvious is the Gondwanaland-Laurasia difference. The Permo-Carboniferous of Gondwana countries is characterized by the *Glossopteris* flora. *Glossopteris* itself produced striate *Protohaploxypinus* pollen, a pollen type that is a signature of the times to come in the "Mesophytic". (See Fig. 2.1 for definition of informal plant-based "eras" such as "Mesophytic".) In general, the Gondwana floras of latest "Paleophytic" time are more "modern" (= more "Mesophytic") in aspect than are Laurasian floras of the same age. Powis (1981) has shown that the immediately preglacial sequences of various parts of Gondwanaland (Australia and South America) have similar palynofloras.

The glacial palynofloras are also broadly similar: dominated by monosaccates and simple trilete spores, and featuring the first occurrence of taeniate bisaccates. However, there are now marked regional differences, with two major palynofloral assemblage types: (a) Australian type (dominant trilete spores, up

to l0% monosaccate pollen), and (b) Indian type (dominant monosaccates, few spores). Antarctica, Australia, and South America yield Australian-type Permian palynofloras, while India has the Indian type, and Africa has some Australian type and some Indian type. Later Permian Gondwanaland palynofloras show increasing importance of bisaccate taeniate pollen.

The justification for using "Paleophytic" and "Mesophytic"(see Figs. 2.1 and 6.1) is that, despite the tremendous significance of the terminal Permian event to animals, especially marine animals, vascular plants do not seem to have changed as much at this interval as they did toward the middle of the Permian (during the Kungurian; see Fig. 9.6), at which point the older plants such as *Cordaites, Calamites* and *Lepidodendron* virtually disappeared, and conifers such as various members of the Voltziales began to dominate in Laurasia, and glossopterids in Gondwana. The result of this is that Zechstein (Kazanian, Tatarian) palynofloras resemble Scythian (Lower Triassic) floras much more than they do Lower Permian floras (which are more like Upper Carboniferous floras). A striking aspect of this similarity is the striate (taeniate) pollen forms, which, as we have seen, appeared as pollen of the glossopterids in Gondwanaland earlier than taeniate pollen became abundant in Laurasia. Striate pollen has some combination of grooves, stripes or taeniae on the main body, which may run either parallel or perpendicular to the line connecting the centers of proximal and distal surfaces. Striate/taeniate pollen may be either saccate or non-saccate (see Fig. 9.7). Some Upper Carboniferous forms, such as *Vittatina*, are striate, but the features explosively evolved in the middle Permian, and even the beginning student with an unknown sample crowded with striate pollen will know immediately, "late Permian-early Triassic". Other sorts of conifer pollen, such as *Lueckisporites, Nuskosisporites*, and a number of other genera, also increase in abundance at the expense of the older Carboniferous forms after early Permian. All in all, from a paleopalynological point of view, the "Paleophytic"/"Mesophytic" boundary is a useful concept.

Remy, for example in Gothan and Remy (1957), defines Känophytikum, Mesophytikum and Paläophytikum with boundaries similar to my "Cenophytic", "Mesophytic", and "Paleophytic." However, Remy called the period before the Paläophytikum the Eophytikum, whereas I call it "Proterophytic," to parallel Proterozoic. It begins with the arrival in abundance of robust-walled acritarchs about one billion years ago, which agrees approximately with the probable arrival of eucaryotes (higher algae). Before the Eophytikum, Remy's oldest era is the Archaikum, which coincides with my "Archeophytic", in which only moneran remains are found. "Paleophytic" has unfortunately been used in quite different senses, and the whole "phytic" idea has had detractors as well as boosters, such as Frederiksen (1972) and Ash (1986). It seems to me reasonable to have "Paleophytic" run from the arrival of land plant spores in the Late Ordovician to the rise to dominance of advanced gymnosperms and their pollen in the Upper Permian. As noted in Chapter 2,

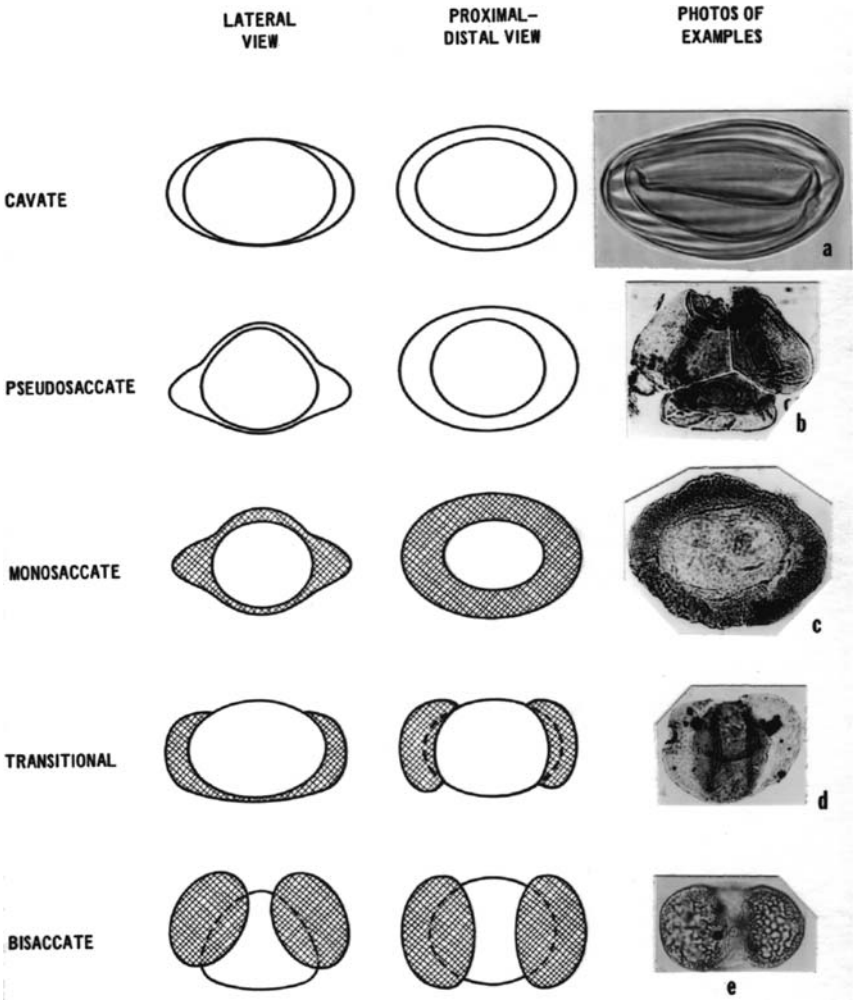

Figure 9.8 Saccate vs. pseudosaccate and cavate spores/pollen morphology. Cavate spores/pollen have a central body of nexine separated by a space from the sexine. (**a**) Example shown in proximal-distal mid-focus is pollen of *Welwitschia mirabilis* Hook. (extant, Namibia), width 60 μm. Pseudosaccate spores have saccus-like structures which, however, are clearly merely a special case of cavate: the pseudosacci enclose hollow spaces between nexine and sexine. (**b**) Example shown is *Alatisporites trialatus* Kosanke (Westphalian D, Carboniferous, Canada), width 90 μm. Monosaccate pollen has an alveolate (spongy) envelope more or less surrounding the grain. The single saccus may enclose the whole grain as shown in the diagram, or may leave (usually distal) areas free of saccus, as in the illustrated grain, (**c**) *Cordaitina* sp. (Westphalian C, Carboniferous, Canada), width 100 μm. Many, especially Mesozoic, forms trend toward bisaccate (= transitional) but the alveolate saccus is actually more or less continuous, especially on the

Gray (1993) published a somewhat different version of the -phytic chronology, without discussion of, or even reference to, this one, which was originally published in 1988.

It should also be emphasized that paleopalynology is very helpful in correlation of rocks according the the zoologically based divisions of the Carboniferous and Permian conventionally used. For example, Love (1994) demonstrates the usefulness of palynological zonation of Upper Carboniferous rocks of the Persian Gulf area, in connection with oil exploration. Peppers (1996) summarizes the key role of fossil spores and pollen in stratigraphic correlation of Pennsylvanian (Middle and Upper Carboniferous) rocks of the coal basins of the central USA, to mention only two contributions among hundreds worldwide on palynostratigraphy of Carboniferous rock. It was the British Carboniferous that Raistrick correlated by fossil spores as a pioneer palynostratigrapher before even the word palynology had been invented.

8 Morphological Comment Regarding Carboniferous/Permian Pseudosaccate and Saccate Spores/Pollen and Related Matters

Carboniferous palynofloras include a number of examples of pseudosaccate spores, such as *Alatisporites* and *Endosporites*, in which the apparent sacci are not true sacci but represent extensions of the cavate (camerate) condition, in which the space between two layers of exine balloons out to produce vesicles (blisters). A true saccus is at least to some extent internally "webby"–the ektexine has obvious structure. Truly bisaccate pollen also developed during the Carboniferous (see Fig. 9.8).

Vesicaspora, for example is bisaccate pollen produced by a seed fern, though at first glance it appears to be very like some extant conifer bisaccate pollen!

Monosaccate pollen also developed during the Carboniferous, e.g., *Florinites*, a genus for pollen produced by cordaitalean and primitive conifers. Monosaccates become very important in the Lower Permian, when forms such as *Nuskoisporites* and *Lueckisporites*,and numerous other, often large, monosaccates are characteristic. Very revealing studies of Paleozoic saccates by Millay and Taylor (1970, 1974, 1976) have contributed greatly to our understanding of such pollen. As

Figure 9.8 proximal side of the grain. Illustrated form (**d**) is *Protohaploxypinus* sp. (Wolfcampian, Permian, Canada), width 70 μm. Bisaccate pollen has two well-demarcated, separate alveolate sacci. Illustrated form (**e**) is *Pityosporites* sp. (Albian, Lower Cretaceous, Canada), width 72 μm. N. B.: See text for discussion of the terms "eusaccate" and "protosaccate." Photos (b)-(d) are courtesy of M. S. Barss and the Geological Survey of Canada, from McGregor, 1965.

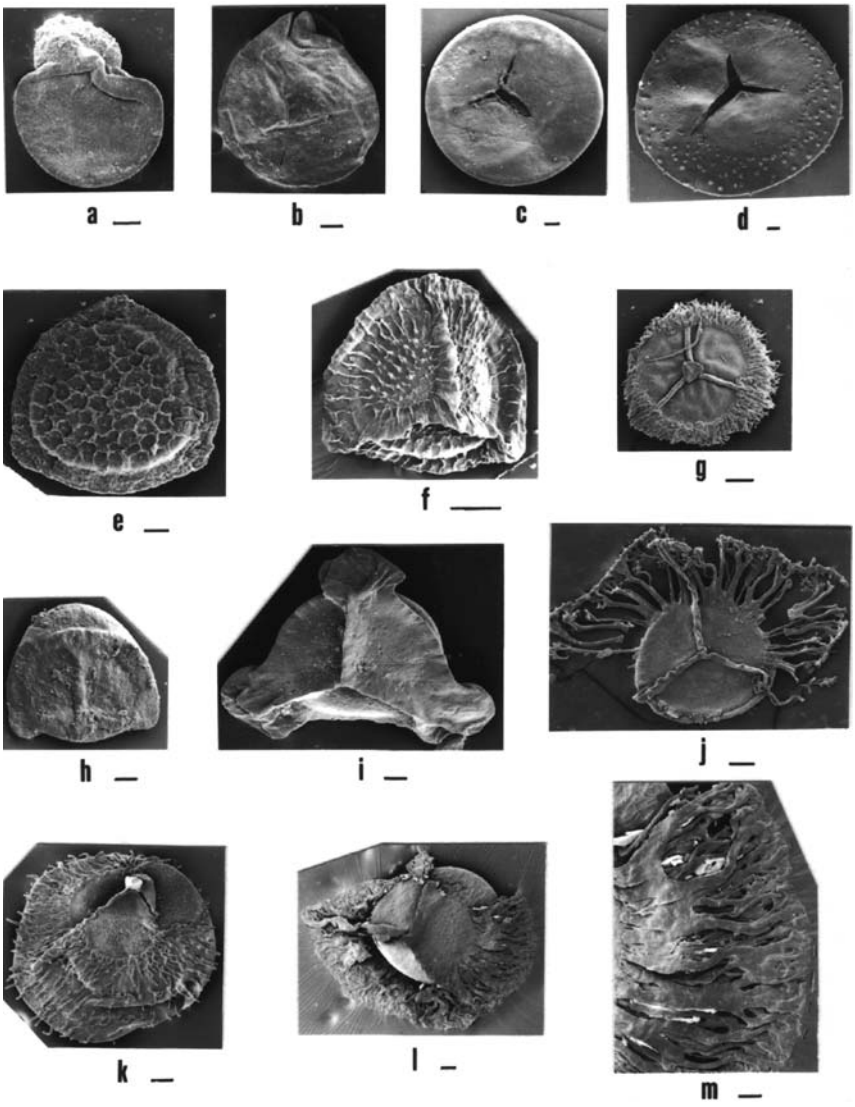

Figure 9.9 SEM micrographs of Late Carboniferous (Westphalian B) megaspores from Barnsley and Lidgett coal seams of the Yorkshire coal field, UK. The small bar to the right of each letter indicates 100 μm. See also caption to Fig. 8.8. (**a**) *Cystosporites varius* (Wicher) Dijkstra. Lateral view of an aborted form. (**b**) *Lagenoisporites rugosus* (Loose) Potonié & Kremp. Lateral view showing gula at top. (**c**) *Laevigatisporites primus* (Wicher) Potonié & Kremp. Proximal view. (**d**) *Tuberculatisporites* sp. Proximal view. (**e**) *Triangulatisporites regalis* (Ibrahim) Potonié & Kremp. Distal view. (**f**) *Triangulatisporites triangulatus* (Zerndt) Potonié & Kremp. Proximal view. Note zona here and in (e).

shown in Fig. 9.8, there are transitional forms between monosaccate and bisaccate. Bisaccate forms are still important today in extant conifers such as *Pinus, Picea, Cedrus, Abies*, etc. Monosaccates also are found in extant conifers, such as *Tsuga*. (In my opinion, the layer of pollen wall of *Taxodium* and some other extant conifers that is usually called perine may really be the relict of a detachable saccus.) The purpose of sacci clearly is related to orientation of the grain for correct germination in liquid drops at the opening of the megasporangium (cf. Hughes, 1994, p. 36).

8.1 About "Protosaccate" and "Eusaccate"

At this point I must also mention two terms about saccate pollen that have crept into the literature of paleopalynology and therefore cannot be ignored, even though they seem to have rather slight significance for practical work with fossil pollen. The terms are *protosaccate* and *eusaccate*. They were introduced by Scheuring (1974), based on Triassic saccate pollen, and have been taken up by many paleobotanists and paleopalynologists. Scheuring (e.g., 1970, 1978), one of the most important investigators of Triassic spores and pollen, noted that many saccate forms he studied have extensive ektexinous ramifications (webbing) in the sacci. Saccate pollen with such webbed sacci forms Scheuring called protosaccate to distinguish them from the sorts of sacci that modern conifers such as *Pinus* have, with only limited webbing, confined to the external part of the sacci. Such pollen is called eusaccate, with the implication that protosaccate is primitive, and eusaccate is advanced. Even though Foster and Balme (1994) show protosaccate-like features in the oldest saccate pollen, *Teichertospora*, that proposition is not supported by the fossil record, as is clear from Taylor *et al.* (1987), Taylor and Taylor (1987), and Taylor and Grauvogel-Stamm (1995). The latter paper demonstrates clearly that the character is mostly confined to the Permo-Triassic and is probably some sort of special pollination-adaptation rather than a phylogenetic link. Zavialova *et al.* (2004), working with the cordaitean pollen, *Cordaitina*, note that the grains vary from clearly protosaccate to clearly

◄

Figure 9.9 (**g**) *Setosisporites hirsutus* (Loose) Ibrahim. Proximal view (see Fig. 8.8t). (**h**) *Valvisporites auritus* (Zerndt) Potonié & Kremp. Obliquely proximal view. (**i**) *Valvisporites appendiculatus* (Kowalewska-Maslankiewicz) Potonié & Kremp, proximal view, note auriculate structures reminiscent of those in miospore form, *Triquitrites*. (**j**) *Rotatisporites rotatus* (Bartlett) Potonié & Kremp. Proximal view of form with elaborate coronate zone. (**k**) *Lagenicula subpilosa* (Ibrahim) Potonié & Kremp. Obliquely proximal view showing rather small contact area and gula (see Fig. 8.8r). (**l-m**) *Zonalessporites brasserti* (Stach & Zerndt) Potonié & Kremp. Proximal view, and detail of densely fimbriate zone, respectively (see Fig. 8.8 m for a specimen of the species without the zone). Micrographs courtesy of K. M. Bartram.

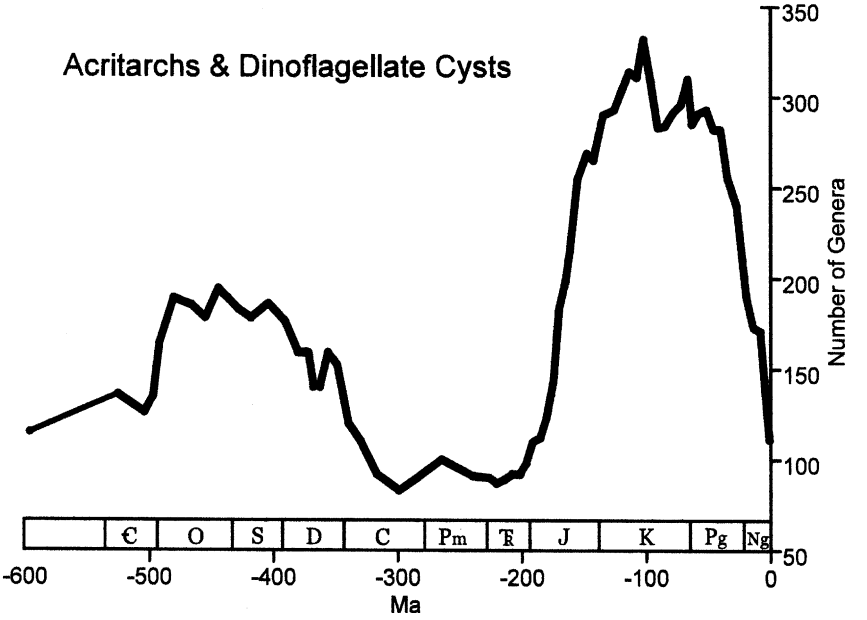

Figure 9.10 Fossil microphytoplankton paucity in Carboniferous, Permian and Triassic sediments, with abundance in the Cambrian to Devonian based on acritarchs and abundance post-Triassic based on dinoflagellates. The curve is of standing diversity of Phanerozoic acritarch and dinoflagellate cyst genera compiled for the author by P.K. Strother, based partly on data from R.A. MacRae, filtered by indices for acritarchs and dinoflagellates to assure use of legitimate taxa. The values displayed are stratigraphically resolved to the epoch/series level.

eusaccate, depending to some extent on the thickness of the individual ektexine, as if the situation is developmental. In any case, as this character can only be demonstrated with certainty by electron microscopy, it clearly is not going to be important for basic paleopalynological work, a view that is shared by Taylor *et al.*, 1996.

9 Late Carboniferous-Permian Megaspores

Although free megaspores are never again as prominent as they were in late Devonian-early Carboniferous time, their study remains an important source of stratigraphic and especially of paleoecological information through the remainder of the Carboniferous, and the Permian, into the Triassic.

SEM pictures of some important forms of late Carboniferous megaspores are displayed in Fig. 9.9.

Dybova- Jachowicz *et al.* (1982) have demonstrated the importance of careful morphological analysis of these complex spores of the Carboniferous. Scott and King (1981) and others have shown the potential significance of megaspore studies in unraveling the environment of deposition of Carboniferous coals.

10 Carboniferous-Permian Acritarchs

Aside from spores/pollen, the only palynomorphs of significance in late Paleophytic rocks are acritarchs, and they have been comparatively little studied, largely because of the dramatic decrease in their relative abundance and diversity in marine sediments after the Devonian. Outline drawings of some representative Permian and Triassic acritarchs are shown in Fig. 10.5, but it should be stressed that acritarch palynofloras even in the Triassic are not very diverse. As mentioned earlier, it is striking that whatever microscopic phytoplankton the Permo-Carboniferous seas contained, the organisms did not produce many microfossils with robust, sporopolleninous walls, and that continued to be the story until the end of the Triassic, when dinoflagellate cysts appear. Fig. 9.10 is a dramatic display of this major "event" in world history. Why the microphytoplankton surely present in those seas gave up making cysts or other disseminules with robust walls would be very interesting to know.

Chapter 10

Permo-Triassic Palynofloras

1 Introduction

Late Permian, from the Kungurian stage on, is palynologically a time of saccates: monosaccates and bisaccates, and especially of striate bisaccates, surely bespeaking conifer or conifer-like gymnosperm dominance (plus glossopterids in Gondwanaland). This trend accelerated across the "Paleophytic"/"Mesophytic" line. (See Fig. 9.6 for Permian/Triassic time divisions.) However, Permian palynofloras follow those of the Carboniferous in showing great provincialization, and one really must look at the Permian floras both spatially and temporally to get an accurate picture. Hart (1974) and others (Truswell, 1981) adopt provinces used by megafossil paleobotanists (Chaloner and Lacey, 1973): (a) Euramerican province (Chaloner and Lacey divide this into Atlantic, North American and Cathaysian in Lower Permian), (b) Angaran province (Central Asia, mostly), (c) Cathaysian province, (China, etc.), (d) Gondwana province (India, Africa, etc.). To this should probably be added an Australian province, or Gondwanan subprovince, as Balme (1964) has ably demonstrated that a distinct palynoflora has characterized it since Carboniferous time, and Truswell (1980) has shown that Gondwana can be further divided to sub-provinces. Playford (1976) demonstrated that even late Devonian Australian palynofloras are to a high degree endemic. Some of Hart's (1971) basic palynofloral types for the Euramerican province are shown in Fig. 10.1. The "Paleophytic"–"Mesophytic" change is very clear in the Euramerican and Cathaysian provinces, but is not so obvious in the Angaran province. It would appear to fall somewhere in the Talchis-Karbarbari transition in the Indian Permian. Hart (1974) later showed that the four major floras can be further subdivided. He also pointed out that the floras comprise palynofloristic

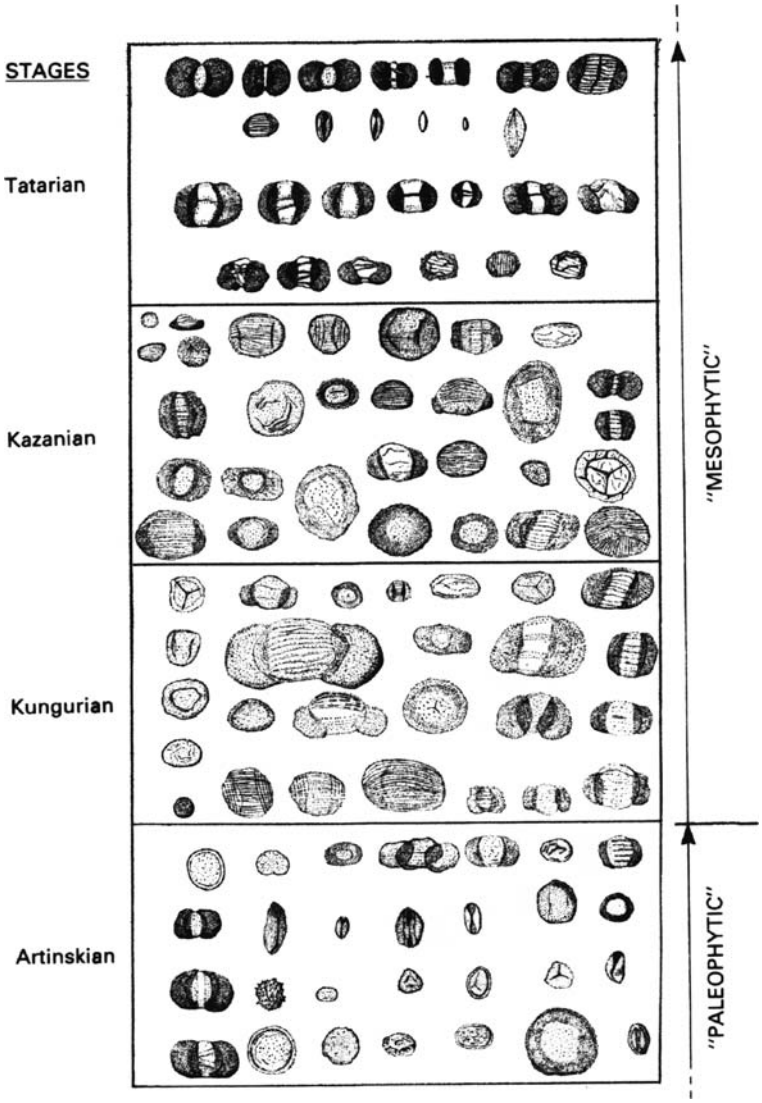

Figure 10.1 Generalized Permian sporomorph succession, Euramerican province, the former USSR. Note that an additional lowest Permian stage, the Sakmarian, exists. A "Mesophytic" era can be informally hypothesized to begin with the Kungurian stage and the coming to dominance of taeniate (striate) and bisaccate pollen, probably corresponding to a profound change in continental climate. The "Mesophytic" would continue until the beginning of the "Cenophytic," at the time of arrival of undoubted angiosperm pollen in the Neocomian, Lower Cretaceous (see Figs. 2.1 and 6.1). By the end of the Permian, conifer-like bisaccates with large sacci were beginning to predominate. Modified from Hart (1971).

zones based on paleolatitudes. The Cathaysian palynoflora, for example, would represent a tropical zone. Akyol (1975) and Horowitz (1973) have shown relationships between the Permian palynofloras of Turkey and Israel, respectively, and the Cathaysian palynoflora.

Wilson (see Truswell, 1981) and others have shown that the Permian palynofloras of Australia and New Zealand are very similar, but Gondwanaland Permian floras seem to have developed their own "intramural" palynofloral provincialism. Truswell, for example, has discussed the interesting case of *Dulhuntyspora* (see Fig. 10.3), a common and biostratigraphically important late Permian trilete spore, essentially confined to Australia. Eshet and Cousminer (1986) report a succession in the Permo-Triassic of Israel. The Permian and Lower Triassic palynofloras are Gondwana-like, those of the Upper Triassic more like Laurasian floras.

It should be noted as a caution here that paleobotanical provinces based on megafossil plants and data from paleopalynology are sometimes difficult to coordinate. Foster *et al.* (1994) note that sporomorph assemblages from quite different paleobotanical provinces appear more similar in their contained taxa than would be expected from the megafossil records from the same areas, suggesting perhaps parallel evolution of sporomorphs in different groups of plants. They observe, however, that detailed study of at least some of the superficially identical sporomorph taxa showed that they actually could be distinguished. It would appear possible that this is an example of the fact that spores and pollen are not easily separated below the level of genera of whole plants.

In several areas the pollen record is important in determining the stratigraphic location of the Permian/Triassic boundary. For example, in Australia the boundary can be placed in relation to the pollen-based *Protohaploxypinus microcorpus* zone (cf. Morante *et al.*, 1994), as it links to carbon istotope excursions.

2 Striates and Bisaccates, Permo-Triassic Hallmarks

When students in my introductory palynology course got a laboratory "unknown," they were always in (preliminary) luck if it was a late Permian or early Triassic sample, because the prevalence of striate bisaccate pollen is very characteristic practically worldwide of palynofloras of this time. The characteristic striate appearance of the corpus of such pollen is produced by deep parallel grooves (striae) and/or parallel straps (taeniae) in the exine. It would appear likely, though this is conjectural, that taeniae resulted from widening of striae, leaving the strap-like taeniae as exine islets. Both striate non-saccate or slightly saccate, e.g., *Vittatina*, and taeniate bisaccate, e.g., *Striatites*, pollen were well established in late Carboniferous and early Permian, but the heyday of bisaccate striate/taeniate pollen was in late Permian and early Triassic. Glossopterid gymnosperms of Gondwanaland have taeniate pollen. The extant gnetaleans, *Ephedra* and *Welwitschia,* have striate pollen. The weirdly "spiral" late Triassic, taeniate

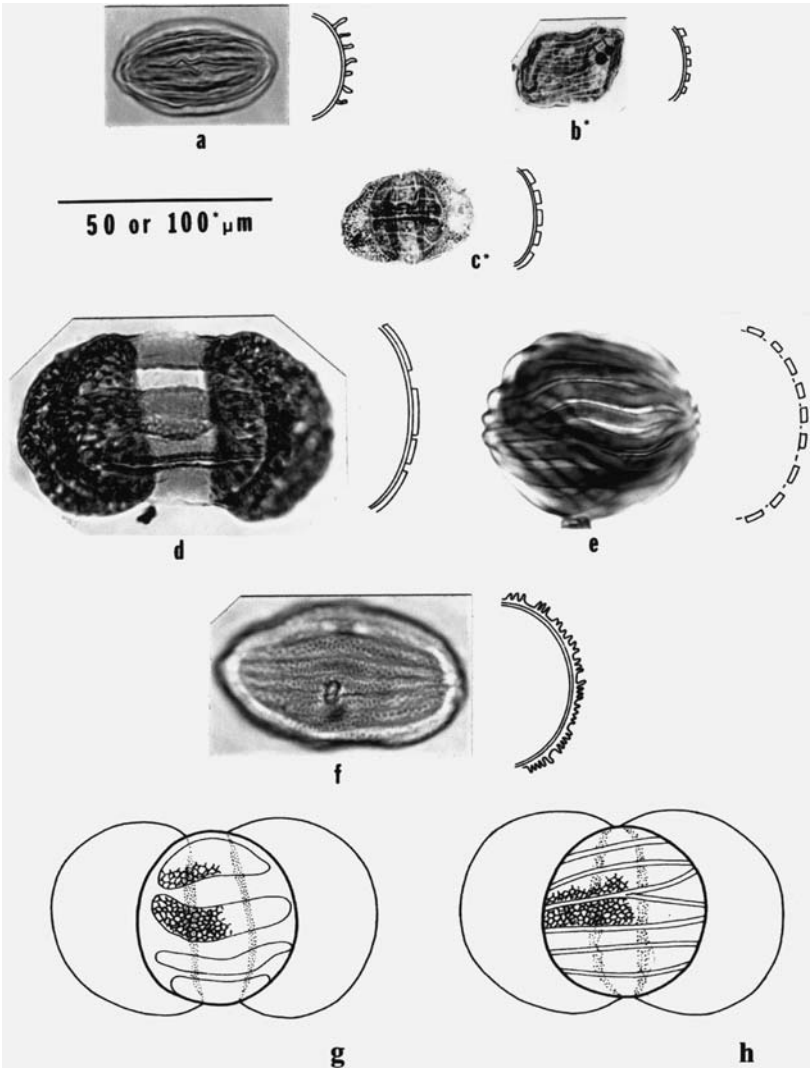

Figure 10.2 Polyplicate and taeniate (= "striate") pollen morphology. One of the most interesting features of Upper Paleozoic and early Mesozoic pollen is the development in a wide range of gymnosperms of pollen, the corpus of which is covered with more or less numerous, more or less widely separated taeniae, or straps of exine. The feature is presumably harmomegathic in nature, allowing for expansion and contraction as required by moisture stress. Among modern plants, the feature is quite rare, being shown by the gnetaleans *Ephedra* (see (a)), *Welwitschia* (see Fig. 9.8a), and by a few angiosperms, such as some members of the family Acanthaceae (see (f)). In both instances, parallel evolution rather than homology to the Permo-Triassic forms is likely. (**a**) *Ephedra tweediana* C.A.

form, *Equisetosporites*, has been found in conifer cones. Clearly, striate/taeniate pollen is a conifer-glossopterid-gnetalean "thing." Fig. 10.2 presents an analysis of the nature of the taeniate/striat construction.

Note that even certain extant dicot angiosperm pollen have adopted this strange pattern, which probably has a harmomegathic function for these angiosperms (family Acanthaceae) as an adaptation to the swelling and contracting caused by considerable losses and gains of moisture, and likely had a similar function for Permo-Triassic gymnosperm pollen.

Foster and Gomankov (1994) have shown that the striate cappa (the thick proximal section of the main body of saccate grains) of *Striatopodocarpites* and *Protohaploxypinus* pollen can detach from the rest of the grain during taphonomic processes and occur separately as an apparent sporomorph resembling other, non-saccate, taxa. Perhaps more disturbing and worth more study is the revelation by Lindstrom *et al.* (1997) that Permian male pollen cones containing mostly *Protohaploxypinus* pollen can contain also as much as 4% pollen referable to *Striatopodocarpites*, as well as aberrant monosaccate and trisaccate pollen that could be placed in other pollen morphogenera. This indicates a certain developmental plasticity in pollen morpohology that warns against over-interpretation of small numbers of sporomorph forms in a sedimentary rock.

Figure 10.2 Mey (extant plant, Uruguay). The plicae are rather thin and not much like fossil pollen taeniae. Note however (Fig. 9.8a) that *Welwitschia* has taeniae. (**b**) *Vittatina vittifer* (Luber) Samoilovitch (Permian of Yukon, Canada). A taeniate form which could accurately be described as striate, as the grooves are as conspicuous as the taeniae. *Vittatina* is one of the few non-saccate Permo-Triassic taeniate pollen forms. (**c**) *Protohaploxypinus* sp. (Permian of Yukon, Canada). This kind of pollen was made, e.g., by *Glossopteris*. The taeniae are perpendicular to the axes of the sacci in this form. In other genera they may be parallel to them, or helically arranged. (**d**) *Lunatisporites* sp. (= *Taeniaesporites*) (Permian, UK). The taeniae in this genus are characteristically four in number, comprising almost all of the corpus exine. (**e**) *Equisetosporites chinleanus* Daugherty (Triassic of Arizona). The exine seems to consist entirely of the taeniae, which interconnect and spiral around the grain. (**f**) *Nilgirianthus warrensis* (Dalz.) Bremak (extant plant of family Acanthaceae, India). The "taeniae" are strips of reticulate ektexine on a triporate grain (pores are subsurface in this specimen, but in related species examined, the pores break through to the surface and interrupt the taeniae). (**g**)-(**h**) Line drawings from Tiwari and Vijaya (1995) provide further help in understanding the difference between bisaccate striate and bisaccate taeniate pollen. The nature of sculpturing is instructive: in taeniate exines (**g**) the sculpturing is confined to the taeniae. In striate (**h**) exines, the striae are channels that cut through sculpture patterns. Photomicrographs (b) and (c) were provided by M. S. Barss, Geological Survey of Canada, originally published in Barss (1967).

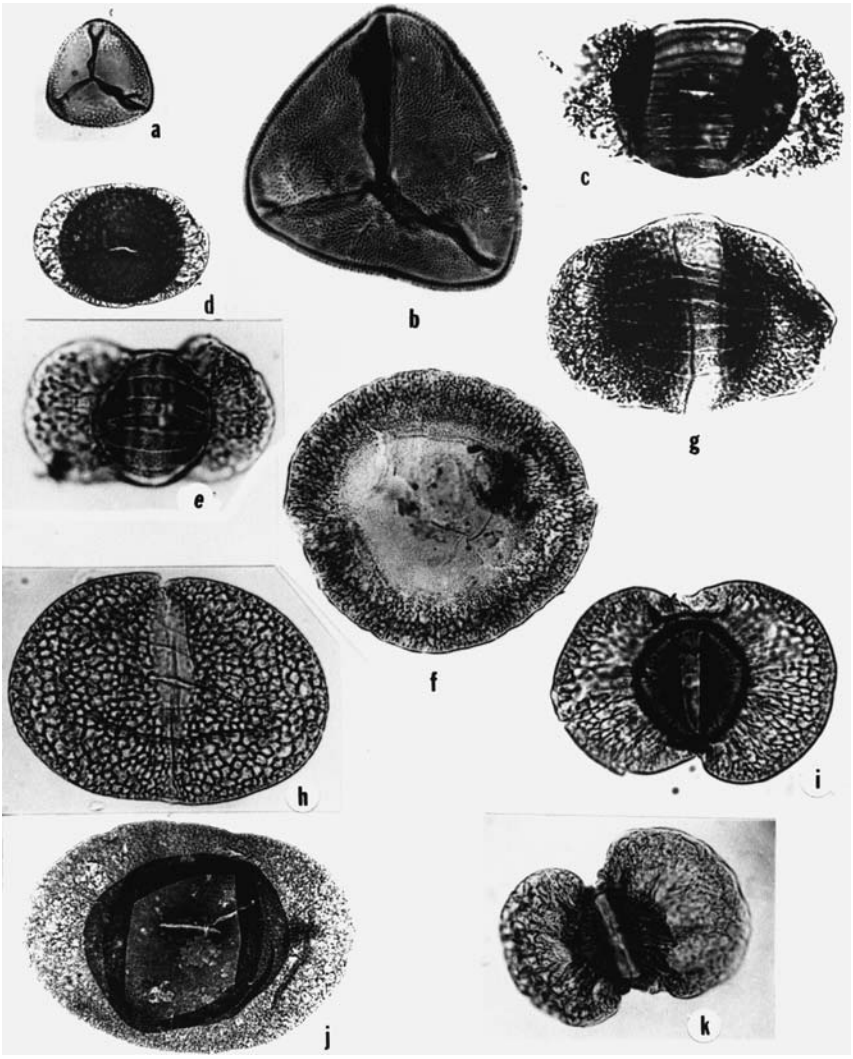

Figure 10.3

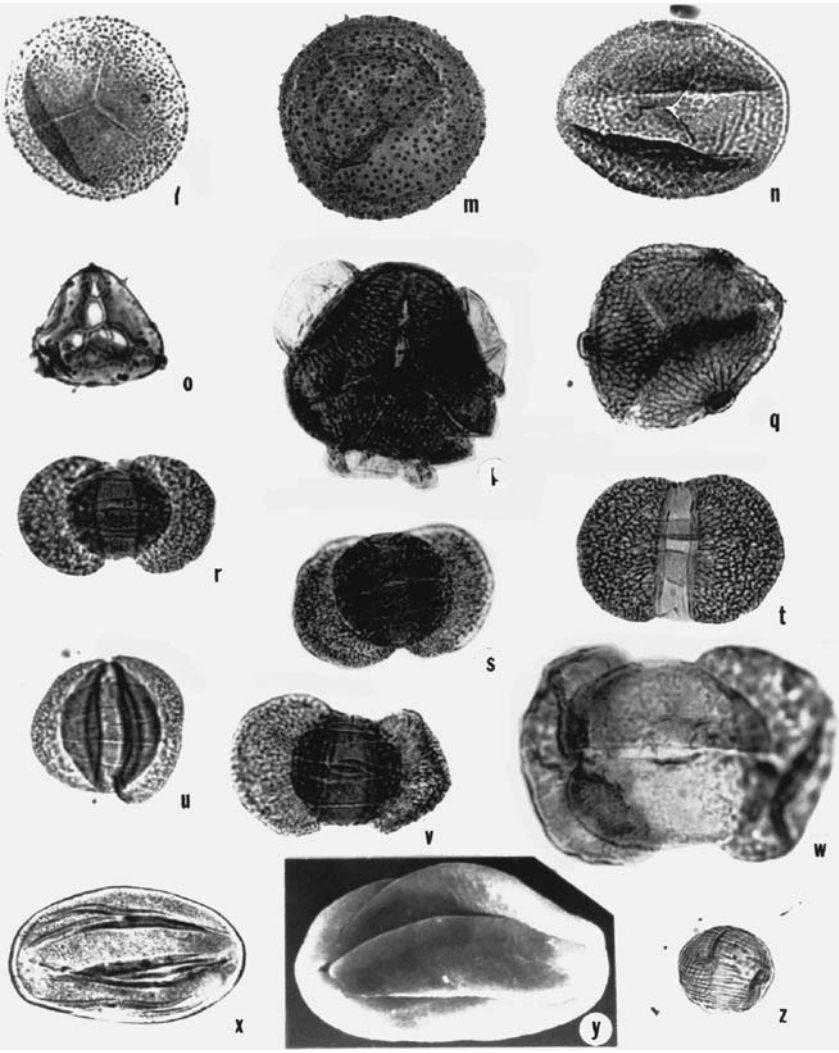

Figure 10.3 *(See caption on page 283)*

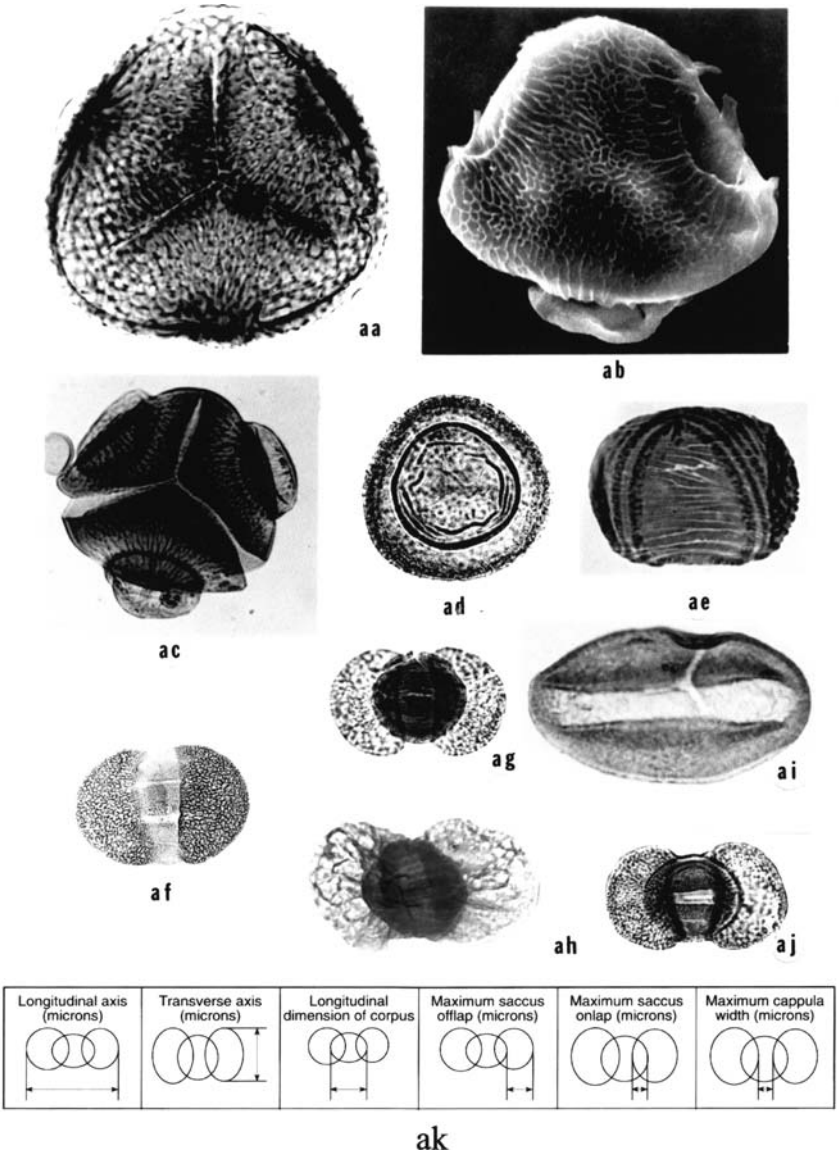
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Figure 10.3

3 Other Spore/Pollen Types of Permo-Triassic

Although bisaccate striate/taeniate pollen are the signature of this time, other spore/pollen forms are also important. Trilete spores, probably mostly of ferns, for example, continue to be important throughout the Mesophytic and some, e.g., *Dulhuntyspora* in Australia, are important stratigraphically. A group of sporomorphs that originated in the "Paleophytic" but became very significant in the Permo-Triassic and remain so through the "Mesophytic" are the monosulcates. *Entylissa* is one form, already present in the Carboniferous, but there are a number of others such as species of *Monosulcites* and *Cycadopites*. Fig. 10.3 shows a range of typical Permo-Triassic sporomorphs from Australia. The stratigraphic range of some of the more important Permian-Triassic-Jurassic forms in Laurasia is given in Fig. 10.4.

Figure 10.3 Permian and Lower Triassic spores/pollen from Australia. (**a**) *Microbaculispora tentula* Tiwari, 40 μm. (**b**) *Microbaculispora trisina* Balme & Hennelly, 85 μm. (**c**) *Striatoabieites multistriatus* Balme & Hennelly, 70 μm. (**d**) *Limitisporites* sp., 67 μm. (**e**) *Striatopodocarpites* sp., 60 μm. (**f**) *Cannaropollis janakii* Potonié & Sah, 115 μm. (**g**) *Protohaploxypinus amplus* Balme & Hennelly, 93 μm. (**h**) *Protohaploxypinus* sp., 102 μm. (**i**) *Platysaccus* sp., 89 μm. (**j**) *Potonieisporites* sp., 160 μm. (**k**) *Platysaccus* sp., 94 μm. (**l**) *Osmundacidites senectus* Balme, Lower Triassic, 78 μm. (**m**) *Lundbladispora willmottii* Balme, Lower Triassic, 80 μm. (**n**) *Marsupipollenites triradiatus* Balme & Hennelly, Upper Permian, 56 μm. (**o**) *Indospora clara* Bharadwaj, Upper Permian, 60 μm. (**p**) *Dulhuntyspora dulhuntyi* Potonié, Upper Permian, 88 μm. (**q**) *Dulhuntyspora* sp., Upper Permian, 80 μm. (**r**) *Taeniaesporites obex* Balme, Lower Triassic, 76 μm. (**s**) *Lunatisporites* sp., Lower Triassic, 80 μm. (**t**) *Lunatisporites pellucidus* Goubin, Lower Triassic 80 μm. (**u**) *Striatopodocarpites* sp., Upper Permian, 74 μm. (**v**) *Lunatisporites* sp., Lower Triassic, 83 μm; (**w**) *Lueckisporites virkkiae* P.& K., Upper Permian of Pakistan, 75 μm. (**x**) *Praecolpatites sinuosus* Balme & Hennelly, Upper Permian, 114 μm. (**y**) As (x), S.E.M., 100 μm; (**z**) *Weylandites lucifer* Bharadwaj & Salujha, Upper Permian, 38 μm. (**aa**) *Dulhuntyspora* sp., Upper Permian, 75 μm. (**ab**) *Dulhuntyspora dulhuntyi* Potonié, S.E.M., 85 μm. (**ac**) As (ab), photomicrograph, 84 μm. (**ad**) *Lundbladispora willmottii* Balme, Lower Triassic, 77 μm. (**ae**) *Weylandites lucifer* Bharadwaj & Salujha, Upper Permian, Pakistan, 54 μm. (**af**) *Lunatisporites pellucidus* Goubin, Lower Triassic, 72 μm. (**ag**) *Taeniaesporites obex* Balme, Lower Triassic, 72 μm. (**ah**) *Striatopodocarpites* sp., Upper Permian, 73 μm. (**ai**) *Marsupipollenites triradiatus* Balme & Hennelly, Permian, 60 μm. (**aj**) *Taeniaesporites* sp., Lower Triassic, 75 μm. (**ak**) Useful parameters for bisaccate measurements from Stephenson and Filatoff (2000). Photomicrographs courtesy of B. E. Balme. Some of them were published in Balme (1964). (ah) is from Utting (1996).

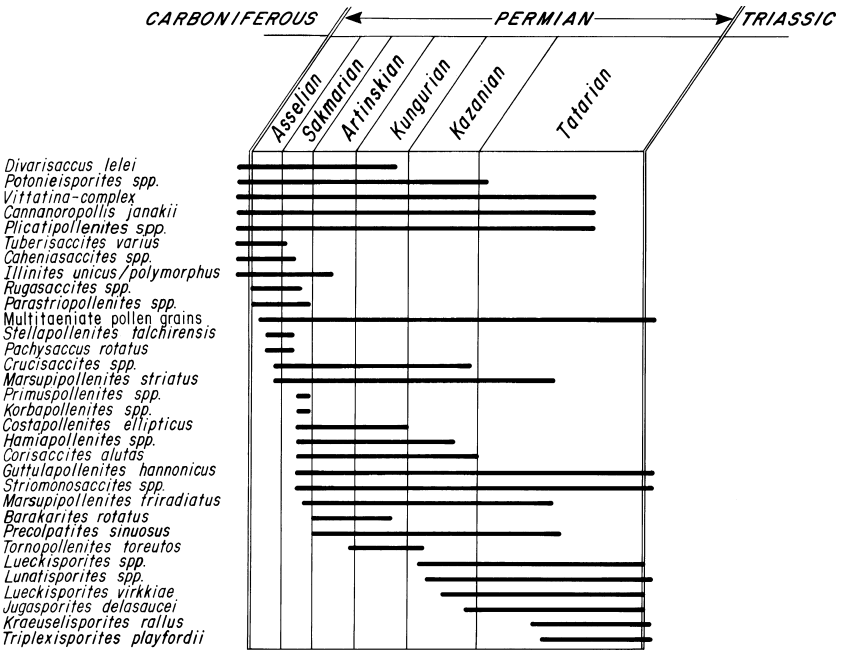

Figure 10.4 Tentative range chart of selected Permian sporomorphs. Some of the forms are restricted to various geographic provinces. This chart was drafted by W. A. Brugman for his informal publication, *Permian-Triassic Palynology* (1983) and appears here in revised form.

4 Permo-Triassic Acritarchs

Fig. 10.5 shows some Permian and Triassic common forms. Marine and near-marine Permian and Triassic sediments often contain abundant and diverse acritarchs. Jacobson *et al*. (1982) have noted that, for some as yet unexplained reason, though apparently sporopolleninous, they are more abundant in some phosphorites than in the associated mudstones (siltstones) where palynomorphs would be expected. The mudstones may even be altogether barren. Permo-Triassic acritarchs have considerable potential stratigraphic usefulness, as noted for example by Jacobson *et al*. and by Sarjeant (1970).

5 Terminal Permian "Fungal Spike" (?) and Related Matters

The end-Permian worldwide extinction also affected plants; it has been suggested that fungi digesting the masses of dead plant and animal material in the basins of the end-Permian world are evidenced by a peak of fungal spore and

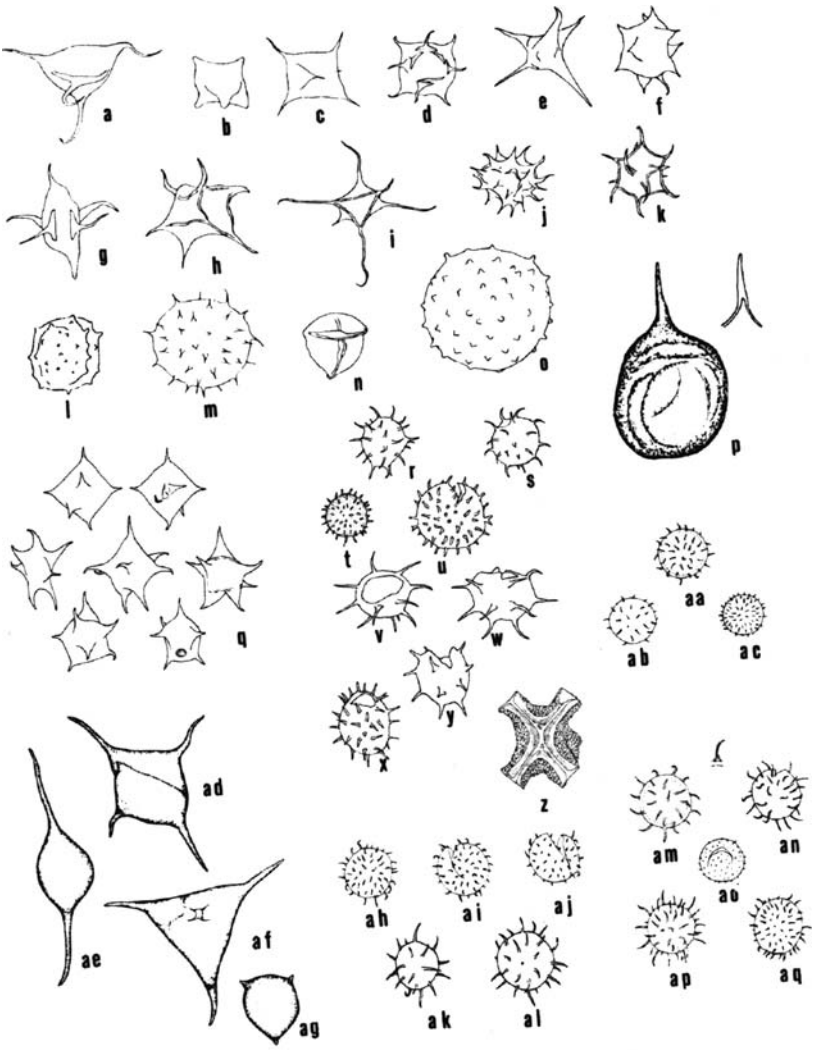
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Figure 10.5

mycelial matter in the palynologic record in various places (cf. Eshet, 1990; Visscher *et al.*, 1996).

Indeed, abundant organic particles and reworked material in the sediments offer much evidence of environmental disruption. Morante *et al.* (1994) note that carbon isotope changes at the boundary bespeak a big alteration in carbon flux, and a reduction in the amount of photosynthesis. Much cellular material that closely resembles fungal fruiting bodies and mycelia is found in some boundary sediments. It has been suggested that the fungal "spike" could be used as a reliable marker event for placing the Permian/Triassic boundary (cf. Steiner *et al.*, 2003). However, this time is well before the first sporadic occurrences of undoubted chitinous fungal spores in late Triassic and Jurassic (Traverse and Ash, 1994) and their rising to abundance in the record beginning in the Cretaceous. Ward *et al.* (2005) have noted that the apparent fungal "spike" is often missing in end-Permian sediments, that it is not always found in such records, and that it sometimes occurs multiple times. Some palynologists are not convinced that the microfossils found in latest Permian sediments and attributed to the Fungi are

Figure 10.5 Outline drawings of Permian and Triassic acritarchs. (a)-(o) Upper Permian (middle and upper Zechstein of Germany (= Tatarian)); (q)-(z) Tatarian of Pakistan; (p), (aa)-(aq) early Triassic (Scythian and Anisian of Pakistan). (**a**) *Veryhachium hyalodermum* (Cookson) Schaarschmidt. (**b**) *V. quadratum* Schaarschmidt. (**c**) *V.* cf. *nasicum*. (**d**) *V. sedecimspinosum* Staplin. (**e**) *V. variabilis* Schaarschmidt. (**f**) *V. conispinosum* Schaarschmidt. (**g**) *V. cylindricum* Schaarschmidt. (**h**) *Polyedryxium kraeuselianum* Schaarschmidt. (**i**) *Polyedryxium* sp. (**j**) *Micrhystridium bistchoensis* Staplin. (**k**) *M*. cf. *albertensis* Staplin. (**l**) *M. microspinosum* Schaarschmidt. (**m**) *Baltisphaeridium brevispinosum* (Eisenack) Downie. (**n**) Undetermined acritarch. (**o**) *Buedingiisphaeridium permicum* Schaarschmidt. (**p**) *Deunffia* sp.. (**q**) Range of forms of *Veryhachium? riburgense* Brosius & Bitterli. (**r**),(**s**) *Micrhystridium breve* Jansonius. (**t**) *M. densispinum* Valensi. (**u**) *M. setasessitante* Jansonius. (**v**),(**w**) *M. circulum* Schön. (**x**) *M*. sp. (**y**) *M. karamurzae* Sarjeant. (**z**) *Polyedryxium* sp.. (**aa**) *Micrhystridium teichertii* Sarjeant. (**ab**) *M. kummelii* Sarjeant. (**ac**) *M. densispinum* Valensi. (**ad**) *Veryhachium* cf. *bromidense* Loeb. (**ae**) *Leiofusa jurassica* Cookson & Eisenack. (**af**) *Veryhachium* sp.. (**ag**) Short-spined variant of *V. valensii* Downie & Sarjeant. (**ah**)-(**aj**) *Michrystridium castanium* Valensi. (ak) M. sp. (al) *Solisphaeridium debilispinum* Wall. (**am**) *Michrystridium teichertii* Sarjeant; includes detail of spine above. (**an**) *M. jekhowskyi* Sarjeant. (**ao**) *M. balmei* Sarjeant. (**ap**) *M. jekhowskyi* Sarjeant. (**aq**) *M. castaninum* Valensi. Magnification various: (a) is about 40 μm wide, and this can be used to measure (a)-(o); (p) is 27 μm high; (ae) is 80 μm long, and this can be used for comparison with (ad)-(ag); (z) is 35 μm long; all the other figures are at about the same magnification, such that (aa) is about 20 μm in diameter. Note the details for spines of (p) and (am), a frequently used illustrative method for acritarchs. Because acritarchs often have delicate processes and hyaline walls and are consequently hard to photograph, line drawings are very commonly used to illustrate them. (a)-(o) are from Schaarschmidt (1963); (p) and (aa)-(aq) are from Sarjeant (1973); (q)-(z) are from Sarjeant (1970).

really fungal. Foster *et al.* (2002), for example, say that *Reduviasporonites*, the genus for the alleged fungal remains is more probably algal. Utting *et al.* (2004) suggest that *Reduviasporonites* sp. may represent an alga itself resistant to the unfavorable conditions at the boundary, rather than an organism that consumed the bounty of destroyed organic matter resulting from such conditions. At this writing the reality of what looked for a time to be a very promising geochronological "golden spike" based on fossil fungal remains, is very seriously challenged.

Chapter 11

Triassic-Jurassic Palynology

1 Introduction

The Buntsandstein, or Scythian stage, of the early Triassic (see Fig. 9.6) would seem qualitatively to "belong" palynologically with the Zechstein in the late Permian, especially on the basis of common bisaccate striate pollen forms, although there were palynological extinctions at the Permian/Triassic boundary. Beginning in the Muschelkalk (Anisian-Ladinian), the once dominant striate bisaccates almost completely disappear. Indeed, very few striates/taeniates of any morphological sort survive after mid-Triassic (exceptions: *Striatoabietites aytugii* Visscher, *Equisetosporites* (see Fig. 11.2), perhaps the striae of some Circumpolles forms would qualify?). Fig. 11.1 illustrates a range of Triassic forms, including early Triassic taeniate forms such as *Lunatisporites* and *Protohayloxypinus*.

The late Triassic to Jurassic palynoflora is dominated by a bewildering array of non-striate bisaccate pollen (especially prominent in the Jurassic), monosaccate pollen, fern spores, monocolpate pollen, and various inaperturate pollen, as well as pollen variously provided with different sorts of apertures, etc., e.g.,

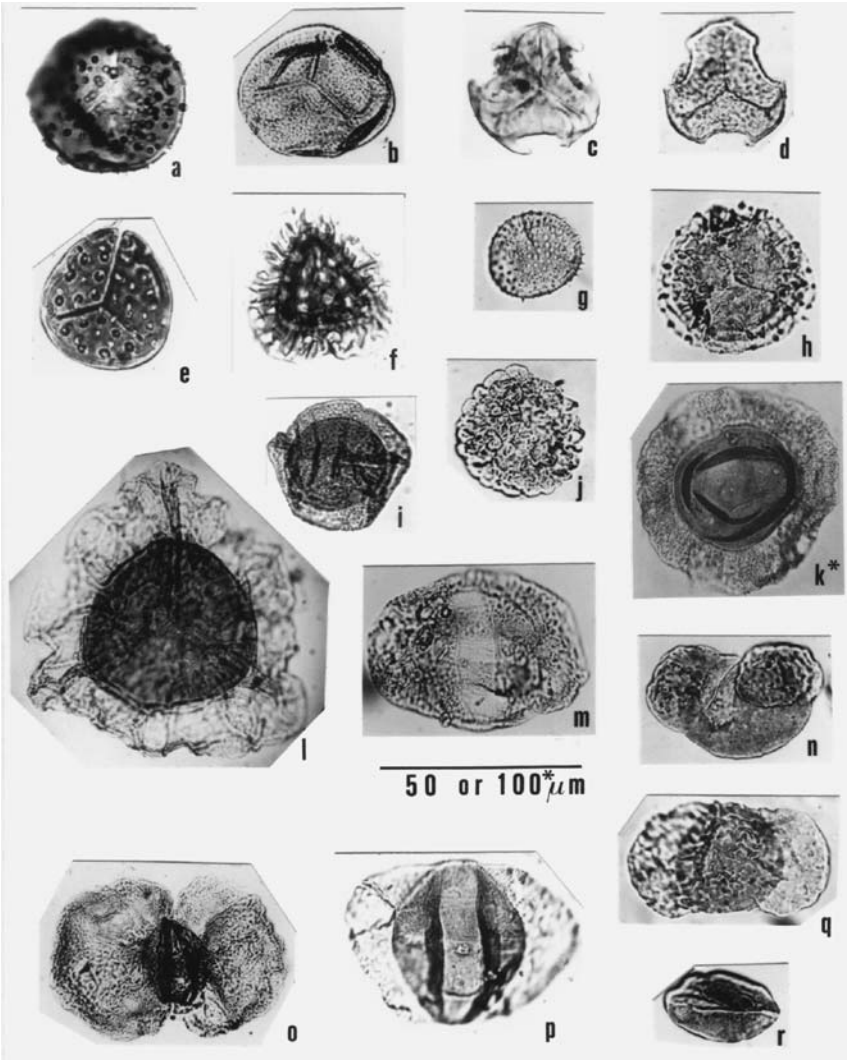


Figure 11.1 Representative Triassic sporomorphs from Poland. Magnification indicated by bar under (m). (**a**) *Cycloverrutriletes presselensis* Schulz, Scythian. (**b**) *Cyclotriletes microgranifer* Mädler, Scythian. (**c**) *Cornutisporites seebergensis* Schulz, Rhaetian. (**d**)*Triancoraesporitess reticulatus* Schulz, Rhaetian. (**e**) *Paraklukisporites foraminis* Mädler, Rhaetian (ranges into Jurassic). (**f**) *Limbosporites lundbladii* Nilsson, Rhaetian. (**g**) *Anapiculatisporites telephorus* (Pautsch) Klaus, Ladinian (ranges Scythian-Lower Jurassic). (**h**) *Kraeuselisporites cuspidus* Balme, Anisian (ranges Scythian-Ladinian). (**i**) *Aratrisporites scabratus* Klaus, Ladinian (ranges at least Scythian-Karnian). (**j**) *Tsugaepollenites oriens* Klaus, Anisian. (**k**) *Heliosaccus dimorphus* Mädler, Ladinian. (L) *Semiretisporis gothae* Reinhardt, Rhaetian. (**m**) *Protohaploxypinus pellucidus*

Eucommiidites, Classopollis. Fig. 11.2 shows characteristic forms from the late Triassic, and Fig. 11.3 gives ranges for some of the more important Triassic forms.

Triassic palynofloras display provincialism, the prominent boundaries seeming to be primarily latitudinal in origin (Truswell, 1981). Australian palynologists have suggested that Triassic floras of the Southern Hemisphere can be plotted on a Triassic paleo-map to show such latitudinal zonation.

Dolby and Balme (1976) showed (see Fig. 11.4) a marked similarity between the "Onslow microflora" of northwest Australia to coeval palynofloras of Laurasia–specifically western Europe, whereas the "Ipswich microflora" characterizes contemporary deposits of eastern Australia, New Zealand, and Antarctica. These probably were latitudinally controlled, the Onslow flora representing forest at 30−35° S, and the Ipswich flora a higher latitude plant association. Two very important publications on palynology of the Australian Mesozoic (almost exclusively Mesophytic within the meaning of this book) are *Studies in Australian Mesozoic Palynology I* (P. A. Jell, ed., 1987) and *II* (J. R. Laurie and C. B. Foster, ed., 2001). It is an interesting comment on trends in paleopalynology that both books are dominated by studies of microphytoplankton, as such microfossils are of increasing importance to applied aspects of the science.

Mid to late Triassic palynofloras of North Africa, North America and Europe have much in common:

1.1 The Keuper Beds of Central Europe: Ladinian (upper part), Karnian, Norian and Rhaetian Stages

Van der Eem (1983) has shown that careful analysis of the palynofloras indicates not only rather rapid floral evolution reflected in what he calls palynologic "phases" (comparable to but distinct from more rigidly defined "zones" for stratigraphic use), but also palynological differences that reflect fluctuating dry vs. wet local climatic conditions. Two important summaries of sporomorph stratigraphy of the Keuper of Germany are those of Beutler (2005) on the megaspores and Schulz and Heunisch (2005) on the miospores, both of which include very useful stratigraphic charts.

Figure 11.1 Goubin, Scythian. (**n**) *Microcachryidites fastidiosus* (Jansonius) Klaus, Anisian (ranges into Ladinian). (**o**) *Platysaccus papilionis* Potonié & Klaus, Scythian. (**p**) *Lunatisporites puntii* Visscher, Scythian. (**q**) *Triadispora plicata* Klaus, Anisian (ranges to Karnian). (**r**) *Cycadopites* cf. *folicularis* Wilson & Webster, Scythian. Photomicrographs courtesy of T. Orłowska-Zwolińska, in whose publication (1979) they originally appeared. The general ranges given in parentheses were provided by W. A. Brugman.

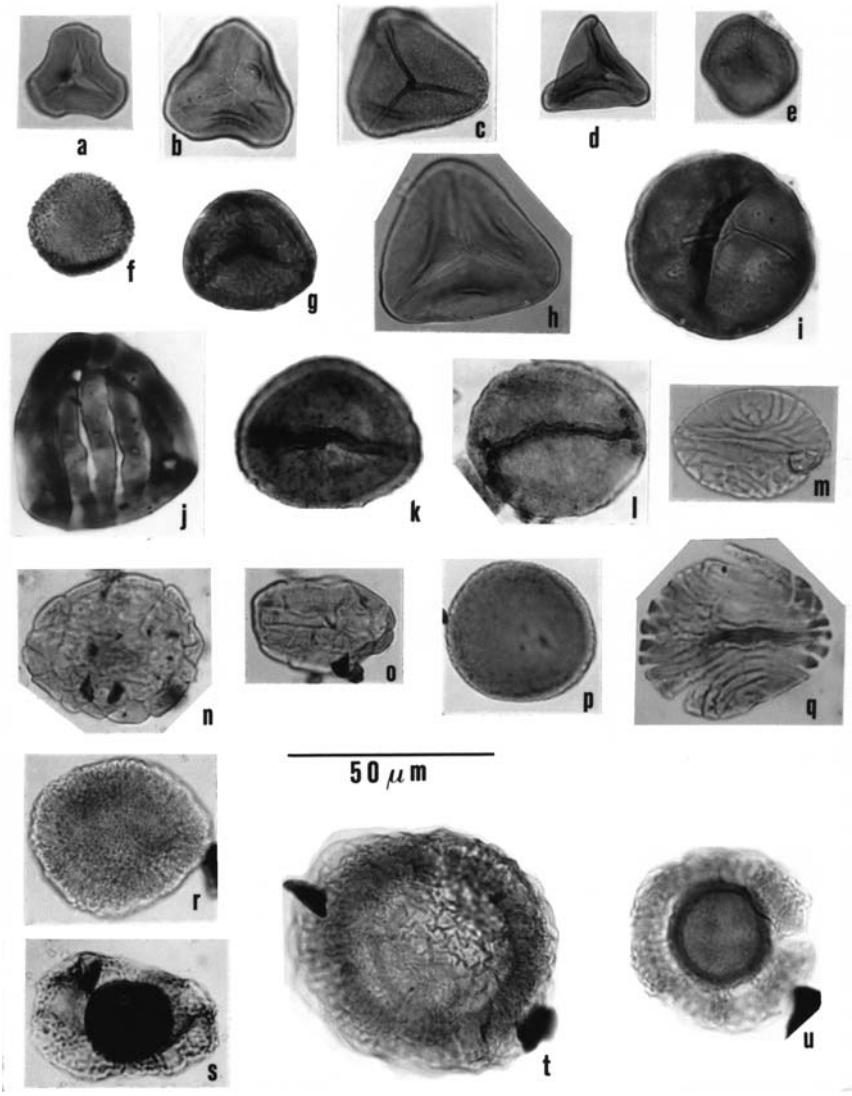


Figure 11.2

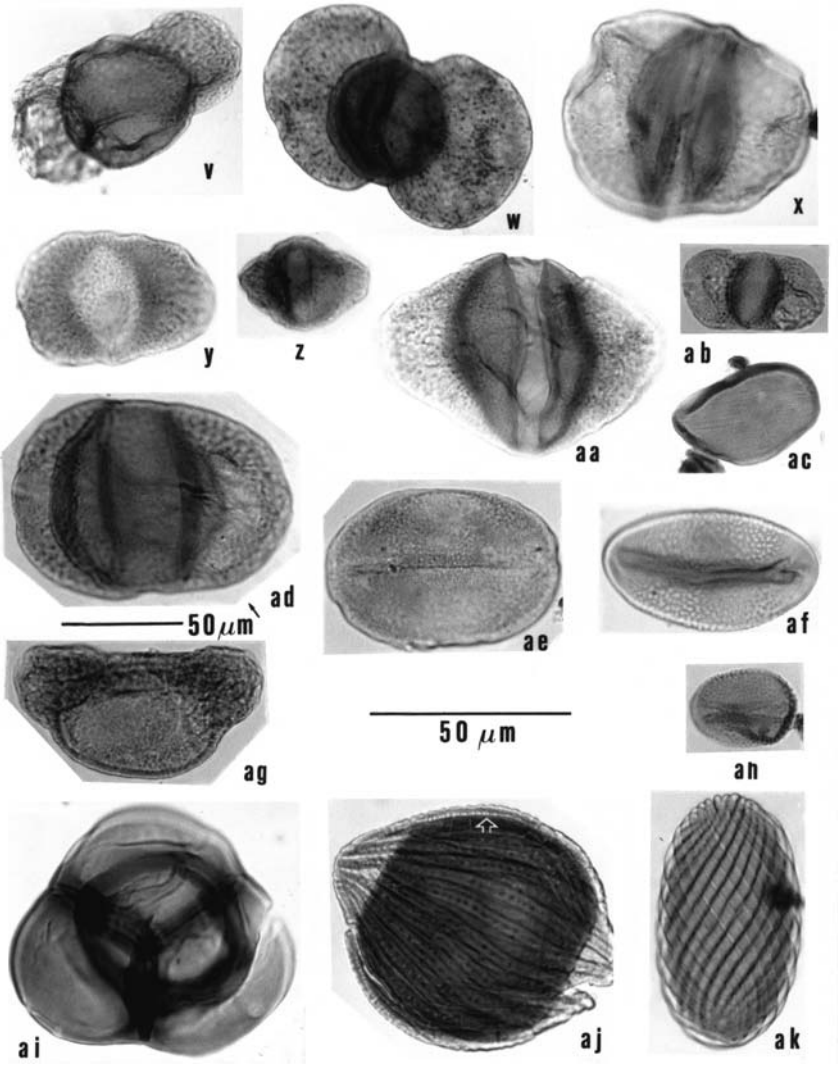


Figure 11.2 *(See caption on page 294)*

1.2 The Chinle Formation and Dockum Group of the American Southwest

Especially well known, they have primarily Karnian, some Ladinian-Norian, floras. Some prominent representatives of the palynoflora are illustrated in Fig. 11.2. Chinle and related palynofloras of the southwest are dominated by bisaccates such as *Alisporites, Falcisporites* and *Klausipollenites* and the odd spiral-striate form, *Equisetosporites*, as well as many taxa of monosaccates that are difficult to separate (*Patinasporites, Vallasporites,* etc.), trilete spore forms such as the odd "lumpy" *Camerosporites*, and other tricolpates such as *Deltoidospora* and *Dictyophyllidites* (Fig. 11.5), and monosulcate forms such as *Cycadopites* and *Lagenella.*

Figure 11.2 Spores and pollen from Middle and Upper Triassic (Ladinian and Karnian) rocks of North America. Magnification indicated by bars under (o) and (ae). (a)-(h), (m), (p), and (t)-(ak) are from the Petrified Forest Member, Chinle Formation, Petrified Forest National Park, Arizona. (i) and (j) are from Karnian portions of the subsurface Eagle Mills Formation, east-central Texas. (k) and (l) are from outcrop samples of the Coal Measures part (Karnian) of the Richmond Basin, Virginia. (n), (o), and (r) are from Ladinian to Karnian parts of the Fundy Basin, Martin Head, New Brunswick, Canada. (**a**) *Cyathidites minor* Couper. (**b**) *Gleicheniidites senonicus* Ross. (**c**) *Granulatisporites infermus* (Balme) Cornet & Traverse. (**d**) *Dictyophyllidites mortonii* (de Jersey) Playford & Dettmann. (**e**) *Stereisporites antiquasporites* (Wilson & Webster) Dettmann. (**f**) *Osmundacidites parvus* de Jersey. Distal view. (**g**) *Camarozonosporites rudis* (Leschik) Klaus. (**h**) *Dictyophyllidites harrisii* Couper. (**i**) *Todisporites* sp. (**j**) *Contignisporites cooksoniae* (Balme) Dettmann. (**k**) *Aratrisporites saturni* (Thiergart) Mädler. An odd monolete, zonate spore, showing prominent spines. (**l**) As (k). Specimen with spines corroded. (**m**) *Brodispora striata* Clarke. See also (q). (**n**) *Camerosporites secatus* Leschik. (**o**) As (n), different specimen. (**p**) *Pseudenzonalisporites summus* Scheuring. (**q**) *Brodispora striata* Clarke. See also (m). (**r**) *Patinasporites toralis* Leschik. (**s**) *Triadispora* sp. (**t**) *Patinasporites densus* Leschik. (**u**) *Daughertyspora chinleana* (Daugherty) Dunay & Fisher. (**v**) *Pityosporites oldhamensis* Dunay & Fisher. (**w**) *Platysaccus triassicus* (Malyavkina) Dunay & Fisher. (**x**) *Alisporites gottesfeldii*. See also (aa). (**y**) *Klausipollenites gouldii* Dunay & Fisher. (**z**) *Protodiploxypinus americus* Dunay & Fisher. (**aa**) *Alisporites gottesfeldii*. See also (x). (**ab**) *Vitreisporites pallidus* (Reissinger) Nilsson. (**ac**) *Lagenella martinii* (Leschik) Klaus. (**ad**) *Alisporites opii* Daugherty. Note different scale. (**ae**) *Ovalipollis pseudoalatus* (Thiergart) Schuurman. (**af**) *Granamonocolpites* cf. *luisae* Herbst. (**ag**) *Samaropollenites speciosus* Goubin. (**ah**) *Retisulcites* sp. (**ai**) *Pyramidosporites traversei* Dunay & Fisher. (**aj**) *Equisetosporites chinleanus* Daugherty. Note columellate structure (arrow). (**ak**) *Equisetosporites*? Specimens of this sort occur on the same slides as specimens such as (aj), and they often show similar tectate-like structure. They may represent a related but different polyplicate pollen grain. Intermediate forms occur.

1.3 The Subsurface Eagle Mills Formation of Northwest Texas

This formation includes Ladinian-Karnian sediments. In wells from the Eagle Mills, *Classopollis* appears as a subdominant to dominant constituent toward the top of the section, but this probably means that drilling mud has caved from upwell Jurassic-Cretaceous material (Cretaceous sporomorphs and dinoflagellate cysts are also present), a common problem when using drilling cuttings rather than cores.

1.4 The Newark Supergroup of Eastern North America

These sediments were deposited in a series of basins produced as a preliminary side effect of the separation of North America and Europe and Africa beginning about 190 million years ago (see Fig. 11.6). Mesozoic rocks of these basins outcrop from Nova Scotia to North Carolina, but related basins are found under the water of the Bay of Fundy and the North Atlantic, and in the subsurface of South Carolina, Georgia, and Florida. Closely related basins exist in Morocco (Cousminer and Manspeizer, 1977).

The sediments of the Newark Supergroup basins were prevailingly presumed until fairly recently to be all Triassic in age. However, Cornet and associates (Cornet 1977a, b; Cornet and Olsen, 1985; Cornet and Traverse, 1975; Cornet *et al*. 1973; Ediger, 1986b; Robbins, 1982; Traverse, 1986) have shown that the sediments range in fact from Karnian or even Ladinian (Deep River Basin, North Carolina; Richmond Basin, Virginia) to Liassic (lower Jurassic = Pliensbachian-Toarcian, see Fig. 11.7) in age (Hartford-Springfield Basin). This means that the Newark Supergroup spans more than 50 million years in time. The principal signatures of the younger age of the Rhaetian-Liassic parts of the sections are the complete dominance of various species of *Classopollis* forms at many levels, along with other Liassic indicators such as species of *Callialasporites, Ischyosporites* and others. Cornet has shown that species differences within the *Classopollis* group can be used to typify various zones, which are then compared with European sections on the basis of other forms as well.

While the Newark Supergroup as a whole is very rich in palynomorph taxa (see Fig. 11.8), the Richmond Basin in particular is especially diverse, though the sediments are all Ladinian-Norian. In addition to the monosaccate, bisaccate and trilete genera typical of late Triassic deposits of North America, some samples are rich in *Aratrisporites*, a wide-ranging genus of lycopod cavate monolete (micro-spores). This genus, abundant in the Australian Triassic, is dominant at some levels in the Richmond Basin, indicating prevalence of marshy environments, a last gasp of dominance of the once mighty lycopsids (de Jersey 1982).

Richmond Basin sediments also sometimes contain specimens of columellate (pseudocolumellate?) reticulate pollen with sulci, sulculi or even multiples of

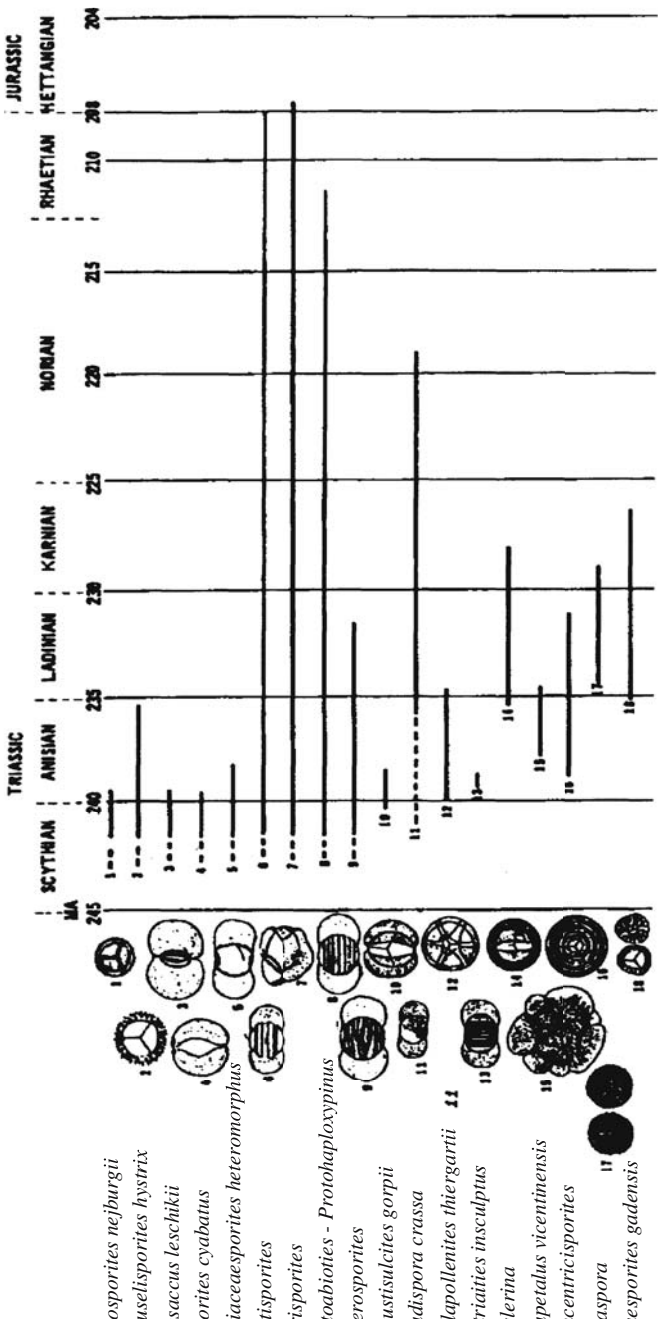

TRIASSIC
JURASSIC
SCYTHIAN
ANISIAN
LADINIAN
KARNIAN
NORIAN
RHAETIAN
HETTANGIAN
MA
245
240
235
230
225
220
215
210
205
1) Densosporites neiburgii
2) Kraeuselisporites hystrix
3) Platysaccus leschikii
4) Alisporites cyabatus
5) Voltziaceaesporites heteromorphus
6) Lunatisporites
7) Aratrisporites
8) Striatoabieties - Protohaploxypinus
9) Stroterosporites
10) Angustisulcites gorpii
11) Triadispora crassa
12) Stellapollenites thiergartii
13) Distriaities insculptus
14) Kuglerina
15) Dgupetalus vicentinensis
16) Concentricisporites
17) Sellaspora
18) Uvaesporites gadensis

Figure 11.3

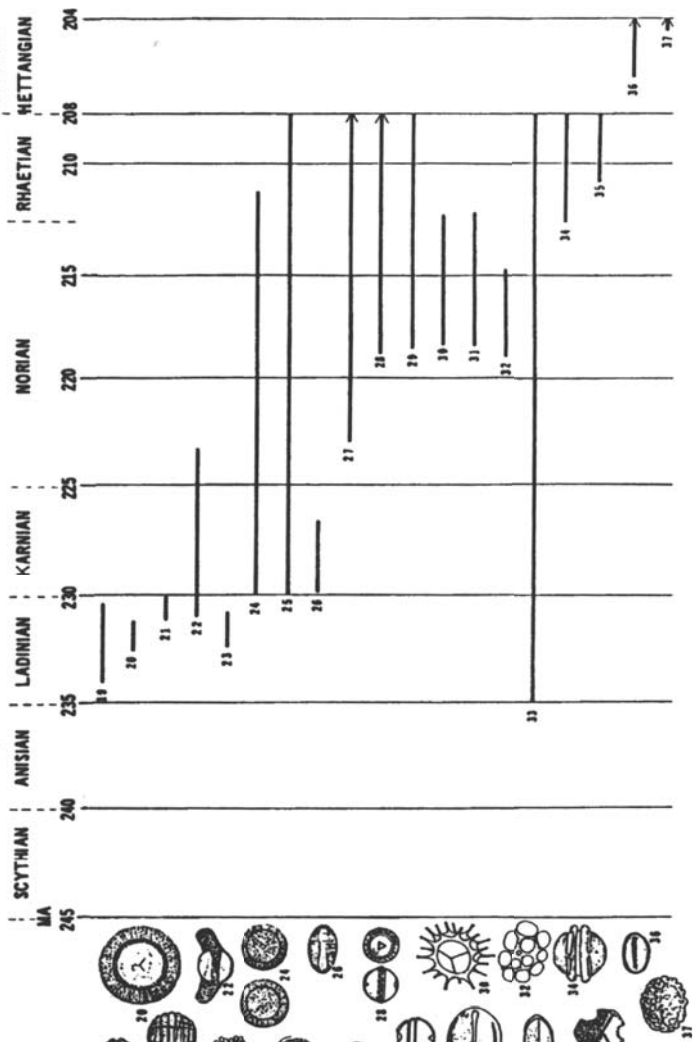
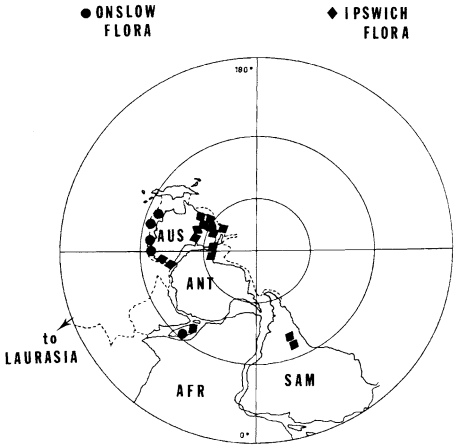


Figure 11.3 Triassic range chart for some selected palynomorphs. Note that *Concentricisporites* (no. 16) is now considered a zynematacean algal spore (cf. Grenfell, 1995), thus neither a sporomorph nor an acritarch. Also note that the three sporomorph forms referred to *Corollina* (nos. 27-29) are now species of *Classopollis*, as explained elsewhere in this chapter. Ranges and most of the palynomorph diagrams are from Brugman (1983); a few of the diagrams are from Jansonius *et al.* (1976-).



	Onslow flora (Euramerican affinities, many dry indicators)	Ipswich flora (Gondwanaland affinities, many moist indicators)
bisaccate pollen	*Falcisporites* (usually dominant)	*Falcisporites*
		Alisporites
	Infernopollenites	
	Staurosaccites	
	Lunatisporites	
	Ovalipollis	
	Samaropollenites	
monosaccate pollen	*Enzonalasporites*	
	Patinasporites	
polyplicate pollen	*Ephedripites*	
	Decussatisporites	
monosulcate pollen	*Cycadopites*	*Cycadopites*
trilete spores	*Camerosporites*	*Duplexisporites* (75% of some counts)
		Osmundacidites
		Dictyophyllidites
		Uvaesporites
monolete spores		*Aratrisporites, et al.*

Figure 11.4 The Onslow and Ipswich mid- to late Triassic floras, originally recognized in Australia (Gondwanaland), seen as if viewed from modern Australia. The Onslow flora, typical of western Australia, has affinities with the Laurasian flora. The Ipswich flora of eastern Australia is Gondwanaland-distributed. Some prominent taxa in these floras are given in the table. Redrawn from Dolby and Balme (1976); floral lists abstracted from the same source.

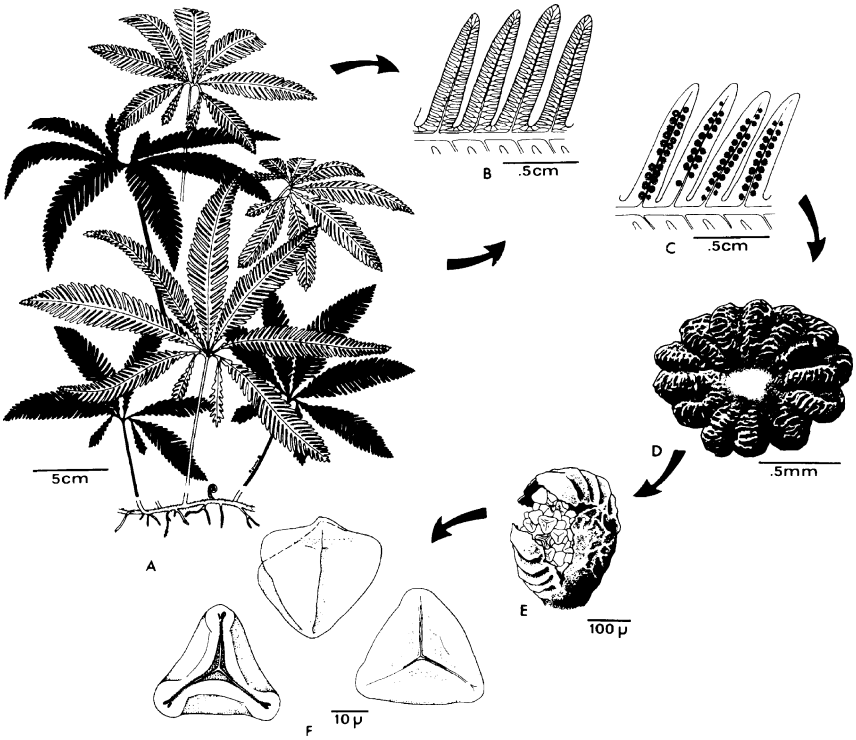


Figure 11.5 Diagrammatic reconstruction of the Chinle fern, *Phlebopteris smithii*, based on specimens collected in the Petrified Forest National Park, Arizona. (**A**) whole plant with suggested rhizome; (**B**) sterile pinnules; (**C**) fertile pinnules; (**D**) sorus; (**E**) sporangium; (**F**) details of spores, isolated by dissection of a mature sporangium. These *in situ* spores are referable to the dispersed spore species, *Dictyophyllidites harrisii* (see Fig. 11.2h). Studies of spores from sporangia on megafossil plants have made possible the assignment of many dispersed spore taxa to the producing plants. Reproduced from Ash *et al*., 1982.

these in a very angiosperm-like manner (see Fig. 11.11). Odd, thick-walled, pollen occurring in tetrads and appearing to be trichotomosulcate, *Placopollis koobii*, also are found in the Richmond Basin sediments. In Europe (Fisher and Dunay, 1981), latest Triassic indicators such as *Rhaetipollis* first show up in the Norian and persist into the Rhaetian and lowest Jurassic (see Fig. 11.3 for ranges of some of the forms). The problem is somewhat bedeviled by arguments about the validity of the Rhaetian as a stage, some regarding it as a terminal substage of the Norian or not using it at all.

Orłowska-Zwolińska (1983) has traced the palynostratigraphic assemblages of the Upper Triassic of Poland, showing that the palynofloras of various levels can

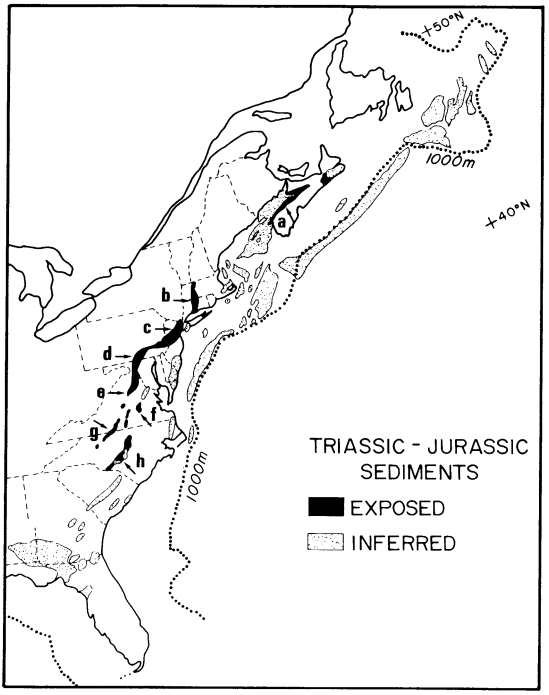


Figure 11.6 The "Newark" basins of eastern North America, which were formed as rift basins in the process of separation of Africa and North America. (Related basins are found in Morocco.) Location of 'inferred' basins is based on extrapolation from drilling information. Palynological and other evidence shows that basin sedimentation began along the whole front in Ladinian-Karnian (late Triassic) time. From central Virginia southward, sedimentation ended after a few million years, but from northern Virginia to Nova Scotia palynological evidence shows that it continued until well into the Jurassic, at least to Pliensbachian, a total of about 40 million years. The principal exposed basins are indicated by letters and arrows: (**a**) Fundy Basin (Nova Scotia and New Brunswick); (**b**) Springfield (Massachusetts)-Hartford (Connecticut) Basin; (**c**) Newark Basin (New Jersey); (**d**) Gettysburg Basin (Pennsylvania); (**e**) Culpeper Basin (Maryland-Virginia); (**f**) Richmond Basin (Virginia); (**g**) Danville (Virginia)-Dan River (North Carolina) Basin; (**h**) Deep River Basin (North Carolina). (Compare with Fig. 11.7.) Redrawn from Olsen (1978).

be assigned to "assemblages" characterized by important palynomorph types and correlating with the established ammonite zones for the Triassic.

A *Heliosaccus dimorphus* assemblage (I) was followed upward by an *Ovalipollis- Triadispora* assemblage (IIb), succeeded by a *Toroisporis-Camarozonosporites- Aulisporites* assemblage (III), and that by a *Classopollis* assemblage (IV), with a *Ricciisporites*-characterized assemblage (V) at the

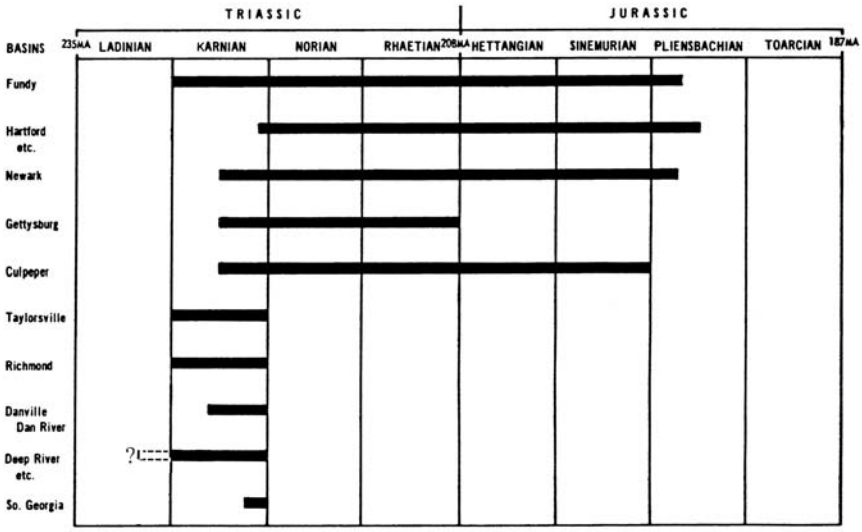


Figure 11.7 Palynologically based ages for the "Newark" Basins. (Compare with Fig. 11.6.) Based on the work of Cornet, Ediger, Robbins, Traverse and others in the palynology program at Penn State University.

top. Orłowska-Zwolińska notes that assemblage I correlates with the Ladinian of western Europe, II-III with Karnian, and IV-V with Karnian-Norian (including Rhaetian). Orbell (1973) found the British "Rhaetic" to be divisible into a lower *Rhaetipollis* zone of latest Triassic age and an upper *Heliosporites* zone of early Jurassic (= Liassic) age. Both zones contained abundant *Classopollis*. A general summary of all levels of Triassic (and Permian) palynostratigraphy in Europe is presented in Brugman (1983).The statements by Mader (1990) in connection with European Triassic sections that sporomorph information is not helpful in understanding stratigraphy and paleoecology have been discussed in Chapter 2. They are based on demonstrably false conclusions and are hence incorrect.

2 Circumpolloid Pollen

This sort of conifer pollen (turmal designation for the group including it is Circumpolles) first appears in the Ladinian stage of the Triassic and seems to characterize new gymnosperms of mid-Triassic to mid-Cretaceous time. As can be seen in Figs. 11.9 and 11.10, this pollen has as its primary feature a girdling colpus-like thinning, which divides the pollen into two "hemispheres", one however usually smaller than the other. The more primitive representatives of

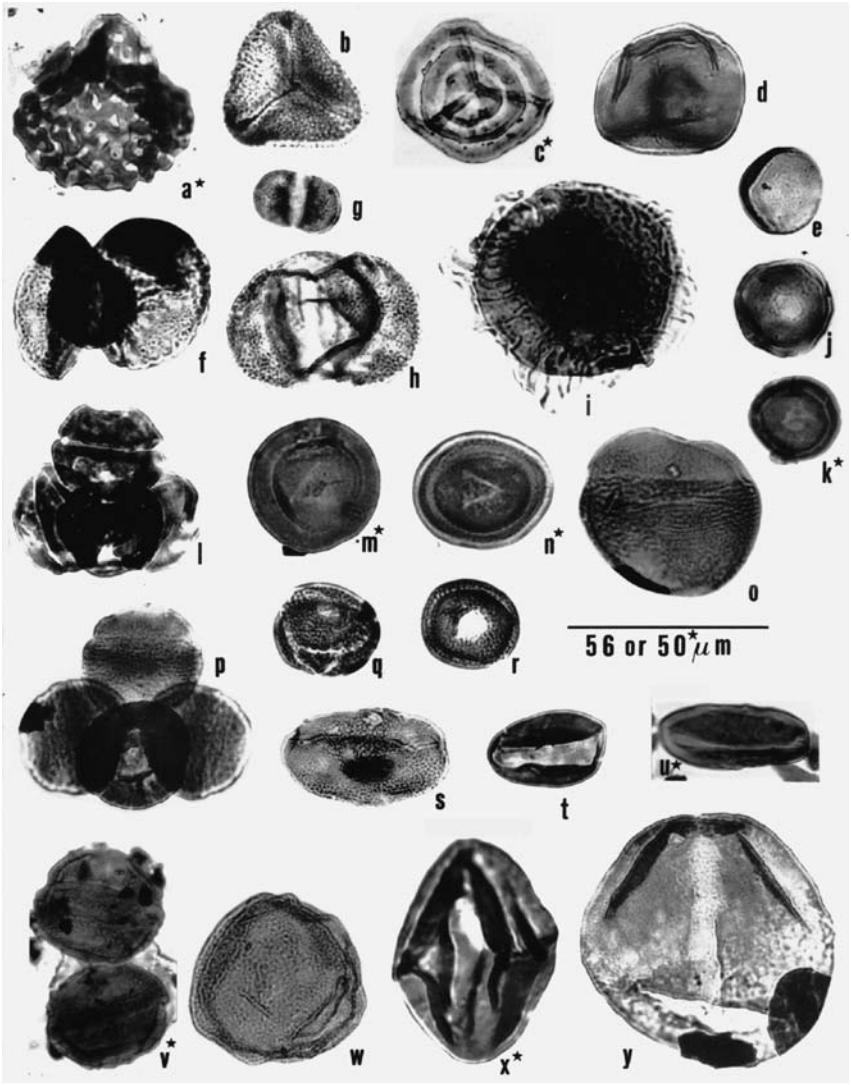


Figure 11.8 Latest Triassic-early Jurassic (Liassic) spores and pollen, North America. Magnification indicated by bar under (o). (a), (c), (m) and (n) (m) and (n) probably from Jurassic upwell caving), and (x) are from upper levels of the Eagle Mills Formation from a borehole in central Texas. Lower portions of this formation in the borehole yield palynomorphs of Ladinian-Karnian age. (k), (u) and (v) are from upper levels of a core (Chinampas Well) in the Bay of Fundy, New Brunswick. (l) is from the upper part of sediments of the Culpeper Basin, Virginia. All other photos are of sporomorphs from latest Triassic and early Jurassic formations in the Hartford-Deerfield Basin, Connecticut and Massachusetts. (**a**) *Ischyosporites variegatus* (Couper) Schulz. (**b**) *Converrucosisporites*

the group (Fig. 11.9) have incomplete equatorial grooves. Some species have a trilete laesura or laesuroid marking on the proximal surface and/or a thin, often more or less triangular, distal colpus-like area, the tenuitas. The two hemispheres sometimes split apart and can then be found isolated (see Fig. 11.10). In some species, tetrads and dyads are very common; in others, only monads are normally found. The exine of the more advanced forms is probably unique among gymnosperms in having very well developed nexinal columellae (see Fig. 11.10). However (Medus, 1977), the structure of various circumpolloid forms differs from that of *Classopollis classoides* Pflug, the "type species," and some forms

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Figure 11.8 *cameronii* (de Jersey) Playford & Dettman. (**c**) *Polycingulatisporites mooniensis* de Jersey & Paten. (**d**) *Todisporites Figure 11.8, continued. rotundiformis* (Malyavkina) Pocock. (**e**) Circumpolloid pollen? Such apparent inaperturate forms have been given various generic names but may be endexines of *Classopollis rotundiformis* (Malyavkina) Pocock. (**e**) Circumpolloid pollen? Such apparent inaperturate forms have been given various generic names but may be endexines of *Classopollis* (see (j)-(r)). (**f**) *Platysaccus* sp. (**g**) *Vitreisporites pallidus* (Reissinger) Nilsson. (**h**) *Alisporites thomasii* (Couper) Nilsson. (**i**) *Callialasporites* cf. *dampieri* (Balme) Sukh Dev. (**j**) *Classopollis meyerianus* (Klaus) de Jersey. Distal view, upper focus. Note distal tenuitas. (**k**) *Classopollis meyerianus*. Distal view in mid-focus, so that the distal, more or less circular tenuitas, the proximal triangular mark, and the pre-equatorial rimula all show. (**l**) *Classopollis meyerianus*, tetrad, with equatorial view of top pollen grain, showing especially the pre-equatorial rimula or groove, and the distal tenuitas in section at the very top. (**m**) *Classopollis meyerianus* Distal view, mid-focus, with the triangular proximal mark showing through, as well as the pre-equatorial rimula. (**n**) *Classopollis classoides* Pflug. View and focus as in (m), showing the prominent internal columellae in the equtorial area. (**o**) *Classopollis itunensis* Pocock. Lateral (= equatorial) view, high focus, emphasizing the large size and the prominent, numerous and complex striations over close to half of the grain in the part below the rimula. (**p**) *Classopollis classoides* Pflug. Tetrad showing the complex post-rimula, girdling striations, as in (o), on the top grain. (**q**) *Classopollis murphyae* (Cornet & Traverse) Traverse. Oblique view showing the tenuitas at the top, the rimula as a crescent, and the thick and complexly structured exine. (**r**) *Classopollis murphyae*. Distal view, mid-focus to show the widely spaced internal rods of the exine with the tenuitas also evident. (**s**) *Cycadopites reticulatus* (Nilsson) Cornet & Traverse. Obliquely distal view, high focus, showing the sulcus and reticulate sculpture. (**t**) *Cycadopites* cf. *jansonii* Pocock. Distal view, mid-focus, showing the widely gaping sulcus and psilate sculpture. (**u**) *Cycadopites* sp. with sulcus flared at ends. (**v**) *Classopollis* sp. Lateral views of grains, upper one with tenuitas up, lower one with it down. This species has very thick, internally complex exine and striate-reticulate sculpture. (**w**) *Araucariacites punctatus* (Nilsson) Cornet & Traverse, high focus of this inaperturate form. (**x**) *Pretricolpipollenites* cf. *ovalis* Danzé-Corsin & Laveine. Lateral distal view, high focus. These puzzling forms are, like *Eucommiidites* sp., probably best interpreted as monosulcate, with supplementary sulculi and folds. (**y**) *Araucariacites fissus* Reiser & Williams. An inaperturate form often, as here, with sulcus- or sulculus-like grooves and folds.

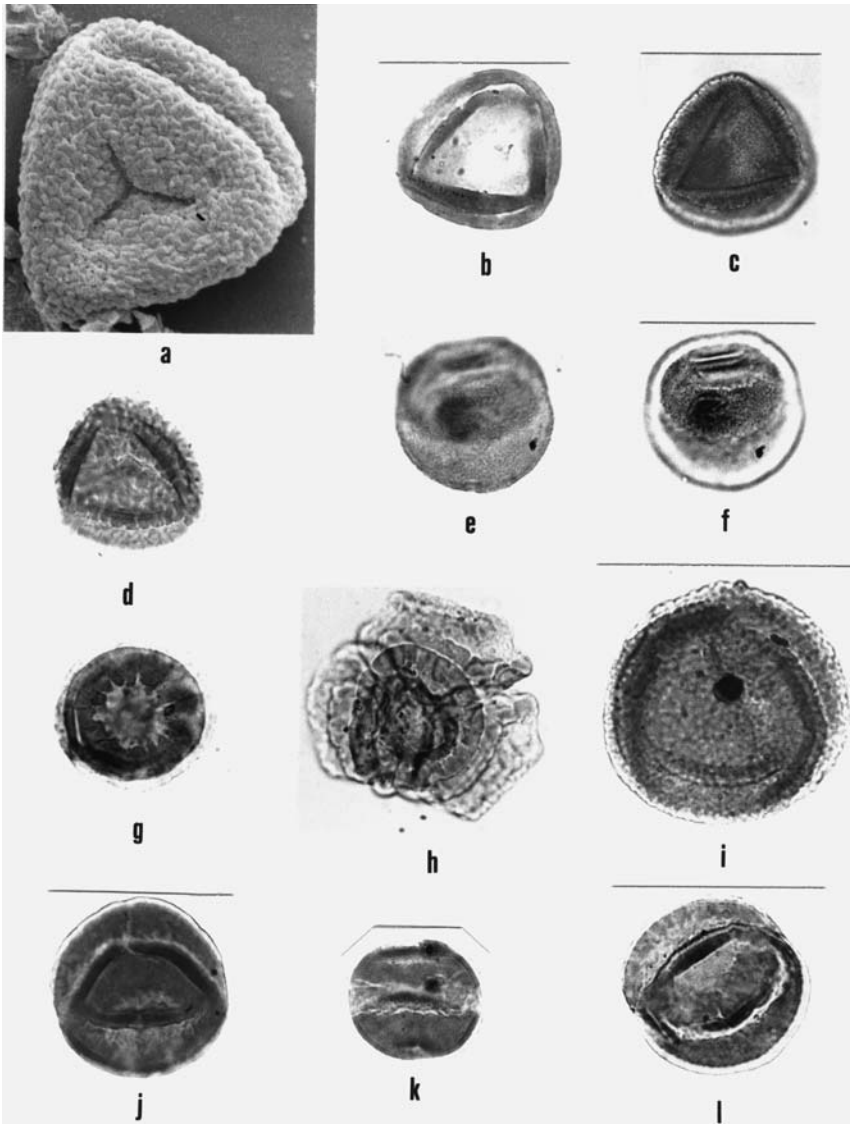

Figure 11.9 *Partitisporites* and *Duplicisporites*, two circumpolloid genera of the mid- and late Triassic. *Praecirculina* has an incomplete semicircular equatorial furrow but is otherwise very similar to *Partitisporites novimundanus* Leschik ((e), (f)). *Camerosporites* (see Fig. 11.2n,o) is another Triassic genus with probable circumpolloid relationship. *Classopollis* is the circumpolloid pollen of the one coniferous taxon of this group that "made it big" (see Fig. 11.10). The magnification of these illustrations varies greatly, so the size is given for each specimen.(**a**) *Duplicisporites verrucosus* Leschik. SEM. micrograph,

seem to lack the multiple levels shown in Fig. 11.10. The botanical relationships of circumpolloid pollen are very certainly known; they are the sort of pollen produced by a variety of Mesozoic conifers, especially by *Hirmerella* (once known as *Cheirolepis*) and other cheirolepidiaceous conifers (whether circumpolloid pollen was produced by non-cheirolepidiaceous conifers is still debated). The ecological significance of the producing plants, often very widespread and dominant in Triassic/Cretaceous time, has been much discussed. At least some of them were apparently warmth-loving shrubs that grew in great thickets in the same sort of low-lying water-margin environment that produced extensive mud flats peppered with dinosaur tracks, as in the Triassic/Jurassic Hartford Basin. Francis (1983, 1984) shows that some *Classopollis* producers were shrubs that tolerated semiarid conditions, and *Classopollis* pollen distribution is correlated with evaporites. However, others may have been upland, xeric plants (Srivastava, 1976a). That they were warmth-loving is indisputable, as they decline sharply with increasing latitude. There seems also to be no doubt that they covered large areas, because the pollen often completely dominates (more than 90%)

Figure 11.9 proximal view showing trilete mark, range, Ladinian-Karnian. The circumpolloid equatorial furrow structure is tripartite (see (b)-(d)) in this genus. Size 35 μm. Karnian, Spain. (**b**) *Duplicisporites kedangensis* Schuurman. Distal view showing the tri-partite equatorial furrow and the distal tenuitas, range Rhaetian-Cretaceous. Size 30 μm. Rhaetian, Italy. (**c**) *Duplicisporites granulatus* Leschik. Proximal view. Range Ladinian-Karnian. Size 33 μm. Karnian, Spain. (**d**) *Duplicisporites verrucosus* Leschik. Proximal view. Data as for (a). (**e**), (**f**) *Partitisporites novimundanus* Leschik. Two levels of focus of obliquely lateral view, showing half of the equatorial furrow, which is bi-partite in this genus, the semilunar segments nearly joining together (see (i)). Range Ladinian-Karnian. Size 35 μm. Karnian, Spain. (**g**) *Partitisporites tenebrosus* (Scheuring) Van der Eem. Distal view showing complex structure of area around the tenuitas. Range Ladinian-Karnian. Size 30 μm. Karnian, Spain. (**h**) *Partitisporites quadruplicis* (Scheuring) Van der Eem. Tetrad showing the flattened distal area in lateral view of top grain. Range uppermost Ladinian-Karnian. Size (one grain) 35 μm. Karnian, Spain. (**i**) *Partitisporites novimundanus* Leschik. Mid-focus of distal view showing bi-partite equatorial furrow (see (e), (f)). Size 35 μm. Karnian, Spain. (**j**) *Partitisporites maljawkinae* (Klaus) Van der Eem. Distal view showing bi-partite equatorial furrow. Range Karnian. Size 35 μm, Karnian, Italy. (**k**) As (j). Lateral view showing somewhat complex equatorial furrow, and the distal tenuitas. (**l**) As (j). Distal view showing bi-partite equatorial furrow and distal tenuitas. (Van der Eem, 1983, grouped *Partitisporites novimundanus, Praecirculina granifer* and "*Paracirculina*" *verrucosa* in the *P. novimundanus* morphon, and *Duplicisporites granulatus, D. verrucosus* and *D. mancus* in the *D. granulatus* morphon.) Brugman and others in the Laboratory of Palaeobotany and Palynology at the University of Utrecht have been the first to make critical observations about the morphology, especially the structure of the equatorial furrows, in these forms. Photos and explanations courtesy of W. A. Brugman (1983, personal communication).

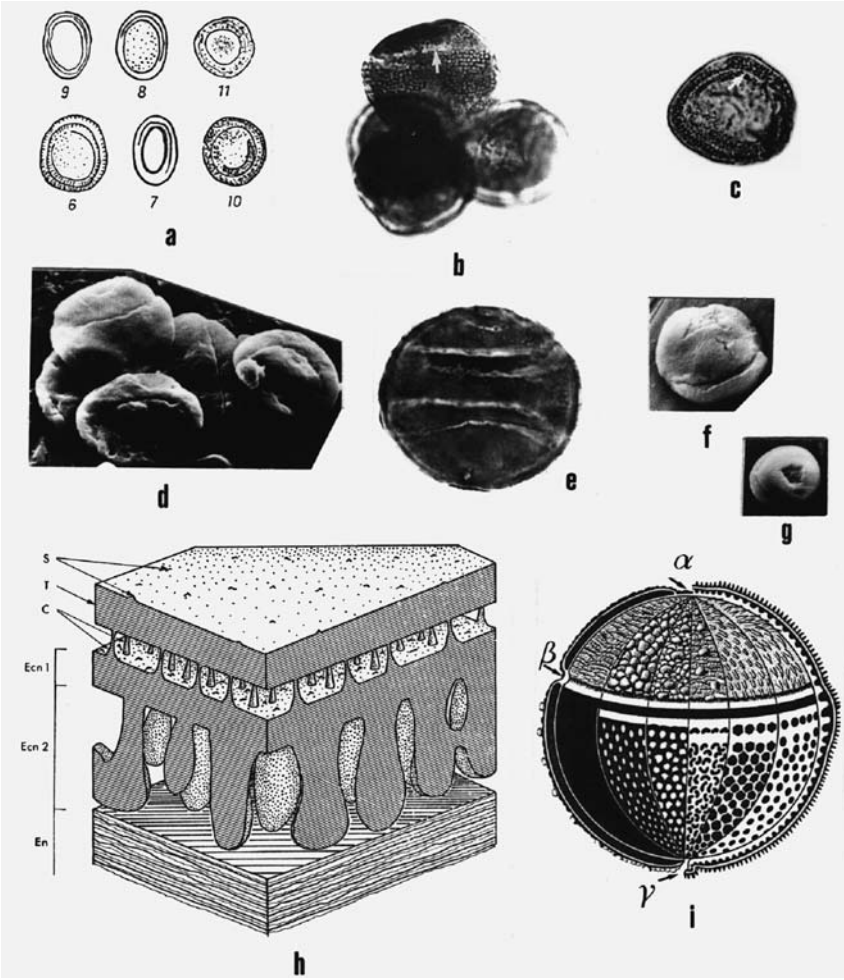

Figure 11.10 The remarkable pollen genus, *Classopollis* Pflug. (**a**) Malyavkina (1949) described from Lower Jurassic rocks of the Soviet Union the group of palynomorphs illustrated here collectively by her line drawings "9, 8, 11, 6, 7, 10". There can be little reasonable doubt that Malyavkina's drawings 6-11 represent what we now call in general "circumpolles" pollen, a group of distinctive, extinct conifer pollen with a pre-equatorial groove or rimula. However, she called numbers 10 and 11 *Corollina compacta* and numbers 6-9 two different species of *Circulina*. (**b**) Tetrad of *Classopollis classoides* showing the complex striate exine in a band encircling the top grain. The encircling groove just above the striate band is the rimula (arrow). (**c**) *Classopollis classoides*. Mid-focus from distal side of single grain, showing the columellate structure of the exine. Rimula (arrow) also visible. Note similarity to Malyavkina's drawing 10 (see (a)). (**d**) A tetrad (left) and an extra grain of *Classopollis meyerianus* in SEM. The rimula is clearly visible on all grains

palynofloras. Some of such dominance characterizes acme zones which have stratigraphic significance. The first one in North America is Hettangian.

2.1 Circumpolloid Systematics

The basic genus is a form that was named *Corollina* Malyavkina 1949, if one accepts that Malyavkina's (1949) simple line sketch (Fig. 11.10) is recognizable as this form. Unfortunately, Malyavkina's type specimen no longer exists. Pflug (1953) described and illustrated what is unequivocally this form, calling it *Classopollis*. That he thought it was angiosperm-like (tri- and tetracolpate) is irrelevant to the nomenclatural problem. Malyavkina (1949) added another complication by publishing another name, *Circulina*, for a circumpolloid form apparently lacking a striate equatorial band.

A solid majority of paleopalynologists have long used the name *Classopollis* despite the priority over it of both *Corollina* and *Circulina*. The reasons were clearly the unambiguousness of *Classopollis*. To solve this problem, I proposed (Traverse, 2004) the formal conservation of the name *Classopollis* against *Corollina* by the nomenclatural session of the International Botanical Congress in 2005, by means of the procedures outlined in the *International Code of Botanical Nomenclature* (Greuter *et al*., 2000). The proposal was accepted by the Congress. However, there are other systematic problems with these pollen forms, e.g., the question of how many genera to recognize. Some have elected just *Classopollis*, or just *Corollina* Mal. for the forms with a striate belt, and *Circulina* for those lacking it. However, other genera have been described, such as *Gliscopollis* Venkatachala.

Figure 11.10 (**e**) *Classopollis zwolinskae* (Lund) Traverse. Lateral view of a peculiar *Classopollis* with two rimulae or furrows, one pre-equatorial, one sub-equatorial (each shows through from the back and thus creates the appearance of four furrows!). Rhaetian, England. This form is diagnostic for the Rhaetian. (**f**) *Classopollis meyerianus*. Obliquely proximal view in SEM, showing the faintly expressed triangular mark. Rimula visible below. (**g**) *Classopollis meyerianus*. Distal view, SEM, showing the tenuitas or distal aperture. (**h**) Drawing illustrating the complex structure of *Classopollis classoides* exine: **S**, sculpture; **T**, tectum; **C**, columellae; **Ecn 1-2** and **En**, layers of the outer exine. (**i**) Drawing showing the sculpture found on various circumpolles exines, displayed on the distal hemisphere (left to right): rugose, verrucose, mixed, 1-formed, echinate-baculate, echinate. The various sorts of internal structure found are shown in the lower hemisphere (left to right): massive, alveolate, reticulate, vermiculate, intrareticulate, punctate. Arrow with α, tenuitas; arrow with ß, rimula; arrow with γ, proximal mark (in lateral section). The magnification is different for each illustration, but each palynomorph is about 30 μm in maximum dimension. (h) is from Pettit and Chaloner (1964); (i) is from Reyre (1970).

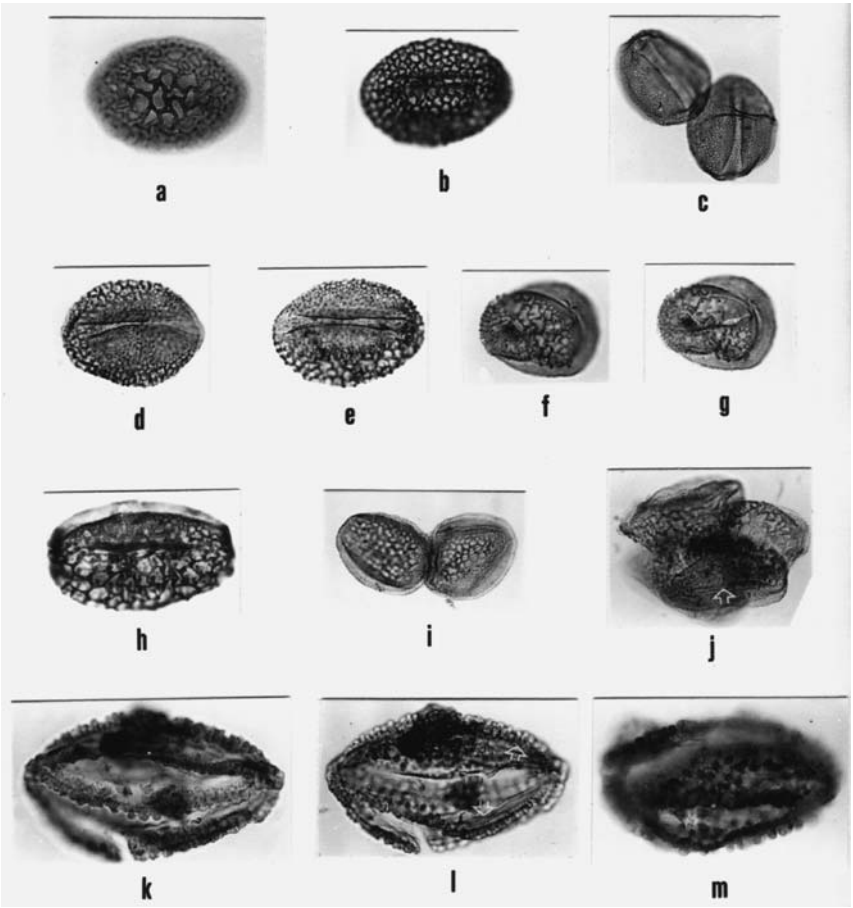

Figure 11.11 Angiosperm-like pollen from the late Triassic. In addition to *Eucommiidites, Pretricolpipollenites*, and other late Triassic pollen with colpi-like furrows suggesting angiospermous affinity, forms are found such as these from the late Triassic Richmond Basin, Virginia, which have not only such furrows but also angiosperm-like sculpture, and even tectate-columellate wall structure. As has been proven for *Eucommiidites*, all these forms are probably best viewed as monosulcates. Thus, these photos are oriented where possible as if monosulcate, according to Erdtmanian convention (presumed primary sulcus parallel to bottom of page). Whether this trend represents a line leading to angiosperms or is the result of convergent evolution is unknown. (**a**), (**b**) Two monosulcate forms. Proximal focus, emphasizing the monocot-like coarse reticulum. (**c**) Pair of monosulcate forms in distal focus with fine-pattern reticulum. (**d**), (**e**) Two monosulcates. Distal view and focus. Style of sulcus and relation of sculpture to it like monocots. (Pollen such as in (a)-(e) is usually put in the form-genus *Retisulcites*.) (**f**), (**g**) Two levels of focus of a distal view of one specimen that is zonasulculate, showing additional furrows, as well as the distal sulcus. (**h**) "Trisulcate" form in lateral view. The reticulate sculpture is modified

Since *Corollina* and *Circulina* are now illegitimate, *Classopollis* having been conserved against them, the specific names previously referred to the suppressed generic names must be formally transferred to *Classopollis*. Ideally this should be done with a separate publication in the journal *Taxon*. However, I am making the necessary transfers in this book for the species to which I refer. As already mentioned, Cornet (1977a) used *Classopollis* species and their relative dominance to typify some of the Triassic/Jurassic palynological zones in his Newark Supergroup work.

3 Colpate (Sulcate) Forms in The Triassic/Jurassic

The encircling colpoid feature that characterizes circumpolloid pollen is very like such structures in the 1-syncolpate (or zonisulcate) pollen in the Angiospermae. Also found in Triassic/Cretaceous palynofloras are forms with other sorts of angiospermous- like ("angiospermid") sulci (colpi). For example, there are monosulcate forms such as *Retimonocolpites, Retisulcites* and *Liliacidites*, with sculpturing suggestive of monocots (in contrast to typical *Cycadopites*, mostly scabrate to psilate, monosulcate pollen). Another important colpate form is *Eucommiidites*, first described by Erdtman from the early Jurassic of Sweden, and thought by him to be possibly angiospermous, because of the apparently tricolpate form (see Fig. 11.3). However, Couper (1956) and Hughes (1961) showed subsequently that the position and orientation of the colpi are wrong for a dicot tricolpate. Dicot Pc0s have the three equal colpi on meridians connecting the proximal and distal poles and 120° apart. *Eucommiidites* has a main colpus on one side and two subsidiary shorter colpi, which may be united to a single ring furrow, on the other side. Further, the three colpi are not equal in length, the central, or main, colpus being longer. *Eucommiidites* pollen has been found in the pollen chambers of gymnosperm seeds by Hughes (1961), by Brenner (1967) and by Reymanówna (1968), who demonstrated that the exine is of gymnosperm type. *Eucommiidites* is now known to range from Triassic to Cretaceous. *Pretricolpipollenites* pollen is another Triassic/Jurassic form best viewed as an angiosperm look-alike.

Cornet (1977a, 1989) has described, however, odd colpate forms from the late Triassic, especially from the Karnian of the Richmond Basin, which also have a columellate exine and in all are very angiosperm-like (Fig. 11.11). Of

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Figure 11.11 near the sulcus. (**i**) Pair of "trisulcates" with reticulate sculpture. (**j**) Tetrad of "trisulcates," with columellate structure clearly showing at arrow. (**k**), (**l**) Different levels of focus of a "pentasulcate" pollen grain in which columellate structure is apparently present (arrows). (**m**) Another specimen of the "pentasulcate" form. Magnification shown by bar under (l). Photos courtesy of Bruce Cornet.

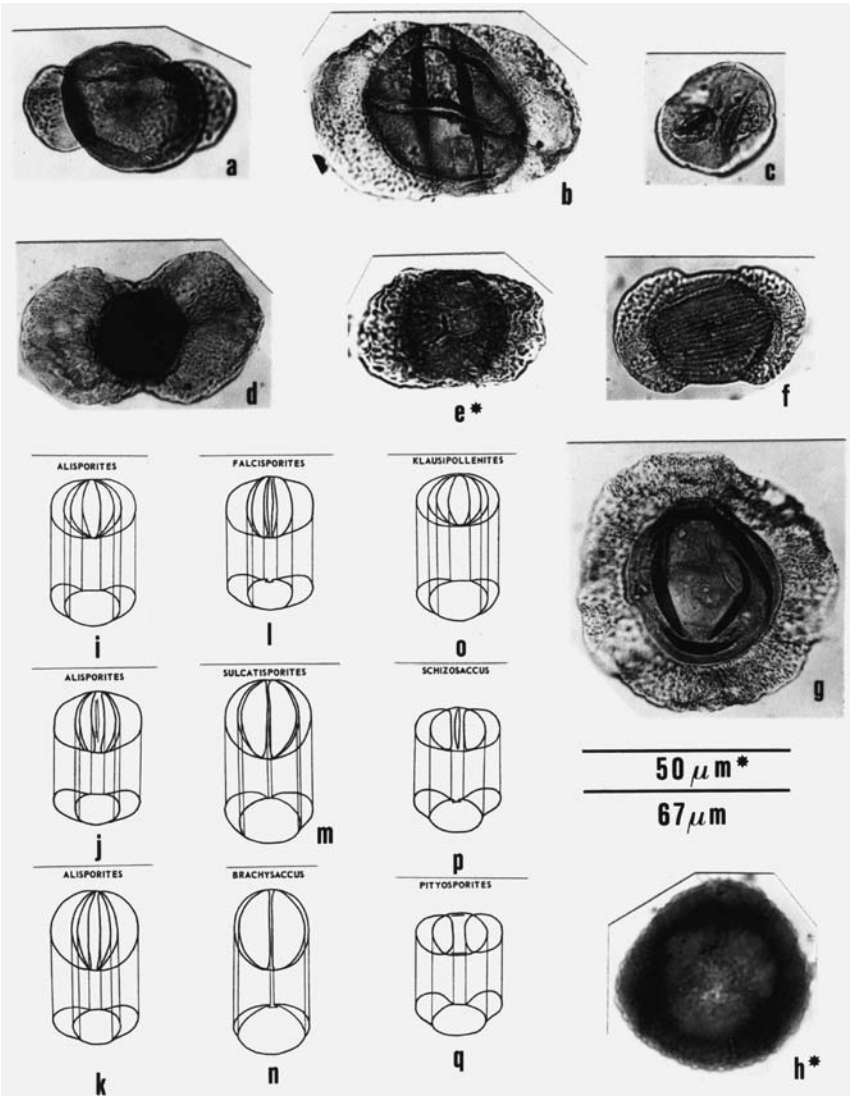

Figure 11.12 Triassic bisaccate and monosaccate diversity. The systematic problems encountered in the classification of saccate pollen are perhaps the most difficult in all of paleopalynology. Those of Triassic-Jurassic palynofloras are, as a group, among the most difficult. (**a**) *Microcachryidites fastidiosus* (Jansonius) Klaus. Anisian, Poland. Proximal view, high focus. (**b**) *Succincitisporites grandior* Leschik. Scythian-Anisian, Poland. Proximal view, mid-focus, showing characteristic monolete-like structure and saccus folds. This form is transitional between monosaccate and bisaccate. (**c**) *Minutosaccus gracilis* (Scheuring) Orłowska-Zwolińska. Ladinian, Poland. Proximal view, high focus. Forms

these, Cornet writes (pers. comm.): "One of the most interesting discoveries from the study of Late Triassic palynofloras…has been the rare (usually less than 1%) but persistent presence…of angiosperm-like monosulcate and zonasulculate pollen grains…." A complex of about eight species of angiosperm-like pollen of late Middle Karnian age from the Richmond Basin of Virginia includes highly reticulate-columellate monosulcates, zonasulculates (trisulcates), and a reticulate-clavate pentasulcate (see Fig. 11.11). Hochuli and Feist-Burkhardt (2004) have published Middle Triassic forms similar to those described from the Barents Sea, in the Norwegian Arctic, and they point out that no gymnosperms are known that produce pollen with reticulate sculpture, exine with angiosperm-like layering, and colpate-like apertures, so these pollen would appear to represent either ancestral angiosperms, or an otherwise unknown gymnosperm group with perhaps ties to such angiosperms.

Perhaps all of these Triassic-Jurassic forms should be viewed as an indication of a trend of various gymnosperms toward the morphological types that angiosperm pollen later typified, and for all we know one or more of them may be somehow directly linked to flowering plant ancestry.

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Figure 11.12 with such tiny sacci are often classified as *Protodiploxypinus* spp. (**d**) *Platysaccus* cf. *papilionis* Potonié & Klaus. Scythian-Anisian, Poland. Mid-focus, illustrating very dense central body and large sacci. (**e**) *Triadispora crassa* Klaus. Scythian-Anisian, Poland. Proximo-distal view, focus on the trilete laesura of proximal side. Lateral views show that sacci almost surround central body. (**f**) *Striatoabietites balmei* Klaus. Scythian-Anisian, Poland. Proximal view, mid-focus, taeniate (= polyplicate or "striate") form that survived into mid-Triassic after most of them had become extinct. (**g**) *Heliosaccus dimorphus* Mädler. Ladinian, Poland. Proximo-distal view, mid-focus, showing alete central body (otherwise resembles the earlier monosaccate form, *Nuskoisporites*). (**h**) *Patinasporites densus* Leschik. Karnian-Norian of Eagle Mills Formation, Texas. Proximo-distal view, mid-focus, showing the "bubbly" saccus that surrounds the grain. This sort of monosaccate is often very abundant in the late Triassic. The faint pseudo Y-mark visible would cause some to place this in *Vallasporites*. There are other forms of probably the same single genus, such as *Daughertyspora*. (i)-(q) Drawings by Bruce Cornet showing some of the variants on the Triassic-Jurassic bisaccate theme. Each pair of drawings presents a distal view above and the corresponding lateral view below: (**i**)-(**k**) variations within the *Alisporites* complex; (**l**) *Falcisporites*, which differs very slightly from *Alisporites*–the transverse sulcus displayed is not always demonstrable; (**m**) *Sulcatisporites*, despite the name, there is no visible sulcus; (**n**) *Brachysaccus*, can be difficult to distinguish from *Sulcatisporites*, but *B*. does have a sulcus; (**o**) *Klausipollenites*–in polar views the small, crescent-shaped sacci are distinctive; (**p**) *Schizosaccus*, which has sacci like *Pityosporites*, but *S*. is sulcate; (**q**) *Pityosporites*, grains resemble modern *Pinus* or *Cedrus* more than do any of the others illustrated. (a)-(g) are courtesy of T. Orłowska-Zwolińska, in whose publication (1979) they originally appeared; line drawings are courtesy of Bruce Cornet.

4 Further Notes on Triassic/Jurassic Saccates

Late Triassic and Jurassic sporomorph assemblages are dominated by gymnosperm pollen, Pv1, Pv2 (and P00-Pa0 trilete fern spores). The monosaccates, *Patinasporites, Vallasporites, Enzonalasporites,* and others, are an interesting illustration of a morphon, or intergrading complex of forms. The bisaccates are extremely difficult to cope with systematically. Some of the more common sorts of monosaccate and bisaccate organization are shown in Fig. 11.12. The bisaccates of the Triassic/Jurassic, because so numerous and of so many forms, are especially challenging. S.A.J. Pocock in a short course on Mesophytic palynology I attended referred to their often large size and rather nondescript nature as "big floppies." A wonderful publication in which to view a series of such pollen from Jurassic rocks of China is the chapter by Liu (2000) in the summary book on Chinese fossil paleopalynology edited by Song (2000).

5 Jurassic Palynomorph Paleogeography

Paleopalynology shows that the Jurassic was not as homogeneous as once thought, though more cosmopolitan than most parts of the Phanerozoic. For example, Filatoff (1975) showed that Jurassic trisaccate pollen is restricted to India, Australia and Argentina. On the other hand, some conifers are indeed cosmopolitan, e.g., the *Classopollis* plant, although there are latitudinal variations in its abundance (Truswell, 1981). Dinoflagellate cyst studies have demonstrated marked provinciality in the Jurassic (Williams, 1975).

6 Major Known Botanical Relationships of "Mesophytic" (Late Permian-Early Cretaceous) Dispersed Spores/Pollen Genera

The "turmal" classification is not as useful in the "Mesophytic" as in the Paleophytic because the system was designed by Potonié primarily for Paleozoic spores/pollen, and has not really been as well developed for many of the "Mesophytic" sporomorphs, e.g., taeniate-striates, bisaccates and monocolpates. Furthermore, at least the broad botanical relationship is known for practically all Mesophytic sporomorphs, and shoe-horning the forms into "turmal" categories is often time-consuming and frustrating. Therefore, I present the data for spores found *in situ* here in broad morphological categories, which follow roughly the turmal classification. With a few exceptions, I do not repeat the genera already treated under Paleozoic spores. However, it should be emphasized that such

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**in situ*, or very strong presumption from association

genera as *Apiculatisporites*, produced by ferns, and *Calamospora*, produced by a variety of sphenopsids, continue through the "Mesophytic." Various authors have produced lists of botanical relationships of Mesophytic sporomorphs without references to the source of the information, and as a general handy guide some of these lists, for example that of de Jersey and Raine (1990: Table 5.1), are nevertheless useful.

I. SPORES (megaspores marked with asterisk)

A. TRILETE

(Fern fossils from "Mesophytic" rocks are sometimes referred to extant genera! Thus, Jurassic/Cretaceous spores obtained from osmundaceous fern megafossils are referred to as *Osmunda* spores by Krassilov, l978).

*Banksisporites**

*Banksisporites** was produced as a trilete megaspore by the Triassic lycopsids, *Cyclostrobus* and *Selaginellites*, according to Helby and Martin (1965). (Microspores of *Cyclostrobus* and *Selaginellites* were monolete *Aratrisporites* and trilete *Lundbladispora*, respectively. See also entries for these two genera.)

Calamospora

Calamospora spores were identified from Triassic megafossils of the genus *Equisetites* by Couper (1958) and by Kelber (1999).

Carnisporites

Carnisporites spores were produced by the fern *Cynepteris*, judging from illustrations in Ash (1969).

Cicatricosisporites

Cicatricosisporites spores were studied by Couper (1958) in the type slide of the Cretaceous schizaeaceous fern, *Ruffordia*. Couper also studied *C*. spores in preparations of other schizaeaceous ferns from Cretaceous to Eocene in age. Skog (1980, 1982) found *C*. spores in the Lower Cretaceous schizaeaceous ferns, *Ruffordia* and *Pelletixia*.

Clathropterisospora

Clathropterisospora was described by Zhang (1980) for dispersed spores identical with those obtained from Upper Triassic *Clathropteris* (Dipteridaceae) sporangia.

Cyathidites

Cyathidites spores were identified by Couper (1958) in preparations of Jurassic ferns probably referable to the Dicksoniaceae, and by Douglas (1973) from *Coniopteris*, in the Lower Cretaceous; see also *Dictyophyllidites* below.

Sukh-Dev (1980) notes that *Cyathidites*-like spores were removed from Indian Lower Cretaceous *Onychiopsis* ferns. (See also *Deltoidospora.*) As explained by Van Konijnenburg-Van Cittert (1989b), *Cyathidites* and *Deltoidospora* (q. v.) are often considered synonymous. She found spores referable to *C. australis* and *C. minor* in ten different species of Jurassic ferns referable to the family Dicksoniaceae and to the genera *Coniopteris*, *Kylikipteris, Eboracia,* and *Dicksonia.*

Deltoidospora

Deltoidospora-like spores were obtained from Lower Cretaceous *Onychiopsis* ferns by Sukh-Dev (1980) (but see also *Cyathidites*).

Densoisporites

Spores referable to this morphogenus were recovered from the tree lycopod, *Pleuromeia*, from the lower Triassic of central Europe by Grauvogel-Stamm (1999).

Dictyophyllidites

Dictyophyllidites was obtained from Jurassic *Dictyophyllum* (cheiropleuriaceous? fern) by Couper (1958). Spores of this type were also obtained from Jurassic *Phlebopteris* and from Lower Cretaceous *Weichselia* ferns (Sukh-Dev, 1980) (see also *Lametatriletes*). Litwin (1985) isolated spores referable here from Triassic *Phlebopteris* (Matoniaceae).

*Dijkstraisporites**

Megaspores referred to *Dijkstraisporites* have been described from *Annalepis*, a lycopod cone also producing *Aratrisporites* microspores (see also *Tenellisporites).*

Gleicheniidites

Gleicheniidites spores were identified by Couper (1958) from figures of Jurassic gleicheniaceous ferns published by Harris.

Granulatisporites

Granulatisporites-type spores were identified by Litwin (1985) in Triassic *Clathropteris* (Dipteridaceae) material.

*Horstisporites**

Horstisporites was found in the Triassic lycopsid cone *Skilliostrobus*, according to Ash (1979).

Klukisporites

Klukisporites spores were studied in preparations from Jurassic schizaeaceous ferns (*Klukia* and *Stachypteris*) by Couper (1958).

Lametatriletes

Spores similar to *Lametatriletes* (and to *Cyathidites* and *Dictyophyllidites*) have been removed from Lower Cretaceous *Weichselia* ferns (see Sukh-Dev, l980).

Lundbladispora

Lundbladispora was produced as a microspore by the lycopod *Selaginellites* (Helby and Martin, 1965).

Marattisporites

Marattisporites spores were obtained from Triassic-Jurassic marattialean ferns by Couper (1958).

Matonisporites

Matonisporites spores were identified by Couper (1958) from figures of Triassic-Jurassic matoniaceous ferns (*Phlebopteris, Selenocarpus, Matonidium*) published by various paleobotanists. *M*. spores were also isolated from sporangia of *Phlebopteris* ferns (Ash *et al*., 1982) from the late Triassic of Arizona, and in Indian Jurassic *Phlebopteris* (*Dictyophillidites* also identified), according to Sukh-Dev (1980).

*Minerisporites**

Minerisporites megaspores were obtained from *Isöetites* megafossils (Lower Cretaceous) (Sukh-Dev, 1980).

Osmundacidites

Osmundacidites spores were identified by Couper (1958) from Jurassic osmundaceous ferns published earlier by Harris. Litwin (1985) found spores referable to this genus in *Todites* sporangia of Triassic age. Van Konijnenburg-Van Cittert (1978) referred *in situ* spores from *Osmundopsis* (osmundaceous megafossil) to *Osmundacidites*.

*Paxillitriletes**

Paxillitriletes is an isöetalean megaspore (Kovach and Dilcher, 1985).

Punctatisporites

Punctatisporites (or *Cyclogranisporites*) spores were described for the Triassic fern, *Anomopteris*, by Grauvogel-Stamm and Grauvogel (1980).

*Tenellisporites**

Tenellisporites marcinkiewiczae Reinhardt and Fricke megaspores have been described by Grauvogel-Stamm and Duringer (1983) from the lycopod fructification *Annalepis*, which produces also *Aratrisporites* microspores (these megaspores also have been referred to *Dijkstraisporites*).

Todisporites

Todisporites spores were obtained by Couper (1958) from Jurassic osmundaceous ferns, and from the Triassic fern *Wingatea* by Litwin (1985). Van Konijnenburg-Van Cittert (1978) said that *in situ* spores from *Todites* spp. (osmundaceous megafossil) are referable to *Todisporites*. Schweitzer et al. (1997) also refer *in situ* spores of *Todites* to *Todisporites*, but they note that one species of *Todites* produces spores that could be placed in other similar morphogenera: *Cyclogranisporites, Granulatisporites, Anapiculatisporites.*

*Triletes**

Triletes megaspores were removed from the Jurassic-Cretaceous probable lycopod, *Synlycostrobus*, by Krassilov (1978).

B. MONOLETE

Aratrisporites

Aratrisporites was produced as a microspore by the Triassic lycopsid *Cylostrobus*, according to Helby and Martin (1965). The same authors note the occurrence of *A*. also in *Lycostrobus*. Ash (1979) found *A*. as a microspore in the heterosporous lycopsid cone, *Skilliostrobus*. Grauvogel-Stamm and Duringer (1983) found spores close to *Aratrisporites minimus* Schulz in the lycopsid fructification *Annalepis zeilleri* Fliche (see also megaspore *Tenellisporites*). Skog and Hill (1992) note that sporangia of *Annalepis* contained either *Aratrisporites* microspores and either *Tenellisporites* or *Dijkstraisporites* megaspores. (Scott and Playford, 1985, report *Aratrisporites* microspores attached to *Banksisporites* and *Nathorstisporites* megaspores.)

Punctatosporites

This form was found in Triassic/Jurassic *Marattia* ferns by Schweitzer et al. (1997). Other authors put such spores in *Marattisporites.* (Schweitzer *et al*. also found trilete spores in the *Marattia* fossils–cf. *Cyclogranisporites.*

II. POLLEN

A. MONOSACCATE

Callialasporites

Callialasporites (also called *Applanopsis*) was produced in pollen cones of the Lower Cretaceous conifer, *Apterocladus* (Archangelsky and Gamerro, 1967; Gamerro 1968).

Cerebropollenites

This morphogenus of pollen has been reported from *Masculostrobus* (conifer) male cones, for example by VanKonijnenburg-Van Cittert and Van der Burgh (1989), but such cones have also been cited as producing many other pollen morpohogenera.

Nuskoisporites

Nuskoisporites, a trilete monosaccate pollen form, was isolated from late Permian and early Triassic conifer cones, belonging to the genus *Ortiseia* (Clement-Westerhof, 1974; Poort *et al*, 1997).

Patinasporites

Patinasporites, a *Tsuga*-like form, was obtained from *Pagiophyllum*-like conifer cones of the Late Triassic of Pennsylvania by Cornet (1977a).

B. BISACCATE (including multi-saccates, pseudosaccates and striate-taeniate bisaccates)

Alisporites

Alisporites pollen of several species was found, and a new species of this dispersed pollen morphogenus was described by Grauvogel-Stamm (1978) from *Willsiostrobus* cones, a conifer from the early Triassic of France. (It does not affect the information here, but it would be better not to propose new *Sporae dispersae* taxa from megafossil plant specimens. The name of the megafossil taxon should simply be used for the palynomorphs.) *Alisporites*. pollen (but see *Favisporites* and *Lunatisporites*) was also found in Triassic pollen organs of *Pteruchus* (a corystosperm) and *Masculostrobus* (a conifer) according to Townrow (1962). *A*. pollen (but see also *Pteruchipollenites*) was described in ultrastructural detail from *Pteruchus* pollen organs from the Triassic of Argentina by Taylor *et al*. (1984). Yao *et al*. (1995) found *A*. pollen in *Pteruchus* organs from Antarctica and were able to demonstrate that they were produced by corystosperm plants. Pollen of this sort also was described by Delevoryas and Hope (1973) from abundant late Triassic male cones associated with the ovulate conifer cone, *Compsostrobus*. *Alisporites* (but see also *Platysaccus*, *Pteruchipollenites,* and *Sulcosaccispora*) has been found in pollen organs similar to *Pteruchus* and probably belonging to *Dicroidium*, a putative member of the Corystospermaceae. *A*. pollen was also described from the conifer fructification *Lelestrobus* by Srivastava (1984). An important summary of structural features of corystospermaceous *in situ* pollen referable to *Alisporites* was published by Osborn and Taylor (1993). It seems likely that the conifer and corystosperm bisaccate pollen referred to this morphogenus will eventually be separated.

Exiguisporites

Exiguisporites (as well as *Vitreisporites* and *Falcisporites*) pollen was reported from pollen sacs of *Caytonanthus* (Jurassic caytonialean) and *Harrisiothecium* (Triassic pteridosperm) by Townrow (1962).

Falcisporites

Falcisporites (as well as *Vitreisporites* and *Exiguisporites*) pollen was reported from pollen sacs of *Caytonanthus* (Jurassic caytonialean) and *Harrisiothecium* (Triassic pteridosperm) by Townrow (1962). Townrow (1965) also illustrates pollen of a corystospermaceous pteridosperm, which Balme (1970) recognized as *Falcisporites*.

Favisporites

Favisporites (as well as *Alisporites* and *Lunatisporites*) pollen was found in Triassic cones of *Pteruchus* (a pteridosperm) and *Masculostrobus* (a conifer) by Townrow (1962).

Gigantosporites

Gigantosporites, a large, non-striate bisaccate, was found in a probable conifer cone of the late Permian by Clement-Westerhof (1974).

Illinites

Illinites (see also information under Paleophytic spores/pollen) was reported from cones of the Lower Triassic conifers *Aethophyllum* and *Willsiostrobus* by Grauvogel-Stamm (1978). She notes that others have called these palynomorphs *Chordosporites, Colpectopollis* and *Sahnisporites*. (Grauvogel-Stamm and Grauvogel, 1973, referred to such pollen from *Masculostrobus acuminata*, a conifer, as *Parillinites*.) Gall and Grauvogel-Stamm (1999) illustrate an *Illinites* grain obtained from a male cone of *Aethophyllum.*

Jugasporites

Jugasporites, a bisaccate having an odd corpus structure with a rent-like opening, was found by Clement-Westerhof (1974) in late Permian coniferous cones.

Kosankeisporites

Kosankeisporites pollen was described from Triassic sporangia of *Pteruchus*, a pteridosperm (but see also *Sulcatisporites* and *Pteruchipollenites*) by Townrow (1962).

Lueckisporites

Lueckisporites, a monolete(!) taeniate bisaccate in which the taeniae form most of the corpus, was isolated from late Permian coniferous cones of Italy by Clement-Westerhof (1974).

Lunatisporites

Lunatisporites (=Taeniaesporites), a taeniate bisaccate, was found in a conifer cone from the late Permian by Clement-Westerhof (1974). *L*. pollen (as well as *Alisporites* and *Favisporites*) was found in Triassic *Pteruchus* (a pteridosperm) and *Masculostrobus* (a conifer) cones by Townrow (1962).

Pityosporites

Pollen referable to this bisaccate morphogenus were found in some specimens of the enigmatic gymnosperm microsporophyll, *Pramelreuthia* (Ash and Litwin, 1996). However other microsporophylls contained pollen referable to *Protodiploxypinus*.

Platysaccus

Platysaccus has been found in cones associated with *Dicroidium*, a probable member of the Corystospermaceae (Anderson and Anderson, 1983) (but see also *Alisporites* and *Sulcosaccispora*).

Podocarpidites

Podocarpidites pollen (as well as *Vesicaspora*) was found in Triassic *Ruhleostachys* (a conifer or cordaite) cones by Townrow (1962).

Protodiploxypinus

This non-striate bisaccate pollen occurs in the microsporophylls of the enigmatic gymnosperm *Pramelreuthia* in the Upper Triassic Chinle Fm. of the SW USA (Ash and Litwin, 1996). However, some forms of the same microsporophyll morphogenus produced pollen referable to species of *Pityosporites.*

Protohaploxypinus

Protohaploxypinus, a striate bisaccate, is known to have been produced by Permian glossopterid gymnosperms, but it was first described from Laurasia. As noted by Retallack (1980), Pant and Nautiyal (1960) illustrated a number of such palynomorphs, and some other sorts, from glossopterid seed pollen chambers. Gould (1981) noted the occurrence of *P*. pollen in *Arberiella*, the pollen-sac organ of *Glossopteris*. However, this sort of pollen also has been found in the cones of a podocarp, *Rissikia* (Anderson and Anderson, 1983).

Pteruchipollenites

Pteruchipollenites pollen was reported from the Triassic, in pollen organs of *Pteruchus*, a corstospermacous pteridosperm (but see *Sulcatisporites, Alisporites*) by Townrow (1962) by Taylor *et al*. (1984) and by DeVore and Taylor (1988). Possible *Pteruchipollenites* was described from preparations of Triassic *Pteruchus* by Couper (1958).

Rimaesporites

Rimaesporites Permian pollen was obtained from *Ullmannia* (a conifer) cones by Townrow (1962).

Satsangisaccites

Satsangisaccites pollen was described from Lower Triassic *Nidistrobus* pollen-bearing organs, an apparent pteridosperm, by Bose and Srivastava (1973).

Striatites

Striatites pollen is illustrated from the Triassic enigmatic (gymnospermous?) fossil, *Nidpuria*, by Pant and Basu (1979). Probable *S*. pollen was obtained from Permian *Arberiella* cones (Townrow, 1962), a glossopterid gymnosperm.

Sulcatisporites

Pollen referable to *Sulcatisporites (= Lorisporites)* from Triassic *Pamelreuthia*, a pteridosperm, possibly a caytoniad, was studied by Townrow (1962). However, Townrow also noted that *S*.-like pollen was obtained from sporangia of *Pteruchus africanus*, a pteridosperm.

Sulcosaccispora

Sulcosaccispora (see *Alisporites* and *Platysaccus*) has been found in cones of *Dicroidium*, a probable member of the Corystospermaceae.

Taeniaesporites: See *Lunatisporites*

Triadispora

Triadispora, an unusual bisaccate form with a trilete laesura, was found as mature pollen in the early Triassic conifer, *Darneya*, and in *Sertostrobus* conifer cones (but see *Inaperturopollenites*), by Grauvogel-Stamm (1978).

Vitreisporites

Vitreisporites (= *Caytonipollenites, Pityosporites*) *pallidus* is well known to be the dispersed pollen of Jurassic *Caytonanthus* (Chaloner, 1968b). The bisaccate nature of *V*. has been regarded by some but not all as a major stumbling block in efforts to connect the Caytoniales with angiosperm ancestry. *V*. pollen was studied by Couper (1958) in preparations of *Caytonanthus*. *V*. (and *Falcisporites* and *Exiguisporites*) pollen was reported from strobili referable to *Caytonanthus* and *Harrisiothecium* (a Triassic pteridosperm) by Townrow (1962).

Voltziaceaesporites

Voltziaceaesporites pollen was reported from early Triassic conifer cones, *Willsiostrobus* and *Yuccites*, by Grauvogel-Stamm (1978).

C. POLYSACCATE

Podosporites

Podosporites (Microcachryidites) trisaccate pollen was described by Vishnu-Mittre (1956) from Jurassic *Masculostrobus* male cones of apparent podocarpacean affinity, according to Balme (1964).

Trisaccites

Trisaccites pollen was found in cones of the Lower Cretaceous podocarpaceous conifer, *Trisacocladus*, by Archangelsky and Gamerro (1967), and by Baldoni and Taylor (1982).

D. INAPERTURATE

Araucariacites

Araucariacites pollen was identified by Couper (1958) in a preparation of the Jurassic conifer, *Brachyphyllum* (but see below under *Classopollis*).

Exesipollenites

Pollen of *Exesipollenites* morphology was described from the type-specimen of the Jurassic cyadeoid flower, *Williamsoniella lignieri*, by Harris (1974a).

Inaperturopollenites

Inaperturopollenites limbatus Balme pollen was shown to be produced by Lower Cretaceous *Brachyphyllum* cones, by Archangelsky and Gamerro (1967) and Gamerro (1968) (but see under *Classopollis* below, and *Araucariacites* above). Pollen attributed to the genus *I*. was also found by Grauvogel-Stamm (1978) as immature grains in Lower Triassic *Darneya* conifer cones, of which the mature pollen was *Triadospora*. (Pollen in some of the illustrations appear circumpolloid. This pollen was later (Archangelsky 1977) transferred to a new genus, *Balmeopsis*.)

Perinopollenites

Perinopollenites pollen was identified by Couper (1958) in cone preparations of the Jurassic taxodiaceous conifer, *Elatides*. Harris (1973) confirmed this, noting that the pollen is quite variable from one cone to another. Van Konijnenburg-Van Cittert and Van der Burgh (1989) described this pollen morphotaxon from an *Elatides* from the Jurassic of Scotland.

E. CIRCUMPOLLOID (*Classopollis, Gliscapollis,* etc.)

Classopollis

Classopollis pollen was produced by the Lower Cretaceous conifer cone, *Tomaxiella* (Archangelsky and Gamerro, 1967; Gamerro, 1968). Couper (1958)

identified it in preparations of Jurassic coniferous male cones of *Pagiophyllum*. He also identified *C*. from illustrations of pollen cones of *Hirmerella* (= "*Cheirolepis"*). However, it should be emphasized (see Barnard, 1968; Medus, 1970) that circumpolloid pollen of various sorts has been obtained from male cones of a variety of Mesozoic conifers: *Brachyphyllum, Hirmerella, Pagiophyllum* and *Masculostrobus*. Some of these genera also have produced non-circumpolloid pollen. The primary association seems to be of *Hirmerella* (Cheirolepidaceae) cones and *Classopollis* pollen, however (see Francis, 1983, 1984).

F. STRIATE (including taeniate, but not saccate)

Equisetosporites

Equisetosporites pollen was obtained from Triassic *Dechellyia* (=*Masculostrobus*) by Ash (1972). It is thought by many that *Equisetosporites/Dechellyia* represents gnetalean plants.

G. MONOSULCATE

Cycadopites

Pollen apparently referable to *Cycadopites* was obtained from Jurassic *Sahnia* (Pentoxylaceae), according to Sukh-Dev (1980), and from *Lepidopteris* (Peltaspermales), per Anderson and Anderson (1983).

Monosulcites

Monosulcites pollen was identified from preparations of a Jurassic cycadalean fructification, *Androstrobus*, by Couper (1958) and, per the same publication, from Rhaetian-Lower Cretaceous ginkgoalean material, and from the Jurassic cycadeoids, *Williamsonia, Williamsoniella*, and *Wonnacottia*. Osborn and Taylor (1995), in a very detailed and important study of the structure of the pollen of *Cycadeoidea* (Bennettitales) show it to be similar to that of the dispersed genus, *Monosulcites.* Especially significant is the existence of a granular infratectum in a number of different cycadeoid pollen forms.

Nomenclatural note: In this second edition I am using the generic name *Classopollis* to replace *Corollina*, as explained earlier in this chapter. This creates a problem with two species illustrated here, viz. *Classopollis murphyae,* and *Classopollis zwolinskae.* These species have apparently never been formally transferred from *Corollina,* although the combination *Classopollis murphyae* was used in a list in Petrosyants and Bondarenko (1983). *Classopollis meyerianus* appears in lists in de Jersey (1971), and de Jersey (1973) later made the transfer, although the gender of the specific epithet must be corrected to *us* from *a*. The new combination for *C. meyerianus* published by Y. Shang in Song (2000, p. 550) was therefore superfluous. I am here making the two additional required formal transfers as follows:

Classopollis murphyae (Cornet & Traverse 1975) Traverse, nov. comb., published here. Basionym: *Corollina murphyi,* Cornet, B. and Traverse, A., 1975, *Geoscience and Man* **11**:19-20, holotype Pl. 5, Fig. 11. The ending of the specific epithet is corrected because the species was named for a woman.

Classopollis zwolinskae (Lund 1977) Traverse, nov. comb., published here. Basionym: *Corollina zwolinskai* Lund, J. J., 1977, *Geol. Surv. Denmark II Ser*. **109**:70, holotype Pl. 7, Fig. 11.5. The ending of the specific epithet is corrected because the species was named for a woman.

Chapter 12

Triassic-Jurassic Megaspores, Dinoflagellates, Other Microplankton

1 Acritarchs and Algal Groups Formerly Classified as Acritarchs

Marine and semi-marine sediments of Permian to Jurassic age often contain abundant but not very diverse acritarchs, and their study has not been as productive as is true of the Paleophytic, especially of Cambro-Devonian time. The reasons for the post-Devonian collapse of the acritarch palynoflora are as yet uncertain. However, a fair amount is known about Mesophytic acritarchs, and their study may be rewarding.

Many forms previously classed as acritarchs have now been removed from that group, because they have been recognized as belonging to specific algal groups, for example, the Prasinophyceae (see Fig. 12.1), Zygnemataceae, and Hydrodictyaceae (see Fig. 12.2). Prasinophyte forms known as tasmanitids, from the genus *Tasmanites* (most of the forms in Fig. 12.1) are especially important constituents of some Triassic-Jurassic marine rocks. The cysts, often called phycomata, are very characteristic in appearance, beset with pores, the openings of internal channels. As all or almost all acritarchs are probably algal in origin, it makes some sense to refer to dinocysts, acritarchs and organic-walled microscopic algal fossils as collectively the palynomorph microplankton. Fig. 12.2 shows some Triassic-Jurassic acritarchs.

2 Megaspores

After the Carboniferous, free-sporing megaspores retreat ever more into the background, the plants that produced them being replaced by seed/pollen-producers. In the modern flora, free megaspores are made by only a few lycopsid

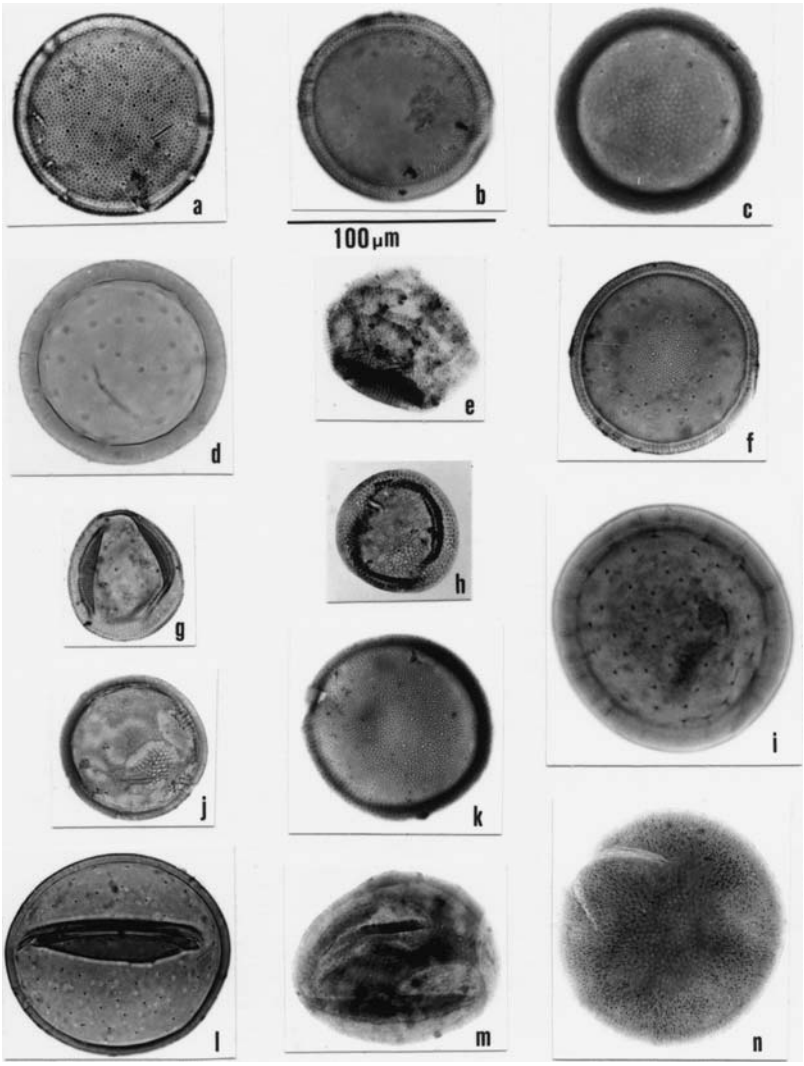

Figure 12.1 Tasmanitids: thick-walled disk-like bodies with walls perforated by canals, formerly referred to the acritarchs, but now recognized as belonging to the algal family Tasmanitaceae. Tasmanitids occur from early Paleozoic to present and have been shown to represent cyst-like parts (sometimes called phycomata, singular phycoma, cf. Guy-Ohlson, 1996) of the life cycle of members of the green alga group, Prasinophyta, which has species in fresh to marine water. *Quisquilites* (Fig. 6.6l) is a Devonian "acritarch" usually put with the tasmanitids. If it is truly referable to the prasinophytes, it is of course not an acritarch. The forms illustrated here are from the Posidonienschiefer, Lower Jurassic (Liassic:Toarcian) oil shales of Germany. The tasmanitids have not been as abundant since the Jurassic as they were in nearshore marine environments of the

and fern genera such as *Selaginella, Isöetes* and *Azolla*. As in the modern flora, Mesozoic megaspores also represented heterosporous lycopods and ferns. Permian, Triassic and later sediments regularly contain free megaspores, and they can be removed from their enclosing rock, using the techniques described in the Appendix. Fig. 12.2 includes illustrations of some Triassic megaspore forms and Fig. 13.17 some Cretaceous forms. About 350 species of megaspores, referable to about 75 genera, have been described from Triassic to Cretaceous sediments (Sweet, 1979). (Fig. 12.3 summarizes internationally accepted Jurassic-Cretaceous stages.) These palynomorphs are clearly of potential biostratigraphic importance, but as yet too few assemblages have been studied to provide adequate biostratigraphic control over most of the world. Important studies have been made, for example, of Triassic megaspores of Australia (Dettman, 196l; Scott and Playford, 1985), Europe (Orłowska-Zwolińska, 1979), and the other continents, including Antarctica. Undoubtedly megaspore study is a field with a future. (See also discussion of megaspores in Chapters 8 and 9.)

3 Dinoflagellates

It could turn out that some acritarchs known from the Paleophytic are really cysts of dinoflagellates or dinoflagellate precursors, because molecular and biogeochemical studies suggest that the group may have originated as early as late Proterozoic (see summary in Hackett *et al.*, 2004). However, the first unquestioned dinoflagellate cysts with all the required characteristics and clearly tied in with subsequent evolutionary developments are late Triassic (see Figs 19.5 and 12.10). All of the many claims for pre-Triassic dinoflagellates have so far been rejected by dinoflagellate experts for one reason or another.

The dinoflagellates are in today's environments an extremely diverse group of protists, including even forms that are parasitic in vertebrate guts. They are also very important constituents of the marine food chain and are the causative organisms of some of the infamous "red tides" that, among other things, can make shellfish toxic to humans. However, the only dinoflagellates of importance to paleopalynologists are those which have a complex life cycle with a thin-walled, motile, characteristically flagellate stage usually called the theca or thecate stage,

Figure 12.1 Paleozoic and early Mesozoic. (**a**) *Pleurozonaria media* Mädler. (**b**) *P. suevica* (Eisenack) Mädler. (**c**), (**d**) *P. wetzelii* Mädler. (**e**) *P. media*, corroded, see (a). (**f**) *P. suevica*, see (b). (**g**) *P. suevica*, not fully developed, see (b) and (f). (**h**) *P. wetzelii*, not fully developed, see (c) and (d). (**i**) *Tasmanites tardus* Eisenack. (**j**) *Pleurozonaria sp.* (**k**) *P. suevica*, see (b) and (f). (**l**) *Tasmanites tardus*, not fully developed, see (i). (**m**) *Tytthodiscus sp.*, corroded example. (**n**) *Tytthodiscus schandelahensis* (Thiergart) Mädler, peculiar preservation makes pore canals visible. Photomicrographs from Karl Mädler, originally published in Mädler, 1963.

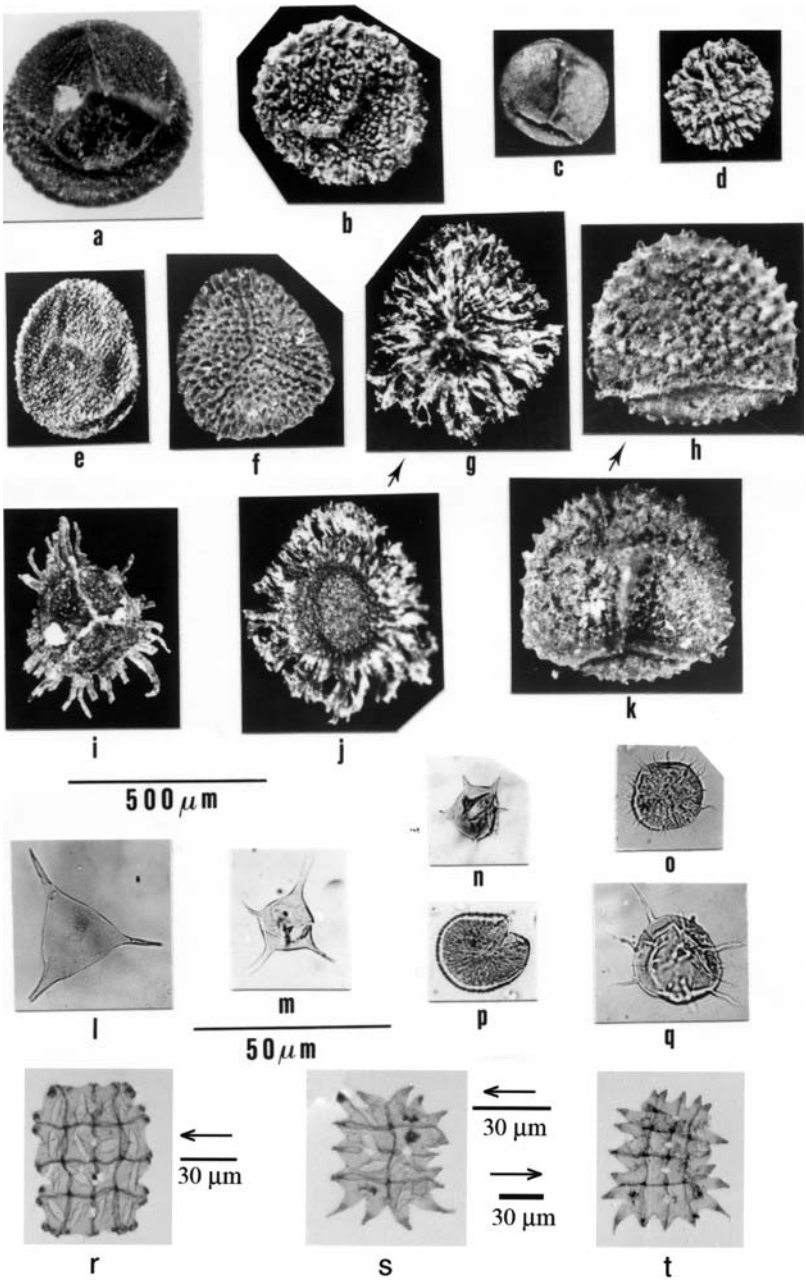

Figure 12.2

and a non-motile, thick-walled encysted stage, the cyst (see Figs. 12.5–12.8). The cysts, or at least the cysts we find as fossils, have walls made of a substance apparently very similar to the sporopollenin of spores, pollen and acritarchs: more or less the same color, the same response to carbonization. The staining reactions and fluorescene characteristics are, however, somewhat different. The substance is often called dinosporin to underline the fact that it comes from

Figure 12.2 The large and the small of Triassic palynology. Free megaspores (a)-(k) reached their heyday in the late Devonian to early Carboniferous. As the seed habit took over in the evolution of vascular plant reproduction, free megaspores declined in importance, and today they are only produced by a handful of heterosporous ferns and lycopods. However, Mesozoic sediments still contain abundant megaspore remains. Methods for processing and photographing megaspores differ somewhat from methods normally employed for miospores, e.g., these photos were made using reflected light. SEM in conjunction with transmitted light microscopy of cleaned (by HNO_3 or Schulze's reagent) specimens is also frequently used for megaspores (see Scott and Playford, 1985). Acritarchs (n)-(q) had their apex of diversity in the early Paleozoic but continue to be abundant and important, especially in marine sediments, to present. (r)-(t) represent microscopic algal coenobia referable to family Hydrodictyaceae of the green algae. The acritarchs and various algal microscopic fossils together comprise the microphytoplankton. They are all presumably algal. The acritarch photographs are of typical Triassic forms (see also line drawings in Fig. 10.5). Magnification for (a)-(k) shown by bar under (i), and for (l)-(o) and (q) by bar under (m); (p) is slightly more magnified–the specimen shown is 23 μm in maximum dimension. The dimensions for figures (r)-(t) are indicated by the indicated bars. All specimens are from the Triassic of Poland, except (r)-(t), which are from the Upper Triassic of Texas, USA. (**a**) *Verrutriletes utilis* (Marcinkiewicz) Marcinkiewicz, Rhaetian. Proximal view showing prominent contact scars. (**b**) *Verrutriletes litchi* (Harris) Potonié, Rhaetian. (**c**) *Trileites pinguis* (Harris) Potonié, Rhaetian. (**d**) *Echitriletes frickei* Kannegieser & Kozur, Karnian. (**e**) *Verrutriletes ornatus* Reinhardt & Fricke, Karnian. (**f**) *Horstisporites cavernatus* Marcinkiewicz, Rhaetian. (**g**) *Dijkstraisporites beutleri* Reinhardt, Ladinian. Proximal view (see also (j)). (**h**) *Narkisporites harrisii* (Reinhardt & Fricke) Kozur, Karnian. Distal view (see also (k)). (**i**) *Tenellisporites marcinkiewiczae* Reinhardt & Fricke, Ladinian. (**j**) *Dijkstraisporites beutleri* Reinhardt. Distal view of same specimen as (g). (**k**) *Narkisporites harrisii* (Reinhardt & Fricke) Kozur. Proximal view of same specimen as (h). (**l**) *Veryhachium reductum* (Deunff) Jekhowsky, Ladinian. (**m**) ?*Veryhachium irregulare* Jekhowsky, Scythian. (**n**) *Veryhachium dualispinum* Wall, Ladinian. (**o**) *Baltisphaeridium debilispinum* Wall & Downie, Ladinian. (**p**) *Baltisphaeridium aciculatum* Orłowska-Zwolińska, Ladinian. (**q**) *Baltisphaeridium longispinosum* (Eisenack) Eisenack, Ladinian. (**r**) *Plaesiodictyon mosellanum* Brenner and Foster ssp. *bullatum* Wood *et al*. (**s**)-(**t**) *Plaesiodictyon mosellanum* ssp. *variable* Brenner and Foster. Megaspore photos are from Marcinkiewicz (1979). Photographs of acritarchs are from Orłowska-Zwolińska (1979). *Plaesiodictyon* photos were provided by Gordon D. Wood and were originally published in Wood and Benson (2000).

SYSTEM	SERIES	STAGE	EUROPEAN "SERIES"
PALEOGENE	PALEOCENE	Danian	
CRETACEOUS	UPPER	Maestrichtian Campanian Santonian Coniacian Turonian Cenomanian	SENONIAN
	LOWER	Albian Aptian Barremian Hauterivian Valanginian Berriasian	NEOCOMIAN
			*
JURASSIC	UPPER	Volgian (±=Portlandian or Tithonian) Kimmeridgian Oxfordian	MALM
	MIDDLE	Callovian Bathonian Bajocian Aalenian	DOGGER
	LOWER	Toarcian Pliensbachian Sinemurian Hettangian	LIAS
TRIASSIC	UPPER	Rhaetian **	

* An upper part of the Volgian, the "Purbeckian", usually regarded as uppermost Jurassic, often turns out to be Cretaceous, but if so is nevertheless classified as "MALM".

** If the Rhaetian is not recognized as a stage, this is late Norian.

Figure 12.3 Internationally recognized sub-divisions of Jurassic-Cretaceous time/rock. Modified from Pocock (1973).

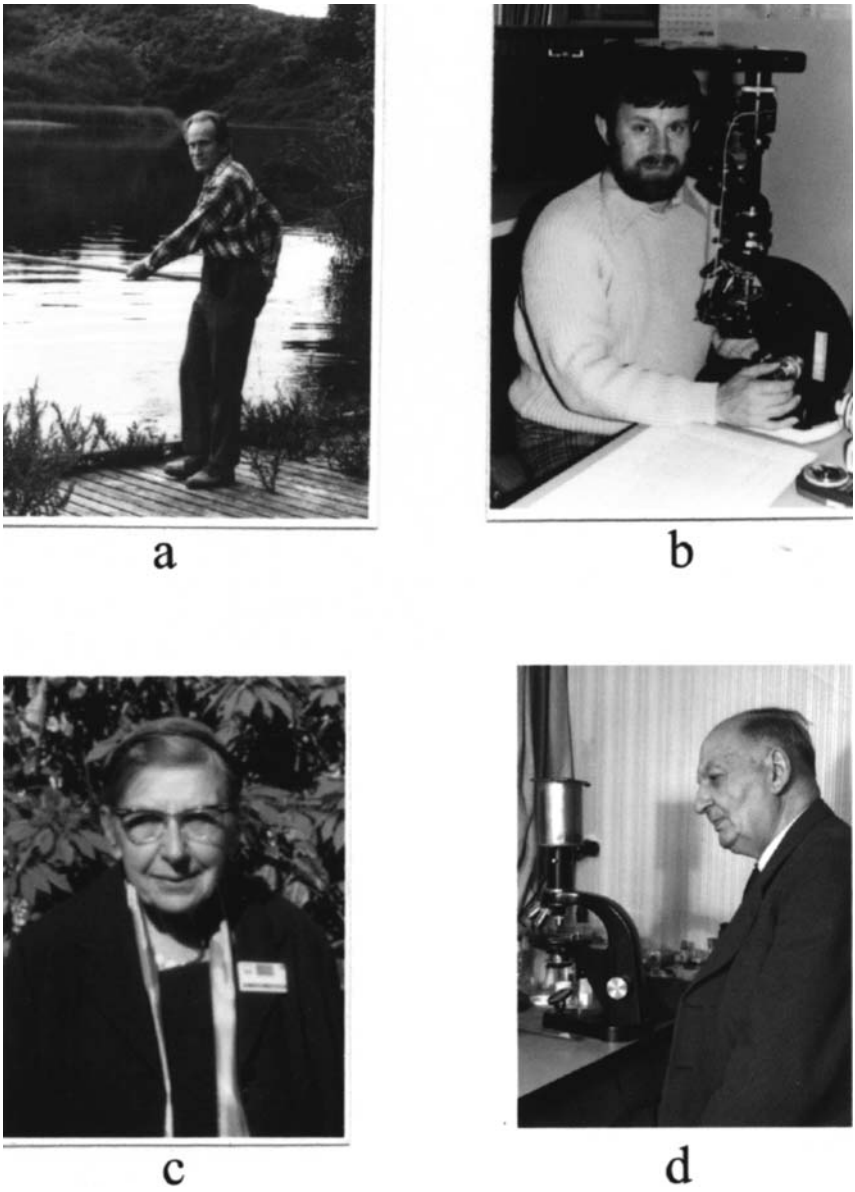

Figure 12.4 Several important persons in the study of fossil dinoflagellates. (**a**) William R. Evitt, born 1923, fishing for freshwater dinoflagellates in a lake near his Stanford, California, laboratory, July 1982. It was Evitt more than any other person who was responsible for recognizing from their morphology that many of the former "hystrichosphaerids" were in fact dinoflagellate cysts. It was Evitt who proposed

organisms that are not related to the producers of sporopollenin. The robustness of sporopollenin/dinosporin accounts for the preservation of most palynomorphs.

It should be emphasized that of extant dinoflagellates only something in the order of 10–15% make resting cysts, not all of which are preservable (cf. Head, 1996). A few dinoflagellates make calcareous cysts, which can be preserved as fossils, but they are not palynomorphs because they dissolve in acid (one species is known that has an organic wall within the calcareous wall that might become a palynomorph, cf. Hultberg, 1985).

Dinoflagellates are usually classed in biology as protists (= Kingdom Protista), but they are now believed to be an independent bunch with a long history separate from other organisms and probably related to ciliates and sporozoans. Spector (1984) noted that the nuclei of dinoflagellates are so different from those of eucaryotes that they might be called "mesocaryotes," to distinguish them from both procaryotes and eucaryotes, and to suggest that they are not closely related to any other group.

Indeed, along with their apparent relatives they are now called alveolates, in reference to possession of cortical ("amphiesmal") vesicles throughout these organisms. The alveolates are not closely related to animals, plants or fungi. When I first began my work as a palynologist (though we weren't called that then), most of us were spore/pollen people and few if any of us knew what the dinoflagellate cysts we found in marine sediments were; we lumped them with

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Figure 12.4 dividing the "hystrichosphaerids" between those which are dinoflagellate cysts, and all others–the acritarchs. (**b**) David Wall, born 1937, at the microscope. Dinoflagellate cysts are often so different from the thecal state of the organism that, despite Evitt's insightful proposals, someone had to grow thecal dinoflagellates from the cysts, in culture, and vice versa, to establish the life cycle and prove that Evitt's proposals were correct. Wall did this many times and for different dinoflagellates. From his work it was obvious that fossil dinoflagellates are always cysts. (**c**) Isabel C. Cookson, 1893–1973, pioneer Australian paleopalynologist. Already well-known for her work with Cenozoic fossil pollen, Dr. Cookson turned her attention to dinocysts about 1953. She recognized the rich opportunities for Australian fossil dinoflagellate studies, and encouraged the interests of many others in this work. (**d**) Alfred Eisenack, 1891–1982. A German whose life was incredibly impacted by the two world wars (prisoner of war in both of them, for a total of more than a decade!) he nevertheless managed to be the effective father of the study of fossil acritarchs and dinoflagellates, while supporting himself mostly as a secondary school teacher. His name is immortalized in the Eisenack Catalog of Fossil Dinoflagellates, which in its original series also had four volumes dedicated to acritarchs. The photo shows evidence of the low-budget nature of Eisenack's research. He never possessed an expensive microscope, or even one with a mechanical stage, and his photomicrographic apparatus consisted of an ordinary tin can that he adapted to his microscope. (b) photo courtesy of D. Wall, taken in 1978; (c) photo by J. G. Douglas, courtesy of M. E. Dettmann, taken in 1971; (d) photo by Werner Wetzel, courtesy of Hans Gocht.

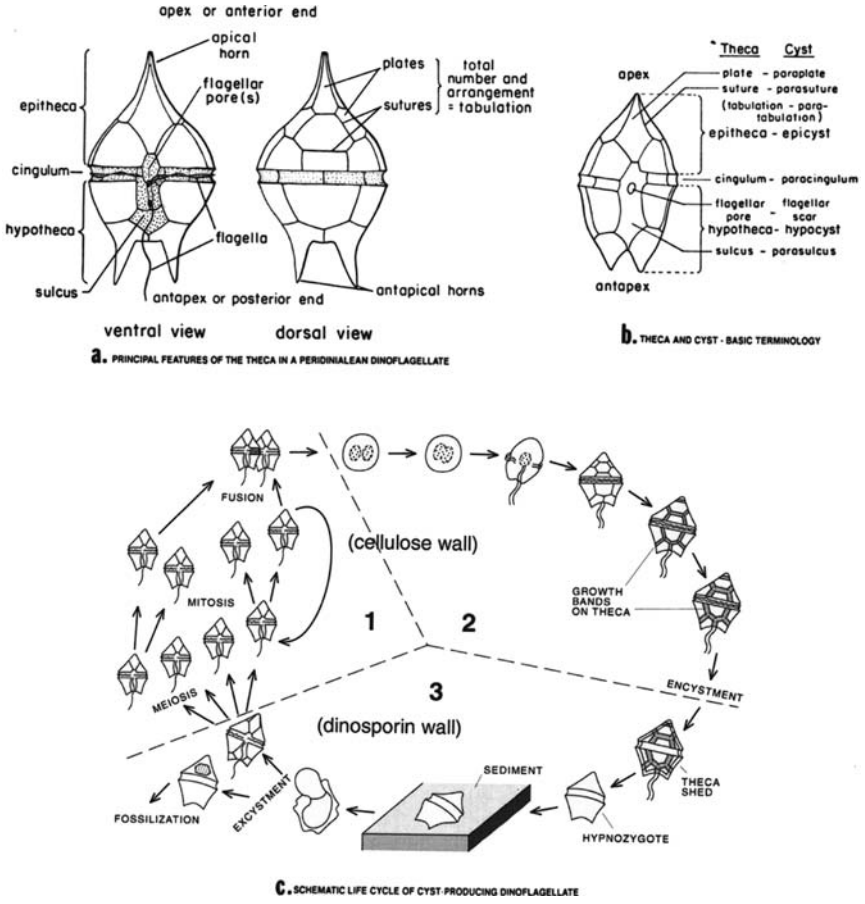


Figure 12.5 Basic aspects of dinoflagellate cell construction and life cycle. The "vegetative" form with a cellulosic theca (wall) is encountered in many free-living dinoflagellates. Almost all fossil dinoflagellates represent the encysted phase, which may be quite different in appearance from the thecal form from which it derives, although at least part of the basic construction of the cyst, e.g., the archeopyle, can be shown to derive from specific plates of the theca. (**a**) Features of a dinoflagellate theca: the principal terms used are the same for theca and cyst, but for cysts, as seen in (**b**), some linguistic alterations are necessary. The prefix "para-" before sulcus and other terms for the cysts (thus, parasulcus, paraplate, etc.) to distinguish them from the same terns for thecae is not used by all who study dinoflagellates. The life cycle of the dinoflagellates that produce resistant-walled (sporopolleninous) cysts is variable, and that displayed in (**c**) is an average picture, not invariably followed even by one species. In the "fusion" shown in step **1,** the haploid cells act as gametes, and fuse to a zygote which becomes the cellulosic-walled theca in step **2**. As cell size increases, bands of new thecal material (growth bands) may appear along sutures. In step **3**, a cyst wall of dinosporin develops inside the thecal wall, and

what we now call acritarchs as "hystrichosphaerids" (spiny spheres–though many are not spiny). This is despite the fact that the pioneers of micropaleontology such as Ehrenberg recognized at least the proximate (non-spiny) dinocysts as dinoflagellates. The early investigators of fossil dinoflagellates were not looking at macerations of rock such as modern palynologists study, but at thin sections. In my doctoral work on the Brandon lignite I had a very puzzling "unknown" that was sent or shown to many micropaleontologists over a period of a year before one of them said that the item was a peridinioid dinoflagellate, a proximate cyst, probably the first fresh water fossil dinocyst to be described. One very famous expert on fossil insects thought they were stonefly eggs. What we now know to be chorate cysts with various sorts of external processes remained "unknowns" when Muller (1959) published them as "hystrix" for modern Orinoco delta sediments, and Traverse and Ginsburg (1966–based on research done about 1960) published many of them as "hystrichosphaerids" for modern sediments of the Great Bahama Bank, where they were abundant constituents of the pollen-poor marine sediment. These chorate cysts with processes look very different from the thecae of the organisms that produced them, and they were not recognized as dinoflagellates even by experts on dinoflagellates. It was one of the great achievements of palynology when Evitt (1961; see Fig. 12.4) demonstrated on morphological grounds that many of the "hystrichosphaerids" are dinoflagellate cysts, even though on first examination they do not look at all like the thecal stages, i.e. the part of the life cycle that was regarded as "normal" for dinoflagellates. Indeed, at the time Evitt solved this riddle I was working with hystrichosphaerids in marine sediments of offshore Florida and sent specimens to several of the then better known dinoflagellate experts, who would not accept them as dinoflagellates. They were accustomed to studying only the very different thecal forms. I said at the time that I would not accept "my" hystrichosphaerids as dinoflagellates unless somebody "hatched" one, to produce a thecal, motile dinoflagellate. Wall (1965) (see Fig. 12.4) soon did just that, many times, and it is now known which cyst goes with which theca for many species pairs. Both cysts and thecae in many cases had names, and the nomenclatural problems created are somewhat troublesome. We no longer use the term "hystrichosphaerid" for any forms. Those known to be dinoflagellate cysts or representatives of various algal groups are so identified, and the others, still not referable to any biological group, are now known as acritarchs (from Greek for "unknown origin"), a term introduced by Evitt (1963).

Figure 12.5 this cellulosic wall then disintegrates. The cyst then settles as a sedimentary particle. Following a period of obligate dormancy, the protoplast excysts,, and meiosis yields new haploid cells which conjugate and produce thecae, completing the cycle. The discarded, resistant dinosporin cyst wall is now available for fossilization. Drawings are taken from Evitt (1985), as modified in Fensome *et al*. (1996a).

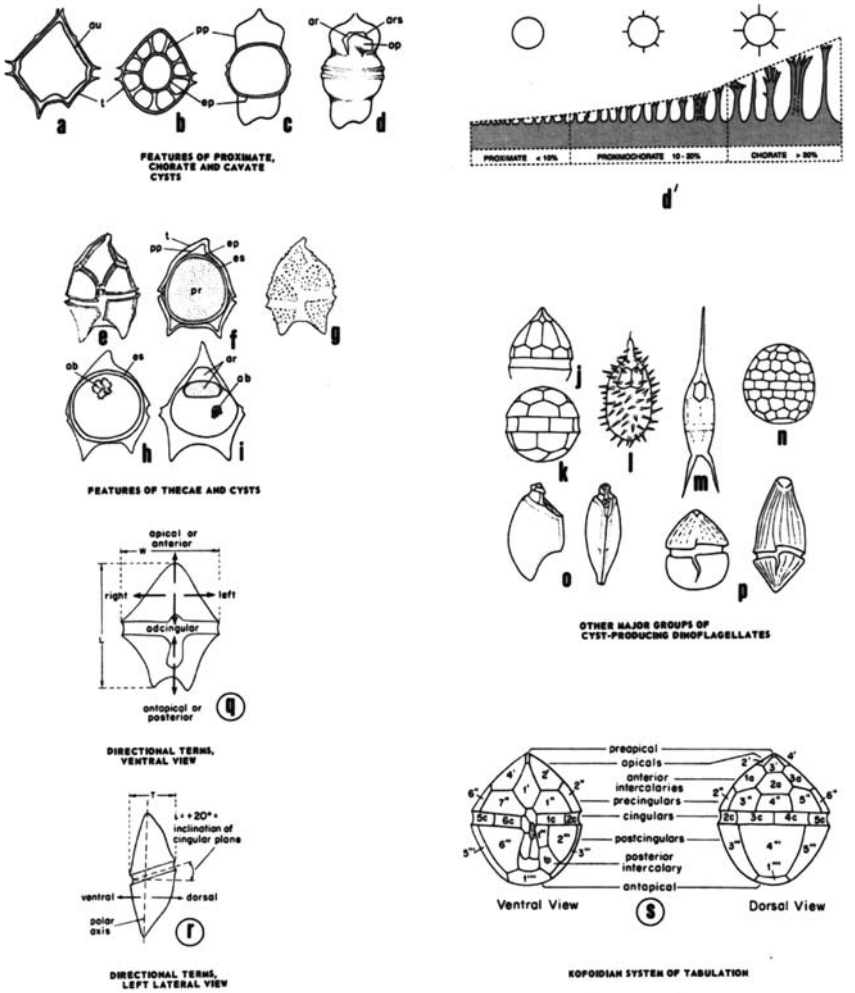


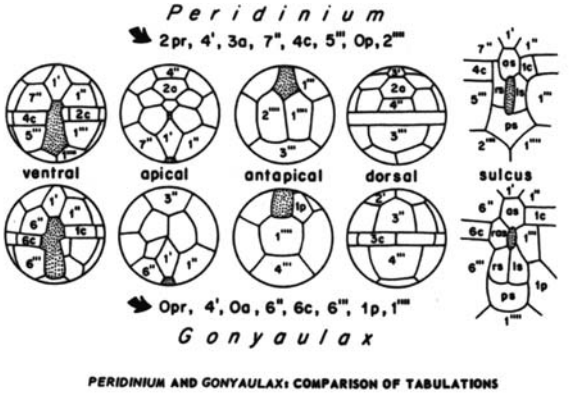
Figure 12.6 More about basic features of dinoflagellate morphology, with special reference to cysts. (**a**) Longitudinal section of a proximate cyst (resistant wall = au, autocyst), which fills the theca (t), inside of which it was formed. Note that the theca would not be found with the cyst in nature, as the theca would have been shed. (**b**) Section, as in (a), of chorate cyst, the contracted body of which is separated from the theca (t) by hollow processes (outer wall = pp, periphragm; inner wall = ep, endophragm). Note that the theca would not be so attached in nature, as it would have been shed. (**c,d**) Cavate cyst with theca shed, in longitudinal section (**c**) and dorsal exterior view (**d**). Periphragm (pp) and endophragm are separated at each end but are appressed in the mid-section. A polygonal archeopyle (ar) opens through the periphragm. The operculum (op) is flap-like and adnate because the suture (ars) is incomplete (see Fig. 19.5). Evidence of the previous thecal tabulation is seen only in the archeopyle and the paracingulum. (**d'**) Explanation

The theca, or motile "normal" dinoflagellate, of the kind that makes palynomorph cysts, has a wall of cellulose, organized into a series of plates (see Figs. 12.5 and 12.6). The theca normally has a ventral furrow or sulcus with a flagellum in it. A more or less equatorial encircling transverse furrow (= cingulum) contains another flagellum.

All of this is more or less irrelevant to paleopalynology because thecae apparently do not occur at all, or hardly at all, as fossils. Fossil dinoflagellates are cysts or "dinocysts" (a nickname not popular with some dinoflagellate experts). Some investigators of dinoflagellate cysts call the parts of cysts by terms similar to those used for thecae, but append the prefix "para . . .," yielding terms such as paraplate, parasulcus, etc., unless the term itself could only refer to a cyst (such as "archeopyle"). This seems to me an unnecessary complication to what is already complicated enough, but many specialists find it helpful and informative (see Fig. 12.5). The cyst is not merely formed by dinoflagellates to survive bad times (though this is perhaps an important matter), but is an essential part of the life cycle. Most encysting dinoflagellates today are marine, but some are brackish-water forms and a few are freshwater forms.

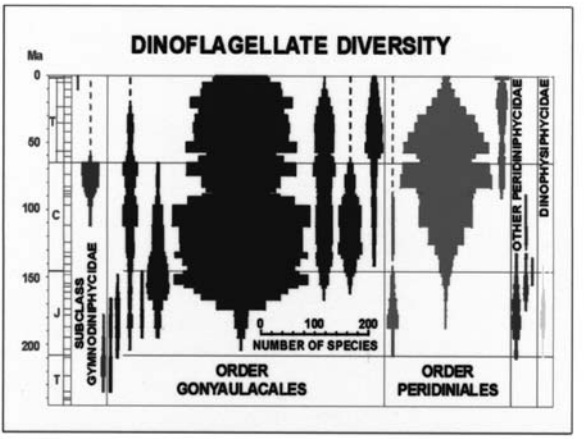
Figure 12.6 of the terms proximate, proximochorate and chorate for cysts, based on process length as a percentage of the shortest diameter of the central body. Compare with illustrations (a) and (b). (**e**)-(**h**) *Peridinium limbatum*, an extant freshwater species whose theca (**e**) shows plates separated by striate intercalary bands, whereas the cyst (**g**) shows the plates marked by sculptural fields, and the intercalary bands are represented by smooth strips. (**f**) An optical section of an encysted specimen, with theca (t) and two resistant layers of cyst wall (pp and ep), plus non-resistant contents, endospore (es) and protoplast (pr); other symbols as for (a)-(d). (**h**) Section of cyst (see (f)) showing accumulation body (ab)–these are also known as "eye-spots" and by other terms–probably metabolic wastes, found in both fossil and living cysts. (**i**) Fossil cyst of *Cerodinium* sp., with endophragm (stippled) showing through the archeopyle (ar). (j-p) Various fossil dinoflagellates not referable to modern peridinioid or gonyaulacoid groups: (j)-(m) Dorsal views, showing large anterior intercalaries with characteristic knee-like points toward the cingulum: (**j**) *Rhaetogonyaulax* (late Triassic), (**k**) *Dapcodinium* (late Triassic-early Jurassic), (**l**) *Gochteodinia* (late Jurassic-early Cretaceous), (**m**) *Broomea* (late Jurassic); (**n**) *Suessia* (late Triassic), schematic dorsal view showing the numerous paraplates; (**o**) *Nannoceratopsis* (Jurassic) in right lateral and ventral views–tabulation is peridinialean only in the epicyst, and the hypocyst consists of just two large and two small paraplates; (**p**) *Dinogymnium* (late Cretaceous), ventral views of two examples, showing lack of paraplates in the resistant-walled test. This could represent a cell-covering of the motile stage. (**q**) Directional terms, ventral view (L = length, W = width); adcingular = toward the cingulum. (**r**) Directional terms, left lateral view (T = thickness). (**s**) Tabulation (arrangement of plates) per the numbering scheme of Kofoid (see also Fig. 19.5). Drawings and explanations are from Evitt (1985), except for (d'), which is from Fensome, *et al*. (1996a). Fensome, *et al*. (1993) and (1996a) may be consulted for more information.

a



PERIDINIUM AND GONYAULAX: COMPARISON OF TABULATIONS

b



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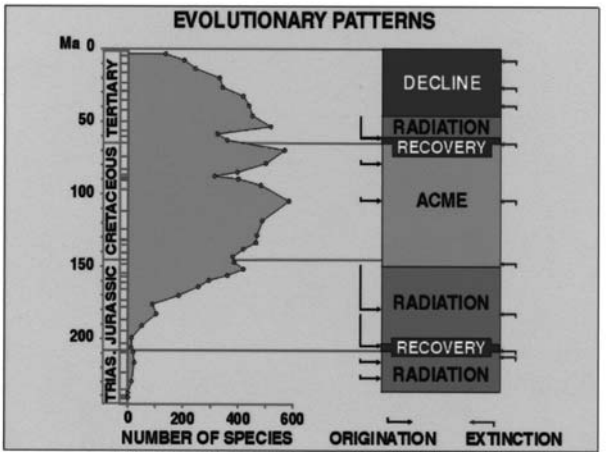

Figure 12.7 *(See caption on page 338)*

The cyst can be, for a one-celled shell, a very complex structure, reflecting the plate arrangement, etc., of the "parent" theca. On the other hand, some cysts, especially of freshwater and brackish-water forms, are more or less unadorned and uncomplicated "bags," affording only occasional glimpses of the presumed precursor thecal structures, such as plates. To prove that a fossil cyst was produced by a dinoflagellate, it is great if the tabulation (the arrangement of the plates), the sulcus and the cingulum can be observed. However, often in relatively featureless forms the one thing that is likely to save the day is the demonstration that the cyst has a true archeopyle, the place at which excystment occurs. To prove this, there must be a clear indication of the original plate boundaries of the piece of cyst wall that drops out for excystment, a trapdoor called the operculum. Without such indication of plate boundaries, the archeopyle could be the exit aperture ("pylome") of an acritarch. Note that detached operculae also consist of dinosporin and can and do occur frequently as palynomorphs. The part of the theca in which the sulcus occurs is the ventral part (see Fig. 12.6), and the section opposite it is the dorsal part (the "front" and "back"). The transverse furrow or cingulum separates two halves, the anterior and posterior (= episome and hyposome), which culminate in the apex and antapex, respectively. The plates are usually numbered for easy description in a scheme introduced by Kofoid in 1907 (see Fig. 12.6s). Note that not all the possible plate types exist in all

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Figure 12.7 (**a**) More about tabulation-notation (see Fig. 12.6s for basic Kofoid system). The two common types within the Peridiniphycidae: typical fossil peridinioid and typical fossil gonyaulacoid tabulation types. The arrows indicate the tabulation (= "paratabulation" for cysts) formulas, showing the number of plates in each series according to the Kofoidian scheme: 2 pr = two preapicals, Op = no posterior intercalaries. In the sulcal area, as = anterior sulcal, rs – right sulcal, ls = left sulcal, ps – posterior sulcal, ras = right anterior sulcal. The Kofoidian notation arbitrarily numbers plates in sequence as they are found, and a homologous plate may end up with quite different numbers in different species, if plates have been added by division. Dinoflagellate palynologists. nowadays mostly use the Kofoid notations with homolgous plates indicated by asterisks, recognized on the basis of standard gonyaulacoid and peridiniod patterns. Note that there have been other proposed systems for the numbering of dinocyst plates, but none of them is in wide usage.. See Fensome et al. (1993;1996a) for more information. (**b**) Graphic demonstration of the predominance of the Peridiniphycidae (Gonyaulacales plus Peridiniales) throughout dinoflagellate evolution as represented by resistant-walled cysts. The graph also shows clearly the important fact of dinocyst explosion in diversity following their first certain appearance in the Late Triassic, and their diminution in the Cenozoic (although gonyaulacacean cysts are still quite diverse), facts also shown in (**c**), underlining the acme abundance of dinocysts in the Late Jurassic and throughout the Cretaceous. The drawings in (a) are from Evitt (1985). (b) is modified from Fensome *et al.*, 1996b, per Fensome (pers. comm., 2005). (c) is from MacRae *et al*. (1996), modified per R. A. Fensome (pers. comm., 2005), from *Can. J. Bot.* **74**:1692.

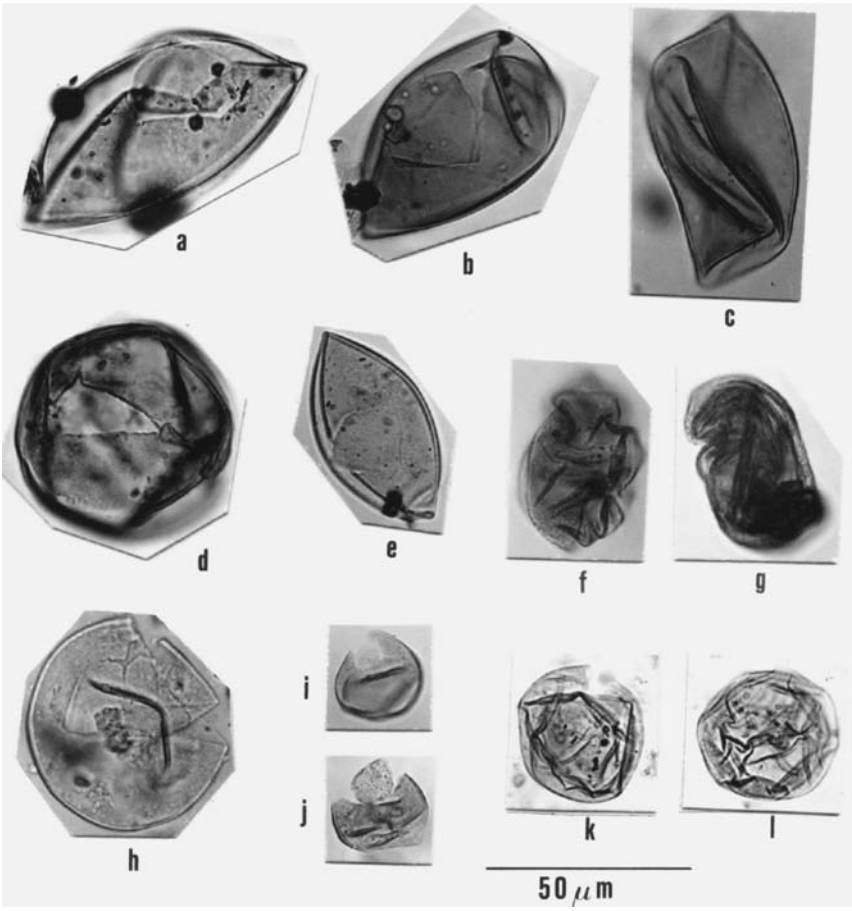

Figure 12.8 Students should not get the impression from neatly labeled diagrams and published dinoflagellate cyst photos that cysts are always easy to recognize as such! "Bag" dinoflagellate cysts of sorts encountered in great numbers at Neogene levels in cores of Black Sea sediment are shown here ((a)-(g) represent the most common kind, but are not necessarily one taxon). Thousands of specimens may be examined without finding even one with any evidence at all of plate boundaries. One might well identify the forms as P00 pollen grains. Then a level will be reached in which some specimens display obvious dinoflagellate archeopyles, mostly of the monoplacoid type. ((h), however, is polyplacoid), also showing principal and sometimes accessory ((d),(h)) sutures (see Fig. 12.9). An adherent operculum is sometimes present ((a),(b),(e),(h),(j)). Sometimes from association and shapes a good identification can be made as to which plate(s) the archeopyle represents, as 2", 3", 4" precingular plates for (h). However, systematic study, description, and later reidentification are very difficult with all of these forms. One should look for a typical specimen with good archeopyle features. In many samples in the Black Sea sediment most of the baggy cysts are folded ((a)-(c), (e)), and some are crumpled as

dinocysts. Fig. 19.5 gives more information about tabulation-notation, which is a complex business, with many new wrinkles added to the original Kofoid system.

The Kofoid system, however, continues to be used by a large majority of dinoflagellate palynologists. One modification to the Kofoid system, known as the Taylor-Evitt system, which assumes an ancestral gonyaulacod model (see Evitt, 1985), has been especially important in unraveling the homology of plates and patterns among dinoflagellates, although it is not specifically applied as such by most present dinocyst palynologists. The subject of dinocyst evolution, basic biology, and morphological detail has grown exponentially since the first edition of this book. Persons who wish to go beyond the very basic explanations of this chapter should consult more advanced works on the subject, such as Fensome *et al*. (1993;1996a).

Fig. 19.5 illustrates the tabulation for basic *Peridinium* and *Gonyaulax* dinocysts. The two genera are the name-bearers for the Peridiniales and the Gonyaulacales, which as can be seen in Fig. 19.5b totally dominate the history of fossil dinoflagellates, although there are other groups that make and have made cysts. We have no way of knowing whether the Peridiniphycidae, the group including the peridinaleans and gonyaulacaleans, really so dominated the dinoflagellate floras. We have only the cysts, and cyst-making dinoflagellates are a tiny fraction of the whole group.

Three principal kinds of dinocysts, based on gross morphology, are recognized (see Fig. 12.6):

(a) Chorate cysts, in which the cyst is beset with processes. The cyst develops within the theca and only the placement of processes, the ends of which formed in contact with the thecal wall, and the eventual operculum-archeopyle production recalls the original plate positions.
(b) Proximate cysts, in which the cyst forms directly within the thecal wall and has practically the same conformation as the theca. Special horns, when present, may show that there are, however, two cyst layers, the endophragm (from phragma, wall) and the periphragm. The plate

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Figure 12.8 well as folded together ((f),(g)). These latter may have been "processed" in animal guts to produce these folds. Without having seen a few specimens with archeopyles, these would be completely unrecognizable as dinoflagellates. Some very small "baggy" types are also commonly found ((i),(j)). (Dinoflagellate experts who have examined these specimens agree that the archeopyle is almost certain proof that these are small dinoflagellate cysts.) Other forms may be leiosphaerid acritarchs ((k),(l)), but even these occasionally give tantalizing hints that they too are really dinoflagellate cysts in very effective disguise.

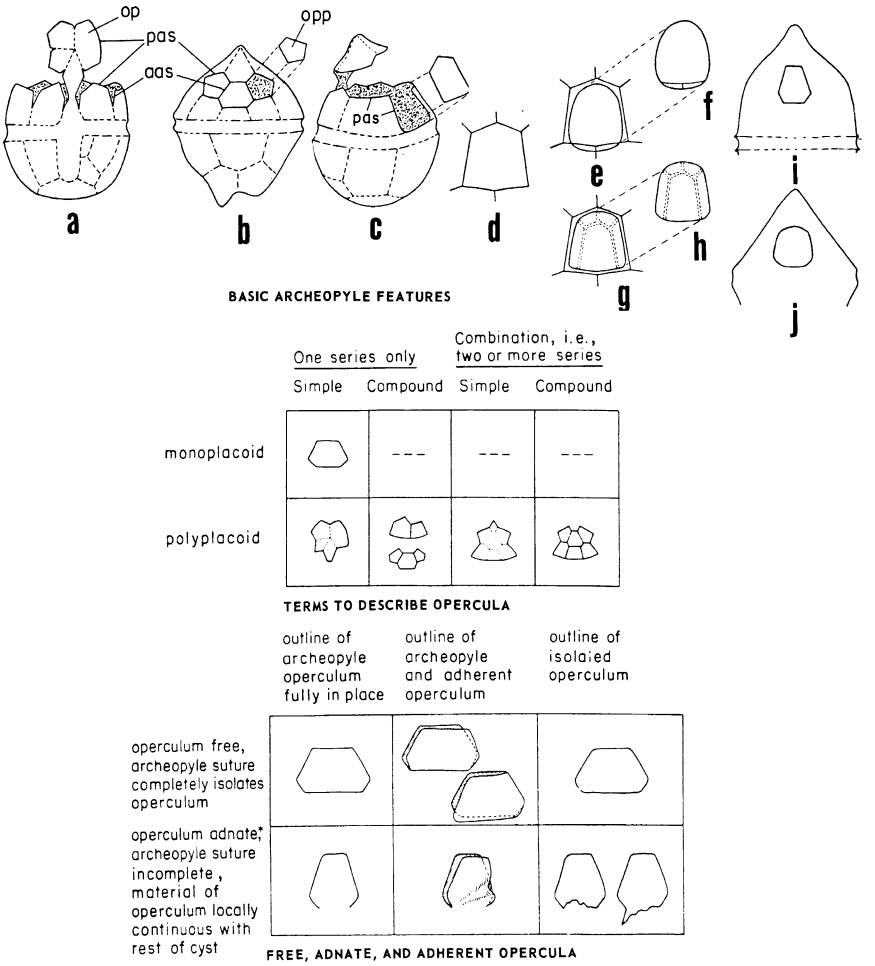

Figure 12.9 Dinoflagellate cyst archeopyle and operculum features and description. Archeopyles are the openings through which excystment occurs. In general, dinoflagellate cyst archeopyles are the "holes" left where opercula have been completely or partly removed. (As they are dinosporinous, free opercula are frequently found as fossils in dinoflagellate cyst-rich sediments.) In ((a)-(j)), aas = accessory archeopyle suture; pas = principal archeopyle suture; op = operculum; opp = opercular piece of compound operculum. (**a**) Apical archeopyle, ventrally adnate operculum (see term explanations in tables following). (**b**) Intercalary archeopyle with compound operculum divided by accessory sutures into three opercular pieces. (**c**) Combination archeopyle with compound operculum, apical portion polyplacoid and adnate. (**d**) Archeopyle and paraplate congruent. (**e**),(**f**) Archeopyle not congruent with paraplate. (**g**),(**h**) Reduced archeopyle involving paraplate, the surface of which bears accessory ridges related to overlap and growth of thecal plates (h is operculum). (**i-j**) Angularity of opening. In (**i**), shape and position

boundaries of the theca, plus archeopyle and other features, are usually clearly observable, at least in some specimens.

(c) Cavate cysts, in which there is a very clear separation between inner wall (endophragm) and periphragm, resulting in a thick-walled inner-body or endocyst. Where there are multiple layers such as this, terms are often used to designate the layers (see Fig. 12.6).

To these I would add in very informal fashion:

(d) "Baggy cysts" ("saccocysts"?), such as those shown in Fig. 12.8, in which relatively few specimens show any trace of plate boundaries. Occasionally specimens are found with an archeopyle showing some plate boundaries, which is enough to prove dinoflagellate relationship, but except for the plates associated with the archeopyle, even these specimens may demonstrate no plates. In many species the average specimen is thin-walled, and the collapsed cyst is folded, sometimes extremely so. Such cysts I found to be very abundant in some Neogene Black Sea sediments.

The nature of the archeopyle is very important to dinocyst classification. The principal features of archeopyles as described by Evitt are shown in Fig. 12.9. Evitt (1985) also presented a rather complex but useful classification of archeopyles, an archeopyle formula, based on numbered position of plates involved in archeopyle formation, such as type I for intercalary archeopyle, to which a prefix number showing the number of plates and subscript numbers indicating the specific plates involved may be added, such as $3P_{2\text{-}4}$. The basic archeopyle letters used are: A = apical; C = cingular; HA = antapical; HI = posterior intercalary; HP = postcingular; I = anterior intercalary; P = precingular; S = sulcal.

Triassic dinoflagellate cysts shown in Fig. 12.10 are considered primitive by most investigators. Some forms, such as *Suessia* (Fig. 12.10g,h) have very numerous small plates, so many plates that it is difficult to assign code-numbers to them according to the Kofoid scheme.

Fig. 12.10 also illustrates a variety of Jurassic dinoflagellates. The Jurassic represents the beginning of cyst-producing dinoflagellates' "finest hour"–the Jurassic/Cretaceous. (See also Fig. 12.6b. and c.) Dinoflagellates were then

Figure 12.9 of opening are sufficient to indicate equivalence of the archeopyle to paraplate 2a of a peridinioid cyst, even in the absence of other tabulation. In (**j**), the rounded opening does not indicate paraplate equivalence. Drawings from Evitt (1985).

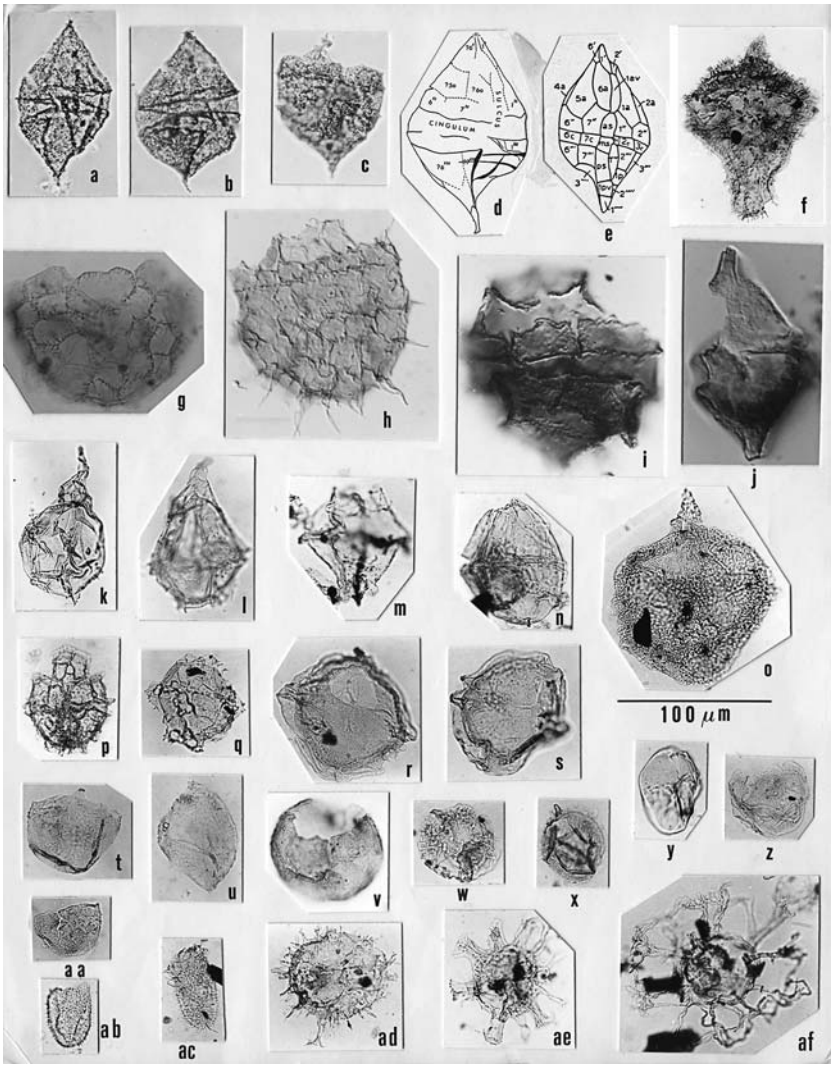

Figure 12.10 Late Triassic and Jurassic dinoflagellate cysts. Although Paleozoic dinoflagellate cysts have been reported, none of the claims has been substantiated. The known range of dinoflagellate cysts is late Triassic to present. The Triassic forms are somewhat unusual, in comparison to modern dinoflagellate cysts, but most of the Jurassic forms represent trends not greatly different from those of extant taxa. Magnifications for (k)-(af) shown by bar under (o); size for all others is given with their captions. (**a**)-(**e**) *Rhaetogonyaulax rhaetica* (Sarjeant) Loeblich & Loeblich, was, when described, the oldest known dinoflagellate cyst for which paratabulation could be demonstrated. (**a**)-(**c**) Specimens from the Rhaetian of England, length about 70 μm: (**a**) ventral view, showing the paracingulum and parasulcus; (**b**) obliquely ventral view; (**c**) cyst with the operculum of apical

evolving dramatically and therefore very useful stratigraphically, at a time when spores/pollen and other palynomorphs are at some levels difficult to use for fine stratigraphy. Plate 13.1 in the next chapter illustrates a group of Late Jurassic dinocysts to emphasize the richness of the dinocyst palynoflora in that time frame.

Figure 12.10 plates missing. (**d**),(**e**) Drawings of ventral views: (**d**) shows the paratabulation as directly discernible in a whole specimen; (**e**) is an interpretative reconstruction of the paratabulation from a similar view. (**f**)-(**j**) Dinoflagellate cysts from marine shales of late Triassic age, North Slope, Alaska: (**f**) *Sverdrupiella spinosa* Bujak & Fisher. $86 \times 78\,\mu$m. An oddly shaped spiny cavate cyst. (**g**) *Suessia* sp. $48\,\mu$m. The multiplate apically located archeopyle and the very numerous, somewhat irregular plates, are evident. (**h**) *Suessia* sp. $44 \times 41\,\mu$m ($+9\,\mu$m spines). Note the numerous plates as in (g), and the apically located archeopyle representing a number of epicystal paraplates. (**i**) *Dapcodinium* sp. Dorsal view showing the intercalary archeopyle. (**j**) *Shublikodinium arcticum* Wiggins, lateral view. The archeopyle in this cyst involves many of the apical, precingular and intercalary paraplates. In the picture, only some of these plates have been shed, others still adhere. (**k**)-(**af**) Cysts from Pliensbachian-Toarcian ("PT"), Bajocian-Callovian ("BC"), and Oxfordian-Kimmeridgian ("OK") levels in the marine Jurassic of East Greenland. (**k**) *Gonyaulacysta* sp. (OK). (**l**) *Gonyaulacysta jurassica* var. *longicornis* (OK). Dorsal view. Note precingular archeopyle. (**m**) *Atopodinium prostratum* Drugg (OK). (**n**) *Leptodinium* sp. (OK). Proximate cyst with clear indication of paratabulation, lateral view, archeopyle to the left. (**o**) *Acanthaulax scarburghensis* (Sarjeant) Lentin & Williams (OK). (**p**) *Meiourogonyaulax* sp. (OK). Ventral view, apical archeopyle. (**q**) *Scriniodinium* cf. *irregularis* (Cookson & Eisenack) Stover & Evitt (OK). (**r**) *Scriniodinium* cf. *playfordii* Cookson & Eisenack (OK). Cavate cyst, dorsal view showing precingular archeopyle. (**s**) *Scriniodinium crystallinum* (Deflandre) Klement (OK). Cavate cyst showing pericyst and endocyst walls very well. (**t**) *Mancodinium* sp. (PT), a cyst with an archeopyle involving the entire epicyst. (**u**) *Nannoceratopsis senex* van Helden (PT). (**v**) *Cassiculosphaeridia* sp. (OK), a cyst without much indication of paratabulation except in the area of the apical archeopyle where the paraplates are clearly demarcated. (**w**) *Stephanelytron redcliffense* Sarjeant (OK). The intricately interwoven processes reveal the tabulation. (**x**) *Kalyptea monoceras* Cookson & Eisenack (OK). (**y**) *Chytroeisphaeridia cerastes* Davey (BC), a relatively featureless cyst, but the precingular archeopyle leaves no doubt of its dinoflagellate affinity. (**z**) *Sentusidinium pelionense* Fensome (BC), a baggy cyst with clearly demarcated apical archeopyle. (**aa**) *Mancodinum semitabulatum* Morgenroth (PT), see (t). (**ab**) *Sentusidinium* sp. (OK), apical archeopyle. (**ac**) *Prolixosphaeridium* sp. (OK). (**ad**) cf. *Systematophora* sp. (OK), chorate cyst. (**ae**) *Compositosphaeridium costatum* (Davey & Williams) Dodekova (OK), chorate cyst with double walls of processes clearly shown. (**af**) *Rigaudella aemula* (Deflandre) Below (OK), chorate cyst with interconnecting processes, the outer limit of which indicates position of original thecal walls. (a)-(c) are courtesy of V. D. Wiggins; (d) and (e) are from Harland *et al.* (1975);(f)-(j) are courtesy of D. Wall; (k)-(af) are courtesy of K. R. Pedersen, originally published in Lund & Pedersen (1985).

It must be emphasized that dinoflagellate paleopalynology has expanded greatly since the publication of the first edition of this book and is now virtually a field of its own with little in common with sporomorph paleopalynology except that dinocysts from the marine realm and sporomorphs from land masses mix in marine sediments and together constitute the palynofloras that we study. Students should consult more detailed treatments of dinocyst-based paleopalynology such as that of Fensome *et al.* (1996a) or Fensome *et al.* (1993) to move beyond the basics presented here.

Chapter 13

Jurassic-Cretaceous Palynology: End of the "Mesophytic." Advent and Diversification of Angiosperms. Dynamic Evolution of Dinoflagellates

1 Introduction

As has been noted already, one of the main palynological stories for the post-Liassic part of the Jurassic has to do with bisaccate, mostly conifer pollen, which never, before or since, were so common. Many of them are large, 100 μm or more in length. As is true of bisaccates in general, these Jurassic Pv2s are very difficult taxonomically, and their classification can best be described as *ad hoc*. The classification of bisaccate pollen, later Triassic to Cretaceous, is badly in need of research. Spores, mostly of ferns, are also a very important part of non-marine Jurassic-Cretaceous palynofloras. A few of these forms from earliest Cretaceous are shown in Fig. 13.1.

A number of pollen types found in Jurassic palynofloras are interesting as possible harbingers of the angiosperm condition, the fully developed arrival of which marks the end of the "Mesophytic" and the beginning of the "Cenophytic." One such form already mentioned is the circumpolloid pollen, *Classopollis*. If it were not known that *Classopollis* was produced by several, at least partly very widespread, dominant conifer shrubs, one might perhaps suspect angiosperm

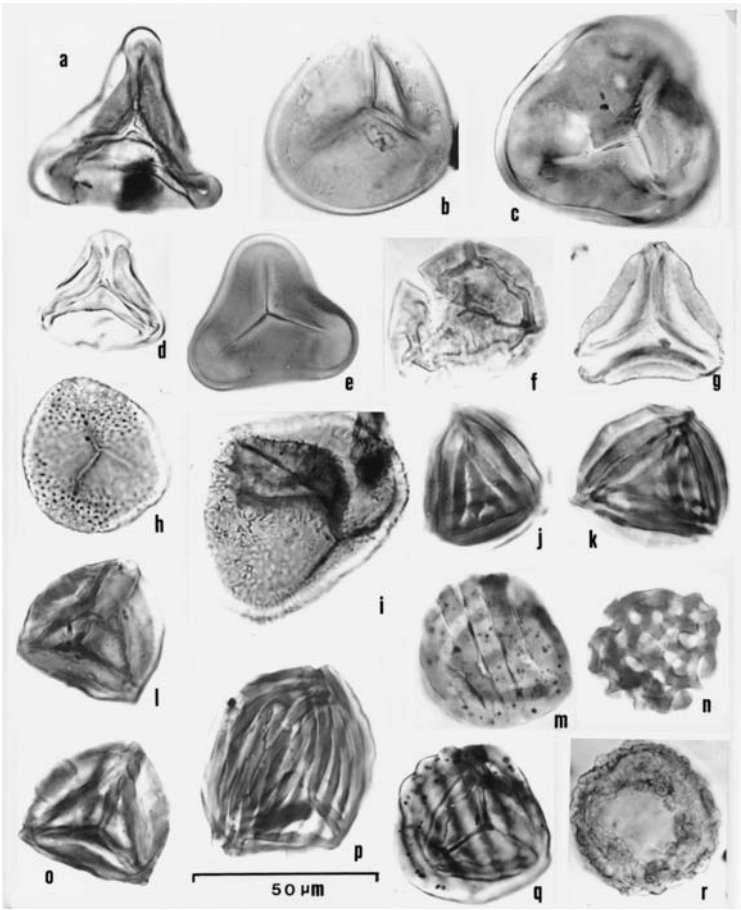

Figure 13.1 Typical earliest Cretaceous sporomorphs from the Hauterivian of Portugal: (**a**) *Auritulinisporites deltaformis* Burger; (**b**) *Dictyophyllidites equiexinus* (Couper) Dettmann; (**c**) *Deltoidospora germanica* Dörhöfer; (**d**) *Dictyophyllidites harrisii* Couper; (**e**) *Cardioangulina crassiparietalis* Döring; (**f**) *Coronatispora valdensis* (Couper) Dettmann; (**g**) *Gleicheniidites circiniidites* (Cookson) Brenner; (**h**) *Faveosporites subtriangularis* (Brenner) Döring; (**i**) *Pilosisporites* cf. *crassiangulatus* (Ivanova) Dörhöfer; (**j**) *Cicatricosispori tes* cf. *hannoverana* Dörhöfer, distal view (see also (k)); (**k**) *Cicatricosisporites* cf. *hannoverana* Dörhöfer, proximal view (see also (j)); (**l**) *Plicatella parviangulata* (Döring) Dörhöfer, distal view (see also (o)); (**m**) *Contignisporites cooksonii* (Balme) Dettmann, distal view (see also (q)); (**n**) *Ischyosporites pseudoreticulatus* (Couper) Döring; (**o**) *Plicatella parviangulata* (Döring) Dörhöfer, proximal view (see also (l)); (**p**) *Cicatricosisporites annulatus* Arch. & Gamerro; (**q**) *Contignisporites cooksonii* (Balme) Dettmann, proximal view (see also (m)); (**r**) *Cerebropollenites mesozoicus* (Couper) Nilsson. Scale shown by bar under (p). Photomicrographs provided and identified by J. Medus, originally illustrated in Medus (1983).

ancestry from the pollen. It displays columellate exines and a circumpolloid colpal-like feature (see Fig. 11.10). One could imagine such a pollen feature evolving into a primitive angiosperm colpus, as did the author of the name *Classopollis,* Pflug (1953).

Although *Classopollis* and the other circumpolloid forms are more typical of Late Triassic and Jurassic rocks almost worldwide, they persist to the end of the Cretaceous and even into the Paleogene, though one needs in the Cenozoic always to consider the possibility of reworking of the forms from older rocks into the Paleogene sediments.

Petrosyants and Bondarenko (1983) published an important summary of worldwide late occurrences of *Classopollis* and related forms.

Another angiosperm-suggesting form already mentioned is *Eucommiidites*, which has two subsidiary shorter colpi in addition to the sulcus-proper. As has been pointed out by Couper and others, the subsidiary colpi are not in the right position on the pollen grain for the dicot tricolpate condition. Hughes (1961) and Brenner (1967) found numerous, obviously intrinsic *Eucommiidites* pollen in gymnosperm seeds. Further, Doyle *et al.* (1975) showed that *Eucommiidites* has a thick, laminated endexine, a generally present gymnosperm character, whereas angiosperms lack laminated endexine, except sometimes in the apertural region. In addition, Friis and Pedersen (1996) published a pollen organ containing sporangia with *Eucommiidites* pollen. The characters of the pollen organ not only are non-angiospermous, but also are non-gnetalean, eliminating another suggested relationship for *Eucommiidites*. It is nevertheless interesting that such forms appear in the fossil record not too long before undoubted angiospermy arrives.

Cornet (1977a, 1989) has found a number of uncommon Triassic-Jurassic forms with multiple colpi and more or less syncolpate forms ("zonasulculate"; see Fig. 11.11) that sometimes have angiosperm-like, more or less columellate exines. More recently, Hochuli and Feist-Burkhardt (2004) have reported somewhat similar forms from the Norwegian Triassic. One should also mention in this connection the Triassic-Jurassic form *Pretricolpopollinites* (see Fig. 11.8), the multiple sulci (colpi?) of which are certainly "angiospermid." Of course, it should be noted that primitive angiosperm pollen probably was not multiaperturate but monosulcate, or perhaps l-syncolpate (zonasulculate), like some extant nymphaeaceous pollen. Another puzzle is that the Jurassic plants perhaps most like angiosperms are pteridosperms (?), the Caytoniales, the "fruits" of which are in fact, "angiospermous," that is, containing the seeds in a closed carpel. The pollen, however, is Pv2 (see Fig. 11.8). Could sacci somehow become colpi?

Crane (1985), however, used cladistic analysis to demonstrate that the angiosperms' closest relatives seem to be the Gnetales, which have almost no megafossil record. Two of the three extant genera make polyplicate pollen resembling forms found in the Jurassic and Triassic, however. Against the Gnetales having much to do with the origin of the angiosperms is the fact that the fossil

pollen is very gymnospermous, for example, with a thick and lamellate nexine (cf. Osborn *et al.*, 1993).

Palynological evidence contributing to the puzzle about where the angiosperms came from botanically is the find of *in situ* pollen of *Cycadioidea* by Osborn and Taylor (1995). The cycadeoids are the only group of gymnosperms that produce fructifications that are flower-like, with pollen organs, seed-bearing organs and sterile appendages. The pollen's infratectum is granular, and the nexine (endexine) is non-lamellate, characters that are angiosperm-like.

2 Origin of the Angiospermae

Toward the end of the Jurassic, pollen forms appear that are very likely angiospermous, based on exine characters, although the megafossil supporting evidence is still very slim. Sun *et al.* (1998) reported an angiosperm fruiting axis (unfortunately without flowers) from the Upper Jurassic of China, and Ren (1998) recorded fossil flies with angiosperm-adapted mouth parts from Upper Jurassic rocks of China. Labandeira (1998) accepted Ren's evidence and seconded the motion by pointing out that various Jurassic insects support in their structure the concept that flowering plants were already co-evolving with them, a concept that Crepet (1996) and Crepet *et al.* (1991) had also endorsed for later, Cretaceous time.

Several decades ago Kemp (1968), Laing (1976), Hughes *et al.* (1979), and Hughes (1984) found a number of pollen forms in the earliest Cretaceous of England with exines suggesting the characteristic columellate condition of angiosperm exines. Similar observations were later made in other parts of the world. *Clavatipollenites*, a monosulcate to trichotomosulcate pollen grain, sometimes has more or less free clavae in the ektexine, suggesting that lateral fusion of the clavae would produce a truly tectate columellate exine (see Fig. 13.2). Furthermore, it had long been hypothesized that a trichotomosulcate form could become tricolpate by simple projection of the "corners" of the three-cornered trichotomosulcate sulcus and "healing" of the distal side of the grain. Indeed, a tricolpate grain with exine structure-sculpture like *Clavatipollenites* does appear in the Aptian of England in sediments just above sediments containing *Clavatipollenites*. Such a form is *Tricolpites albiensis* Kemp (see Fig. 13.2). The *Clavatipollenites*-like tricolpate forms are joined worldwide in the Neocomian (see Fig. 13.2) by other primitive angiosperm monocolpate and tricolpate forms with just barely columellate exines. Fig. 13.2e from Doyle *et al.* (1977) shows that in equatorial areas of Africa the advent of protoangiosperm pollen is even earlier than at high latitudes, and involves more forms. Among the oldest such things as yet reported are tiny inaperturate and monosulcate forms from the Valanginian of Israel (Brenner, 1996). Brenner (1984) had earlier found monoaperturate and inaperturate probable angiospermous pollen in the Hauterivian of Israel at one

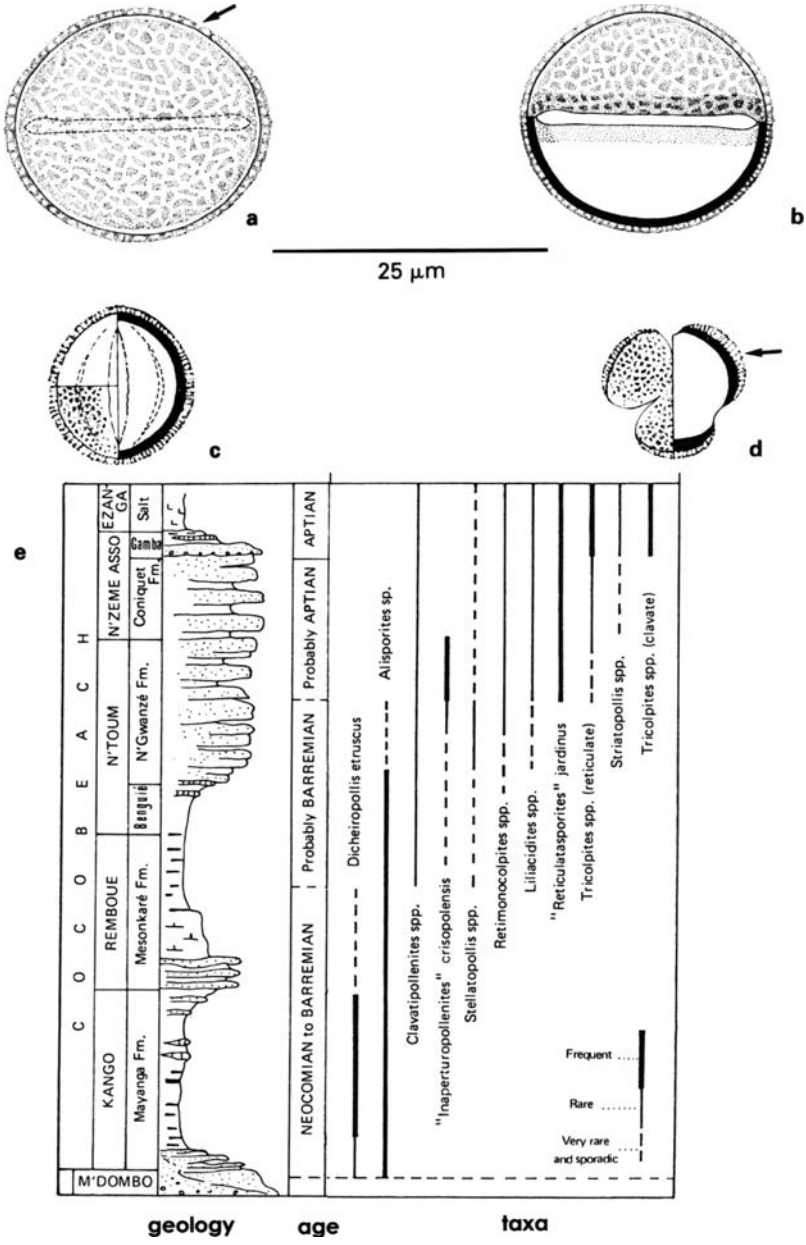

Figure 13.2 The "*Clavatipollenites* link" and the earliest appearance of angiosperm pollen. Kemp (1968) observed, in Barremian-Albian rocks of England, monosulcate pollen of the type pictured in (**a**) (proximal view) and (**b**) (distal view). This pollen type clearly has columellate structure (see arrow). The species illustrated is *Clavatipollenites rotundus*

locality, and Brenner (1996) also found tricolpates, monosulcates and monoporates in the Aptian of his Kokhav 2 Well in Israel. Fig. 13.3 illustrates some early protoangiosperm forms. Walker, Doyle, and others have shown that the evolution of the columellate angiosperm ektexine is the culmination of a long evolutionary process. Fig. 13.4 illustrates evolutionary trends in exine structures of gymnosperms and angiosperms.

As Le Thomas (1980-81) has emphasized, some of the *Clavatipollinites*-type pollen of the Lower Cretaceous lacked ektexinous columellae, having instead a granular exine. The arrival of the tricolpate condition is linked to the advent of a clearcut endexine-ektexine distinction in dicots, with a thin non-lamellar endexine typically present. (Gymnosperms typically have relatively thick lamellar (= laminated) endexine.)

Another illustration of the eudicot distinctiveness is that the endexine is not thickened under the apertures, whereas it is in monoaperturate forms. ("Eudicot" is a term introduced by Doyle and Hotton (1991) for angiosperms with pollen of Pc0-Pc3 type or some pollen form obviously derived from tricolpate morphology.) Both the peculiar colpal arrangement of most dicots and the complex exine structure of most angiosperms have undoubtedly to do with the reproductive processes that are critical to angiosperm success. The columellate exine provides a strong sporopollenin meshwork in the interstices of which a very complex set of organelles and compounds are dispersed (Rowley 1976, 1978, 1981). One function of some of these compounds is to provide sophisticated recognition mechanisms by which angiosperms are able to reject pollen-tube growth by unwanted pollen. The whole structural-chemical complex is clearly related to insect pollination, and the coevolution of insects and angiosperms is nowhere better illustrated than in palynology Friis *et al.* (1986) have shown that floral structures (including *in situ*

Figure 13.2 Kemp. In Albian samples from the same area, the tricolpate form, *Tricolpites albiensis* Kemp, shown in (**c**) (equatorial view) and (**d**) (polar view) occurs commonly. This tricolpate, obviously dicot, grain has the same sort of structure (arrow) as *C. rotundus*, and it is likely that it evolved from such a monosulcate–one possibility would be through an intermediate trichotomosulcate form, though this is very controversial. (**e**) The very early appearance of primitive angiosperm pollen in equatorial Africa is shown here, from the work of Doyle *et al.* (1977). *Dicheiropollis* (circumpolloid) and *Alisporites* (bisaccate) are conifer pollen. Tricolpate pollen appeared much earlier in equatorial Africa than in Laurasia. After the appearance of *Clavatipollenites* (in a broad sense) in late Neocomian time, a number of other pollen with columellate-type structure appear, so that before the Albian there was already a large range of angiosperm pollen present. Primitive angiosperm fossil pollen has also been found in the Hauterivian. Representation of types of sedimentary rock follows conventional usage: dotted patterns for sandstone, black bands for coal, block vertical line patterns for limestone, horizontal lines for shale, small circles for conglomerate. (a)-(d) rearranged from Kemp(1968), (e)rearranged from Doyle *et al.* (1977).

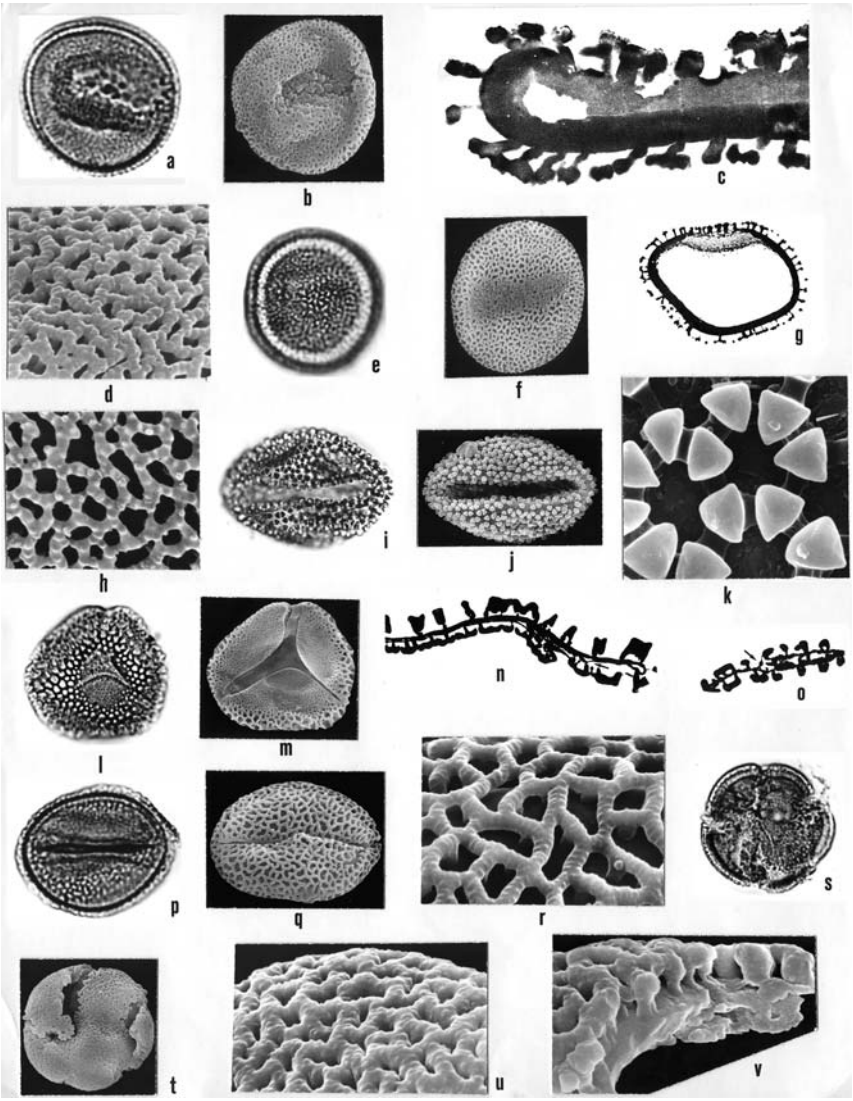

Figure 13.3 Early Cretaceous *Clavatipollenites* pollen and some of its friends and relatives. From the pioneering work of James W. and Audrey G. Walker we have learned many details of morphology of this ancestral angiosperm pollen form. Walker and Walker (1984) show that *Clavatipollenites* includes forms with two quite different pollen structures. *Clavatipollenites hughesii* Couper, illustrated here ((a)-(d)) has well developed endexine–but only in the apertural regions–and is tectate-columellate. Pollen of the living taxon *Ascarina diffusa* A. C. Smith (Chloranthaceae) ((e)-(h)) is

Figure 13.3 practically identical to *C. hughesii*, and there are other reasons for pinpointing this primitive angiosperm family as a living relic of the basal angiosperm at or near the ancestry of both monocots and dicots. Also shown are other key pollen types among the early Cretaceous angiosperms. *Clavatipollenites, Retimonocolpites* and *Liliacidites* are very difficult to limit in light microscopy, but do show differences in electron microscopy. (a)-(d) *Clavatipollenites hughesii* Couper, Barremian-Lower Aptian, Potomac Group, Maryland (maximum dimension of pollen 23 μm): (**a**) photomicrograph, distal view; (**b**) SEM micrograph, distal view, showing the sulcus and the reticulate exine organization; (**c**) TEM micrograph of whole grain section, with sulcus on top, showing its (lighter) endexine, and individual columellae with laterally fused heads; (**d**) SEM micrograph, much higher magnification than (b), with beaded muri. (e)-(h) *Ascarina diffusa* A. C. Smith, extant Chloranthaceae pollen for comparison with *C. hughesii* (maximum dimension 26 μm): (**e**) photomicrograph, distal view (see (a)); (**f**) SEM micrograph, distal view, showing sulcus (see (b)); (**g**) TEM micrograph, whole grain section, sulcus at top showing (lighter) endexine, and structure very like that of *C. hughesii* (see c); (**h**) SEM micrograph, much magnified, beaded muri as in (d). (i)-(k) *Stellatopollis barghoornii* Doyle, Albian, Potomac Group, Delaware (maximum dimension 53 μm): (**i**) photomicrograph, distal view showing the triangular-appearing sculptural units in linked groups–such sculpture is seen in extant members of the quite advanced genus *Croton* (Euphorbiaceae), presumably because of convergent evolution, hence "crotonoid" sculpturing; (**j**) SEM micrograph showing the same features as (i); (**k**) high-magnification SEM micrograph showing that the triangular exine blocks seen in (i) and (j) are mounted on an underlying reticulum with circular muri. (l)-(n) *Liliacidites* sp., Albian, Potomac Group, Delaware (maximum dimension 33 μm): (**l**) photomicrograph, proximal view, medium-high focus; (**m**) SEM micrograph, distal view, showing the trichotomosulcate morphology and reticulate sculpturing with larger pattern on proximal side; (**n**) TEM micrograph of whole grain section, sulcus showing on underneath of right side–the additional layer interpolated here is endexine (arrow). (o)-(r) *Retimonocolpites dividuus* Pierce, Albian, Potomac Group, Delaware (maximum dimension 30 μm): (**o**) TEM micrograph, one side of whole grain section, showing infolding (arrow) presumably the same as seen at edge of sulcus in (p) and (q); (**p**) photomicrograph, distal view–the apparent thick-bordered sulcus is due to infolding of the exine; (**q**) SEM micrograph, distal view, showing sulcus with tucked-in edge, and reticulate sculpture; (**r**) SEM micrograph, high magnification, showing the corrugated band structure. (s)-(v) "*Stephanocolpites*" *frederickburgensis* Hedlund & Norris, Albian, Potomac Group, Oklahoma (maximum dimension 28 μm) (quotation marks refer to fact that the generic name commonly used for this form is illegitimate): (**s**) photomicrograph, polar view; (**t**) SEM micrograph, polar view showing the irregular colpal margins; (**u**) SEM micrograph, much higher magnification, showing that the densely organized reticulate-type sculpture is actually perforate (foveolate) because the perforations are far less than 50% of the surface–the exine is very thick, as demonstrated in SEM micrograph of broken edge of grain in (**v**), with apertural region to the right. All photomicrographs and electron micrographs provided by James W. and Audrey A. Walker. They appeared originally in Walker and Walker (1984).

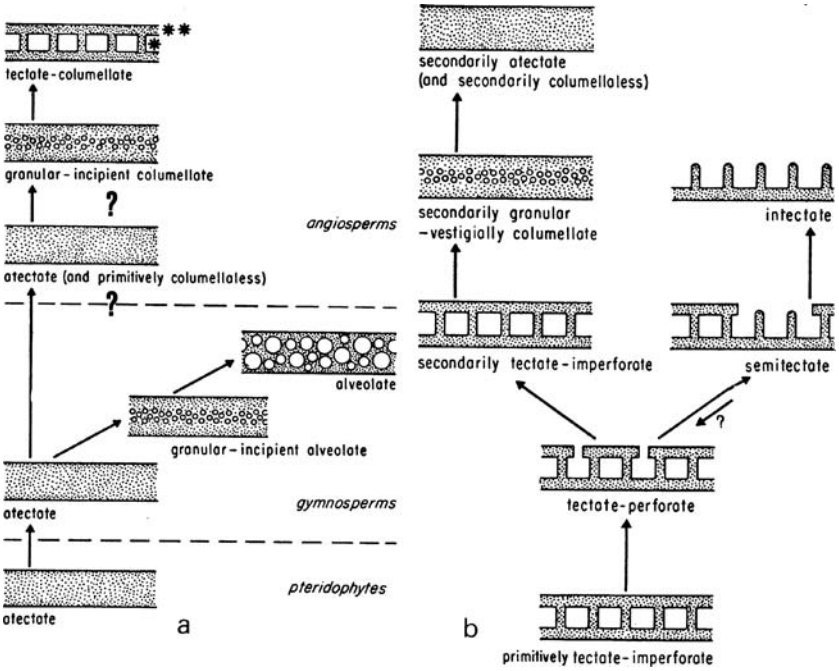

Figure 13.4 Evolutionary trends in outer exine (sexine or ektexine) structure. (**a**) Trends in vascular plants generally. Tectate sexine is always columellate because it is the columellae (single asterisk, upper left) which produce the extra "roof" or tectum (two asterisks). The "bubbly" (alveolate) outer exine of gymnosperms usually overlies a laminated nexine (not shown), whereas angiosperms have a non-laminated nexine or may have no nexine, or nexine only for part of the exine. (**b**) Trends in angiosperm pollen. "Intectate" refers to the presence of some indication of columellae but no tectum, whereas "atectate" refers to the total absence of columellae. Columellate pollen is the characteristic angiosperm condition, and even forms lacking columellae are mostly derived from forms that had them. However, the ancestral angiosperms in earliest Cretaceous time (see (a)) were only incipiently columellate and probably derived from atectate gymnosperms. The question-marks in (a) indicate uncertainty as to whether the line between angiosperms and gymnosperms should be put where shown by the brokenline or higher. It should be noted that Jurassic-Cretaceous or earlier pollen with columellae cannot be presumed to be either angiospermous or non-angiospermous on the basis of this feature alone. Diagrams modified from Walker (1976).

pollen) referable to the modern family Chloranthaceae (Magnoliales) were already present at least by Albian time. The pollen (see Fig. 13.3) is quite similar to pollen of the *Clavatipollenites* complex and seems clearly to have been insect-pollinated. *Archaefructus*, a megafossil fruiting axis from the Upper Jurassic of China was described by Sun *et al.* (1998) as having an assortment of magnoliid characters,

some that associate with the Magnoliaceae, but others more like Chloranthaceae. The mixture of features was noted by Crepet (1998) in stressing the significance of the Sun *et al.* discovery.

Other studies have also emphasized the significance of the connection of the Chloranthaceae with Early Cretaceous pollen forms such as *Clavatipollenites* spp. and *Asteropollis* spp. Unfortunately, *Archaefructus* lacks stamens and therefore pollen. The Chloranthaceae are a magnoliid group that includes trees, shrubs and herbs–itself interesting in terms of the plasticity and heterogeneity of that plant family.

Pedersen *et al.* (1991) showed that fruits from the mid-Cretaceous with associated *Clavatipollenites* pollen were probably referable to the Chloranthaceae. Archangelsky and Taylor (1993) described *Clavatipollenites* comparable to chloranthaceous pollen from fossil anthers of the early Aptian of Argentina. Herendeen *et al.* (1993) have described *Chloranthus*-like stamens from the Upper Cretaceous, with *in situ* pollen very similar to some of the Early Cretaceous angiosperm pollen referred to the Chloranthaceae. However, Crane *et al.* (1986) have shown that Albian sediments also contain flowers of non-magnoliid, higher angiosperms close to modern Platanaceae, probably bespeaking considerable pre-Albian evolution.

It is clear that we must be careful in assigning the earliest angiosperm pollen too rigorously to particular lines of evolution until and unless we have more information. Brenner (1996) points out that the oldest angiosperm pollen doesn't fit well into schemes for evolution of angiosperm pollen morphological types. The earliest forms are very small inaperaturates (P00) or monoaperturates (closer to P01 than to Pa0). Brenner suggests that the angiosperm apertures may have in part evolved de novo, rather than being derived from apertural types of the ancestral plants. He also suggests that his Valanginian forms are more like the pollen of Piperales herbs than they are like pollen of a woody magnoliid. In this connection, the paper by Poinar and Chambers (2005) on a flower perhaps referable to Monimiaceae from Myanmar amber at least as old as Albian is interesting: the associated pollen is inaperturate with striate exine.

With the arrival of undoubted tricolpate pollen, we can say with certainty that the "Cenophytic" has begun, and that is where I would now put the Mesophytic/Cenophytic boundary. However, some presumed "primitive" angiosperm forms, such as Magnoliaceae, have monosulcate pollen, and most monocots also have monosulcate pollen or some obvious derivative of Pa0, such as P01, Pac, or P00. Indeed, the monocots, if they have a common origin with the dicots, as usually assumed, probably diverged very early from them–most likely in the Jurassic. Based mostly on analysis of characters of modern monocot groups, but partly also on diversity of fossil monocots, Walker (1986) suggested that this group had a temperate, Northern Hemisphere (Laurasia) origin, in contrast to the dicots, which quite clearly arose in the tropics of the Southern Hemisphere (Gondwana). At least one family (Nymphaeaceae) of modern angiosperms is difficult to assign

definitively to either the dicots or monocots on the basis of pollen morphology, and another family (Annonaceae) retains apparently primitive characters such as weakly granular exine structure and distally sulcate pollen, which this family shares with the monocots (Le Thomas, 1980–81). Friis *et al.* (1997) describe angiosperm fruits from the Lower Cretaceous (*Anacostia*), which have associated Pa0/Pac pollen, indicating possible relationship to both extant magnoliids and extant monocots. Friis *et al.* (2001) assert that the Magnoliidae are in fact a paraphyletic (i.e., including some but not all the descendants of an ancestral form) basal grade of angiosperms in which the monophyletic (includes an ancestral species and all its descendants) monocots and eudicots are embedded. Friis *et al.* (2000b) showed that in Early Cretaceous of Portugal 85% of the angiosperms are magnoliids, and Friis *et al.* (2000a) describes monocolpate, probably alismatalean pollen of the same general source. Other publications by Friis and associates (Friis *et al.*, 1991, 1999) stress the relative abundance of monoaperturate pollen early and tricolpate forms later in the Cretaceous, with a trend from thicker endexine to thinner exine.. Friis *et al.* (2004) describe *Mayoa* and other araceous pollen forms from the Lower Cretaceous, illustrating the relatively early differentiation of the monocots from the ancestral angiosperm plexus, whereas eudicot forms are rare early and explode in diversity later. Frederiksen (1980b) has stressed that monosulcate pollen has never been a dominant pollen type, though produced by six different plant orders, the vegetative parts of which are frequently common as fossils. This could be a matter of pollination strategy. It is interesting in this connection that Friis *et al.* (1999) suggest that relative paucity of pollen diversity in some Early Cretaceous deposits, compared to mesofossil angiosperm diversity in the same deposits, may be due to the early angiosperms being mostly insect-pollinated.

The truth is that when the first irrefutable angiosperm exines appear in the fossil record, in Late Jurassic to earliest Cretaceous time, it is probably not appropriate to apply the classificatory schemes for modern angiosperms to them. It is comparable to trying to decide to which modern mammalian orders Triassic mammals should be referred. This is evident from Doyle and Hotton's (1991) cladistic studies of angiosperms and possibly related ancestral groups, in which comparatively short cladistic trees root in or near the woody Magnoliales, but almost equally well among herbaceous plants of the magnoliids and monocots.

Whatever it meant, the arrival of tricolpate (Pc0) pollen with columellate ektexine and non-lamellar endexine does provide a watershed. Doyle and Hotton (1991) suggested the term "eudicot" for the angiosperm line with such pollen or obviously tricolpate-derived forms, and the term is now widely used. Even molecular data support the monophyletic integrity of the group (E. M. Friis, 2005, personal communication; see also Soltis, *et al.*, 2005). Magallan *et al.* (1999) point out, in an important extensive review of the group, that 75% of extant angiosperm species are "eudicots," ranging from the Ranunculaceae to the Asteraceae. Brenner (1976) and others (Hickey and Doyle, 1977; see Fig. 13.5)

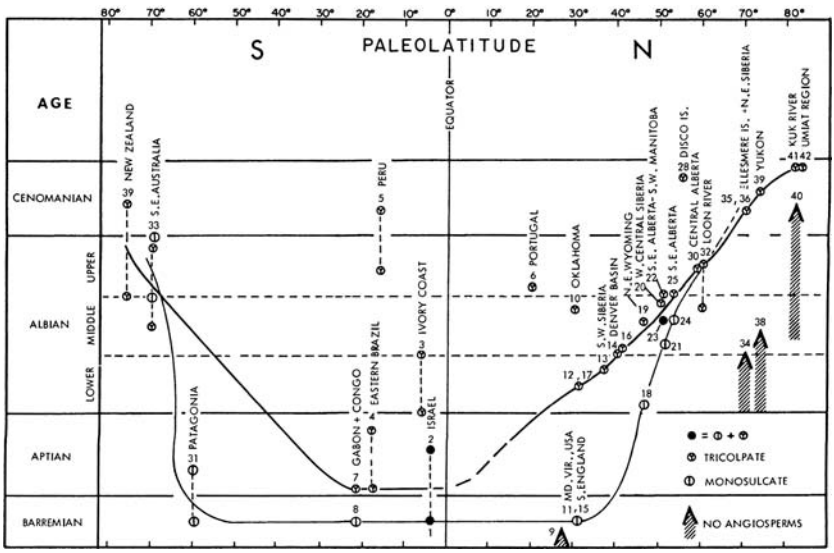

Figure 13.5 The angiosperms seem to have spread poleward from an equatorial or near-equatorial origin. This figure plots first occurrences of angiosperm pollen types. Note the poleward spread of tricolpates (all dicots), reaching high latitudes by Cenomanian time. Broken lines indicate a range where there is uncertainty about time of first appearances. Monosulcates (representing monocots and dicots) seem to have begun poleward migration before the tricolpates, which caught up later. Numbers associated with symbols refer to original publication-sources, of which there is a list in Hickey and Doyle (1977), which publication is the source of this diagram.

have shown that Pc0 pollen arrives first in equatorial, Southern Hemisphere areas in Barremian time; it reaches middle latitudes of the Northern Hemisphere in Aptian-Albian time and only penetrates to Arctic areas by the Cenomanian.

Crepet and Nixon (1998) suggested that Turonian (Upper Cretaceous) flowers which made prolate reticulate Pc3 pollen referable to the Clusiaceae that they studied, could show magnoliid roots on the one hand and connections with bee-pollinated plants of mainline eudicots on the other. Hickey and Doyle (1977) have shown from megafossil evidence that in the coastal plain of eastern North America the *Clavatipollenites-Tricolpites* sort of flux was coterminous with a complex of primitive angiosperm leaves suggesting a stream-margin pioneer flora, perhaps indicating that the angiosperms arrived at mid-latitude pre-adapted for marginal environments, perhaps where regular moisture supply is a problem or in marginal marine environments. Doyle *et al.* (1977) showed, for example, that even *Tricolpites* was present in west Africa by the Aptian (Fig. 13.2), and a complex of possible monosulcate, columellate precursors by Barremian or earlier. Burger (1981) shows possible spreading pathways for *Clavatipollenites*, tricolpates and

tricolporates, from usually equatorial or low- to middle-latitude origins. Others have ecological suggestions as to angiosperm origins, for example that they arose in coastal areas as mangrove-like plants (Retallack and Dilcher, 1981a), or as quick colonizers of coastal river levees (Retallack and Dilcher, 1981b). Heimhofer *et al.* (2005) theorize that once established in Barremian to Albian time, the angiosperms' rapid radiation, as evidenced by increase in diversity and abundance, was keyed to coordinated climatic changes. As to an ultimate or unified solution to Darwin's "abominable mystery" of the origin of the angiosperms–where and when– we still cannot make an authoritative pronouncement, although Crepet (1998) predicted solution of the mystery by the year 2008 (!–to paraphrase Caesar on Cassius, "such predictions are dangerous").

After the arrival of well authenticated angiosperms in the Neocomian, their subsequent history, of great significance to paleopalynology, is reasonably clear. Doyle, Muller and others have traced angiosperm (mostly dicot) pollen "evolution." It should be emphasized that it is the plants that evolve–pollen is only a single organ, representing one side of the haploid generation! However, Muller (1984) and others have called attention to the fact that mosaic evolution does occur in Cretaceous angiosperms–that is, pollen can evolve at different rates from other organs. Some peculiar combinations therefore occur, such as amentiferous (Amentiferae are all dicot shrubs and trees in the modern flora) inflorescences with monosulcate pollen (Dilcher, 1979)! As can be seen in Fig. 13.2, the first tricolpate pollen was small (less than 20 μm), and isodiametric. That is, the ratio of the pole-to-pole axis to the diameter at the equator is about 1. These are sometimes called "Longaxones." As can be seen in Fig. 13.6a, d-f-h, i, a trend to shortening of the polar axis was a very early development. Tricolporate (tricolporoidate) pollen appears in the late Albian.

Triporate forms, which are usually bowl- to disk-shaped, were well established at middle latitudes by Cenomanian time. In other words, "Brevaxones" forms, with a ratio of polar axis to diameter of 0.5 or so, had arrived. (Many extant angiosperms still have Longaxones pollen. Some are even perprolate, with a ratio of polar axis to diameter of 2 or more.) Possible patterns of evolution are displayed in Fig. 13.7. Angiosperms were already the dominant land plants worldwide by late Cenomanian time (see Fig. 13.8), demonstrating their unique competitive edge. All of the major morphological variants of angiosperm pollen had appeared by late Cretaceous time. By that time the unique pollination relationships between various insect groups (especially Lepidoptera and Hymenoptera) and the angiosperms were well developed. Stanton *et al.* (1986) suggest indeed that selective pressures may well have been in the direction of "male fitness"–that is, in attractiveness of flowers to pollinators. For example, the tricolporate form developed from the tricolpate, with intermediate tricolporoidate forms, apparently to provide a stronger "accordion pleat" for harmomegathic expansion and contraction, while retaining an efficiently thin area for germination. The conversion of many angiosperms to wind pollination is a secondary phenomenon, primarily of the Cenozoic. By the end of the Cretaceous many forms are already referable with some confidence

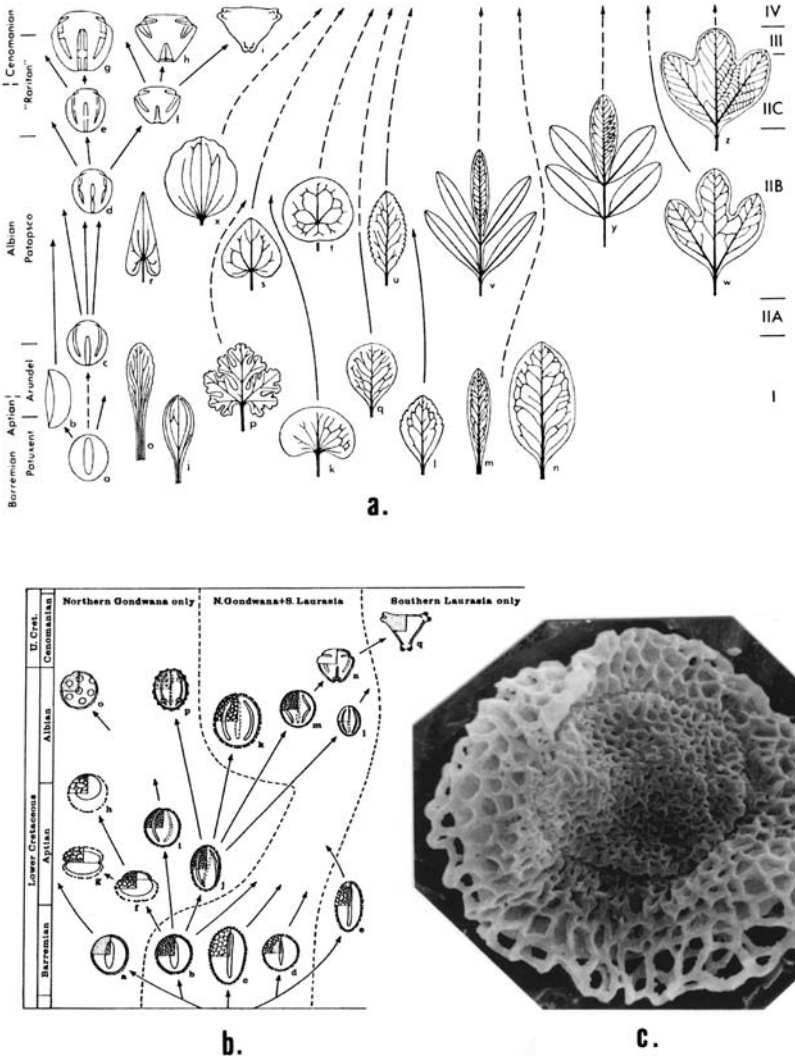

Figure 13.6 Adaptive radiation of angiosperms in about the middle of the Cretaceous (see Fig. 12.8: about ll5 to 90 million years ago). (**a**) The story from the Potomac Group of Maryland, eastern Coastal Plain, USA, and vicinity: the pollen picture on the left and the coordinate leaf fossil picture on the right. (From Doyle and Hickey, 1976.) "Patuxent," etc., at the left refer to the local lithologic units; I, IIA, etc., on the right refer to the pollen-based stratigraphic zonation (originally proposed by Brenner, 1963). Pollen types indicated: a, generalized tectate-columellar monosulcates (*Clavatipollenites, Retimonocolpites, Stellatopollis*); b, reticulate monocotyledonoid monosulcates (*Liliacidites*); c, reticulate to tectate tricolpates (*Tricolpites*); d, reticulate to tectate tricolporoidates (*Tricolpites, Tricolporoidites*); e, small, generally smooth-walled prolate tricolporoidates

to modern families (see Muller,1981). Supporting this referability to families is work on *in situ* pollen from Cretaceous angiosperm flowers, such as that of Friis and Skarby (1982), Friis (1985b), and Basinger and Dilcher (1984). For some monocot families, assignment to modern families is probably even possible for Early Cretaceous families, such as Alismataceae and Araceae (cf. Friis *et al.*, 2004).

3 Normapolles Pollen

An early divergence from the basic tricolpate form of dicot pollen was the development in Cenomanian time of the triporate (P03) condition, in which the germinal openings are more or less isodiametric pores (larger axis of opening less than two times the smaller axis), 120° apart, more or less on the equator of the grain. A variant on this theme was the development, also in the Cenomanian,

Figure 13.6 (*Tricolporoidites*); f, small, generally smooth-walled, oblate-triangular tricolporoidates (*Tricolporoidites, Perucipollis*); g, larger, smooth-walled to reticulate prolate tricolpor(oid)ates (*Tricolporopollenites*); h, larger, generally smooth-walled, oblate-triangular tricolpor(oid)ates (*Tricolporopollenites*); i, early members of the triangular triporate Normapolles complex (*Complexiopollis, Atlantopollis*). Leaf types indicated: j, acrodromous, narrowly obovate, monocotyledonoid (*Acaciaephyllum*); k, first rank, pinnately veined, reniform (*Proteaephyllum reniforme*); l, first rank, serrate (*Quercophyllum*); m, first rank, narrowly obovate (*Rogersia*); n, first rank, broadly elliptical (*Ficophyllum*); o, parallelodromous, elongate (*Plantaginopsis*); p, lobate reniform (*Vitiphyllum*); q, first rank, obovate (*Celastrophyllum*); r, campylodromous, sagittate (*Alismaphyllum*); s, actinodromous ovate-cordate-lobate ("*Populus*" *potomacensis, Populophyllum reniforme*); t, actinodromous, peltate (*Menispermites* "*tenuinervis*"); u, pinnately veined, serrate (*Celastrophyllum*); v, second rank, pinnatifid (*Sapindopsis magnifolia*); w, second rank, palinactinodromous, palmately lobed (*Araliaephyllum*); x, acrodromous, lobate elliptical (*Menispermites potomacensis*); y, third rank, pinnately compound, sometimes serrate (*Sapindopsis* spp.); z, third rank, palinactinodromous, palmately lobed (*Araliopsoides*, "*Sassafras*", etc.). (**b**) Development of most major dicot pollen types during Barremian to Cenomanian time (From Doyle, 1984). Forms appearing later in the Cretaceous presumably had their origins in one of the lines shown. Non-Normapolles triporates, for example, probably also derived from "n." Pollen types indicated: a, tectate-granular relatives of *Clavatipollenites*; b, *Clavatipollenites* and *Retimonocolpites*; c, *Stellatopollis*; d and e, *Liliacidites* spp.; f, *Afropollis operculatus*; g, *A. zonatus*; h, *A. jardinus*; i, monosulcate with extended sulcus; j, early tricolpate; k, large, sculptured tricolpate; l, small, smooth tricolpate; m, tricolporoidate; n, oblate-triangular tricolporate; o, polyforate; p, tricolpodiorate; q, early Normapolles. (**c**) *Afropollis operculatus* Doyle *et al.*, SEM, for comparison with types f-h to the left in (b), distal view, diameter of grain 34 um (from Doyle *et al.*, 1977). Others of the ancestral types are illustrated in Fig. 13.2. (a) illustrations and caption material from Doyle and Hickey (1976); (b) slightly revised from Doyle (1984); (c) SEM micrograph provided by J. A. Doyle, originally published in Doyle *et al.* (1977).

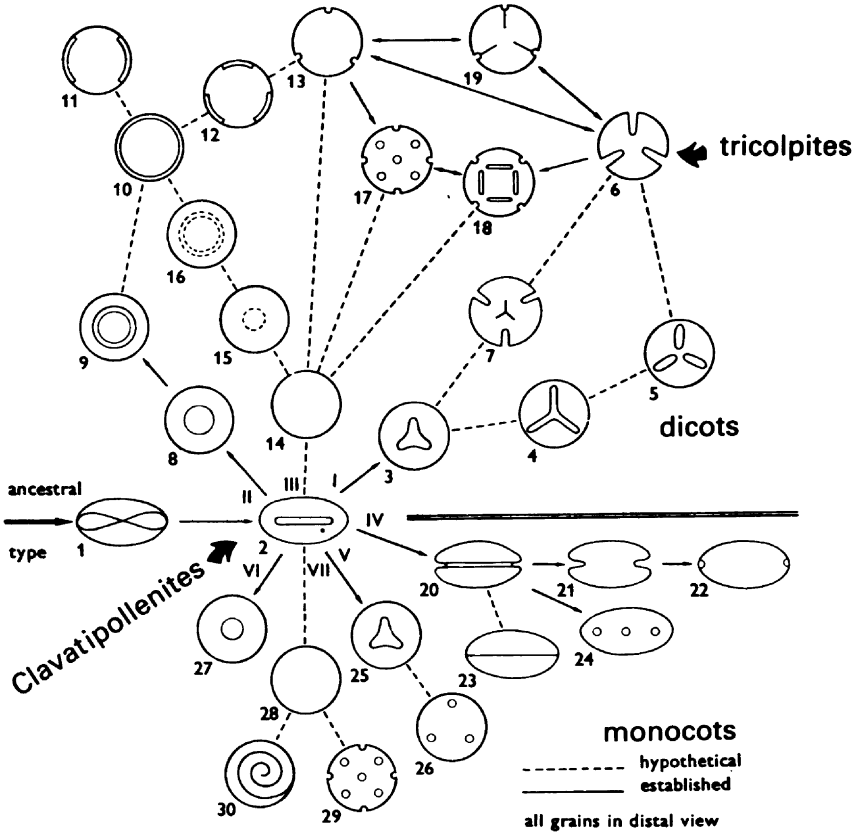

Figure 13.7 Probable paths for evolution of different aperture types in angiosperm pollen. The time frame for these developments is seen in Fig. 13.6. This scheme, proposed by Muller (1970), was mostly hypothetical, as shown by the dominance of broken lines, but later work has increased its plausibility. "Ancestral type 1" represents a cycad or ginkgoid monosulcate with the sulcus flared at the ends. Type "2" refers to the sort of sulcus shown by *Clavatipollenites* (and also made by palms and canellaceous dicots). The roman numerals I-VII refer to distinct trend lines in evolution. The other, arabic, numerals refer to specific pollen-morphological categories: (3,4) trichotomosulcate; (5) distally tricolpate; (6) tricolpate; (7) trichotomosulcate and tricolpate; (8) distally monoporate; (9) distally op erculate; (10) equatorially zonocolpate; (11) equatorially dicolpate; (12) equatorially tricolpate; (13) equatorially triporate; (14) inaperturate; (15) proximally monoporate; (16) proximally operculate; (17) periporate; (18) pericolpate; (19) tricolporate; (20) monosulcate; (21) dicolpate; (22) diporate; (23) meridionally zonocolpate; (24) distally meridionally triporate; (25) trichotomosulcate; (26) distally sub-equatorially triporate; (27) distally monoporate; (28) inaperturate; (29) periporate; (30) spiraperturate. This diagram originally appeared in Muller (1970).

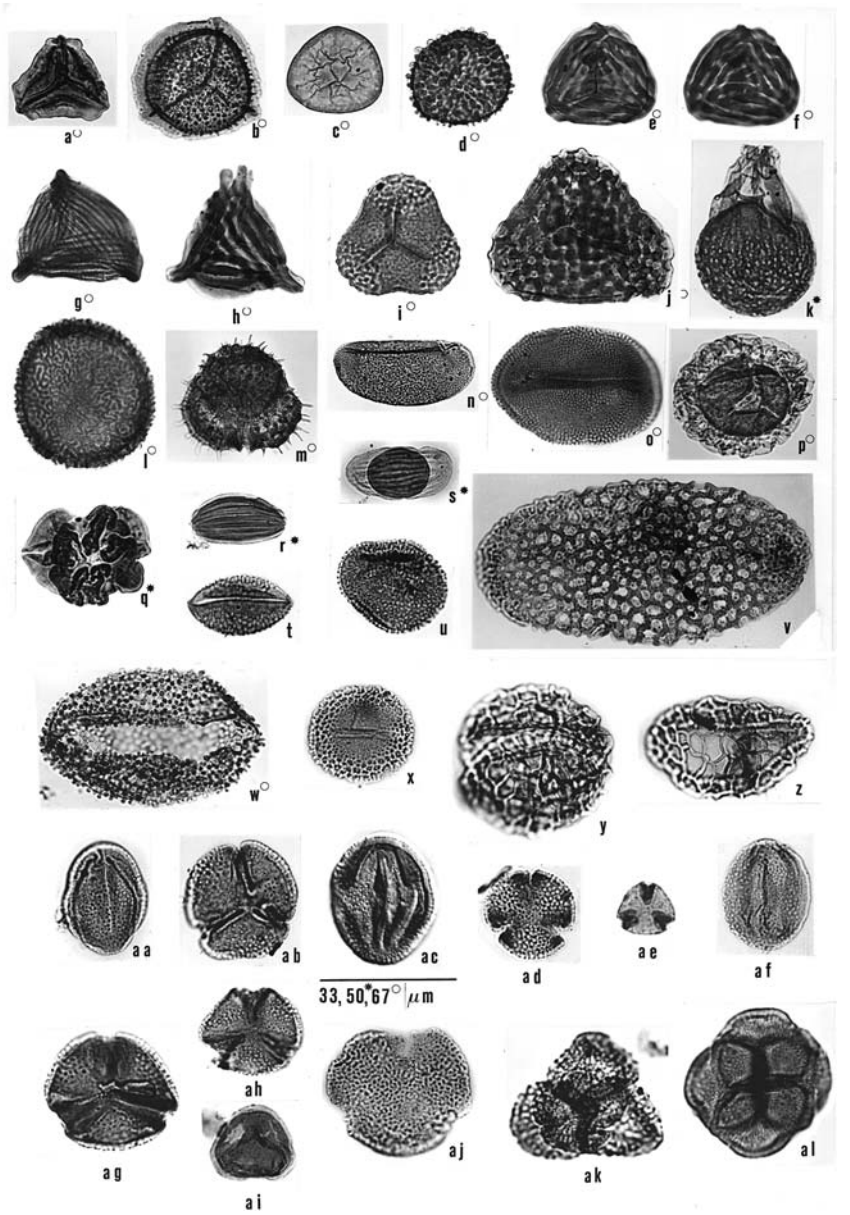

Figure 13.8 Early to middle Cenomanian (that is, about middle Cretaceous) spores/pollen from Peace River area, northwestern Alberta, Canada. Note that monosulcate forms (t-z) of rather primitive aspect and rather generalized tricolpate, tricolporoidate, and tricolporate forms (aa)-(aj), as well as obligate tetrads (ak),(al), have arrived in some abundance and diversity. Magnification is shown by line under (ac). (**a**) *Gleicheniidites*

of triporate (in a broad sense) pollen with internally complex pore structure (see Fig. 13.9). These are collectively called Normapolles. They diversified through the Cretaceous and remained, reduced in diversity, in the early Paleogene, but were much reduced by early Eocene (Batten, 1981b), and gone by early Oligocene (Hochuli, 1984).

Figure 13.8 *bolchovitinae* Döring, proximal view. (**b**) *Aequitriradites ornatus* Upshaw. Proximal view. (**c**) *Triporoletes cenomanianus* (Agasie) Srivastava. Distal view. (**d**) *Gemmatriletes clavatus* Brenner. Focused on distal surface. (**e**) *Cicatricosisporites crassiterminatus* Hedlund, Focused on proximal surface. (**f**) Same specimen as (e), distal view. (**g**) *Appendicisporites auritus* Agasie. Mid-focus. Proximal-distal view. (**h**) *Appendicisporites insignis* (Markova) Khlonova. Distal view. (**i**) *Trilobosporites purverulentus* (Verbitskaya) Dettmann. Proximal view. (**j**) *Cibotiidites arlii* Srivastava. Distal view. (**k**) *Crybelosporites bellus* C. Singh. Lateral view. This spore has a spherical inner body and a loosely fitting, cavate outer coat which is described by the non-committal term "sculptine." It is perhaps a perine. (**l**) *Rugulatisporites* sp. Distal view. (**m**) *Heliosporites kemensis* (Khlonova) Srivastava. Tetrad. (**n**) *Microfoveolatosporis pseudoreticulatus* (Hedlund) C. Singh. Proximo-lateral view. (**o**) *Reticulosporis foveolatus* (Pierce) Skarby. Proximal view. (**p**) *Crybelosporites pannuceus* (Brenner) Srivastava. Proximal view. See comments under (k). (**q**) *Rugubivesiculites multisaccus* C. Singh. Lateral view of unusual bisaccate grain. (**r**) *Equisetosporites fissuratus* Phillips & Felix. Mid-focus; (**s**) *Equisetosporites ambiguus* (Hedlund) C. Singh. Mid-focus. (**t**) *Liliacidites lenticularis* C. Singh. Distal view. (**u**) *Clavatipollenites tenellis* Phillips & Felix. Distal view. (**v**) *Liliacidites giganteus* C. Singh. Proximal view with heads of columellae showing as dark dots. (**w**) *Stellatopollis largissimus* C. Singh. Distal view. (**x**) *Liliacidites tectatus* C. Singh. Distal view. (**y**) *Dichastopollenites dunveganensis* C. Singh. Lateral view of this strange, apparently zonisulculate grain, of which the two halves separated by the encircling sulculus frequently break apart and are found as separate fossils. See (z). (**z**) A single half ("hemisphere") of the same taxon as illustrated in (y). (**aa**) *Fraxinoipollenites constrictus* (Pierce) Khlonova. Equatorial view. (**ab**) *Foveotricolporites callosus* C. Singh. Polar view. (**ac**) Same taxon as (ab), equatorial view. (**ad**) *Rousea doylei* C. Singh. Polar view. (**ae**) *Nyssapollenites nigricolpus* C. Singh. Polar view. (**af**) *Rousea candida* C. Singh. Equatorial view. (**ag**) *Foveotricolporites callosus* C. Singh. Polar view. (**ah**) *Retitricolporites pristinus* C. Singh. Polar view; (**ai**) *Phimopollenites tectatus* C. Singh. Polar view. (**aj**) *Phimopollenites megistus* C. Singh. Polar view. (**ak**) *Senectotetradites varireticulatus* Dettmann. Obligate tetrad. Polar view of central grain. (**al**) *Foveotetradites fistulosus* (Dettmann) C. Singh. Obligate tetrad, showing "pretzel contact figure." All grains showing are in lateral views. For (aa)-(aj), note that with the advent of tricolpate pollen, it becomes important to guard against classifying polar and equatorial views as different taxa! They look very different–see (ab) and (ac)–and the sculpture is a good key to linking them. Where possible, it is also desirable to examine the same specimen in different views by rotating it in a liquid mountant by tapping or pushing very gently on the coverslip, but fossil grains are almost always flattened, so tapping is seldom helpful. Tricolpate-tricolporate pollen is prevailingly flattened so as to produce polar views. Photomicrographs provided by Chaitanya Singh, in whose publication (1983) they originally appeared.

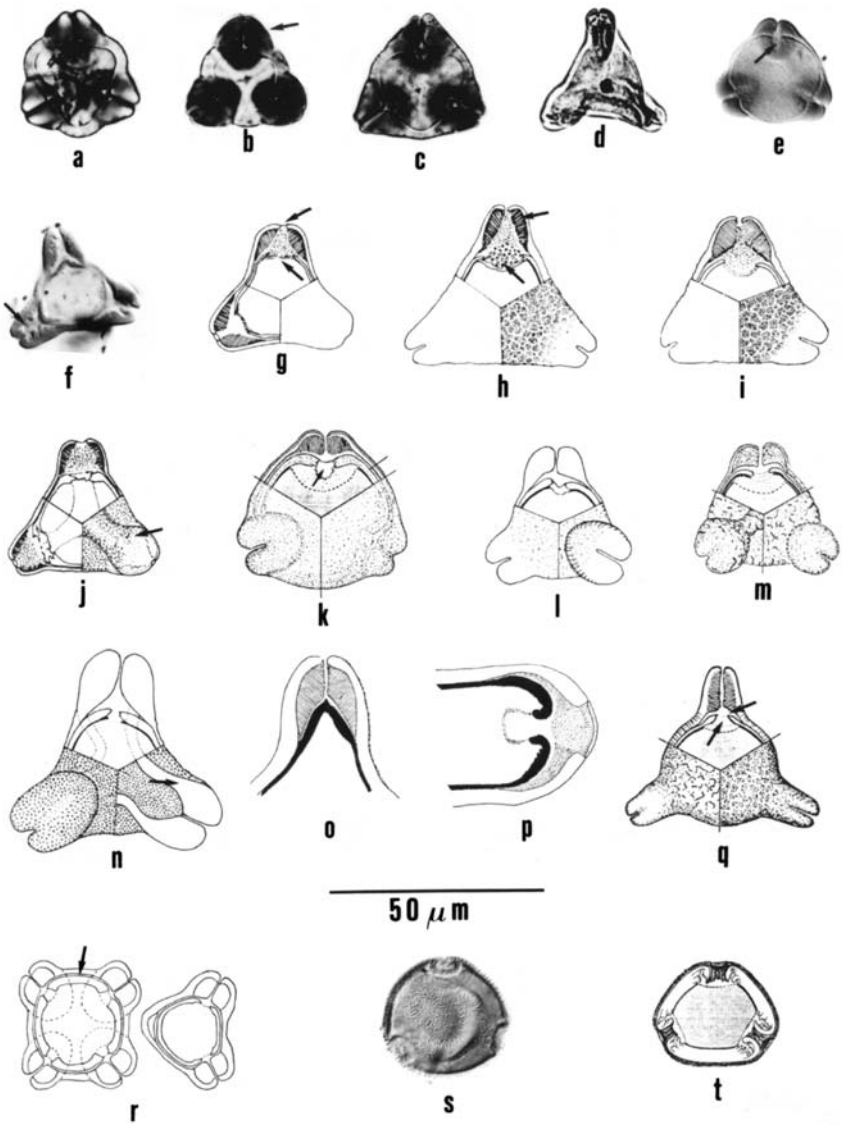

Figure 13.9 The Normapolles pollen group. This distinctive triporate pollen form characterizes the Normapolles palynofloral province of eastern North America and western Eurasia. The pore-structure (germinal) is internally complex and is difficult to illustrate photographically. Hence the popularity of line drawings for illustration of such structure. Normapolles first appears in about the middle of the Cretaceous and continues through the Paleocene into the Eocene. Magnification for the photomicrographs is indicated by bar under (o) and (p). The line drawings are at various magnifications, but the actual

Figure 13.9 size of the specimens drawn is comparable to that of the photographed specimens. (**a**) *Oculopollis orbicularis* Góczán, Senonian, Hungary. Mid-focus, showing the pore canals (see also (b)). (**b**) *Oculopollis orbicularis* Góczán, Senonian, Hungary. High focus, showing (arrow) the extraordinarily thick-walled oculus structures (**c**) *Oculopollis parvooculus* Góczán, Senonian, Hungary. Mid-focus as in (a). (**d**) *Complexiopollis vulgaris* (Groot & Groot) Groot & Krutzsch, Cenomanian, Spain. Mid-focus, showing complex internal pore structure. This is representative of the earliest Normapolles form. (**e**) *Trudopollis pertrudens* (Pflug) Pflug, Paleocene, Texas. Interference contrast photo, mid-focus, showing the oculus structures with prominent pore canal (arrow) (see also (k)). (**f**) *Basopollis basalis* (Thomson & Pflug) Pflug, Paleocene, Texas. Interference contrast photo, mid-focus showing the complex internal pore structure, a centripetally developed polyannulate annulus (arrow). (**g**) *Osculapollis aequalis* Tschudy, Campanian, Tennessee. Sections of drawing showing internal structure at different levels. The exine openings, which in Erdtman terms would be the pore (external) and os (internal), are shown by arrows. Normapolles experts usually call these openings germinals (exogerminal and endogerminal). (**h**) *Vacuopollis munitus* Tschudy, Maastrichtian, Missouri. Sections showing germinal structure and sculpture pattern. The endexine is two-layered. There are internal verrucae (lower arrow) in the atrium between inner and outer germinals. The upper arr ow points to the characteristic "baculate" structure of the wall of the vestibulum, a feature found in many Normapolles pollen. (**i**) *Extremipollis versatilis* Tschudy, Maastrichtian, Kentucky. Sectional view of germinal and surface view. Note baculate structure as in (h), but even more pronounced. (**j**) *Plicapollis retusus* Tschudy, Campanian, Tennessee. Sectional views and a surface view (lower right) showing the sculpture and a plica (arrow), a common Normapolles feature. (**k**) *Trudopollis pertrudens* (Pflug) Pflug, Paleocene, Germany. Optical section above showing prominent endogerminal (arrow) and surface features (left) and surface features reflecting internal structure (right) (see also (e)). (**l**) *Semioculopollis* sp., Maastrichtian, Tennessee. This has characteristic "oculi" (much thickened annuli) on one side of grain only. The slit-shaped exogerminals extend farther toward the poles on the side with the oculi. Lower right of drawing shows one side and lower left the obverse side. (**m**) *Pseudooculopollis principalis* (Weyland & Krieger) Krutzsch, Late Cretaceous, central Europe. Lower left and right show appearance of opposite sides of grain. Note plica on one side (see (j)). (**n**) *Pseudoculopollis* sp., Maastrictian, Tennessee. Oculus present on one side only. Arci (arrow) present only on side without oculi. Arci are thickenings similar to plicae, but arc-shaped. (**o**),(**p**) *Choanopollenites conspicuus* (Groot & Groot) Tschudy, Paleocene, Maryland: (o) the apertural region in polar view, (p) the same region in a sectional equatorial view. In (o) the densely packed baculae show very clearly. In (p) the exogerminal's opening appears funnel-shaped, though in polar view and surface expression it is a slit. The great difference of these two views of the same apertural area illustrates well the complexity of Normapolles morphology. (**q**) *Extratriporopollenites fractus* (Pflug) Pflug, Paleocene, Germany. This shows difference in sculpture on opposite sides of grain, atrium (lower arrow) and vestibulum (upper arrow). (**r**) As pointed out by Skarby (1968), many observed variations in basic Normapolles morphology are teratological ("freaks"): left, a 4-germinal form; right, a two-pored form. Extensive spaces between the outer and inner exine are a common feature of Normapolles, as shown here. The space (arrow) is called an interloculum. (**s**) *Thomsonipollis magnificus* (Thomson & Pflug)

Kedves (1983) noted that major trends in Normapolles evolution included decrease in number of exine layers and development of secondarily granular sexine from the columellate condition of the ancestral Brevaxones forms. Skarby (1968) has stressed the evident plasticity of this pollen.

4 Late Cretaceous Angiosperm Pollen and *Wodehouseia* and *Aquilapollenites*

Late Cretaceous terrestrial palynofloras are rich in forms unlike known modern angiosperm pollen, yet possessing features seen in various modern families. Fig. 13.10 illustrates some significant late Cretaceous pollen forms.

Two outstanding examples of late Cretaceous pollen which are clearly dicotyledonous but not referable to a modern group are *Wodehouseia* and *Aquilapollenites* (see Fig. 13.11). *Wodehouseia* is a loaf-shaped pollen grain with a very thick exine and four pores, two on either side of the grain. *Wodehouseia* and related forms such as *Azonia* have been collectively referred to as the *Oculata*-group (Wiggins, 1976; Takahashi, 1984). The group as a whole is mostly confined to the late Cretaceous, but *Wodehouseia* and *Aquilapollenites* species do get into the Paleocene. *Aquilapollenites* is a larger genus than *Wodehouseia*, with something like 80 species in the whole complex. Some palynologists, however (Takahashi, 1984), split the genus into a number of genera: *Triprojectus, Hemicorpus, Mancicorpus, Integricorpus, Bratzevaea*, and others (see Fig. 13.11). The group of genera, including *Aquilapollenites*, can be called "triprojectate" or the Triprojectacites-group. It is mostly a late Cretaceous group, but a few Triprojectacites occur in the Paleocene and even Eocene (Choi, 1983). Many variants on the basic theme exist, but that theme is a tricolporate grain in which the three colpi occupy the termini of branch-like extensions from the main body, which in turn has polar extensions. The three colpal and two polar extensions give the whole the appearance of the 6-pointed pieces in the old-fashioned child's game of "jacks," although the name comes from the Latin *aquila*, meaning eagle, suggesting bird-like appearance.

Figure 13.9 Krutzsch, Paleocene, Texas. Interference contrast photo. *Thomsonipollis* is a Cretaceous-Eocene form usually grouped with Normapolles forms because of the unusual, very complex, pore (germinal) construction. Whether *Thomsonipollis* really is related to Normapolles, however, is problematical. (**t**) Drawing of *Thomsonipollis* illustrating the multiple exine layers and the invagination of layers in connection with the germinal structure. (An important summary of Normapolles morphology is to be found in Batten and Christopher (1981).) (a)-(d) are from G. F. W. Herngreen, in whose paper (Herngreen and Chlonova, 1981) they were originally published; (e), (f) and (s) provided by D. J. Nichols; (g)- (j), (l) and (n) are from Tschudy (1973); (k), (m), (q), and (t) are from Góczán *et al.* (1967).

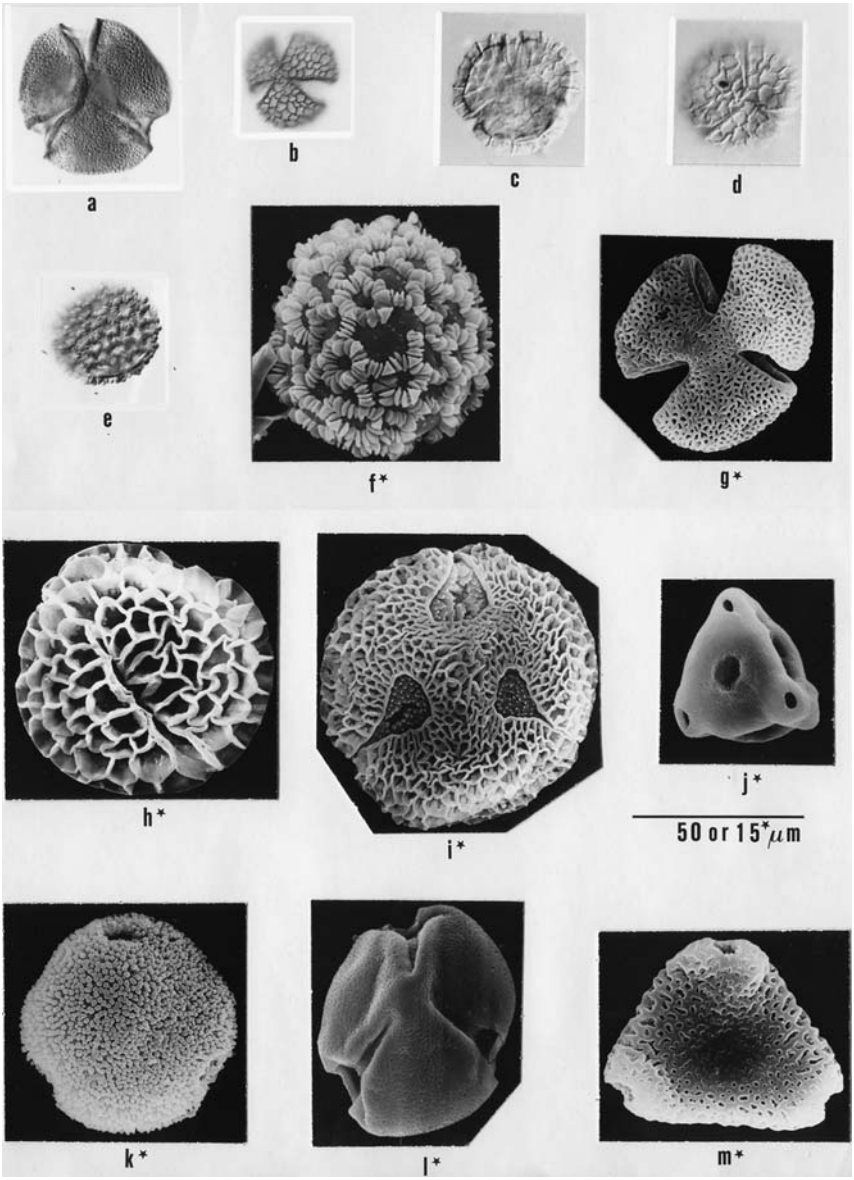

Figure 13.10 Illustrations of some significant late Cretaceous dicot pollen from Colorado, USA (a)-(e) Interference contrast photomicrographs; (f)-(m) SEM pictures. Magnification indicated by bar under (j). Magnification for SEM pictures is approximate. (**a**) *Tricolporopollenites* sp. Polar view. A very nearly syncolporate form with prominent colpal margos. (**b**) *Retitrescolpites* sp. Polar view. (**c**) *Retitrescolpites* sp. Polar view, mid-focus. (**d**) Same as (c). High focus. (**e**) *Erdtmanipollis pachysandroides* Krutzsch. (f) Same as

It has been suggested that *Aquilapollenites* was produced by the family Loranthaceae, which in the modern flora is mostly a parasitic family (mistletoe, for example). The form of the grains may well have made it buoyant in air, which would account for occasional finds of the grains far removed from the zones where it is typically abundant.

5 Cretaceous Palynofloral Provinces

Palynological provincialism has been noted throughout the Cretaceous, and is especially marked in the late Cretaceous. Batten (1984) points out that Cretaceous floral provincialism is a continuation of Jurassic trends, in which the Northern Hemisphere was already broadly divided into two paleofloristic realms, the Siberian-Canadian, and the Indo-European. The middle to late Cretaceous provinces are largely based on distinctive palynomorphs of restricted geographic and stratigraphic distribution, with broadly latitudinal boundaries.

Herngreen and Chlonova (1981) have published Neocomian through Senonian palynological provinces for the former USSR and vicinity; see Fig. 13.12 for their provinces for the early and late Cretaceous. One fact about provincialism long ago observed in the Northern Hemisphere is that palynofloras including Normapolles are found from mid-continent North America eastward to western Asia, whereas palynofloras including *Aquilapollenites* and *Wodehouseia* are found eastward from eastern Asia to central North America (see Fig. 13.12). However, isolated *Aquilapollenites* pollen grains are found in sediments from the Normapolles pollen province, suggesting that it may have been anemophilous.

Toward the polar regions, longitudinal precision is lost. Abundant *Aquilapollenites* occurs, for example, in the Eureka Sound Formation of Ellesmere Island, which is on about the same meridian as Maryland, well within the Normapolles province if defined meridionally. However, as Batten (1982) has shown, the *Aquilapollenites*-Normapolles zone boundaries may be more or less latitudinal in the North Atlantic area. Srivastava (1981) has also pointed out that the late Cretaceous vegetational zones based on pollen data were at least semi-latitudinal rather than meridional. (*Wodehouseia*, though much less common than *Aquilapollenites*, is found in the *Aquilapollenites* province.)

Figure 13.10 (e). SEM picture. (**g**) *Gunnera microreticulata* (Belsky *et al.*) Leffingwell. Polar view. (**h**) *Retitrescolpites* sp. Equatorial view. Compare with light pictures (c),(d) to see the advantages of SEM for interpretation of sculpture. (**i**) *Libopollis jarzenii* Farabee *et al.* Polar view. (**j**) *Interpollis sapplingensis* (Pflug) Krutzsch. Polar view. (**k**) *Thomsonipollis mangnificus* (Thomson & Pflug) Krutzsch. Polar view. (**l**) *Tricolporopollenites* sp. Polar view. (**m**) *Proteacidites* sp. Polar view. Photomicrographs and SEM micrographs provided by D. J. Nichols.

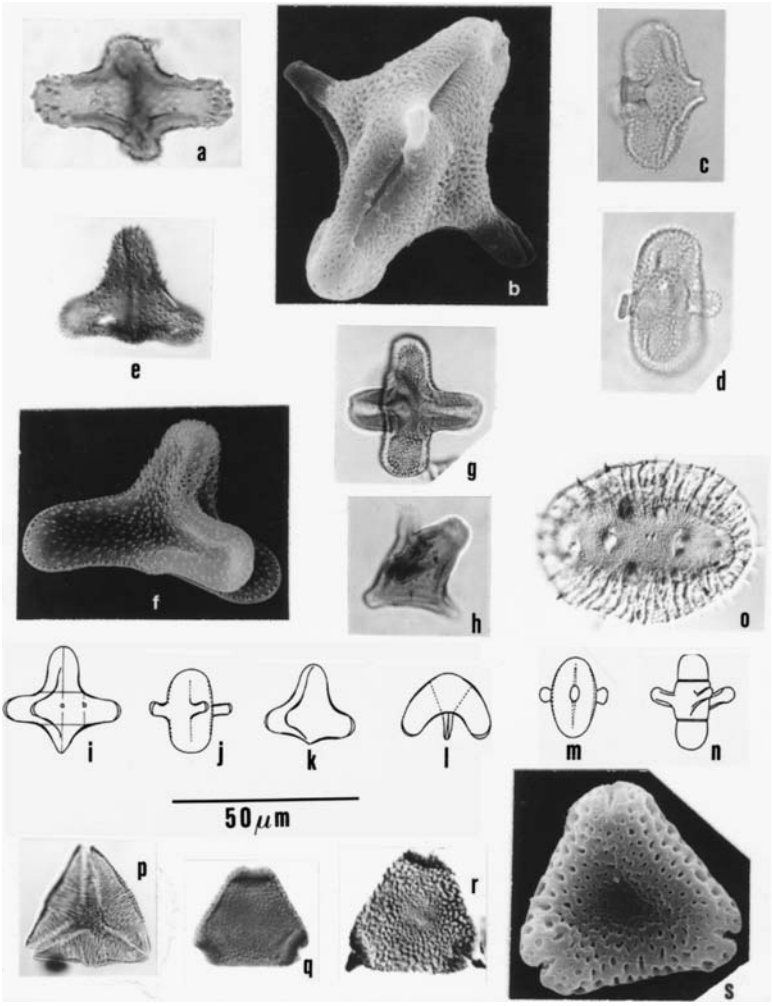

Figure 13.11 "Triprojectate" pollen and a few fellow travelers. The curious, mostly Cretaceous, characteristically multi-pronged pollen form, *Aquilapollenites*, is the form-genus which gives its name to the *Aquilapollenites* late Cretaceous palynofloral province. In a very broad sense, all of these pronged pollen could be shoe-horned into the single, original genus, *Aquilapollenite*s. Various other genera are usually recognized, but palynologists have not yet agreed on how many, or which ones. The whole group comprises the "triprojectate complex." (i)-(n) Line drawings from Takahashi & Shimono (1982), illustrating some of the triprojectate genera they recognize. The colpal apparatuses are located on the ends of each of the (usually three) lateral arms. Associated with *Aquilapollenites* spp. and other triprojectates in the *Aquilapollenites* palynofloral province are a number of other genera. Examples of three of these genera, *Wodehouseia, Cranwellia*, and

Nichols (1984) has noted that, within the *Aquilapollenites* province in western North America of late Cretaceous time, subprovinces can be delineated on the basis of taxa occurring with *Aquilapollenites*:

(1) *Expressipollis* subprovince (Arctic)
(2) *Callistopollenites* subprovince (Canadian plains)
(3) *Proteacidites retusus* subprovince (northern Rockies, USA)
(4) *Thomsonipollis magnificus* subprovince (southern Rockies, USA)

Wodehouseia spinata is associated also in subprovinces 1–3 but not in subprovince 4.

Brenner (1976) pointed out the existence of Cretaceous palynoflorally-based provinces in the Southern Hemisphere, e.g., a northern Gondwana province, and a southern Gondwana province, each with a distinctive palynoflora. Herngreen and

Figure 13.11 *Proteacidites*, are illustrated here. (**a**) *Aquilapollenites* sp Rouse, late Cretaceous, Canadian Arctic. Equatorial view. (**b**) *Aquilapollenites trialatus* Rouse, Maastrichtian, Colorado. SEM, oblique equatorial view, 35 μm. (**c**) *Triprojectus echinatus* Mchedlishvili, late Cretaceous, Canadian Arctic. Equatorial view. (**d**) Same as (c). Different specimen showing one of colpal arms in optical section. (**e**) *Aquilapollenites quadrilobus* Rouse, Maastrichtian, Utah. Equatorial view, interference contrast. See also (f). (**f**) *Aquilapollenites quadrilobus* Rouse, Maastrichtian, Colorado. SEM, equatorial view, 44 μm. See also (e). (**g**) *Aquilapollenites rigidus* Tschudy & Leopold, Campanian, Montana. Equatorial view. Note the thickenings in the colpal arms as seen in optical section. (**h**) *Integricorpus* sp., late Cretaceous, Canadian Arctic. Oblique equatorial view. The poles are in the upper right and lower left. The colpal arms, of which one is shown in the center of the grain, have pronounced costae. (**i**) *Aquilapollenites*. Equatorial view. The small "a" refers to the length of the polar axis, and "b" refers to the width (thickness) of the equatorial (colpal) projection. Takahashi and Shimono use the ratio a/b as a character in describing the genera (see (a),(b)). (**j**) *Triprojectus*. Equatorial view (see (c),(d)). (**k**) *Hemicorpus*. Equatorial view (see (e),(g)). (**l**) *Mancicorpus*. Obliquely polar view. (**m**) *Integricorpus*. Equatorial view (see (h)). (**n**) *Bratzevaea*. Equatorial view. (**o**) *Wodehouseia spinata* Stanley, Maastrichtian, Montana. Equatorial view. (**p**) *Cranwellia rumseyensis* Srivastava, Maastrichtian, Montana. Polar view. *Cranwellia* is believed by some to be related to the triprojectates. It is an important fellow traveller in any event. (**q**) *Proteacidites* sp., Maastrichtian, Colorado. Interference contrast, polar view. Note characteristic exinal thickenings associated with the pores (see (r)). (**r**) *Proteacidites* sp., Maastrichtian, Utah. Interference contrast, polar view (see (q)); (**s**) *Proteacidites* sp., Maastrichtian, Colorado. SEM picture, polar view, about 30 μm. Magnification for photomicrographs is shown by bar under (j) and (k). The line drawings are at various magnifications. For the SEM, the size for each grain is given with the listing. (b), (e)-(g), and (o)-(s) courtesy of D. J. Nichols, who also provided identifications and other information; (i)-(n) are from Takahashi and Shimono (1982).

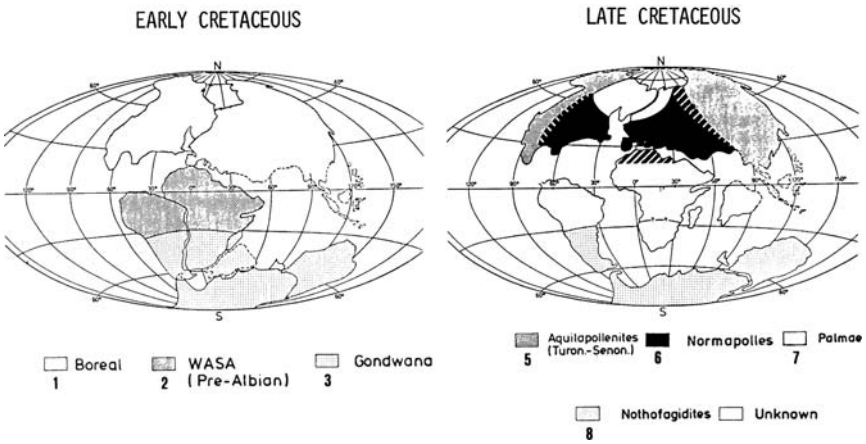

Figure 13.12 Cretaceous palynofloral provinces. See Figs. 13.13–13.15 for photomicrographs of examples of many of the characteristic sporomorphs. (Aquilapollenites, Normapolles and Nothofagidites provinces are not much illustrated there, because there are a number of illustrations of the pertinent forms in other figures.) Diagrams and information modified from Herngreen and Chlonova (1981). Note that Herngreen *et al.* (1996) have published considerably revised versions of Cretaceous palynofloral provinces generally and of these diagrams, especially for the Early Cretaceous.

Chlonova (1981) have summarized distribution data for a number of sporomorph taxa characterizing provinces from early to latest Cretaceous (see Fig. 13.12, and representative pollen forms in Figs. 13.13–13.15). The mid-Cretaceous ASA province is characterized by *Galeacornea, Afropollis* and various elater-bearing pollen, and other unusual forms. In this province the earliest pollen unquestionably referable to dicot angiosperms appears (see Livingstone and Van der Hammen, 1978). An important contribution to the *Afropollis*/Elatero-complex of the ASA flora was published by Schrank (2001). Srivastava (1983) has pointed out that, in latest Cretaceous time (Maastrichtian), there is mixing of elements from the previously distinct palynofloral provinces, caused by worldwide regression. Normapolles and *Aquilapollenites* producers, for example, were able to migrate to South America and Africa. Many of the significant early Cretaceous spore forms persisted for very long times, whereas the late Cretaceous pollen types were relatively short-lived, as is shown in Fig. 13.16. Nichols et al. (2006) have shown that some matters about angiosperm evolution, as reflected in the palynofloras, can be of critical importance in the dating of rocks worldwide. They were able to show from the presence of tricolporate (Pc3) pollen in rocks of Mongolia and China previously dated as early Cretaceous could not be older than early Cenomanian at the base of the Late Cretaceous.

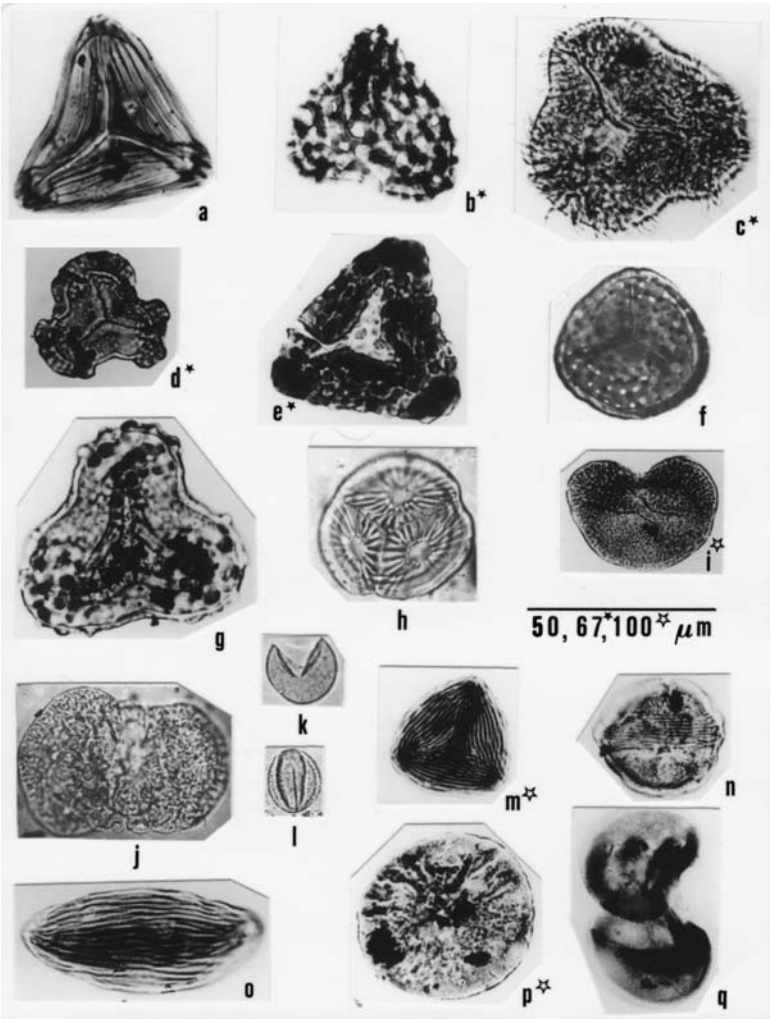

Figure 13.13 Pollen and spores characteristic of the early Cretaceous, Boreal palynofloral province ((a)-(l)), and of the pre-Albian early Cretaceous WASA (= West African-South American) province ((m)-(q)). See Fig. 13.12 for more information about the Cretaceous palynofloral provinces. (a)-(e), and (i) are from the Upper Jurassic to Lower Cretaceous of the Netherlands; (g) is from the Aptian of Germany; (f),(h), and (j)-(l) are from the former Soviet Union; (m)-(q) are from Brazilian boreholes. Magnification indicated by bar under (i). (**a**) *Cicatricosisporites abacus* Burger. Proximal view. (**b**) *Ischyosporites pseudoreticulatus* (Couper) Döring. Distal view. (**c**) *Pilosisporites trichopapillosus* (Thiergart) Delcourt & Sprumont. Proximal view. (**d**) *Trilobosporites hannonicus* (Delcourt & Sprumont) Potonié. Proximal view. (**e**) *Trilobosporites bernissartensis* (Delcourt & Sprumont) Potonié. Proximal view. (**f**) *Foveosporites cenomanicus* (Khlonova)

6 Cretaceous Fern Spores

Fern spores continue to be important in Cretaceous non-marine sediments, as they are in the Jurassic. Markova (1966), for example, shows that in Siberian sediments fern spores referable to the family Schizaeaceae reached a peak of abundance in the Hauterivian-Barremian, just before the arrival of tricolpate angiosperm pollen on the scene. Although it is not conventional to use modern fern generic names for Cretaceous fern spores, most of the Cretaceous forms do seem to be similar in form to modern fern spores, though there are exceptions. This is in contrast to Cretaceous pollen, which is mostly different from the pollen of Cenozoic plants, even of those believed to be related. On the other hand, the demonstration by Hughes and coworkers (Hughes and Moody-Stuart, 1966, 1969; Hughes and Croxton, 1973) that fern spores were diverse and evince rapid enough evolution to be the basis for successful stratigraphic use in the British Cretaceous shows that Cretaceous ferns were still an important and dynamic floral element.

7 Cretaceous Megaspores

As noted earlier, free megaspores were never in center-stage in the post-"Paleophytic." However, heterosporous ferns and lycopods continued to produce megaspores that were preserved as fossils. Cretaceous megaspores are characteristic of specific environments of deposition and can be locally relatively abundant in fine sandy sediment. Hueber (1982) noted the relative abundance of such genera as *Arcellites* (Fig. 13.17m) and *Paxillitriletes* (Fig. 13.17e,f,j) in the lower Cretaceous Potomac Group of Virginia. Singh (1983) has described a rich megaspore palynoflorule from the mid-Cretaceous of Alberta, Canada (see Fig. 13.17 for representative forms), and Batten (1969, 1974) studied megaspores from the Wealden (Lower Cretaceous) of Great Britain, mostly representing lycopods growing on the Wealden delta, and showed their usefulness in reconstructing paleoenvironments. Kovach and Batten (1989) present a useful summary

Figure 13.13 Schvetzova in Bolkhovitina & Fokina. Proximal view. (**g**) *Imparde-cispora apiverrucata* (Couper) Venkatachala, Kar & Raza. Proximal view. (**h**) *Steno-zonotriletes radiatus* Khlonova. Proximal view. (**i**) *Parvisaccites radiatus* Couper. Lateral view. (**j**) *Rugubivesiculites aralicus* (Bolkhovitina) Khlonova. Mid-focus, distal-proximal. (**k**) *Taxodiaceaepollenites hiatus* (Potonié) Kremp. Lateral view. (**l**) *Tricolpopollenites micromunus* Groot & Penny. Equatorial view. (**m**) *Cicatricosisporites australiensis* (Cookson) Potonié. Distal view. (**n**) *Classopollis* sp. Lateral view. (**o**) *Ephedripites* sp. Lateral view. (**p**) *Araucariacites* sp. or *Inaperturopollenites* sp. (**q**) *Dicheiropollis etruscus* Trevisan. Lateral view. This form occurs normally as an apparent dyad. Photomicrographs from G. F. W. Herngreen. They originally appeared in Herngreen and Chlonova (1981).

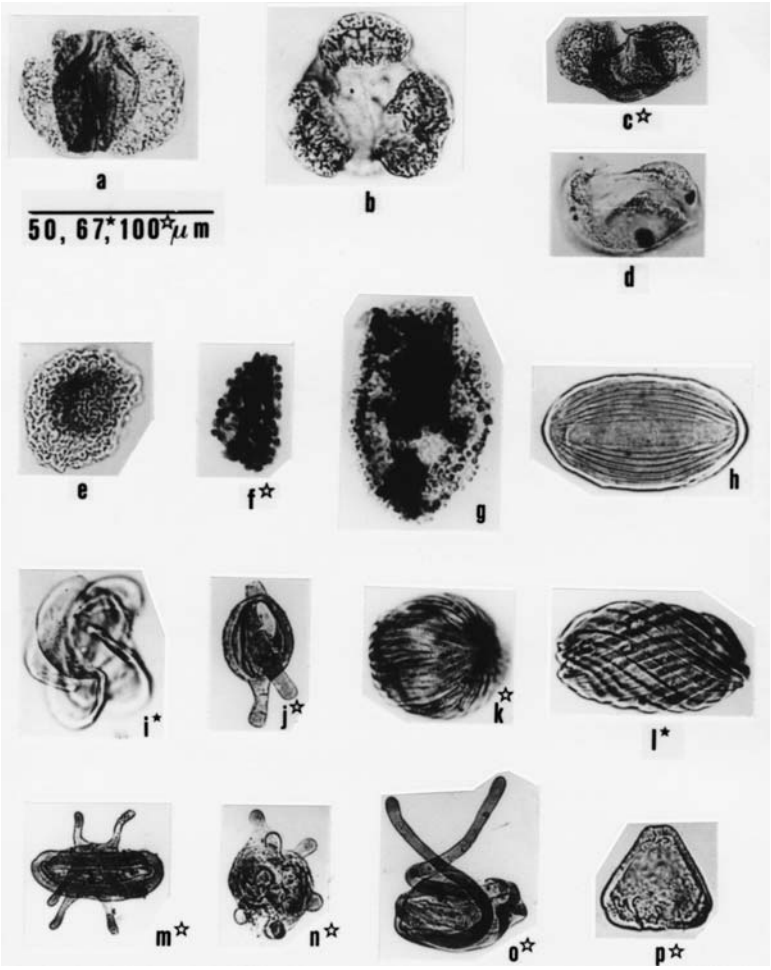

Figure 13.14 Characteristic pollen and spores of the early Cretaceous Gondwana palynofloral province ((a)-(d)), and of the later early to mid Cretaceous (Albian-Cenomanian) ASA (= African-South American) province ((e)-(p)). See Fig. 13.12 for more information. (a)-(d) are from Albian levels in a borehole in Australia; (e)-(p) are from Albian-Cenomanian levels in Brazilian boreholes. Magnification indicated by bar under (a). (**a**) *Podocarpidites* cf. *ellipticus* Cookson. Proximal-distal view, mid-focus. (**b**) *Microcachryidites antarcticus* Cookson. Distal view. (**c**) *Alisporites grandis* (Cookson) Dettmann. lateral view. (**d**) *Podosporites microsaccatus* (Couper) Dettmann. Oblique lateral view. (**e**) *Afropollis jardinus* (Brenner) Doyle *et al.* (**f**) *Reyrea polymorphus* Herngreen. (**g**) *Stellatopollis* sp. This genus is a representative early-appearing, monosulcate, angioperm pollen grain. (**h**) *Ephedripites* sp. Distal view. (**i**) *Galeacornea causea* Stover. (**j**) *Sofrepites legouxae* Jardiné. (**k**) *Ephedripites elsikii* Herngreen.

of the stratigraphic occurrence and usefulness of Mesozoic and Cenozoic free megaspores, based on study of about 700 species of the spores from about 500 publications.

Kovach and Batten (1993) summarize the changes in diversity of lycopsid and fern megaspores in time. They note that lycopsids, a Paleozoic survivor group, declined dramatically in the Late Cretaceous, whereas heterosporous aquatic ferns such as Marsileaceae and Salviniaceae, which first appeared in the Cretaceous, continued in stable diversity across the Cretaceous/Paleogene boundary.

8 Dinoflagellates and Acritarchs of Jurassic-Cretaceous

Dinoflagellate cysts first appear abundantly and very recognizably in paleopalynological preparations of marine sediments from late Triassic on. In the Jurassic they are very abundant and very fast-evolving, making them ideal subjects for palynostratigraphy. Williams and others (Williams, 1977; Bujak and Williams, 1979) have described the very rapid evolution of Jurassic dinoflagellates. This is very fortunate for palynologists, as non-marine Jurassic sediments, dominated by rather difficult to work with Pv2s and Sc0s, can be troublesome for stratigraphy. Charts in Wilson and Clowes (1980) show the range of principal general forms, late Triassic to Neogene. An important book edited by Laurie and Foster (2001) is devoted mostly to profuse illustration and description of the dynamically evolving Jurassic dinocyst "floras" of Australia, especially of the Timor Sea area. Plate 13.1 illustrates some diverse Jurassic dinocyst forms (and one acritarch!) from chapters by Riding and Helby (2001a-d) in the Laurie and Foster book. Fig. 13.18 illustrates some Cretaceous dinoflagellate cysts.

Jurassic dinoflagellate palynofloras (cf. Fig. 12.9 and Plate 18.1) show considerable provinciality, and zonations based on them cannot be extended worldwide (Williams, 1975). Dinoflagellate-based palynostratigraphy remains important in marine sediments of the Cretaceous and also ties in with the non-marine spores/pollen zonations, which from the end of the Neocomian on are also quite well controlled because of rapid angiosperm evolution. Truswell (1981) has summarized this situation, and has noted that the Cretaceous dinoflagellate work

Figure 13.14 Obliquely lateral view. (**l**) *Ephedripites jansonii* (Pocock) Muller. (**m**) *Elaterosporites klaszi* (Jardiné & Magliore) Jardiné. (**n**) *Elaterocolpites castelaini* Jardiné & Magloire. (**o**) *Elateroplicites africaensis* Herngreen. (**p**) *Triorites africaensis* Jardiné & Magloire. Note that the odd forms (i),(j), and (m)-(o) are characteristic ASA forms and their peculiar elater or elater-like appendages probably were an adaptation to arid climate, a suggestion strengthened by association with ephedroid pollen ((h),(k),(l)). Indeed, *Elateroplicites* combines elaters with the polyplicate (taeniate) condition characteristic of *Ephedra* and relatives. Photomicrographs from G. F. W. Herngreen. They originally appeared in Herngreen and Chlonova (1981).

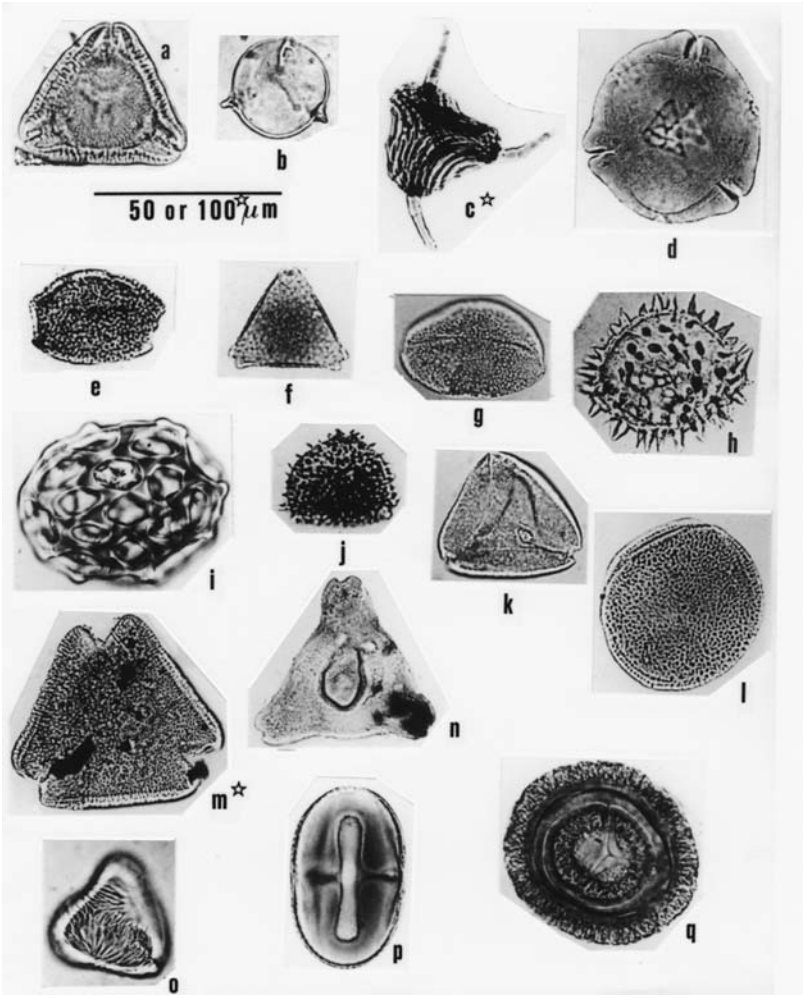

Figure 13.15 Spores and pollen of the late Cretaceous (Turonian-Senonian) *Aquilapollenites* palynofloral province ((a),(b)), and late Cretaceous Normapolles palynofloral province ((c),(d)), and the late Cretaceous (Senonian) Palmae palynofloral province ((e)-(q)). See Fig. 13.12 for more information. For other representatives of the *Aquilapollenites* province, see Fig. 13.11 and for other Normapolles province forms see Figs. 13.9 and 13.10. (a) and (b) are from the former Soviet Union; (c) and (d) are from the Senonian of Hungary; (e) and (h) are from the Senonian of Venezuela; (f),(g),(i)-(k) and (m)-(q) are from the Upper Senonian of Brazil; (l) is from the Senonian of Nigeria. Magnification indicated by bar under (a) and (b). (**a**) *Borealipollis bratzevae* Khlonova. Polar view, mid-focus. (**b**) *Orbiculapollis globosus* (Khlonova) Khlonova. Polar view. (**c**) *Appendicisporites tricuspidatus* Weyland & Greifeld. Distal view. (**d**) *Pseudopapillopollis praesubherzynicus* (Góczán) Góczán. Polar view, mid-focus. This is a Normapolles form in which

has also been used to indicate factors in sedimentation such as sediment source and energy levels.

Acritarchs continue to be important in marine sediments of late Mesozoic age. Some characteristic forms from the Cretaceous and Paleogene of the Canadian Arctic are shown in Fig. 13.19 (see also Plate 13.1). Habib and Knapp (1982) have shown that some very small (less than 10 μm) acritarchs of the Cretaceous can be of considerable stratigraphic importance. Conventional palynological investigation often misses forms so small. As mentioned elsewhere, study of "Mesophytic"-"Cenophytic" acritarchs is a wide-open field.

9 Note on Classification of Jurassic-Cretaceous Spores/Pollen

The taxonomy of (that is, the classification of) Mesozoic, especially post-Triassic, spores/pollen is a very difficult matter. Although some, especially older, Soviet palynological works use names of extant plants for some mid-Mesozoic pollen, most of the forms are usually placed in form-genera (= morphogenera): *Classopollis, Ovalipollis, Triadispora, Aquilapollenites, Wodehouseia*, etc. It is possible to follow some rough grouping: all trilete spores together, all bisaccate pollen together, etc. It would be possible to develop a "turmal" listing, and indeed many Mesozoic palynologists do use modifications of Potonié's turmal system. The problem ceases to be a problem by Eocene-Oligocene, when enough certainty can be attached to family assignments to use an Engler-Prantl, or one of the more modern botanical classification schemes, plus broad morphological groupings for morphogenera of unknown relationship.

Figure 13.15 some of the characteristic structures (see Fig. 13.9) are not as strongly expressed as in other taxa. (**e**) *Retidiporites magdalenensis* Van der Hammen & Garcia. Equatorial view. (**f**) *Proteacidites sigalii* Boltenhagen. Polar view. (**g**) *Retimonocolpites* sp. Distal view. (**h**) *Spinizonocolpites echinatus* Muller. Proximal-distal view, mid-focus. (**i**) *Buttinia andreeva* Boltenhagen. (**j**) *Echitriporites trianguliformis* Van Hoeken-Klinkenberg. Polar view. (**k**) *Cupanieidites* sp. Polar view showing the syncolpate morphology. (**l**) *Proxapertites operculatus* (Van der Hammen) Van der Hammen. Proximal-distal view. This genus is zonisulculate (has a ring furrow: in a sense, monosulcate and syncolpate). (**m**) *Foveotricolpites irregularis* Herngreen. Polar view. (**n**) *Aquilapollenites sergipensis* Herngreen. Polar view. (**o**) *Scollardia srivastavae* Herngreen. Polar view. (**p**) *Crassitricolporites brasiliensis* Herngreen. Equatorial view. (**q**) *Gabonisporis vigourouxii* Boltenhagen. Proximal view. Photomicrographs from G. F. W. Herngreen. They originally appeared in Herngreen and Chlonova (1981).

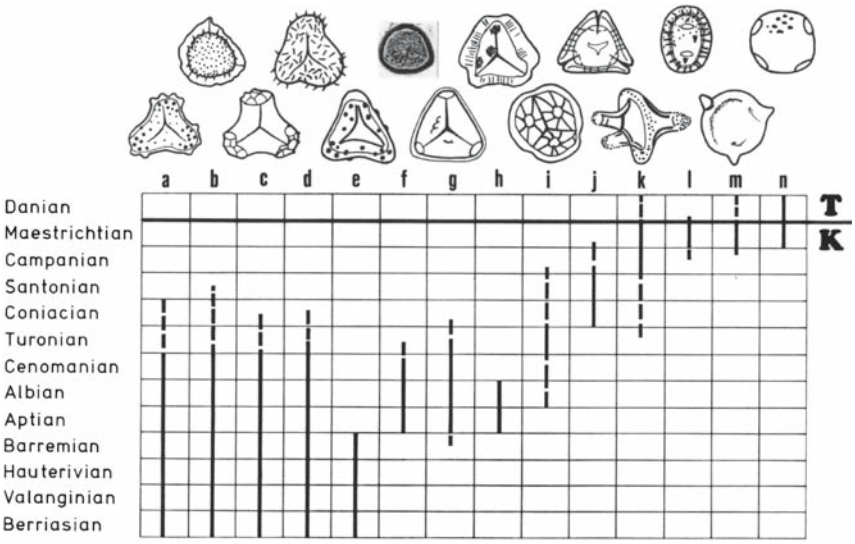

Figure 13.16 Stratigraphic ranges of selected key species of Cretaceous spores and pollen. This figure illustrates that early Cretaceous spore forms tended to persist for long periods, whereas later Cretaceous taxa tended to have shorter periods of stasis, facilitating both stratigraphic and palynofloral (provincial) subdivision. Broken lines mark sporadic occurrence. Except for (f), the taxa are here represented by line drawings. They are mostly illustrated by photographs elsewhere in the book. (**a**) *Impardecispora apiverrucata* (Couper) Venkatachala *et al.* (**b**) *Aequitriradites spinulosus* (Cookson & Dettmann) Cookson & Dettmann. (**c**) *Impardecispora trioreticulosa* (Cookson & Dettmann) Venkatachala. (**d**) *Pilosisporites verus* Delcourt & Sprumont. (**e**) *Trilobosporites bernissartensis* (Delcourt & Sprumont) Potonié. (**f**) *Coptospora paradoxa* (Cookson & Dettmann) Dettmann. (**g**) *Triporoletes singularis* Mchedlishvili. (**h**) *Asbeckiasporites borysphenicus* (Voronova) Theodorova- Shakhmundes. (**i**) *Stenozonotriletes radiatus* Khlonova. (**j**) *Borealipollis bratzevae* Khlonova. (**k**) *Aquilapollenites unicus* (Khlonova) Khlonova. (**l**) *Wodehouseia spinata* Stanley. (**m**) *Orbiculapollis globosus* (Khlonova) Khlonova. (**n**) *Ulmoideipites krempii* Anderson. Chart modified slightly from Herngreen and Chlonova (1981).

10 Terminal Cretaceous Event ("TCE")

It is well known that marine organisms suffered a crisis at the end of the Cretaceous ("K-T boundary"–perhaps a better term would K-Pg boundary, meaning the boundary between the Cretaceous and the Paleogene). This was also an era boundary, between the Mesozoic and Cenozoic, and it represents the second greatest extinction event of Earth history, exceeded in magnitude only by the Permian/Triassic (= Paleozoic/Mesozoic) extinction. The event at the K-T

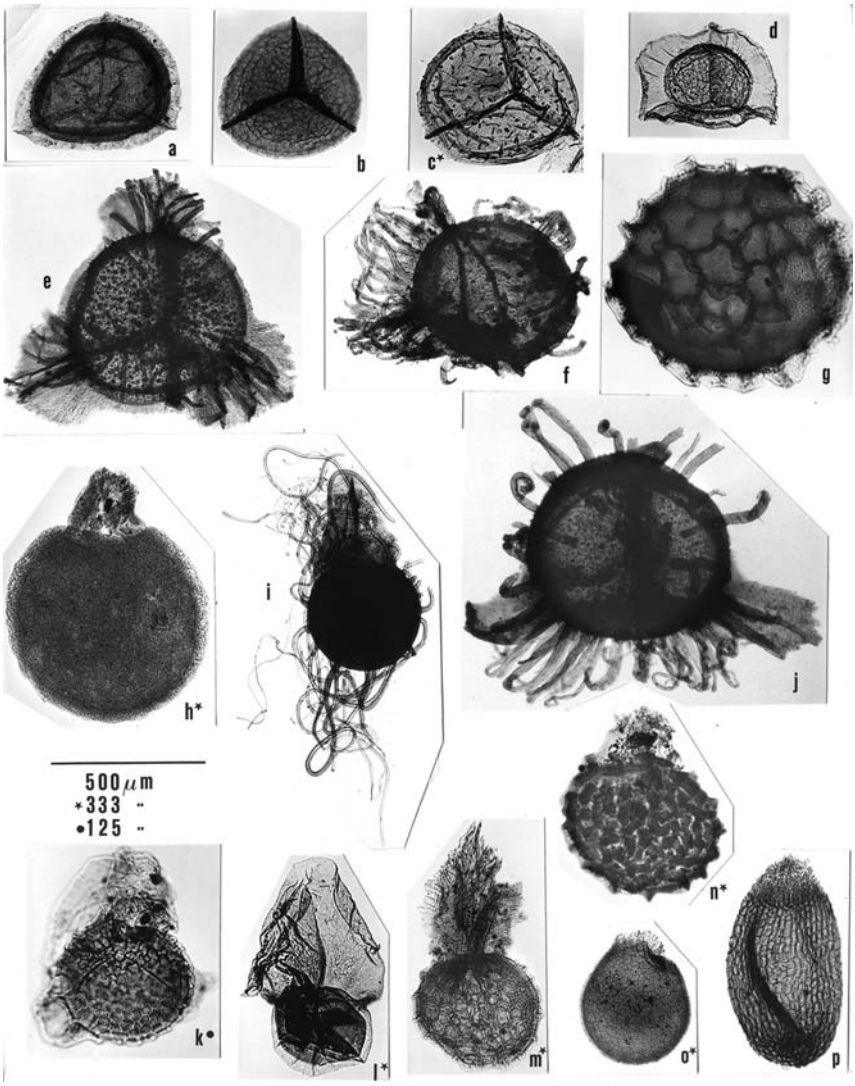

Figure 13.17 Cenomanian Cretaceous megaspores. From the Peace River area, northwestern Alberta, these megaspores illustrate that free-megaspore-producing heterosporous ferns and lycopsids were still a factor in mid-Cretaceous time, though free-sporing megaspores were never as diverse or numerous again as in the late Devonian and Carboniferous. Magnification indicated by bar under (h). (**a**) *Minerisporites* sp. Proximal view. (**b**) *Minerisporites dissimilis* Tschudy. Proximal view. (**c**) *Henrisporites angustus* Tschudy. Proximal view. (**d**) *Minerisporites pterotus* C. Singh. Proximal view. This species has a membranous zona. (**e**) *Paxillitriletes dakotaensis* (Hall) Hall & Nicolson. Proximal view (see also (f) and (j)). (**f**) As (e) and (j). Lateral view. (**g**) *Erlansonisporites erlansonii* (Miner) Potonié.

boundary is sometimes referred to as the TCE = Terminal Cretaceous Event. Indeed, the total extinction of ammonites is one *raison d'être* for this period (and era) boundary. Marine vertebrates and invertebrates generally were decimated. Many kinds of land animals also perished: all dinosaurs and pterosaurs, indeed all land animals except the relatively small mammals, small reptiles and amphibians, and, of course, arthropods. Many authors in the past have suggested a worldwide catastrophe such as an epidemic of volcanoes. The bolide (an exploding meteor or meteorite) explanation is now widely accepted–indeed the collision has been geographically located in the Yucatan area of Mexico and given a name derived from that locality: the Chicxulub impact. Impact ejecta are often found, associated with anomalies in the element iridium in sediments just below the major extinction interval, not only in North America but also elsewhere in the world One would expect that vegetation must have been affected by such an event. Tschudy and Tschudy (1984) showed that, at many locations in the northwest USA where sediments straddle the K-T boundary, a short-lived but profound ecological crisis (in the words of Nichols *et al.*, 1990) is mirrored in the palynological record. There is a blotting out of many pollen types and a "fern spike" with great abundance of monolete and trilete fern spores (see Fig. 13.21). This spike presumably represents an expansion of ferns into decimated forests, as occurs today in areas of forest fires or volcanic disasters. The palynological record of extinction is less dramatic than that shown by megafossil floras, but there was considerable loss of sporomorph taxa.

Among the pollen forms that do not come back after the K-T event are *Proteacidites* spp., and some kinds of *Aquilapollenites* (see Fig. 13.20). Nichols (2003) notes that this disappearance at the TCE of the major plant taxa (probably trees and shrubs) that made these pollen forms must have meant a major shift in biodiversity of the vegetation. However, a few triprojectates–*Aquilapollenites* in

Figure 13.17 Distal view. (**h**) *Molaspora fibrosa* C. Singh. Lateral view. (**i**) *Ariadnaesporites cristatus* Tschudy. Lateral view. The tangling, tubular threads presumably served to attach the spore to substrates for germination or to trap microspores. (**j**) as (e) and (f).Oblique view showing the long, hooked processes of the distal surface. (**k**) *Balmeisporites glenelgensis* Cookson & Dettmann. Obliquely lateral view showing laesura on proximal surface. (**l**) *Ariadnaesporites antiquatus* C. Singh. Lateral view. (**m**) *Arcellites reticulatus* (Cookson & Dettmann) Potter. Lateral view. The apical leaf-like appendages on this megaspore (see (e),(l),(n) and (k)) are a characteristic megaspore feature, probably having to do with "capture" of microspores. (**n**) *Rugutriletes comptus* C. Singh. Lateral view. (**o**) *Ricinospora pileata* (Dijkstra) C. Singh. Lateral view. (**p**) *Spermatites ellipticus* Miner. Lateral view. Although in the same size range and found in the same preparations, *Spermatites* is presumably not a megaspore, but a seed, of which the seed cuticle with cellular structure is preserved. Photographs provided by Chaitanya Singh, originally published in Singh (1983).

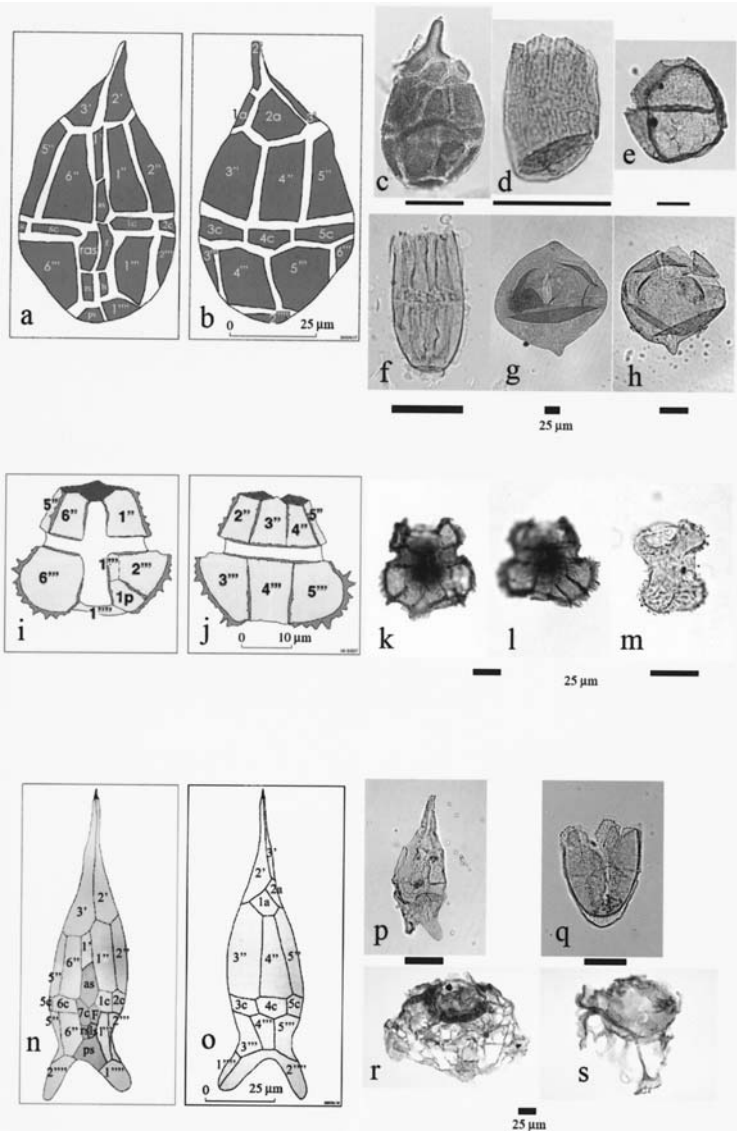

Plate 13.1

Plate 13.1 Jurassic dinoflagellate cysts and one non-dinoflagellate cyst fellow traveler. Can you pick out the acritarch? The dinocysts are examples of the explosive evolution of dinoflagellates after their appearance in the Late Triassic. (**a-c**) *Tabulodinium senarium* Dodekova. (**a**)-(**b**) line drawings of an idealized specimen in ventral (**a**) and dorsal (**b**) view, with notations for the Kofoid tabulation pattern. Compare with photomicrograph of a lateral view of the same species in (**c**). (**d**). *Striatodinium lineatum* Riding & Helby, showing the apical archeopyle and the non-tabular ridges that somewhat obscure the tabulation. (**e**) *Nummus apiculus* Riding & Helby, an acritarch showing that non-dinoflagellate cysts, in the same size range as dinoflagellate cysts, were present in the Jurassic and might be confused with them by the unwary. Note the apical pylome, not an archeopyle, and in this specimen an equatorial fold even simulates a cingulum. (**f**) *Striatodinium ottii* Riding & Helby, with apical archeopyle (cf. **d**), and linear crests tending to hide the tabulation although the cingulum is obvious. (**g**)-(**h**) *Fusiformacysta terniana* Riding & Helby, with blunt apical and antapical horns and a precingular archeopyle. Note that in (**h**) the apical horn appears to be missing because the opercular pieces have detached. (**i**)-(**l**) *Fostericysta eclipsiana (*Riding & Helby) Riding. (**i**)-(**j**) are line drawings of an idealized specimen, showing the gonyaulacalean Kofoid tabulation pattern, in ventral (**i**) and dorsal (**j**) view. The archeopyle is apical. This taxon is characterized by a very dense accumulation body in center of the cyst (cf. **k-l**), and this is omitted in the diagram for clarity. (**k**) specimen showing the apical archeopyle very well. (**l**) specimen in low focus to show the accumulation body. Accumulation bodies are of uncertain significance, but they obviously share the resistance to attack of dinosporin (**m**) *Aidelocysta clavata* Riding, Helby & Stevens, an odd dinoflagellate cyst with quadrate form, a pronounced cingular waist-like constriction and an anterior intercalary archeopyle. There is a dense cover of short processes. (**n**)-(**p**) *Voodooia tabulata* Riding & Helby. (**n**)-(**o**) are line drawings of an idealized specimen showing the Kofoid tabulation pattern in ventral (**n**) and dorsal (**o**) view. The parasulcal area is shaded a little darker in (**n**). (**p**) is a photomicrograph of a lateral view in which the cingulum is well displayed. (**q**) *Gardodinium angustum* Riding, Helby & Stevens, showing the two-layered nature of the cyst (endophragm and ectophragm layers), and the archeopyle with very obvious accessory archeopyle sutures. (**r**) *Hadriana cincta* Riding & Helby. The complexity and variety of form of this genus is a marvelous example of the dynamic evolution of dinoflagellates in the Jurassic. This sort of cyst drives a novice palynologist trying to interpret it to distraction! This is a lateral view of the cyst and when studied under the microscope with the possibility of focusing up and down, the plate structure can be interpreted. The dark circular area at the top is the archeopyle. The web-like ectophragm of the cyst is described as consisting of trabeculae. (**s**) *Belowia* sp. A of Riding & Helby. Slightly oblique apical view. Another very complicated cyst with trabeculae emerging from the cingular area and making up much of the ectophragm. There are also postcingular processes, one of which projects downward in the lower center of the photo. Interpretation of the tabulation pattern is obviously very difficult. All of the above illustrations are of fossils from sediments of Northwest Australia and adjacent parts of Indonesia in the Timor Sea region. They are from the publications of Riding and Helby (2001a-d), and are published here with the permission of the authors and of the Association of Australasian Palaeontologists.

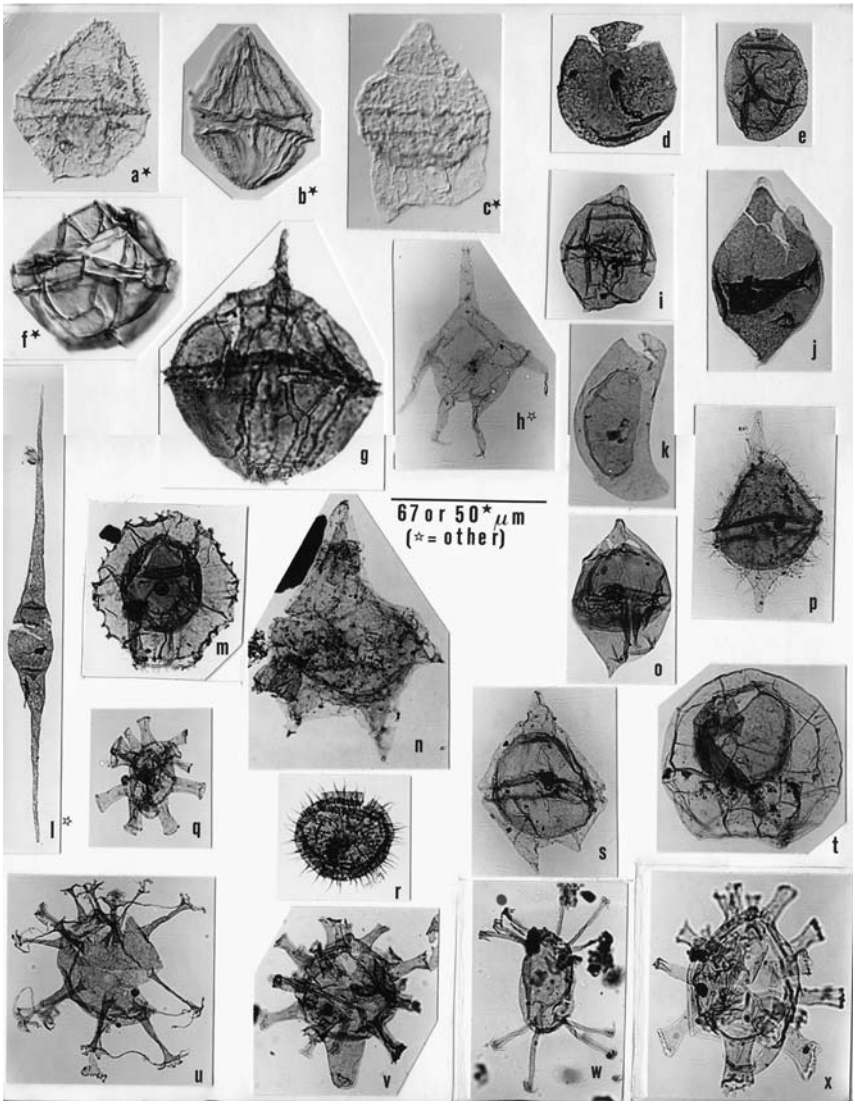

Figure 13.18 Selected dinoflagellate cysts of early and middle Cretaceous age from North America. (a)-(c) are interference contrast photomicrographs of specimens from the early Cretaceous of Wyoming. All others are bright-field (except as noted) photomicrographs of specimens from the Cenomanian of northwestern Alberta, Canada. Size of specimens indicated by bar under (h). Size of specimens marked "other" indicated in caption. (**a**) *Chichaouadinium vestitum* (Brideaux) Bujak & Davies. Dorsal view of spiny proximate cavate cyst showing intercalary archeopyle. (**b**) *Dinogymnium* sp. Ventral view of this characteristically pleated taxon of proximate cysts. Many species of this

a very broad sense–persist well into the Paleocene, and Choi (1984) has described a new genus of them in the Eocene of the Canadian Arctic.

Many Normapolles forms drop out at the end of the Cretaceous, but others persist until they terminate in the Eocene. (Obviously, in cases of such anomalous extentions upward in the record, one must always consider the possibility of

Figure 13.18 genus were formerly known as *Gymnodinium* spp. (**c**) *Ascodinium verrucosum* Cookson & Hughes. Dorsal view of cavate cyst showing separation of the large apical operculum. (**d**) *Batiacasphaera macrogranulata* Morgan. Proximate cyst with apical archeopyle. (**e**) *Fromea granulosa* (Cookson & Eisenack) Stover & Evitt. Proximate cyst with apical archeopyle. (d) and (e) are "bag-like" cysts with very limited expression of paratabulation. (**f**) *Leptodinium modicum* Brideaux & McIntyre. Dorsal view of proximate cyst with clearly shown paratabulation and precingular archeopyle. (**g**) *Cribroperidinium intricatum* Davey. Ventral view, proximate cyst with clearly expressed paratabulation and apical horn. (**h**) *Muderongia pentaradiata* C. Singh. Proximate cyst with one apical, two cingular and two antapical horns. Specimen 140 μm long. (**i**) *Subtilisphaera?inaffecta* (Drugg) Bujak & Davies. A slightly cavate cyst with a small apical horn and a clearly demarcated paracingulum. (**j**) *Trithyrodinium rhomboideum* C. Singh. Dorsal view of proximate cavate cyst with intercalary archeopyle–the three intercalary paraplates are released separately. The picture shows one of these paraplates partially separated. (**k**) *Wallodinium anglicum* (Cookson & Hughes) Lentin & Williams. Lateral view of curved cavate cyst with a small endocyst and apical archeopyle. Operculum shown separating. (**l**) *Odontochitina singhii* Morgan. Unusual cavate proximate cyst. There is an apical horn and two antapical horns, one of which is vestigial. Length of cyst: 400 μm. (**m**) *Catastomocystis spinosa* C. Singh. Dorsal view of proximate cavate cyst with precingular archeopyle. The endocyst is dark and smooth, and its wall (the endophragm) is closely appressed to the dorsal side of the pericyst wall (the periphragm). (**n**) *Endoceratium pentagonum* C. Singh. Proximate cavate cyst with apical archeopyle. Dorsal view, with open archeopyle suture. (**o**) *Alterbidinium daveyi* (Stover & Evitt) Lentin & Williams. Proximate cavate cyst, mid-focus, lateral view. (**p**) *Palaeohystrichophora infusorioides* Deflandre. Proximochorate, cavate cyst, dorsal view, with prominent cingulum. (**q**) *Discorsia nanna* (Davey) Duxbury. Skolochorate cyst. (**r**) *Cleistosphaeridium* cf. *aciculare* Davey. With apical archeopyle, paratabulation not evident. (**s**) *Subtilisphaera hyalina* C. Singh. Cavate proximate cyst, dorsal view, with prominent cingulum, paratabulation not evident. (**t**) *Stephodinium australicum* Cookson & Eisenack. Cavate proximate cyst with small endocyst, lateral view, clearly delimited paraplate boundaries. (**u**) *Oligosphaeridium trabeculosum* C. Singh. Skolochorate cyst, apical archeopyle. The stringy connections between the processes represent the approximate level of the original thecal wall. (**v**) *Florentinia* cf. *deanei* (Davey & Williams) Davey & Verdier. Skolochorate cyst with precingular archeopyle, dorsal view. (**w**) *Bourkidinium psilatum* C. Singh. Skolochorate cyst with apical archeopyle, processes with filiform, recurved spines. (**x**) *Florentinia cooksoniae* (Singh) Duxbury. Skolochorate cyst with precingular archeopyle, dorsal view. (a)-(c) are courtesy of D. J. Nichols, originally published in Nichols and Jacobson (1982); (d)-(x) were provided by Chaitanya Singh and originally appeared in his 1983 publication.

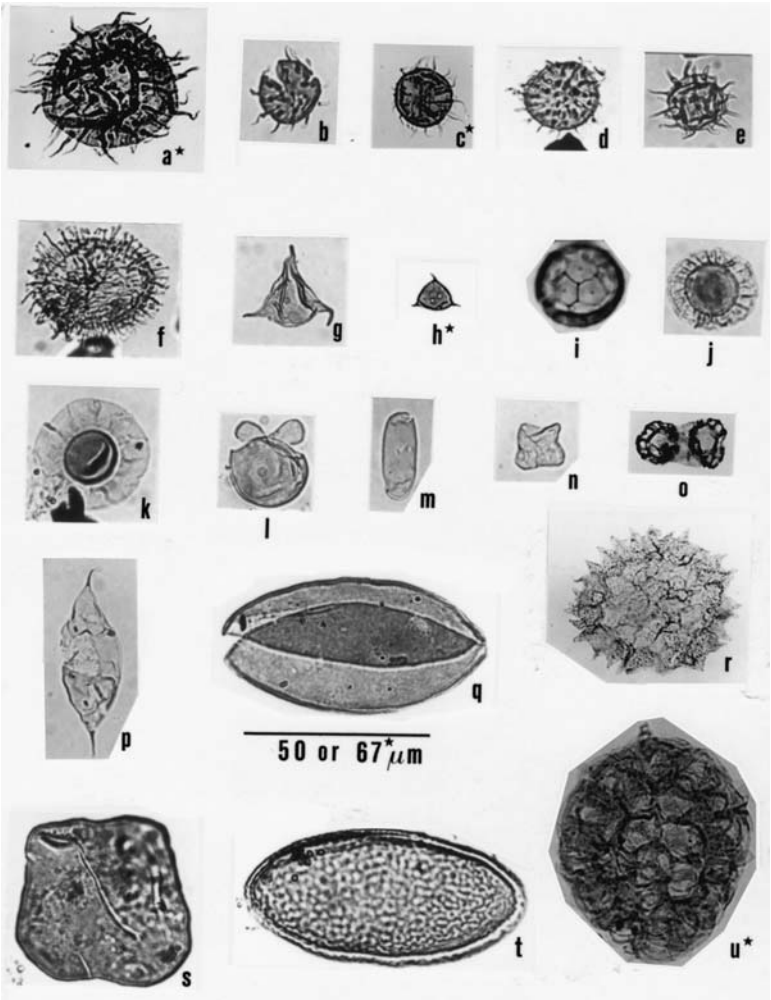

Figure 13.19 Cretaceous and Paleogene acritarchs and miscellaneous algal-derived palynomorphs. Marine shales containing palynofloras usually have among these floras various bodies that survive sedimentation, post-depositional processes, and laboratory maceration. Some of these are acritarchs–algal cysts and cyst-like bodies not referable to the dinoflagellates or some algal group. Others are such colonial algae as *Pediastrum* (r), *Botryococcus* (illustrated elsewhere in the book), and *Palambages* (u). Although acritarchs are especially rich in numbers and diversity in early Paleozoic marine rocks, they have remained important to the present. Algal bodies, e.g. *Botryococcus* and *Pediastrum*, and acritarchs occur also in non-marine rocks but are not as abundant or diverse there as in sediment generated in marine environments. Magnification indicated by bar under (q). Most of the specimens illustrated are from northern Canada (AH = Axel Heiberg Island; EI = Ellesmere Island). (**a**) *Baltisphaeridium* sp., Cenomanian, northern Alberta;

reworking.) Some forms, such as *Casuarinidites granilabrata*, actually become more abundant in the Paleogene (Fleming,1984). Sweet and Braman (1992) note that a variety of opportunistic survivor species from the Upper Cretaceous generated the new Paleocene floras. At first they were rather depauperate, but Johnson and Ellis (2002) report a high-diversity tropical rainforest flora from Colorado at 1.4 million years after the K-T boundary, showing that vegetation had recovered a Maastrichtian-like richness. Knobloch *et al.* (1993) report that in central Europe angiosperm evolution seems to have been relatively little interrupted by the TCE, and even in parts of the world where the maximum extinctions of plant taxa have been demonstrated it must be conceded that Paleocene floras were much more like Maastrichtian floras than were the coordinate faunas like each other.

Fig. 13.21 shows the TCE "fern spike"and the much more spike-like, bolide-caused iridium incursion into the sediment at a locality in Wyoming.

The extinction rate at this locality for sporomorph taxa is about 30%. This rate is observed at many other localities in western North America, for example in Saskatchewan, Canada (Nichols *et al.*, 1986) and in North Dakota (Nichols, 2002; Nichols and Johnson, 2002). It is significant that very thorough studies of the megafossil flora, such as that of Wilf and Johnson (2004), show about 60% extinction of megafossil plant morphospecies; Johnson *et al.* (1989) even reported 70%–both teams were working on the K-T boundary in North Dakota. Wolfe (1986) somewhat earlier had observed extensive extinction at the boundary

◄

Figure 13.19 (**b**) *Micrhystridium fragile* Deflandre, Paleocene-Eocene, AH; (**c**) *Micrhystridium recurvatum* Valensi, Cenomanian, northern Alberta; (**d**) *Baltisphaeridium* sp., Santonian, AH; (**e**) *Micrhystridium breve* Jansonius, Paleocene, AH; (**f**) *Baltisphaeridium fimbriatum* (White) Sarjeant, Paleocene-Eocene, AH; (**g**) *Veryhachium reductum* (Deunff) Jekhowsky, Santonian, AH; (**h**) *Veryhachium reductum* (Deunff) Jekhowsky forma breve Jekhowsky, Cenomanian, northern Alberta; (**i**) *Pterosphaeridia* sp., Campanian, AH; (**j**) *Pterospermella microptera* (Deflandre & Cookson) Eisenack & Cramer, Campanian, EI; (**k**) *Pterospermella australiensis* (Deflandre & Cookson) Eisenack & Cramer, Campanian, EI; (**l**) *Sigmopollis psilatus* Piel, Paleocene, EI; (**m**) *Navifusa* sp., Paleocene, EI; (**n**) *Tetraporina* sp., Campanian, EI; (**o**) *Bipatellifera clathrata* C. Singh, Cenomanian, northern Alberta; (**p**) *Leiofusa jurassica* Cookson & Eisenack, Paleocene, EI; (**q**) *Pilospora parva* (Cookson & Dettmann) Filatoff, Campanian, EI (van Geel and Grenfell, 1996, illustrate apparently identical forms as zygnematacean algal spores) ; (**r**) *Pediastrum* sp., Paleocene, Mississippi; (**s**) *Petalosporites quadrangulus* Agasie, Campanian, EI; (**t**) *Ovoidites ligneolus* (Potonié) Potonié, Eocene, EI (Grenfell, 1995, van Geel and Grenfell, 1996, and Rich *et al.*, 1982, consider *Ovoidites* a probable zygnematacean algal spore); (**u**) *Palambages* sp., Campanian, EI. Photomicrographs (a), (c), (h), and (o) were provided by Chaitanya Singh and first appeared in his 1983 publication. (r) is courtesy of D. J. Nichols. All other illustrations are from the doctoral dissertation of D. K. Choi (1983).

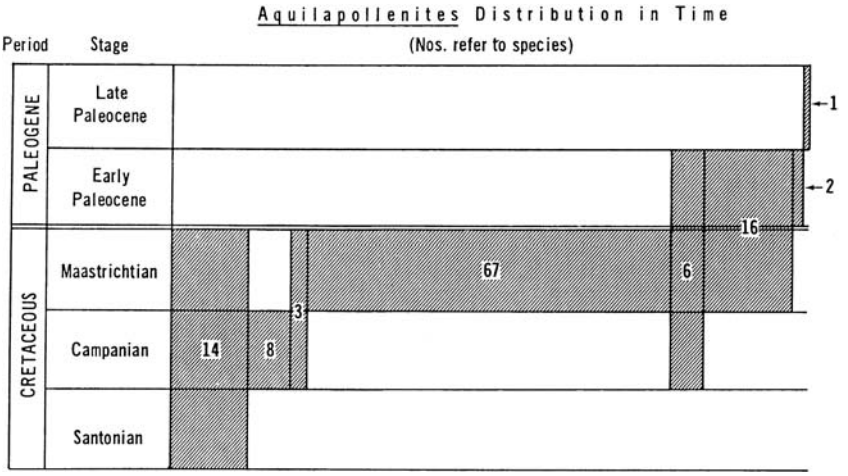

Figure 13.20 This summary of the behavior of *Aquilapollenites* (in a broad sense) pollen across the Cretaceous/Cenozoic ("K-T") boundary illustrates well what happened to palynofloras across this period and era boundary. The shaded areas of the diagram represent the numbers of species with the indicated ranges:14 species extend from Santonian through Maastrichtian, 8 species are confined to the Campanian, 3 species range from Campanian through Maastrichtian, etc. In total, 92 species occur in Cretaceous only, 22 in both Cretaceous and Paleogene, and 3 in Paleogene only. *Aquilapollenites* was decimated at the end of the Cretaceous, but some species survived, after the setback, into the Paleocene. All but a tiny remnant became extinct several millions of years later, in about the middle of the Paleocene. Similar phenomena apply to other Maastrichtian pollen genera that survived into the Paleocene. Since the compilation of these data, more triprojectate pollen–*Aquilapollenites* in the broad sense–have been described (see, for example, Farabee, 1993), but the general picture remains similar. Data compiled for the author by D. K. Choi.

and few Cretaceous megafossil plant fossil morphotaxa that survived into the Cenozoic. It is likely that this difference between megafossils and sporomorphs reflects the fact that the microfossil morphospecies represent primarily plant taxa at the genus or family level, not plant species, a fact I have stressed elsewhere in this book. The iridium evidence for bolide impact and its palynological consequences has been found far from the Americas, for example in New Zealand (Vajda *et al.*, 2001). Some have reported lack of palynological evidence for the impact in sediments at the K-T boundary, for example, Fernández-Marrón *et al.* (2004), in Spain. In this connection it should be emphasized that the fact that a sedimentary sequence seems to be astride the K-T boundary does not necessarily mean that sedimentation was occurring there at the moment in geological time when the bolide impact occurred. However, it should also be emphasized that various authors (e.g., Song *et al.*, 1995) have reported palynofloral and megafossil floral extinctions at the K-T boundary, quite apart from reported association with

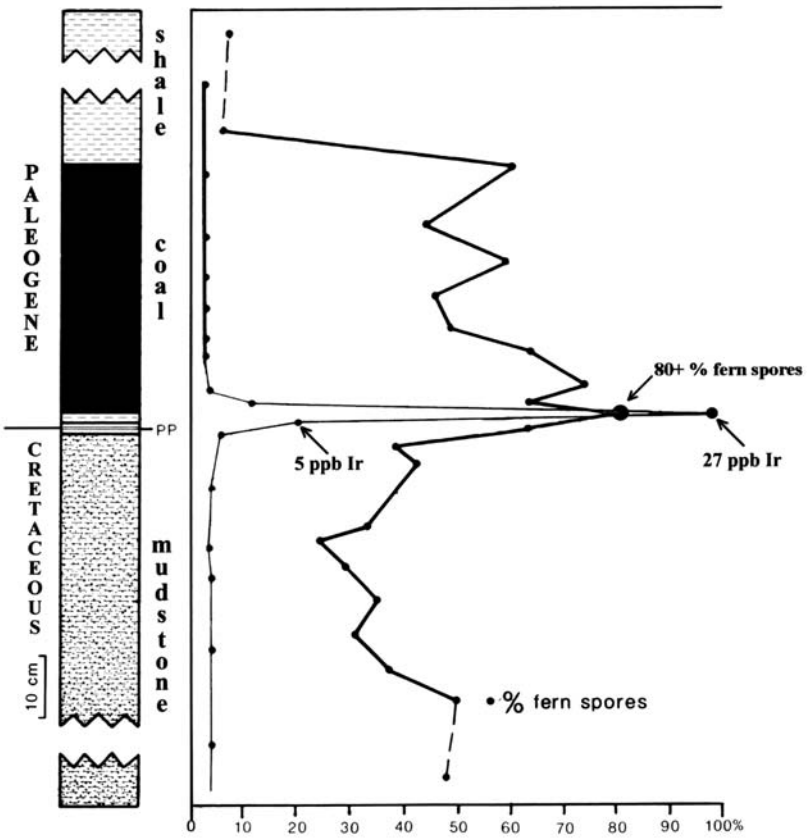

Figure 13.21 Iridium (Ir) anomaly and "fern spike" at the Cretaceous/Tertiary boundary, Powder River Basin, Wyoming. Lithology of the section shown on the left. Scale of the section is indicated on the left just below the word Cretaceous. "pp"represents the 1 to 2 cm. thick boundary clay layer, which contains shocked quartz and elevated Ir, as well as a palynoflora depleted of 30% of the Upper Cretaceous forms. The 2 cm. layer just above "pp" is claystone layer containing the spike of Ir, as well as the beginning of elevated fern spore concentrations which collectiveliy make up the "fern spike," though it is less dramatic than the Ir spike. This illustration was made by simplifying and conflating two figures from Nichols *et al.*, 1992.

iridium and other evidences of bolide impact. One must mention that dinoflagellate floras in central Europe, as represented by dinocyst fossils, are reported to show some acme zones but only relatively minor changes directly related to the boundary, as evidenced by iridium anomalies (Gedl, 2004). At least one paper (Vajda and McLoughlin, 2004) reports a fungal spore "spike" just above the

boundary, as might be expected from the activities of saprophytic fungi working on massive dead plant remains.

Several paleobotanists/paleopalynologists have supported the bolide-impact explanation for the TCE by secondary studies of the paleobotanical/palynological data. For example, Wilf *et al.* (2003) call attention to the fact there is no support from extensive data on fossil floras of western North America for the concept that climatic shifts and alterations could account for the extinctions at the boundary. There must therefore be a non-meteorological causative agent, and Chixulub is the only plausible one. Its reality is abundantly supported by iridium anomalies and ejecta phenomena such as shocked quartz at many localities.

This is in contrast to Sweet and Braman (1992), who recognized considerable change in palynofloras at or near the boundary but who held that paleoecological factors related to climate were part of the explanation. Hotton (2002), working with the Hell Creek Formation in eastern Montana, used statistical analysis of the palynofloras at the K-T boundary, associated with iridium anomalies, noting that the data showed 30% extinction at the boundary, but also indicated a 20–30% reduction in abundance of taxa that were not obliterated. She concluded that such a broad scale change in the absence of adequate explanation from general environmental changes is best explained by the Chixulub impact.

Chapter 14

Paleogene Palynology

1 Introduction

Pollen and spore floras of the Cenozoic are systematically very well known, for a number of reasons. One is that the German brown coals were among the first sediments to which paleopalynological methods were applied. Indeed, the first fossil pollen grains (*Alnus*) ever illustrated (by Goeppert in 1838) were from these beds. Pollen is comparatively easy to separate from lignitic coals. Potonié (1934) obtained his early Tertiary floras from the same sort of German brown-coal-bearing sediments as Goeppert investigated.

In North America, other Paleogene sediments were targeted early, the Eocene Green River Oil Shale being investigated by Wodehouse (1932, 1933) even before the Potonié studies. The early to late Paleocene Fort Union Formation or Group (Wilson and Webster, 1946), and the late Paleocene Wilcox Formation or Group (very little published until Elsik, 1968a,b), both lignite-bearing, were inviting problems. My doctoral work (Traverse, 1951, 1955, 1994) on the Brandon

Lignite of Vermont came about fortuitously, because Professor E.S. Barghoorn was working on that lignite when I needed a doctoral problem. Another factor favoring Cenozoic studies is that sediments of this age are the oldest from which palynofloras can be obtained that offer strong possibilities for reliable paleoecological analysis, based on comparison with modern related taxa. A very important summary of North American vegetational history for the Late Cretaceous and all of the Cenozoic, based both on palynofloras and megafossil floras, is the book by A. Graham (1999) on that subject.

During the Paleogene, modern plant distribution began to take shape, as was amply demonstrated by megafossil paleobotanists, such as Axelrod (1958) and others, before paleopalynology played a major role in paleobotany. For example, in the Northern Hemisphere there were already in the Paleocene-Eocene "Arcto-Tertiary" elements in more northerly locations such as Ellesmere Island in the Canadian Arctic. From these elements came eventually the modern temperate forests. Although Wolfe (1977) and others have cast doubt on the validity of the "Arcto-Tertiary" flora concept, because it is oversimplified, and some of the data on which it was originally based are flawed, the existence of temperate plant taxa of the families Betulaceae, Fagaceae, Ulmaceae, Juglandaceae, etc., in the far North during the Paleogene is amply illustrated by studies of Arctic Paleogene palynofloras. The far northern deciduous forests of Paleogene time were of course unlike any modern deciduous forests that contain some of the same elements (Wolfe, 1980). On the other hand, middle- and low-latitude floras included elements of "paleotropical" vegetation which featured taxa now components of the subtropical and tropical forests. The Cenozoic mountain building resulted in perhaps the highest stand of the continents in geologic history, creating rain-shadows from prevailing moisture sources. At the same time there was an increase of seasonality (hot-cold; wet-dry) and a very great increase in proportions of the Earth characterized by "abnormal geography:" huge semiarid areas, as well as deserts and glaciers. Above all, there was a general decline in world temperatures (see Fig. 14.1) related in part to some of the above-mentioned factors, in part probably also to astronomical factors causing cyclic decline in effective insolation. Already in the Paleogene the development of precursors of semiarid and desert vegetation such as in the Madro-Tertiary flora (Axelrod, 1958) and the Cordilleran flora (Axelrod and Raven, 1985) indicate the response of angiosperms to Cenozoic climatic trends. As pointed out by Frederiksen (1985), some sorts of plant communities from the Paleogene have been much more thoroughly studied than others. For example, coastal brackish-water environments and coastal plain peat swamp communities are much better known than upland communities of the interior.

Fig. 14.1 shows the overall chronology and major paleopalynological high points of the Cenozoic 66-million-year time segment. The traditional division of the Cenozoic into Tertiary (about 64 Myr) and Quaternary (about 2 Myr) periods is a relict of the old division of Earth history into Primary (Paleozoic), Secondary (Mesozoic), Tertiary, and Quaternary. The "Primary" and "Secondary" are now

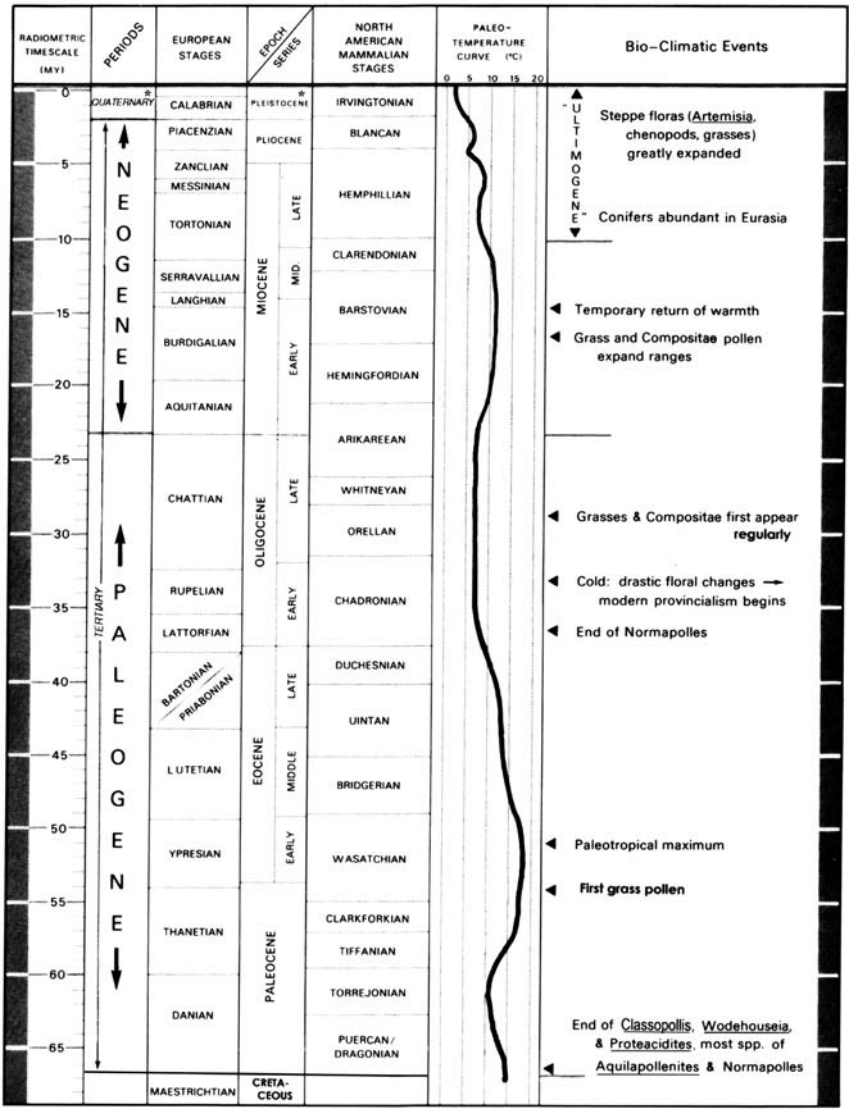

Figure 14.1 Cenozoic framework for palynostratigraphy. Paleogene and Neogene, as used in this book, are the two periods/systems of the Cenozoic, and the Neogene extends to the present, per Berggren (1998) and Berggren *et al*. (1985). The outmoded but beloved term,"Quaternary," should really be abolished, along with the "Tertiary" (see discussion in the text). The paleotemperature plot is much smoothed out and averaged for high latitude ocean surface water temperature, based on oxygen-isotope data measured from foraminifera, from the work of Shackleton and Kennett (1975) and other sources. In the periods and epoch/series columns, 11,500 years B.P. to present is the Holocene,

almost never used, and Tertiary and Quaternary should logically join them in the dustbin. If that were done, the Neogene and its last epoch, the Pleistocene, should run to the present, and both Quaternary and Holocene would be unnecessary terms; the last 11,500 years would be "present interglacial" or some such term. However, the terms Tertiary and Quaternary both have long traditions from much use and are unlikely to disappear. In the now majority opinion, they are the two periods/systems of the Cenozoic. The Paleogene and Neogene are then subsystems of the Tertiary, and the Neogene terminates at the end of the Pliocene. The Quaternary system includes only the Pleistocene and Holocene epochs, totaling around 2 million years, and the Pleistocene has well over 99% of the time, a weird way to divide up a system!

The arguments for "saving" the Quaternary were well set out by Pillans and Naish (2004) and by Gibbard *et al.* (2005). Aubry, Berggren *et al*. (2005) recently proposed solving the problem by recognizing Tertiary and Quaternary as *sub-eras* of the Cenozoic, and having the Paleogene and Neogene serve as *periods* of time (systems of rock) of theoretically lower rank, but including the same 68 millions of years. In the proposal, the Neogene Period runs to the present. As at present recognized, the Paleogene period is about 44 million years long.

It is quite clear that there was a climatic crisis on land at the Cretaceous/Paleocene boundary, and that the characteristic Cretaceous palynofloras were greatly altered, at least locally. For example, *Aquilapollenites* managed to make it across the boundary but was much diminished in the Paleocene (see Fig. 13.20). Normapolles survived the terminal Cretaceous event in diminished numbers and persisted through the almost 30 million years of the Paleocene and Eocene epochs as well, finally passing out of the picture in the Oligocene.

2 Paleogene Climatic Matters

As can be seen in Fig. 14.1, geomagnetic data and oxygen-isotope ($\delta^{18}O$) measurements provide, respectively, control on stratigraphic position and presumed world temperatures for our conclusions about the nature and timing of floral evolution in the Cenozoic. Radiometric and biostratigraphic methods are also helping to provide information on the timing of events. Another important matter has been the gradual acceptance that Cenozoic time-rock segments must depend ultimately on stratotypes. Before these developments, palynologists' conclusions about the meaning of Cenozoic floras were sometimes wrong simply because a correct stratigraphic position "call" was not possible.

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Figure 14.1 but the scale prevents the word from appearing, as is true of the final North American mammalian stage, the Rancholabrean, which however represents a considerably longer period of time than does the Holocene.

As Fig. 14.1 shows, the late Paleocene and early Eocene were mostly very warm, characterized by truly tropical floras in England and warm temperate floras even in what is now the Canadian Arctic. This thermal event is referred to as the PETM, the Paleocene-Eocene Thermal Maximum (Wing *et al*., 2005). Also seen in Fig. 14.1, the temperature increases are on the order of 5–10 °C. Wing *et al*. show that the warming was responsible for large and rapid plant range shifts. Maximum tropicality is at the early/middle Eocene boundary. The early Eocene is sometimes called the paleotropical maximum, as this was the time of greatest expansion of the paleotropical flora in the Northern Hemisphere. The last stand of Normapolles occurred much later. Note that, whatever other disagreements exist, all paleobotanists and most other paleontologists are agreed on the Eocene tropical expansion. Some angiosperm families that become important later, in the Neogene, first are found in the Paleogene; Crepet and Feldman (1991) report unquestionable grass fossils, including the pollen, from Paleocene/Eocene deposits. They note that the well developed organs and tissues of the fossils make it very likely that the roots of the family are in the Cretaceous.

Also recognized by paleontologists in different specialties, and shown by oxygen-isotope data, is pronounced cooling beginning in the earliest Oligocene, though there is some disagreement about its duration within the Oligocene. In any event, the Oligocene was a watershed time, as this cooling was both preceded by, and followed by, significantly warmer times. (Collinson *et al.,*1981, note that evidence from British fossil plants suggests that cooling began in about the middle of the Eocene, rather than being sudden, at the end of the Eocene, as others have suggested.) It was during the Oligocene that very marked drastic floral changes leading to the development of modern plant associations began. Temperate deciduous forests expanded greatly. Grasses (family Poaceae) and composites (family Asteraceae) begin to appear in palynofloras, though not as important floral elements. Conifer forests apparently developed in mountainous areas. Van Simaeys *et al*. (2005) show that migrations of Arctic taxa of dinoflagellate cysts, such as *Svalbardella*, at lower and middle latitudes in Europe in middle Oligocene time (ca. 27.1 Ma) mark strong glaciation expansion in Antarctica. It is evident that local variations are superimposed on rather general climatic alterations shown in Fig. 14.1 such as Oligocene cooling. It is also evident that the overall Cenozoic story shows a fluctuating, but progressive, cooling trend to the Pleistocene.

3 "Postnormapolles"

The decline of Normapolles was accompanied in the late Cretaceous and Paleocene-Eocene by the appearance of many forms of triporate pollen that seem likely to have been produced by plants that evolved from Normapolles producers. The probability that this is so is increased by Skarby's (1981) and Friis' (1983) studies indicating the probability of a Juglandales alliance for the plants that produced

Normapolles pollen. These newer sorts of triporates are called "Postnormapolles" and included *Carya*-like pollen (*Caryapollenites*) and *Myrica*- and *Engelhardia*-like pollen (*Momipites*), among others. Most of the Postnormapolles pollen, as Normapolles, was probably produced by amentiferous trees and shrubs. (Pflug, 1953, introduced Postnormapolles as a suprageneric unit or "Stemma" for fossil porate pollen lacking the Normapolles special structural features.)

4 Characteristic Paleogene Spore/Pollen Floras

Fig. 14.2 illustrates some representative Paleocene spores/pollen from various localities, especially from the Fort Union Formation of Wyoming. A variety of Postnormapolles triporates, a few sorts of Normapolles, various Pc0 and Pc3 forms, and fern spores characterize the Paleocene palynoflora. The latest Paleocene Wilcox Group of Louisiana, Arkansas, Texas, and adjoining Gulf Coast areas of Mexico and the USA is represented by specimens from Texas. This is a considerably different association, with Postnormapolles, especially *Momipites*, very similar to modern genera, abundant palm pollen, and forms probably referable to mostly tropical families. Fig. 14.3 shows some characteristic Eocene sporomorphs of mid-latitude North America and elsewhere. At this level tricolporates of more or less tropical affinity dominate, such as pollen referable to Nyssaceae, Cornaceae, Tiliaceae, and Bombacaceae, plus many sorts of Postnormapolles, palm pollen, bisaccate, and inaperturate conifer pollen. Megaspores continued to be produced by Paleogene lycopods and heterosporous ferns, as they are today, and they are found in Paleogene sediments. For example, *Minerisporites* was produced by isöetaleans, and megaspores of various species of the still extant heterosporous fern *Azolla* (Salviniaceae) also occur and have been described (see Collinson, 1980; Collinson *et al*., 1985). One of the best, readily available, places to look at hundreds of good illustrations of representative Late Cretaceous and Cenozoic sporomorphs is Song *et al*. (1999).

4.1 Nothofagidites

In the Southern Hemisphere a characteristic constituent of late Cretaceous and Cenozoic palynofloras is very distinctive stephanocolpate pollen related to the modern southern beech, *Nothofagus*. This fossil pollen, at least in the Paleogene, is usually referred to the form-genus, *Nothofagidites*. Fig. 14.4 illustrates significant forms.

4.2 Oligocene Palynofloras

Oligocene palynofloras include forms carried over from the Eocene, such as nyssoid pollen, many triporates, and many forms referable to modern families

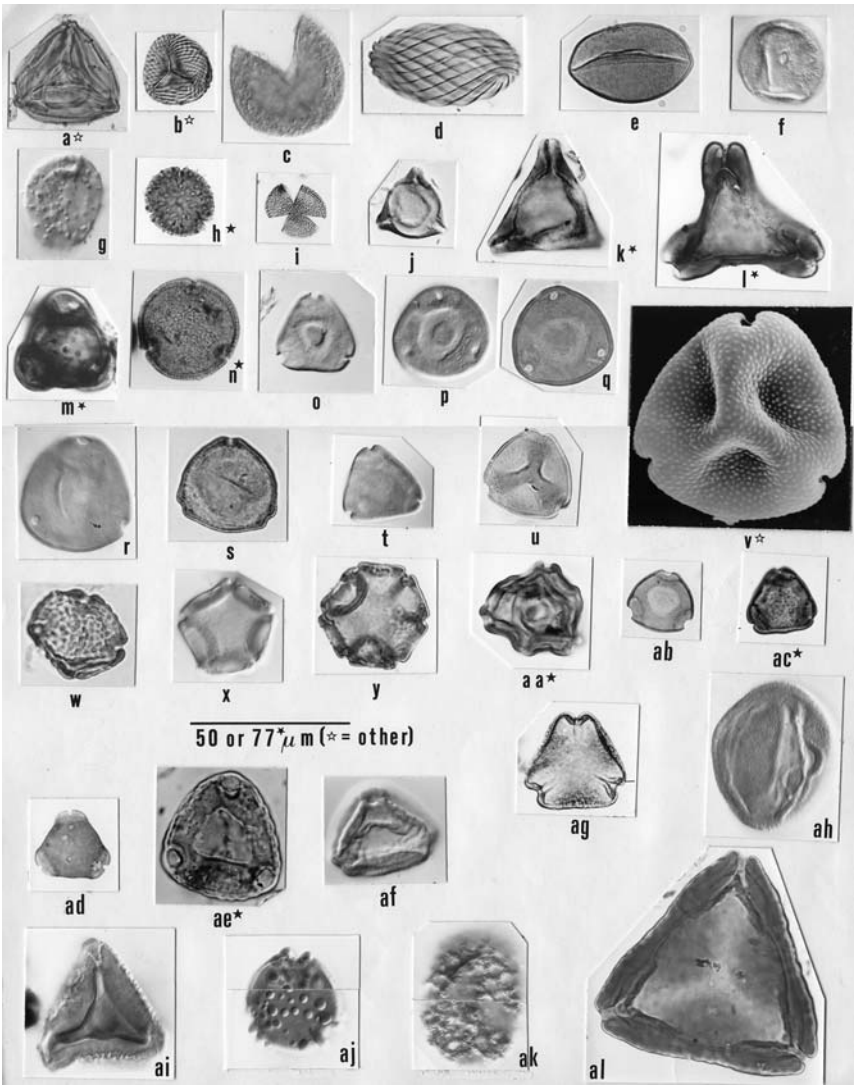

Figure 14.2 Some characteristic Paleocene spores and pollen. Magnification indicated by bar under (x) and (y), except for (a),(b) and (v), the sizes for which are given with the names of the taxa. (N.E.R. = Paleocene levels of DSDP cores at Ninetyeast Ridge, Indian Ocean; T.R.F.U. = Tongue River Member, Fort Union Formation, late Paleocene of Wyoming and Montana; E.F. = Evanston Formation, early Paleocene, Wyoming; W.G. = Wilcox Group, late Paleocene, Texas. (**a**) *Appendicisporites crassicarnatus* Harris. Proximal view, spore 48 μm, N.E.R. (species typical of Paleocene levels, but this particular specimen is from an Eocene-Oligocene level in N.E.R.). (**b**) *Cicatricosisporites* sp. Proximal view, spore 70 μm (note small magnification), W.G. (**c**) *Taxodiaceaepollenites* sp. Lateral view showing

Figure 14.2 characteristic splitting-open, T.R.F.U. (see also (f)). (**d**) *Equisetosporites jansonii* Pocock. A polyplicate form, W.G. (**e**) *Arecipites pseudotranquillus* Nichols *et al*. Distal view of monosulcate grain, W.G. (**f**) *Taxodiaceaepollenites* sp. Distal view of germinal papilla (not a pore), T.R.F.U. (see also (c)). (**g**) *Pandaniidites radicus* Leffingwell. Interference contrast photo, showing the baculate sculpture, T.R.F.U. (**h**)? *Tubulifloridites* sp. Polar view, N.E.R. (**i**) *Tricolpites* sp. Polar view, E.F. (**j**) *Nudopollis terminalis* (Thomson & Pflug) Pflug. Polar view, W.G. ((j)-(m) and (ai) are representative of continuing Normapolles influence in the Paleocene.). (**k**) *Nudopollis endangulatus* (Pflug) Pflug. Polar view, late Paleocene, South Carolina. (**l**) *Choanopollenites discipulus* Tschudy. Polar view, early Paleocene, Alabama. (**m**) *Interporopollenites turgidus* Tschudy. Polar view, early Paleocene, Missouri. (**n**) *Intratriporopollenites pseudinstructus* Mai. Polar view, late Paleocene, South Carolina. (**o**) *Momipites leffingwellii* Nichols & Ott. Polar view of juglandaceous form thought by Nichols to be ancestral to *Caryapollenites*, E.F. (**p**) *Caryapollenites veripites* (Wilson & Webster) Nichols & Ott. Polar view, interference contrast photo emphasizing the "moat-and-island" in the center of the polar area (see (q)), T.R.F.U. (**q**) Same species as (p). Bright field photo showing opercula on pore membranes, W.G. (**r**) *Caryapollenites imparalis* Nichols & Ott. Polar view, interference contrast photo, T.R.F.U. (**s**) *Triporopollenites* sp. Polar view, W.G. (**t**) *Momipites wyomingensis* Nichols & Ott. Polar view, T.R.F.U. (**u**) *Momipites wodehousei* Nichols. Polar view, W.G. (**v**) *Momipites triradiatus* Nichols. Polar view, SEM micrograph, grain 24 μm, W.G. (**w**) *Ulmipollenites undulosus* Wolff. Polar view of 5-stephanoporate form, W.G. (**x**) *Alnipollenites verus* Potonié. Polar view, interference contrast photo, emphasizing the arci (thickened bands arching between pores), T.R.F.U. (**y**) *Alnipollenites* sp. Polar view, bright field, (see (x)), W.G. (**aa**) *Paraalnipollenites confusus* (Zaklinskaya) Hills & Wallace. Distorted polar view, late Paleocene, Alabama. (**ab**) *Momipites tenuipolus* Anderson. Polar view, showing thinned polar area and large vestibules associated with pores, W.G. (**ac**) *Pseudoplicapollis serena* Tschudy. Polar view, showing vestibular areas around pores, early Paleocene, South Carolina. (**ad**) *Momipites dilatus* (Fairchild) Nichols. Polar view, W.G. (**ae**) *Interpollis paleocenica* (Elsik) Frederiksen. Polar view, early Paleocene, South Carolina. (**af**) *Ulmipollenites tricostatus* (Anderson) Frederiksen. Polar view, interference contrast photo, T.R.F.U. (**ag**) *Nyssapollenites* sp. Showing the tricolporate form clearly even in polar view, W.G. (**ah**) *Nyssapollenites* sp. Equatorial view, interference contrast photo, T.R.F.U. Despite reference to same form-genus, this form clearly lacks the sort of clearcut pore (ag) would display in equatorial view. (**ai**) *Insulapollenites rugulatus* Leffingwell. Polar view, interference contrast photo showing the syncolpate morphology, T.R.F.U. (**aj**) *Pistillipollenites mcgregorii* Rouse. Polar view. Two-level mosaic interference contrast photo, the top part showing lower level focus and the arrangement of gemmae around one of the three pores, T.R.F.U. (**ak**) *Erdtmanipollis pachysandroides* Krutzsch. Two-level mosaic interference contrast photo, showing the muri of the reticulum consisting of small exine blocks, T.R.F.U. (**al**) *Choanopollenites eximius* Stover. Polar view of very large Normapolles-type pollen (see also (l)), W.G. Forms identified as N. E. R. are courtesy of E. M. Truswell, in whose paper (Kemp and Harris, 1977) they were originally described; forms identified as T.R.F.U. are courtesy of David Pocknall; forms identified as W. G. are courtesy of D. J. Nichols; all other photos are courtesy of N. O. Frederiksen, and some of them appeared in Frederiksen (1980a).

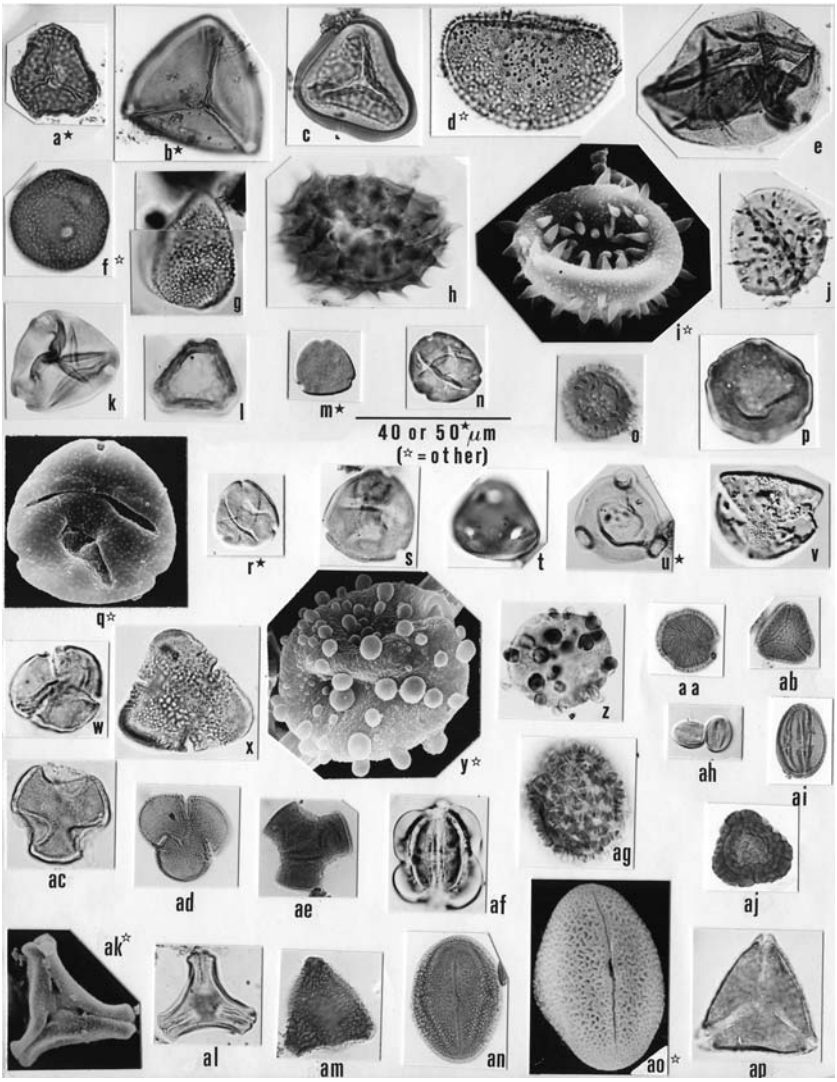

Figure 14.3 Representative Eocene and Eocene-Oligocene sporomorphs. In addition to the forms shown, bisaccate coniferous pollen resembling modern genera is common. Magnification shown by bar under (m)-(n). A few forms are at other magnifications, and their size is given in the caption. Some of the forms are from Eocene to Oligocene levels of DSDP cores at Ninetyeast Ridge, Indian Ocean (N.E.R.). Some others are from the Middle Eocene of San Diego, California (M.E.S.D.). The others are separately identified. (**a**) *Foveotriletes palaequetrus* Partridge, proximal view, N.E.R. (**b**) *Deltoidospora* sp. Proximal view, N.E.R. (**c**) *Polypodiaceoisporites* cf. *tumulatus* Partridge. Proximal view, showing pronounced labra along the laesural rays and heavily sculptured interradial contact

Figure 14.3 areas, N.E.R. (**d**) *Punctatosporites. varigranulatus* Kemp. Lateral view of monolete spore, length 42 μm, N.E.R. (Because such monolete spores are very generalized, this generic name is used for monolete spores from Carboniferous to Cenozoic! *Deltoidospora* for smooth trilete spores such as (b) is also a much used generic name.) (**e**) *Araucariacites australis* Cookson. A collapsed, thin-walled P00 form, such as several extant conifers make, N.E.R. (**f**) *Milfordia hungarica* (Kedves) Krutzsch. Distal view of this P01, diameter 42 μm, M.E.S.D. (Such Restionaceae-like forms presage modern grass pollen.) (**g**) *Longapertites* sp. Composite photomicrograph of two focal levels, length 35 μm, M.E.S.D. (a pear-shaped Pa0). (**h**) *Mauritiidites* sp. Distal view, length 42 μm, M.E.S.D. (echinate Pa0's resembling this are found among modern palms). (**i**) *Echiperiporites rotundus* Kemp. P03-echinate, pore showing at lower left, SEM micrograph, diameter 20 μm, N.E.R. (see (o)). (**j**) *Pandaniidites* sp. Early Eocene, Wyoming. (**k**) *Plicatopollis plicata* (Potonié) Krutzsch. Polar view, showing vestibulate pore structure, early or mid-Eocene, Wyoming. (**l**) *Ulmipollenites tricostatus* (Anderson) Frederiksen. Polar view, early Eocene, Wyoming. (**m**) *Momipites coryloides* Wodehouse. Polar view, early Eocene, Wyoming. (**n**) *Platycarya platycaryoides* (Roche) Frederiksen & Christopher. Polar view, showing characteristic curving arcoid streaks (= pseudocolpi) (see (q)), early Eocene, Wyoming. (**o**) *Echiperiporites rotundus* Kemp. Photomicrograph for comparison with SEM micrograph of (i), diameter 19 μm, N.E.R. (**p**) *Polyatriopollenites vermontensis* (Traverse) Frederiksen. Polar view of stephanoporate form, early or mid-Eocene, Wyoming. (**q**) *Platycarya platycaryoides* (Roche) Frederiksen & Christopher. Polar view, SEM, of P03 for comparison with (n) and (r), diameter 18 μm, early Eocene, Wyoming. (The pseudocolpi are thin-walled depressions.) (**r**) Same data as for (q). Photomicrograph. (**s**) *Platycarya* sp. Mid-Eocene, Mississippi (see (n), (q), and (r)). (**t**) *Anacolosidites reklawensis* Elsik. Polar view of periporate form (six-pored, three pores on each hemisphere), early Eocene, Alabama. (**u**) *Corsinipollenites oculis-noctis* (Thiergart) Nakoman. Polar view of onagraceous-type pollen with remains of viscin threads near the pole, M.E.S.D. (**v**) *Dicolpopollis* sp. Polar view of odd dicolpate form, early Eocene, Alabama. (**w**) *Tricolpites* sp. Polar view, mid-Eocene, Wyoming. (**x**) *Bombacacidites nacimientoensis* (Anderson) Elsik. Polar view, M.E.S.D. (The colporate apertures are situated not at the angles of the amb–the more normal position–but midway between them; this is a normal apertural position for Bombacaceae.) (**y**) *Pistillipollenites mcgregorii* Rouse. SEM micrograph (compare with photomicrograph in (z)), diameter 28 μm, early Eocene, Wyoming, characteristic gemmate sculpture. The grain is P03; Crepet & Daghlian (1981) showed this dispersed pollen form to have been produced by an extant plant belonging to the modern gentian family. (**z**) Same data as for (y) (**aa**) *Simpsonipollis mulleri* Kemp. Polar view, striate sculpture, N.E.R. (**ab**) *Myrtaceidites* sp. Polar view of Pcs form similar to extant Myrtacese, N.E.R. (**ac**) *Cercidiphyllites* sp. Polar view, mid-Eocene, Wyoming. (**ad**) *Tricolpites reticulatus* Cookson. Polar view, N.E.R. (The generic name "*Tricolpites*" really isn't very helpful, as a wide range of more or less Brevaxones tricolpate forms can be put in it–see (w) and (ae); note also that though this taxon is common in the Eocene, this specimen came from a Paleocene level at N.E.R.) (**ae**) *Tricolpites asperamarginis* McIntyre. Polar view of form with gaping colpi, N.E.R. (**af**) *Nuxpollenites crockettensis* Elsik. Equatorial view of form with extraordinarily thickened ektexine, mid-Eocene, Alabama. (**ag**) *Erdtmanipollis pachysandroides* Krutzsch. This displays the characteristic blocks of ektexine making up the surface reticulum, M.E.S.D.

but living far out of the modern range of those families. The cooler circumstances of Oligocene time are reflected in the first abundant appearance of grass and grass-like pollen (the first reliable record of grass pollen is Paleocene) and of composite pollen (Muller, 1981). Fig. 14.5 illustrates some characteristic Oligocene spores/pollen.

5 Fungal Spores in the Paleogene

The fungi have a long fossil record, probably back to the Precambrian Bittersprings Limestone Chert, Australia, about one billion years old (Schopf, 1968; Schopf and Blacic, 1971). Butterfield (2005) describes maceration-resistant forms which he refers to *Tappania* and attributes to the fungi from late Proterozoic rocks of NW Canada. They could also be interpreted as acritarchs, however. An assemblage of maceration- resistant, probable ascomycete fungi, consisting of both spores and hyphae, has been documented from the Silurian (Ludlow) of Sweden (Sherwood-Pike and Gray, 1985). This find is somewhat perplexing because it is so far removed in time from other resistant-walled fungal remains. Fungi were certainly well established by Carboniferous time: many and well preserved fungal remains have been reported from Pennsylvanian coal balls, e.g., by Stubblefield *et al*. (1983). *Microsporonites cacheutensis* Jain, from Permian and Triassic rocks (Jain, 1968; Ecke, 1984) may very well be a chitinous-walled fungal spore. Nevertheless, robust chitinous-walled fungal disseminules, separable from the substrate rock by maceration have not been regularly encountered in palynological macerations older than late Jurassic (Elsik, personal communication, 1982). Traverse and Ash (1994) found a well preserved suite of fungal

Figure 14.3 (**ah**) *Cupuliferoidaepollenites minutus* (Brenner) Singh. Equatorial views of small, more or less smooth tricolporoidate, probably fagalean forms that characterize many parts of the Cenozoic, early Eocene, Wyoming. (**ai**) *Rhoipites microluminus* Kemp. Equatorial view, N.E.R. (see also (an) and (ao). (*Rhoipites* is a broad form-generic concept for such Pc3 forms, a very generalized dicot pollen type common throughout the Cenozoic.) (**aj**) *Myrtaceidites oceanicus* Kemp. Polar view of Pcs pollen with heavy verrucate sculpture, N.E.R. (**ak**) *Gothanipollis* cf. *gothanii* Krutzsch. Polar view, an oddly syncolporate form., SEM micrograph for comparison with photomicrograph in (al), diameter 24 μm, N.E.R. (**al**) Photomicrograph. Same data as for (ak). (**am**) *Proteacidites* cf. *symphonemoides* Cookson. Polar view, N.E.R. (**an**) *Rhoipites grandis* Kemp. Equatorial view for comparison with (ao), N.E.R. (**ao**) Same data as (an). SEM micrograph, length 45 μm. (**ap**) *Boehlensipollis* sp. Polar view of Pcs with very small polar area, middle Eocene, Wyoming. Photos identified as N.E.R. are courtesy of E. M. Truswell, in whose paper (Kemp and Harris, 1977) many of them originally appeared; all photos identified as M.E. S. D. appeared originally in. Frederiksen (1983). Most of the rest of the photos are courtesy of N. O. Frederiksen, but (m), (q), (r), (y), and (ah) are courtesy of D. J. Nichols.

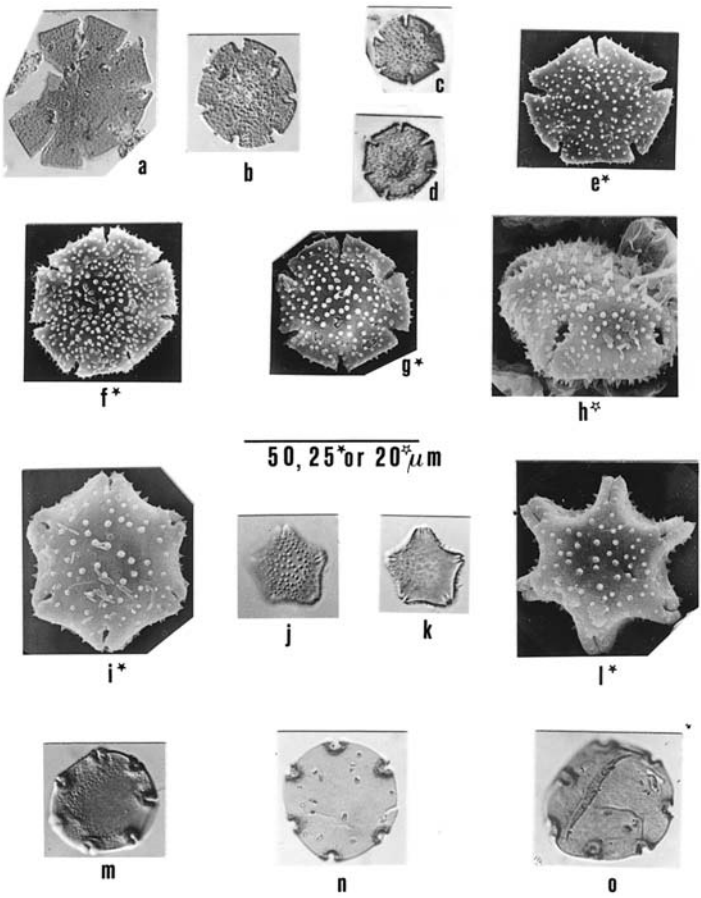

Figure 14.4 *Nothofagidites*, an important constituent of Southern Hemisphere latest Cretaceous and Cenozoic palynofloras. This pollen type is clearly represented in the extant flora by the southern beech, *Nothofagus*. The pollen of *Nothofagus* is very distinctive and diagnostic, but the fossils are usually referred to the form-genus, mostly on the general and debatable principle held by most that fossil material should never be placed in an extant genus. Nevertheless, the range of *Nothofagidites* is assumed to indicate that the genus *Nothofagus* extends back to the Santonian (late Cretaceous) (Muller, 1981). *Nothofagus* (and *Nothofagidites*) pollen is referable to three groups or types (Cookson, 1959): 1. *menziesii*-type (a), with unrimmed, usually gaping colpi; 2. *brassi*-type (b)-(l), relatively small, more or less angular amb, the colpus margins firm though unthickened (it is this type that extends back to Santonian; the other two types begin in the Maestrichtian.); 3. *fusca*-type (m)-(o), rimmed apertures, actually colpate but resembling pores. Magnification shown by bar under (g). The specimens come from: sub-basaltic sediments at Bungonia, New South Wales, Australia, early Eocene (N.S.W.); Ulgnamba Lignite, Hale River Basin, central Australia, middle to late Eocene (C.A.); Ross Sea, Antarctica, recycled specimens

spores in Early to Middle Jurassic rocks of western North America. They become somewhat more abundant during early Cretaceous time and are first really abundant and diverse by late Cretaceous and Paleogene time. Kalgutkar *et al.* (1993) and Kalgutkar and Sigler (1995) reported Late Cretaceous to Oligocene fungal floras from India and Canada. In Neogene and Quaternary sediments they are abundant when environmental circumstances provide the organic matter on which the ascomycete fungi that make almost all fossil fungal spores feed. This rise of chitinous-walled fungal parts is so coincident with the origin and rise to dominance of the angiosperms that it is logical to wonder if there might not be a connection, such as adaptation to requirements of parasitizing, digesting or otherwise making a living from the flowering plants.

Fungi can and do live in all sorts of substances, including, for example, palynological samples. When I first worked on a sample of Brandon Lignite in 1947, the sample was one that had long been stored in the Harvard Museum. The palynological residue was rich in a variety of fungal spores. However, freshly collected samples obtained the next summer yielded no or relatively few fungal spores. Elsik (1976) and others have pointed out, however, that this fact does not at all preclude the stratigraphic use of fungal spores. It is possible to prevent fungal growth in samples by storing them in alcohol or protecting them with some other fungiostatic substance such as a dilute solution of phenol, or by storing them frozen. In my experience, hardly any palynologists routinely do this for rock samples. More importantly, however, the fungi, especially ascomycetes, produce

Figure 14.4 of uncertain age (R.S.). All except (h) are polar views. (**a**) *Nothofagidites asperus* (Cookson) Stover & Evans, R.S. (**b**) *Nothofagidites lachlanae* (Couper) Truswell. 7-colpate form with bluntly echinate sculpture, interference contrast, R.S. (**c**),(**d**) *Nothofagidites* spp. Two gold- coated specimens prepared for SEM, interference contrast, showing that light microscopy is possible on such specimens without removal of gold, N.S.W.; (**c**) same specimen as (g); (**d**) same specimen as (f). (**e**) *Nothofagidites emarcidus* (Cookson) Harris. SEM micrograph, a 5-colpate specimen showing the broad-based spines, N.S.W. (see also (g),(j), and (k)). (**f**) *Nothofagidites vansteenisi* (Cookson) Stover & Evans. SEM micrograph. A 7-colpate specimen, N.S.W. (**g**) *Nothofagidites emarcidus* (Cookson) Harris. SEM micrograph. A 6-colpate form. (**h**) *Nothofagidites* sp. Probably *N. emarcidus*. SEM micrograph, obliquely equatorial view, showing at higher magnification the broad-based biform echinae and the relatively simple colpal structure, C.A. (**i**) *Nothofagidites falcatus* (Cookson) Stover & Evans. SEM micrograph, C.A. (**j-k**) *Nothofagidites emarcidus* (Cookson) Harris. Interference contrast, two levels of focus, (see (e) and (g)), C.A. (**l**) *Nothofagidites falcatus* (Cookson) Stover & Evans. SEM micrograph of form with protruding colpal structures, C.A. (**m**) *Nothofagidites* sp. Fusca-type with pore-like colpi, N.S.W. (**n**) *Nothofagidites* sp. Corroded specimen, 6-pored form, R.S. (**o**) cf. *Nothofagidites flemingii* (Couper) Potonié. Shows folds developed by thin-walled specimens, R.S. All pictures and identifications are courtesy of E. M. Truswell and M. Dettmann. (a), (b), and (o) appeared in Truswell (1983).

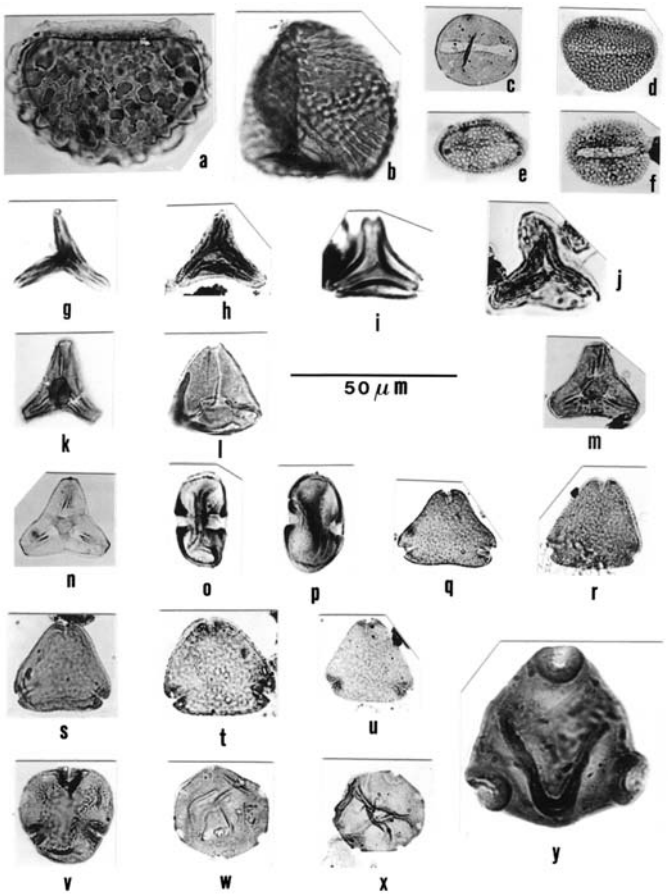

Figure 14.5 Typical middle Oligocene pollen and spores from boreholes in the Bristol Channel, England. By Oligocene time most sporomorphs are very similar to spores or pollen of extant genera and can with some degree of confidence be referred to extant families. Nevertheless, most paleopalynologists use form-generic names for Oligocene sporomorphs. Usually specific names are used with the form-generic names, but opinion is divided as to the usefulness of such specific names in the Oligocene. Most of these photos are from Boulter and Craig (1979). Boulter and Craig did not use specific names for these forms, only giving form-generic references. Magnification indicated by bar under (i). (**a**) *Polypodiidites* Ross. Monolete spore, lateral view. (**b**) *Cicatricosisporites* Potonié & Gelletich. Trilete spore, obliquely proximal view. (**c**) *Monocolpopollenites* Pflug & Thomson. Monosulcate pollen, distal view. (**d**) *Arecipites* Wodehouse. Monosulcate pollen, proximal view, mid-focus. (**e**) *Arecipites* (see (d)). Proximal view, high focus. (**f**) *Arecipites* (see (d)). Distal view, high focus. (**g**) *Boehlensipollis* Krutzsch. Polar view of this oddly tricolpate, nearly syncolpate pollen grain. (**h**) *Boehlensipollis* (see (g)). A form that is apparently fully syncolpate. (**i**) *Boehlensipollis* (see (g)). A form with

many kinds of very distinctive spores and spore-like bodies. They have evolved rapidly during the Cenozoic, with many forms useful as boundary markers, such as are found at the top of the Paleogene. Since they cannot be confused with extant fungi. the Cenozoic range of some species of these genera is potentially very useful stratigraphically. Parsons and Norris (1999), for example, demonstrate the utility of fungal spores for stratigraphy in Paleogene sections in northern Canada. Modern contaminating fungal spores in, say, an Eocene sample are only an annoyance. It is true, however, that fungal spores are a very abundant constituent of the palynomorph load in the modern atmosphere. *Alternaria*-type spores (Fungi Imperfecti) are an important pollinosis vector, and various fungal spores in toto may in some situations be as abundant as embryophytic spores/pollen encountered in spore/pollen traps used by aerobiologists (see Ogden *et al*., 1974). Presence of fungal spores in Pleistocene samples may be an indication that the sample has been extensively degraded and is no longer good for radiocarbon dating of bulk sediment (C. W. Whitlock, personal communication, 1986).

Especially for this reason, samples for radiocarbon analysis should be frozen after collection.

W. C. Elsik, the nestor of fungal palynology (see Fig. 14.7) presented a useful classification of fungal palynomorphs, based on the principal morphologic features of fungal spores and hyphae, permitting their description and separation. The classification, shown here in Fig. 14.6, is simplified from Elsik (1979).

Figure 14.5 kyrtome-like structures. (**j**) *Boehlensipollis* (see (g)). A more robust form. (**k**) *Gothanipollis* Krutzsch. Polar view of tricolpate pollen with weakly developed apertures. The pollen is most characterized by the "trilete" ridge structure, and by the "polar pad" showing as a dark oval in center of photo. (**l**) *Boehlensipollis* (see (g)). A less angular form. (**m**) *Gothanipollis* (see (k)). (**n**) *Gothanipollis* (see (k)). A form in which the 'polar pad" is tri-pronged. (**o**) *Mediocolpopollis* Krutzsch. Tricolporate pollen in which the exopores and endopores are much more prominent than the colpi, prominent costal thickenings, equatorial view. (**p**) *Mediocolpopollis* (see (o)). Equatorial view showing the sinuous costal thickenings. (**q**) *Porocolpopollenites* Pflug. A tricolporate form with very short colpi and therefore large polar areas. Polar view. Some extant members of the extant family Symplocaceae make very similar pollen. (**r**)-(**u**) *Porocolpopollenites* (see (q)). (**v**) *Tiliaepollenites* Potonié. A tricolporate form in which the costal thickenings give the grain a "padded triporate" appearance in polar views such as this. Virtually identical with extant *Tilia* pollen. (**w**) *Polyatriopollenites* Pflug. A 6-stephanoporate form in polar view, each pore provided with an annular thickening. Practically identical pollen is produced by the extant genus Pterocarya (Juglandaceae). (**x**) *Polyatriopollenites* (see (w)). A seven-pored specimen. (**y**) *Corsinipollenites* Nakoman. With "automobile tire"-like thickenings around the pore structures, polar view. Virtually identical pollen is made by members of the extant Onagraceae. Photos courtesy of M. C. Boulter; all but (y) appeared originally in Boulter and Craig (1979).

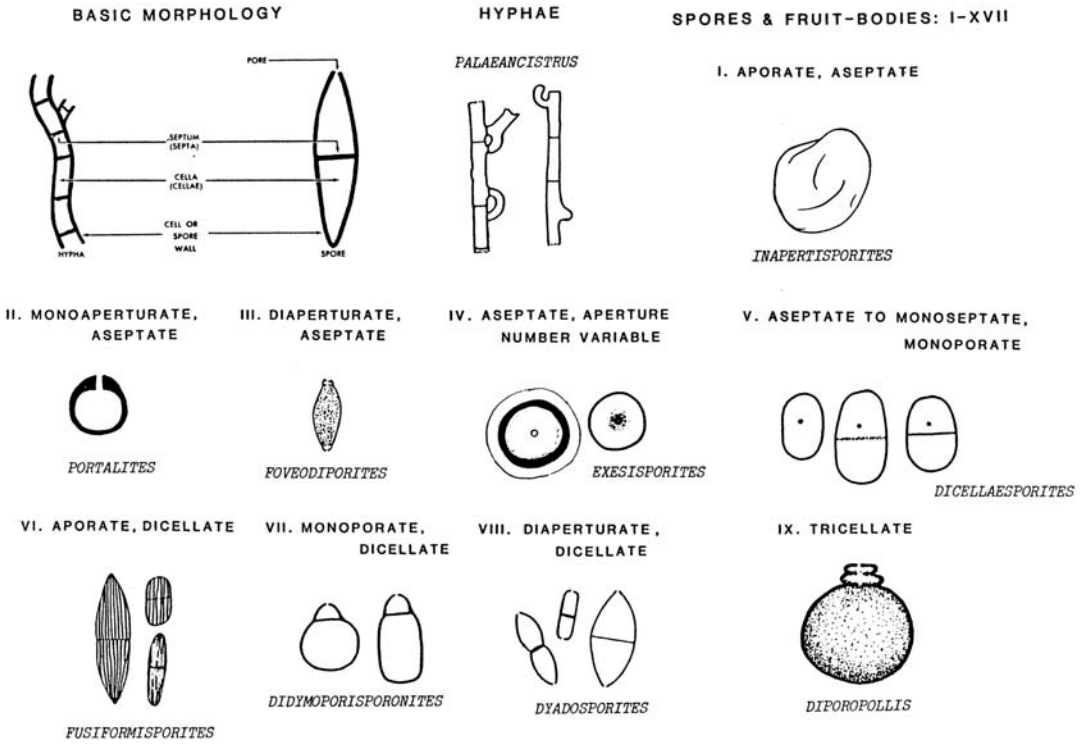

Figure 14.6 *(See caption on page 407)*

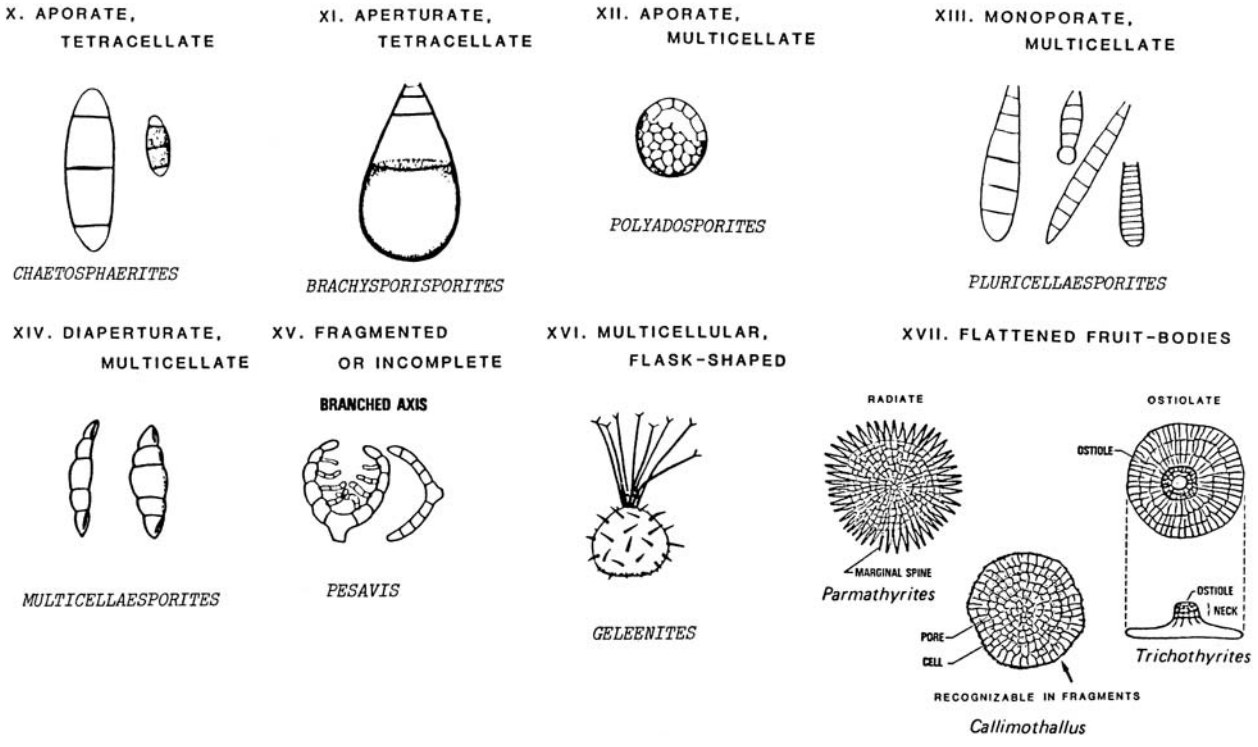

Figure 14.6 Simplified Elsik classification of fungal palynomorphs. Only one example is shown for each large class. In the expanded version of the classification, each class is subdivided into a number of sub-units, based on smaller morphological feathres, and on sculpture. See Fig. 14.8 for photomicrographs of fossil representatives of some of the classes.

Figure 14.7 William C. Elsik, born 1935, in his laboratory at Exxon Co., Exploration Department, Houston, Texas, 1985. Elsik more than any other person has been responsible for promoting the systematic study and stratigraphic use of fossil fungal spores, fruiting bodies and hyphae. Photo courtesy of W. C. Elsik.

It must be emphasized that "spore" is a very general term that palynologists have come to think of as representing only the meiotically derived spores of the embryophytic plants. Fungal "spores" are many sorts of propagules: unicellular, multicellular; sexual, asexual. The chitinous-walled fungal propagules we encounter as palynomorphs are prevailingly produced by ascomycetes and imperfect fungi, although basidiomycetes also occur. Uncarbonized fungal spores in recent sediments are usually a darker color than sporopolleninous exines from the same sample. This color results from a melanin pigment (Elsik, personal communication). However, fresh fungal spore walls can also be colorless (see Fig. 18.1).

Fig. 14.8 illustrates some of the important Paleogene fungal forms. The multicellular fructifications (= "fruit bodies") and the germlings of the epiphyllous family Microthyriaceae (Ascomycetes) are especially characteristic of some Paleogene sediments. Fossil fungal spores are often referred to artificial form-genera, the names of which stress the number of pores and/or cells, or chambers (they usually communicate by holes in the septa between chambers): *Diporicellaesporites, Monoporisporites, Dicellaesporites,* etc. The pores (see Fig. 14.6) at the ends of fungal spores may be either true exit-pores or traces of the attachment point of the spore to the producing organ. (Ascospores are formed free in an ascus and lack attachment scars; most other fungal spores have them.) "Germinals," more or less random openings on the sides of fungal spores, may be produced

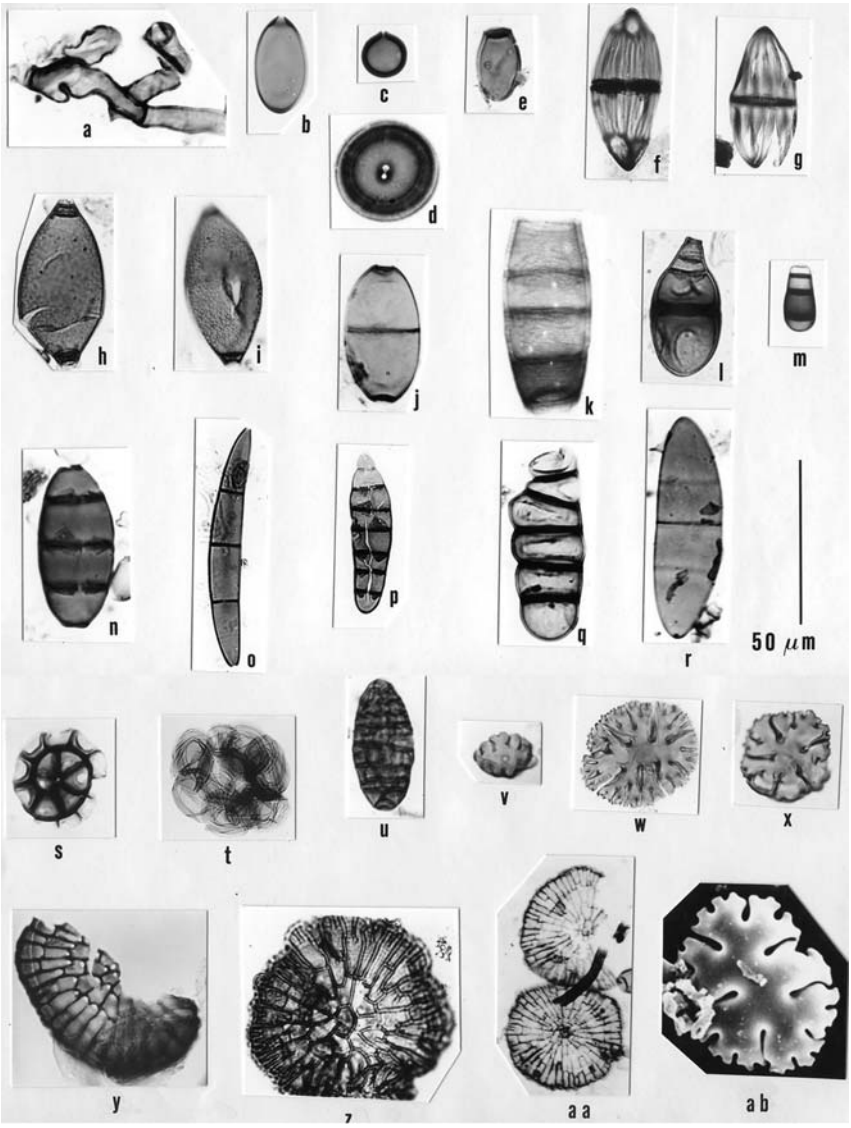

Figure 14.8 Fossil fungal spores, fruiting bodies and hyphae. Although the kingdom Fungi has a fossil record back to the Proterozoic, chitinous-walled, "robust," fungal remains that survive maceration are not abundant until the Cretaceous. They especially characterize the Cenozoic, from which these specimens were obtained. Compare with Fig. 14.6 for the abbreviated Elsik classification according to which these fossils are mostly arranged. All specimens except (b),(c), (f),(g), (k), (m), (p), (s),(t) (x), and (y) come from Eocene-Oligocene levels of Deep Sea Drilling Project Site 254, Ninetyeast Ridge, Indian Ocean. (b),(c), etc., are also Cenozoic, as separately noted. (**a**) Branching,

by bio-solution from within the wall, and there may be one or several such "germinals," in addition to the fixed pore. Where as pores are often accentuated by processing, septa are sometimes lost in fossilization or during laboratory processing (Elsik, 1979). For paleopalynological purposes, an observable opening in a fungal spore is a "pore" regardless of original biological function. Most fossil fungal spores are inaperturate or monoporate. (Fungal hyphae and mycelia occur abundantly in palynological macerations of Cenozoic sediments, especially those of deltaic origin.) The maceration process for fungal spores is the same as for sporopolleninous sporomorphs. Fungal spores seem in my experience to be a little more resistant to geothermal alteration and to oxidation than are sporopolleninous fossils. They occur reasonably well preserved in some Franciscan Melange samples from California, in which most of the embryophyte spores and dinocysts are badly carbonized. However, Elsik (personal communication) says that fungal spores may be either more *or* less resistant to both carbonization and oxidation, depending on as yet poorly understood factors. He also says that fungal spores do not change gradually in color as carbonization progresses but instead become suddenly black. They take biological stains only if they have been oxidized.

◄

Figure 14.8 septate hyphae. (**b**) *Polyporisporites* sp. Despite the name, a monoporate form, middle Eocene, Arkansas. (**c**) *Portalites* sp. Monoporate, middle Eocene, Arkansas. (**d**) *Exesisporites* sp. Pore number variable (1-2), Paleogene, Arkansas. (**e**) *Monoporisporites* abruptus Sheffy & Dilcher. Monoporate. (**f**) *Fusiformisporites* sp. Aporate, dicellate, Eocene, Texas. (**g**) *Fusiformisporites crabbii* Rouse. Aporate, dicellate, Paleogene, Texas. (**h**) *Foveodiporites anklesvarensis* Varma & Rawat. Diporate. (**i**) Same as (h). Different specimen, interference contrast photo emphasizing dense internal granulation of wall. (**j**) *Dyadosporites* sp. Diporate, dicellate. (**k**) *Diporicellaesporites* sp. High focus showing transverse sculptural striae of the wall, mid-Eocene, Arkansas. (**l**) *Brachysporisporites pyriformis* Lange & Smith. Monoporate, tricellate. (**m**) *Brachysporisporites* sp. (see (l)). Eocene, Texas. (**n**) *Diporicellaesporites* sp. Shows flaps of ruptured septa. (**o**) *Diporicellaesporites* sp. (**p**) *Pluricellaesporites* sp. Monoporate, multicellate, Paleogene, Arkansas. (**q**)?*Pluricellaesporites* sp. A phragmospore (one with 2 or more transverse septa) of uncertain relationship. (**r**) A tetracellate spore. Non-porate, dicellate but with "shadow bands" suggestive of incipient or incomplete additional septa. (**s**) *Involutisporonites* sp. Spiral form, multicellate, mid-Eocene, Arkansas. (**t**) *Polyadosporites* sp. Aporate, multicellate, Paleogene, Arkansas. (**u**) *Dictyosporites* sp. Multiple cells in irregular series. (**v**) *Desmidiospora* type. Invaginations and central hyaline spot characteristic (see (w)-(ab)). (**w**) Same as (v). More developed stage (see (v), and (x)-(ab)). (**x**) *Desmidiospora* type. As (v),(w), late Eocene, Texas. (**y**) *Callimothallus pertusis* Dilcher. Microthyriaceous flattened fruit body, recognizable even from fragments; note pores in the individual cells. (**z**) *Paramicrothallites* sp. Microthyriaceous, flattened fruit body. (**aa**) *Paramicrothallites* sp. (see (z)). (**ab**) *Desmidiospora* type. SEM. Photos (b), (c), (f), (g), (k), (m), (p), (s), (t), (x), and (y) are courtesy of W. C. Elsik; all other photos courtesy of E. M. Truswell, reprinted from a paper by her (Kemp, 1978).

Muller (1959) noted some time ago elevated abundance of fungal spores in sediments of the Orinoco River Delta, and I have observed in my research on recent sediments a similar phenomenon in Gulf Coast, USA, deltas. Fungal spores are abundant in sediments in which organic matter (such as wood fragments, cuticles, and other tissue pieces) abound, presumably as a reflection of saprophytic fungi at work. Deltaic sediments provide such substrates.

The study of Paleogene and Neogene fungal spores deserves much more attention, as studies by palynologists such as Smith (1978) in England, Ediger (1981) in Turkey, and Germeraad (1979) in Jamaica have shown. Smith comments on the obviously difficult nomenclatural problem with (usually multicellular) fungal spores ("fruit bodies") because of their great variability in form. The massive synopsis-book by Kalgutkar and Jansonius (2000) on fossil fungal spores is an invaluable aid in studying the fungal spores that are so frequently significant in work on Cenozoic sediments. I would also recommend consultation of Plates 1-12 on Chinese fossil fungal spores in the book by Song *et al.* (1999).

6 Taxonomy and Nomenclature of Paleogene Spores/Pollen

An outsider to our field might expect that, in the "Cenophytic"-Cenozoic, the difficult problems of classifying and naming fossil sporomorphs would become somewhat easier because the fossils belong prevailingly to the Angiospermae and to extant ferns and conifers. On the contrary, however, the paleopalynological taxonomic problems in the Cenozoic are the worst of all, and this has always been true. The most important reasons for this perplexing situation are as follows.

6.1 Identity Problems *per se*

Even extant angiosperm pollen is for the most part only identifiable to the genus (sometimes only to the family). For all we know, this is also true of, say, Devonian spores, but palynologists feel less compunction about frequent genus transfers, such as *Spelaeotriletes lepidophytus* (Kedo) Streel = *Retispora lepidophyta* (Kedo) Playford = *Hymenozonotriletes lepidophytus* Kedo in the Devonian, than they do about referring an Oligocene pollen grain to *Nyssa* today and some other genus tomorrow. For most palynologists, use of form-generic names is somehow less controversial than risky use of a perhaps incorrect modern generic name.

6.2 Scarcity of Fossil Angiosperm Flowers

Another sort of identity problem with angiosperms is that relatively few fossil angiosperm flowers have been found; therefore, identification of fossil angiosperm pollen has so far depended mostly on comparison with modern reference material.

6.3 Mosaic Evolution and Problems of Range

It has long been recognized that the various organs of angiosperms have evolved at different rates; this is called "mosaic" evolution. Pollen resembling the pollen of an extant genus might come from a plant that was otherwise quite different, although, in the Cenozoic, fossil flowers have usually yielded pollen not too unlike the pollen of modern relatives of the flower-producing plants (see Crepet, 1979). On the other hand, Wing (1981) and Hickey and Wing (1983) reported early Cenozoic *Platycarya* pollen and other organs coming from plants with leaves not referable to *Platycarya* or in some cases even to its family, Juglandaceae. Potonié (1951, 1956b, 1975) long ago warned about this problem as part of his bill of particulars against use of extant generic names for fossil pollen. As Potonié put it, to describe fossil pollen as a species of an extant plant genus "unfairly" expands the circumscription of plants referable to that genus, which is limited by the type specimen of that genus of modern plants.

It should also be noted that, during the Cenozoic, angiosperm genera were rearranging their distributions more than they were becoming extinct or evolving new forms. (In this connection, it is important to remember that palynology really can dependably recognize only generic differences.) For example, Germeraad *et al*. (1968) show the ranges of taxa of Cenozoic palynomorphs used in practical stratigraphy by Royal Dutch/Shell, and it is clear that many forms have quite different ranges when the forms are studied in the Caribbean, West Africa, and the Indonesia area.

6.4 Philosophic-Taxonomic Considerations

Some object that, as the pollen grain is a haploid organ representing only the brief gametophytic segment of the life cycle, it is inappropriate to refer fossil pollen to extant genera, or to create species of such genera for fossil pollen. As I have noted above, some say this represents an unfair extension of the circumscription of extant taxa. Of course, bryologists have always based taxa on gametophytic-haploid information, and megafossil paleobotanists have for a century without controversy referred fossil leaves to extant genera, often as "leaf-genera" thereof.

Potonié was the primary writer on these matters, and his prolific productivity of publications on the subject has substantially carried the day. It is largely forgotten that his earlier writings on the question of what to do with Cenozoic spores/pollen were badly confused about the purpose and methods of botanical nomenclature. He long advocated what amounted to three parallel systems of classification and nomenclature:

(a) *Natural*, where reference to extant taxa is certain. The modern generic name could be used, but naming of new species based on fossil pollen was to be avoided. Example: *Pinus silvestris*.

(b) *Half-natural*, where reference to an extant taxon is suspected but not proven. A generic name is coined that purports to show the alleged relationship. Example: *Betulaceaepollenites*.
(c) *Artificial*, where the relationship is not known at all, and a form-generic name based on morphological features is created. Example: *Tetracolporites*.

Erdtman, not a paleopalynologist, had ideas very similar to Potonié's on these matters (see Potonié *et al*., 1950). Erdtman objected to the use of extant generic names for fossil pollen–at least, pre-Pleistocene. He perhaps was even the source of Potonié's ideas on this matter (Potonié said not). He published very few names but managed to confuse nomenclature by proposing simultaneous publication of "natural" and "half-natural" generic names for generic names for pollen; he even published a few such non-binomial names. Unfortunately, coworkers of Erdtman (e.g., Cookson, 1947) actually did this also for a time, which has confused the nomenclature of many fossil sporomorphs.

However, all names of plant taxa, fossil or extant, are governed by one code, the *International Code of Botanical Nomenclature* ("ICBN") (Greuter *et al*., 2000), and it provides a means of referring to the population concerned. It is not illegal to formulate private rules for making up generic or specific names, but such rules have no standing in the *Code*. Under the present *Code*, "half-natural" names are just morphogeneric names, the same as "artificial" names, providing they are validly published. The real question is whether it is allowable to use modern generic names for fossil spores/pollen, or whether one must always use morphogeneric names. The question of how to coin the form-generic names and how to list them subsequently is all smoke screen. At the moment it is clear that those who favor use of only form-generic names in the Cenozoic are by far in the majority. For years I felt that, where the generic reference is absolutely clear, there is no reason at all to avoid the extant generic name. However, after decades of thinking about the matter, I have changed my mind and now feel that pre-Pleistocene sporomorphs should be referred to morphotaxa (morphogenera, morphospecies) such as *Nyssapollenites*, not *Nyssa*, even though, for example, association with other organs makes it clear that the *Nyssa* pollen in the Brandon Lignite described by me (Traverse, 1955) was produced by plants that probably were congeneric with the extant genus *Nyssa*. In short, I have concluded that Potonié's ideas on typification limits were correct, and I have (Traverse, 1994) therefore transferred the Brandon lignite species to morphotaxa units such as *Nyssapollenites, Gordonipollenites* (instead of *Gordonia*), etc. Because of the known time range of genera, very few paleopalynologists would now call a dispersed Jurassic fern spore *Aneimia*, even though it seems inseparable morphologically from that genus. In Pleistocene palynology, extant names are almost always used, even if only to family or other suprageneric units. Of course, this is mostly because pollen identifications based on comparison with

modern material can be made, but it is also true that the purpose of Pleistocene palynology is mostly paleoclimatological and paleoecological intepretation, for which "*Tricolporites* sp." is not of much help! An ecological study in the Paleogene, such as Collinson's (1983), makes sense of the pollen record, because the megafossils are coordinately studied and referred mostly to extant plant taxa. Without the megafossil information, and only dispersed sporomorphs to work with, "*Tricolporopollenites* spp.," with suggestions as to natural affinity is better science than use of modern plant names. Boulter and Wilkinson (1977) have noted that great numbers of late Cretaceous to present angiosperm pollen consist of tricolpate, tricolporate, and triporate forms that are very difficult to distinguish consistently, and neither the application of modern plant names nor the application of form taxa is very useful. Boulter and Wilkinson suggested a non-Linnaean, non-binomial approach by using a grid system based on basic morphological type, size, and sculpture. Though this suggestion has considerable merit for dealing with such forms, it has not been widely adopted. Hughes (1970, 1975) has suggested broad-scale substitution of such a non-binomial classification approach to palynological systematics. Hughes' proposal, unlike Boulter and Wilkinson's, called for the virtual abandonment of formal description of palynomorph taxa by traditional methods. Both the Boulter and Wilkinson, and the Hughes suggestions represent practical approaches to dealing with the huge bulk of paleopalynological data on difficult to separate forms, particularly in the "Cenophytic." Such approaches will be more widely used if their authors avoid conflict with standard paleobotanical/paleopalynological nomenclature and emphasize instead the practical purposes of their methods. (See also discussion of general nomenclatural considerations affecting palynology in Chapter 19.)

7 "Cenophytic" (± Cenomanian-Pleistocene) *Sporae Dispersae* Botanical Relationships

As noted earlier in this chapter, the botanical affinity of "Cenophytic" spores/pollen (mostly angiosperm pollen) is still known mostly from comparison with modern reference pollen slides, because relatively few fossil flowers have as yet been studied. Thus, very curiously we at present know far more about the relationship of Carboniferous dispersed spores/pollen to the producing fructifications than we do about similar Cretaceous-Paleogene dispersed spores/pollen. (In the Neogene there is not really much doubt about the generic or at least, familial, reference of all the abundant and important forms encountered–they are nearly all extant.) The "Cenophytic" begins with the arrival of undoubted angiosperm fossils in the record, both reticulate-veined leaves and more or less columellate pollen of angiosperm character. This event is time-transgressive, occurring earlier toward the equator (about Barremian) than at middle latitudes (about Aptian) or high latitudes (about Cenomanian). Despite the angiospermous nature of much

Cretaceous and Paleogene pollen, however, it has not generally been possible in the past to refer any pollen to extant angiosperm taxa smaller than order until latest Cretaceous. In a much quoted monograph, Muller (1981) summarized the then accepted references of fossil pollen to extant plant families. More recently, Song *et al*. (2004) have expanded Muller's study into more parts of the world, especially China, and in some cases have extended the range of families somewhat deeper into the Cretaceous. It remains true that although some angiospermous families are recognized in the Cretaceous, most are first identified in the Paleogene. Not until about 20 million years ago (Muller, 1981, pers. comm.) do *all* angiosperms encountered belong to extant families. Beginning about 10 million years ago almost all angiosperms were referable to extant genera. Many very important Paleogene and Cretaceous angiosperm pollen forms are still enigmatic as to relationship, awaiting the discovery of flowers bearing them, e.g. *Aquilapollenites* and *Wodehousia*. In the "Cenophytic," fern spores are usually referable to extant genera, or at least to extant families. Fossil conifer and other gymnosperm pollen is often quite like that of extant genera, but studies of fossil and extant cones and the related pollen have shown that this resemblance of pollen form often reflects parallel or mosaic evolution.

The following very short list presents data on "Cenophytic" spores/pollen whose botanical relationship has been proven paleobotanically. In many hundreds of other cases, e.g., *Nyssapollenites* and *Gordonipollenites*, the botanical relationship is nearly certain but has not been proven by finding fossil spores/pollen-bearing organs. In many instances, the presumed botanical relationship shows in the name, as discussed under taxonomic considerations above. However, only in the relatively few instances in which flowers have been studied is the evidence absolutely certain. The complexity of the situation is illustrated by the work of Crepet and Daghlian (1980), in which Eocene castaneoid inflorescences yielded beautifully preserved pollen appearing identical to modern *Castanea*, though the generic assignment of the inflorescence is by no means so certain; this is an illustration of mosaic evolution. Another problem is that megafossil paleobotanists working in the Cenozoic are not especially interested in the referability of *in situ* pollen/spores from their inflorescences to taxa of dispersed sporomorphs. The relationship to modern forms is a more pressing problem. For example, Manchester and Crane (1983) describe in great detail the pollen of a fagaceous plant of Oligocene age, and compare the pollen with pollen of the genera of the modern beech-oak alliance. They do not, however, even mention whether the pollen if dispersed would be *Quercoidites, Cupuliferoipollenites* or something else. The literature includes hundreds of generic names for dispersed Cretaceous-Cenozoic spores/pollen, replete with taxonomic reference to extant genera or families. Much of this information is probably all right, but it is humbling to see from this list how little of it is backed up by megafossil evidence. Paleobotanists have since the first edition of this book made much progress in the search for fossil flowers, and there will undoubtedly be much

more information before many more years. In the meantime, the following short list is representative of how much we have to learn from *in situ* fossil evidence about the botanical relationships of "Cenophytic" *Sporae dispersae*. Most of what we know is still derived from detailed study (including SEM/TEM) of the fossil dispersed pollen itself.

I. SPORES

A. TRILETE

Cyatheacidites

Dispersed spores of this morphogenus, found in rocks of Cretaceous and Cenozoic age, are virtually identical to those of the living monotypic fern, *Lophosoria* (Kurmann and Taylor, 1987).

Deltoidospora

Deltoidospora spores were described from Eocene-Oligocene polypodiaceous ferns close to *Acrostichum* by Collinson (1978).

II. POLLEN

A. MONOSULCATE

Monocolpopollenites

Pollen referable to *Monocolpopollenites tranquillus* (Pot.) Thomson & Pflug was found in palm flowers by Schaarschmidt and Wilde (1986) in the Eocene of Messel, Germany. Harley *et al.* (1991) show by TEM/SEM studies that Eocene dispersed specimens of this taxon are very probably palms (family Arecaceae), with the only real question being which extant palm sub-family to refer the fossils.

Spinizonocolpites

Harley *et al.* (1991) have shown by detailed TEM/SEM study that Eocene specimens of this dispersed pollen morphogenus is so nearly the same as the pollen of the extant *Nypa fruticans* Wurmb, a palm, as to make reference of the fossil pollen to the Arecaceae certain. This pollen form is actually zonosulcate (Paz), a variant of monosulcate.

B. MONOPORATE

Graminidites

Pollen referable to the dispersed morphogenus *Graminidites* was described from grass flowers of the Paleocene/Eocene by Crepet and Feldman (1991).

Pandaniidites

Pandaniidites pollen was found in Paleocene flowers of Lemnaceae by Stockey *et al*. (1997).

C. TRICOLPATE-TRICOLPORATE-STEPHANOCOLPORATE

Pistillipollenites

Pistillipollenites (brevicolpate, gemmate) pollen was obtained from flowers of Paleocene-Eocene age, apparently referable to the family Gentianaceae, by Crepet and Daghlian (1981). However, Wing and Daghlian (1989), working with flowers of the same age, suggest rosid affinity. Stockey and Manchester (1988) describe an Eocene flower with similar characteristics, bearing this morphogenus of pollen, and suggest Euphorbiaceae relationship, and go on to say that this sort of gemmate pollen may have evolved several times by convergent evolution. This very interesting and important pollen form has been described in detail by Rouse and Srivastava (1970).

Striatopollis

Drinnan *et al*. (1991) described pollen from probable buxaceous flowers of the Mid-Cretaceous which is referable to this morphogenus.

Tetracolporopollenites

Harley *et al.* (1991) show by TEM/SEM study that Eocene specimens of this 4-stephanocolporate morphogenus are surely referable to Sapotaceae and probably to the near vicinity of one sapotaceous genus.

Tricolpites

Pollen similar to *Tricolpites minutus* (Brenner) Dettmann was found in staminate flowers of platanaceous plants of the Lower Cretaceous (Potomac Group) of Maryland by Crane *et al*. (1986), and Friis *et al*. (1988).

Tricolporites

Pollen referable to *Tricolporites* was obtained from *Actinocalyx* (probably ericalean) flowers of the Upper Cretaceous by Friis (1985a). Friis (1985) also reported obtaining pollen referable to *Tricolporites* in *Scandianthus* flowers (probably saxifragalean).

Tricolporopollenites

Call and Dilcher (1993) record the presence of the dispersed pollen of *T. parmularis*-type in *Eucommia* (a hamamelid dicot) flowers from the Eocene of Mississippi, USA.

Call and Dilcher (1997) review the extensive record of *T. parmularis* in the early Paleogene and its attribution to *Eucommia*.

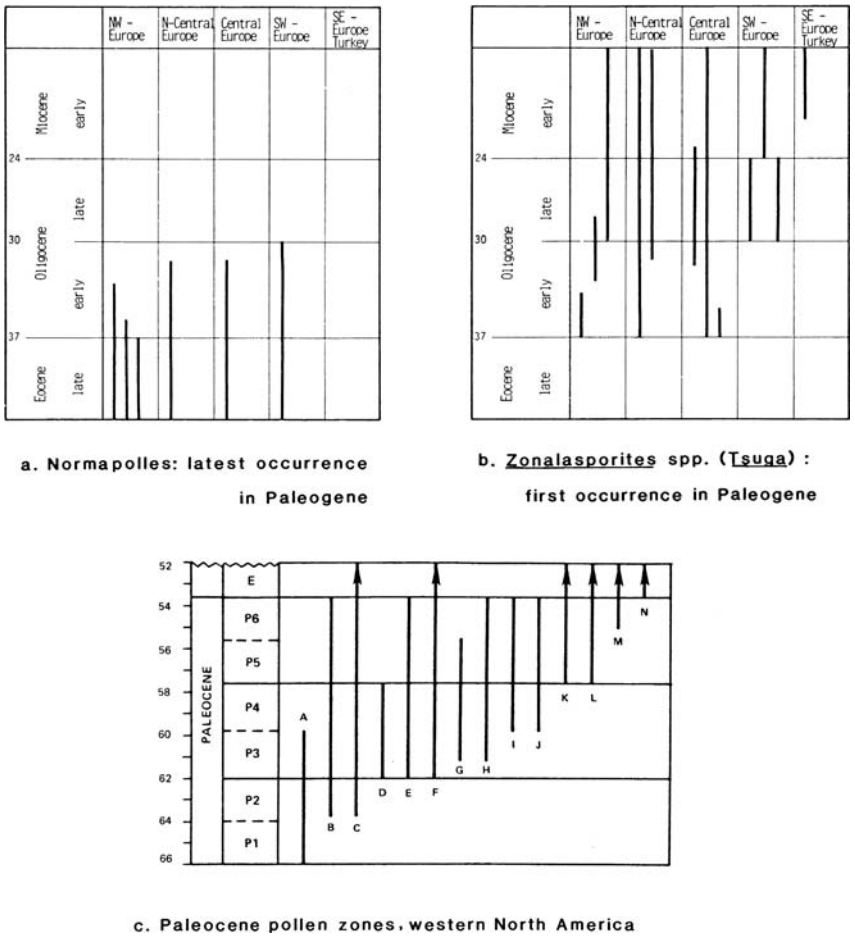

Figure 14.9 Examples of Cenozoic pollen ranges in the Northern Hemisphere. (**a**) Normapolles "tops" (last occurrences). The extra bars for northwest Europe represent data from different sources. Clearly, however, the top is early Oligocene. (**b**) *Zonalasporites* (= *Tsuga*) "bottoms" (first occurrences). As in (a), the multiple bars in most segments represent data from different sources. It is evident that *Tsuga* moved into northwest Europe earlier than into southern Europe. (**c**) Pollen zones for the Paleocene of western North America based on juglandaceous pollen. The zones are mostly based on first ("bottoms") and last ("tops") occurrences of included taxa. Zones so delimited are referred to in a general sense as Oppel zones (similar to concurrent range zones). The taxa are: **A**, *Momipites* leffingwellii Nichols & Ott; **B**, *Momipites waltmanensis* Nichols & Ott; **C,** *Momipites* **wyomingensis** Nichols & Ott; **D**, *Momipites actinus* Nichols & Ott; **E**, *Caryapollenites prodromus* Nichols & Ott; **F**, *Momipites anellus* Nichols & Ott; **G**,*Momipites triorbicularis* (Leffingwell) Nichols; **H**, *Momipites ventifluminis* Nichols & Ott; **I**, *Caryapollenites wodehousei* Nichols & Ott; **J**, *Caryapollenites imparalis*

D. TRIPORATE-STEPHANOPORATE

Caryapollenites

As the name suggests, this triporate pollen form, found in the Eocene, is juglandaceous, according to Manchester *et al*. (1994)

Momipites

Momipites pollen has been obtained by Crepet *et al*. (1975) from *Eokachyra*, a form-genus for Eocene juglandaceous catkins. Crepet *et al*. (1980) reported it also from *Eoengelhardia*, another Eocene juglandaceous catkin. Juglandaceous-like triporate pollen of this sort is also found in the literature under *Engelhardia* or *Engelhardtioipollenites*. Manchester *et al*. (1994) note that *Momipites* from the Eocene is indistinguishable from extant *Engelhardia* pollen.

Extratriporopollenites

Extratriporopollenites pollen in the broad sense (which includes most Normapolles) have been found in Upper Cretaceous floral material of Sweden by Skarby (1981) and Friis (1981, 1985b). Friis (1984) feels that the flowers are referable to the Juglandales-Myricales alliance but probably not to an extant family. *Trudopollis*, in particular, was obtained from one fossil flower, *Manningia*, and *Plicapollis* from another, *Caryanthus*.

Platycaryapollenites

Pollen of this morphogenus from the Eocene is referable to Juglandaceae according to Manchester *et al*. (1994).

Plicatopollis

This form of Po3 pollen found in the Eocene belongs to the Juglandaceae, but not to an extant sub-family, according to Manchester *et al*. (1994).

Pterocaryapollenites

This morphogenus of stephanoporate pollen, found in the Eocene, is referable to the Juglandaceae, according to Manchester *et al*. (1994)

E. TETRADS

Ericipites

Ericipites-like pollen tetrads were described from Eocene mimosoid (Leguminosae) inflorescences by Crepet and Dilcher (1977).

Figure 14.9 Nichols & Ott; **K**, *Caryapollenites veripites* (Wilson & Webster) Nichols & Ott; **L**, *Caryapollenites inelegans* Nichols & Ott; **M**, *Juglans-Pterocarya* type; **N**, *Platycarya platycaryoides* (Roche) Frederiksen & Christopher. (a) and (b) are slightly modified from figures in Hochuli (1984); (c) is from Jacobson and Nichols (1982).

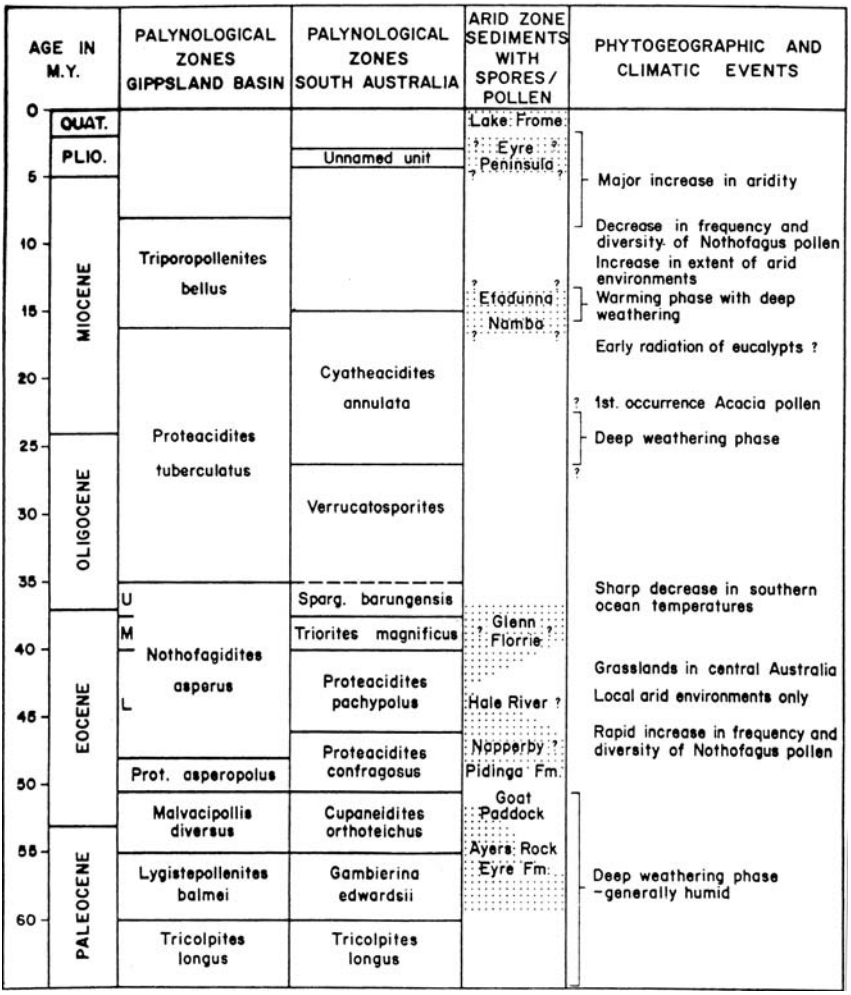

Figure 14.10 Palynological stratigraphic zones for Cenozoic of Gippsland Basin (Victoria) and South Australia, Australia. This zonation dramatizes the very important point (see Fig. 14.9) that in the Cenozoic pollen/spore zonation applies only locally. Note early Oligocene cooling, Miocene warming and the late Neogene major aridity increase, reflecting mostly Australia's northern drift toward the equator. Figure is from Truswell and Harris (1982).

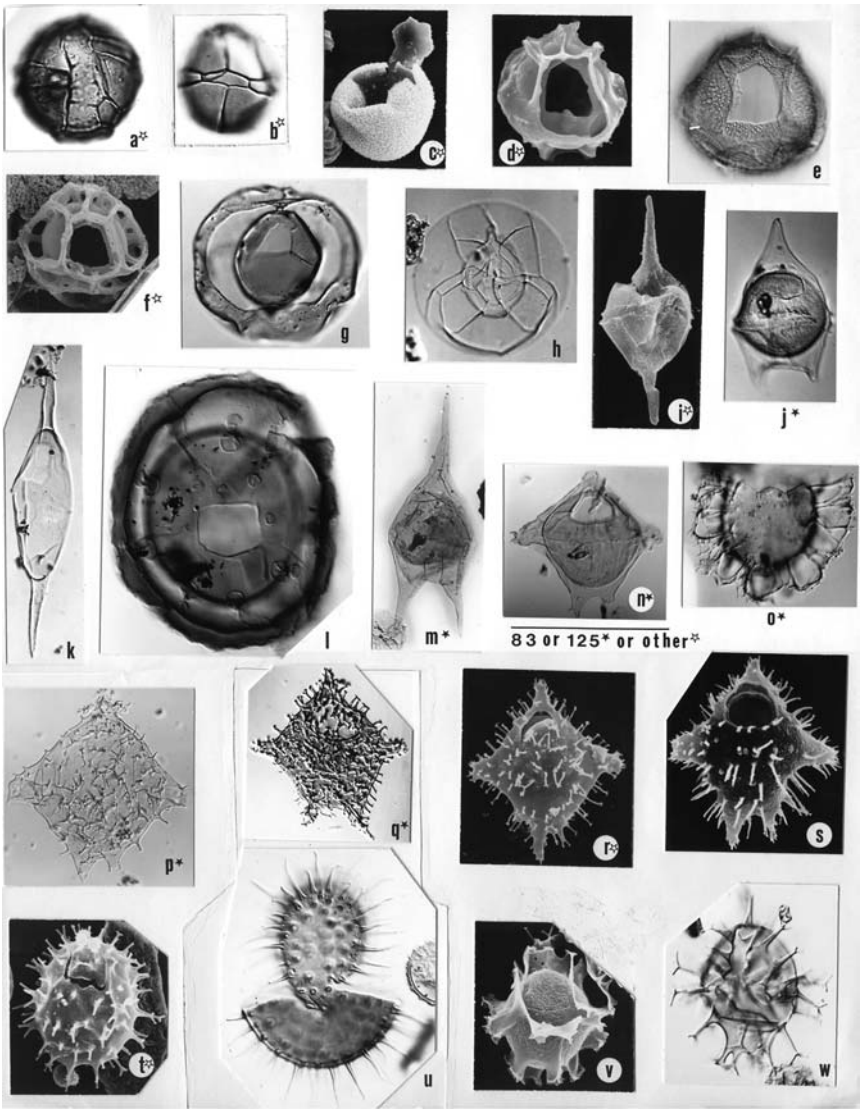

Figure 14.11 Some Cenozoic dinoflagellate cysts from North America and the eastern North Atlantic, in interference contrast light microscopy (IC) and SEM. The North Atlantic samples are from DSDP Leg 81, Rockall Plateau, and are designated "DSDP." Magnification in micrometers shown by bar under (n). Sizes for specimens for which "other" is indicated are given in the caption. Note that for each specimen, not only the surface shows, but the aspect from which that surface is seen is indicated. This is a recommended practice for photos of dinoflagellate cysts, because a ventral surface seen from the ventral side is a mirror image of a ventral surface seen by focusing through from the dorsal side,

Figure 14.11 and this confuses perception of plate arrangement. For SEM, however, the view is only exterior, and this is not a problem. (**a**) *Impagidinium californiense* Damassa. Proximate cyst, IC, ventral view of ventral surface, maximum dimension 43 μm, early-middle Eocene, Alaska. (**b**) *Impagidinium patulum* (Wall) Stover & Evitt. Proximate cyst, IC, ventral view of dorsal surface, maximum dimension 70 μm, late Miocene, DSDP (**c**) *Kallosphaeridium brevibarbatum* De Coninck. Proximate cyst, SEM, oblique apical view showing the apical archeopyle with the multiplate operculum attached at the parasulcus, maximum dimension 41 μm, Paleocene-Eocene, Virginia. (**d**) *Pentadinium polypodum* Edwards. Proximochorate cyst, SEM, dorsal view showing clearly the precingular archeopyle, maximum dimension 65 μm, middle Eocene, Alabama. (**e**) *Pentadinium favatum* Edwards. Proximate cavate cyst, IC,ventral view of dorsal surface, (see (d)), middle Eocene, Alabama. (**f**) *Impagidinium aquaductum* (Piasecki) Lentin & Williams. Proximate cyst, SEM, dorsal view showing precingular archeopyle and parasutural crests which form an open network reflecting original tabulation, maximum dimension, 47 μm, middle Miocene, DSDP (**g**) *Invertocysta lacrymosa* Edwards. Strangely cavate cyst with the relatively dwarfed endocyst and the precingular archeopyle showing within, IC, ventral view of dorsal surface, late Miocene, DSDP (**h**) *Invertocysta tabulata* Edwards. Cavate cyst as in (g). IC, dorsal view of ventral surface, middle Miocene, DSDP (**i**) *Biconidinium longissimum* Islam. Proximate cyst with long apical and antapical horns, SEM, oblique ventral view, maximum dimension 96 μm, early Eocene, Virginia. (**j**) *Deflandrea phosphoritica* Eisenack. Cavate cyst with intercalary archeopyle outline showing, IC, dorsal view of dorsal surface, late Paleocene, Virginia. (**k**) *Palaeocystodinium golzowense* Alberti. Cavate cyst with the periphragm continuing into apical and antapical horns, intercalary plate comprising the operculum showing through from dorsal surface in this mid-focus ventral view, IC, middle Miocene, DSDP (**l**) *Tuberculodinium vancampoae* (Rossignol) Wall. Odd cavate cyst with the antapical archeopyle showing in this antapical view, IC, late Miocene, DSDP (**m**) *Ceratiopsis* sp. Proximate cavate cyst with thin-walled periphragm. IC, ventral view of ventral surface, Paleocene, Alabama. (**n**) *Rhombodinium* sp. Proximate cavate cyst with faint indications of tabulation showing, intercalary archeopyle, IC, dorsal view of dorsal surface, lower Eocene, Virginia. (**o**) *Glaphrocysta* sp. Chorate cyst with processes united at the level of original theca, showing the apical archeopyle, involving several plates, IC, dorsal view of ventral surface, Paleocene, Virginia. (**p**) *Gochtodinium* sp. Chorate cyst, intercalary archeopyle showing in this dorsal view of dorsal surface, IC, early Oligocene, Alabama. (**q**) *Wetzeliella hampdenensis* Wilson. Characteristically angular chorate cyst with processes of medium length, the level of the grapnel ends indicating original thecal wall position, intercalary archeopyle showing, IC, early to middle Eocene, Alaska. (**r**) *Wetzeliella* sp. (see information for (q)). Endocyst showing behind the partially detached operculum, dorsal view, SEM, maximum dimension 111 μm, early Eocene, Virginia (**s**) *Wetzeliella varielongituda* Williams & Downie. Information basically as for (q), intercalary archeopyle in both pericyst and endocyst showing in dorsal view, SEM, early Eocene, Virginia. (**t**) *Apectodinium homomorphum* (Deflandre & Cookson) Lentin & Williams. Cyst with intercalary archeopyle, little or no other evidence of tabulation, SEM, maximum dimension 70 μm, late Paleocene-early Eocene, Virginia. (**u**) *Lingulodinium machaerophorum* (Deflandre & Cookson) Wall. Skolochorate cyst with long processes, with an archeopyle involving the entire epicyst attached at the sulcus, IC, middle Miocene, DSDP

8 Cretaceous-Present Spores/Pollen Ranges

Unfortunately, relatively little is available in the literature regarding spores/pollen ranges in the "Cenophytic." Some broad generalizations have already been noted and can be seen in earlier figures: first appearance of tricolpate pollen in Neocomian- Cenomanian (depending on latitude), first Normapolles in Cenomanian (southern Laurasia), disappearance of many *Aquilapollenites* spp. at the end of the Maastrichtian (and most of the rest of "Aquila" at the end of the early Paleocene), end of Normapolles in late Eocene to early Oligocene, etc. It should be emphasized, however, that the spores/pollen correlations in the Cenozoic are dependent on local climatic conditions more than on well-documented, widespread episodes of extinction (Hochuli, 1981, personal communication). For example, Fig. 14.8 shows that the last appearance of Normapolles (= *Plicapollis*) and the first appearance of *Tsuga* (= *Zonalapollenites*) are rather different in different parts of Europe, and this perhaps indicates a gradual adjustment of vegetation to changing climates. Fig. 14.8 also shows some Paleocene pollen zones from western North America. The zones shown are Oppel zones, determined by tops (ends) and bottoms (beginnings) of some pollen taxa. (Concurrent range zones are very similar but emphasize the mutual occurrence in each zone of a specified suite of fossils.) Fig. 14.9 shows some stratigraphic zones for the Cenozoic of Australia. The zones displayed are assemblage zones, of which a particular taxon is selected as typical. Note that the appearance of *Acacia* and *Eucalyptus* pollen, supertypical of modern Australia, is a Neogene phenomenon.

9 Paleogene-Neogene Dinoflagellates

After some extinctions at the K/T boundary, dinoflagellates rapidly diversified in the Paleogene and are hence very important stratigraphically, especially in marine sediments. As always, in some, especially nearshore marine sediments, they provide an invaluable link between the critical marine animal fossil stratigraphic indicators and spores/pollen from land. (There are also freshwater dinoflagellate cysts, but they are relatively spotty in occurrence.) A number of dinoflagellate cyst taxa terminate at or near the end of the Cretaceous (*Dorocysta, Triblastula,*

Figure 14.11 (**v**) *Hafniasphaera goodmanii* Edwards. Skolochorate cyst, dorsal view showingthe endophragm within, SEM, early Eocene, Maryland. (**w**) *Spiniferites mirabilis* (Rossignol) Sarjeant. Skolochorate cyst, a generic name introduced by Ehrenberg over a century ago, dorsal view of dorsal surface, IC, late Miocene, DSDP. Photomicrographs and SEM micrographs are all courtesy of L. E. Edwards. Several of them appeared in Edwards (1980, 1982b, 1984a) and in Edwards *et al.* (1984).

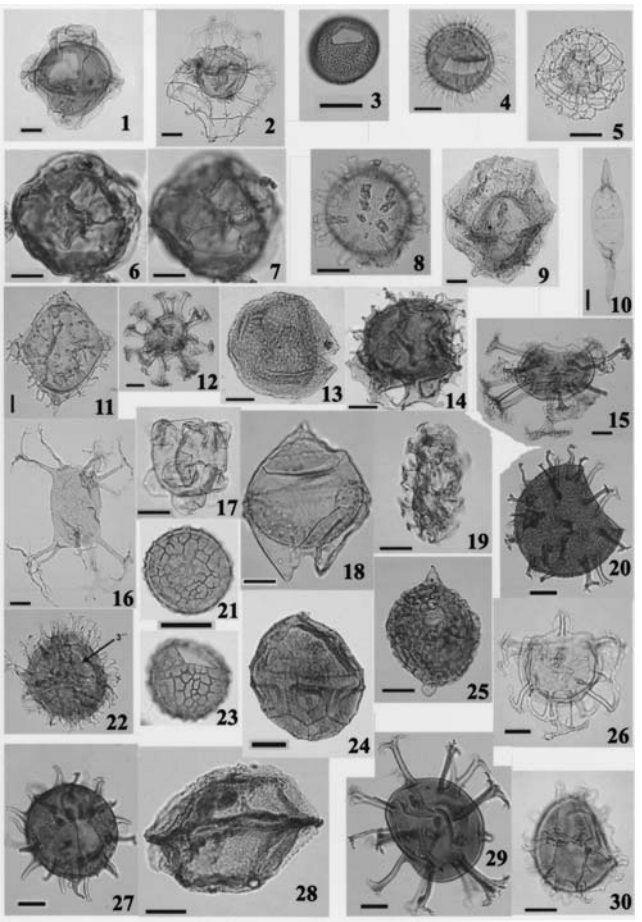
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Plate 14.1

Dinogymnium, etc.), but many other taxa "sail" unabashedly across the boundary (*Oligosphaeridium, Cordosphaeridium, Leptodinium*, etc.), and it is evident that the terminal Cretaceous "event" was not as cruel to dinoflagellates as to the Coccolithophoridae and many other organisms.. The picture seems to be more like that for pollen and spore taxa. One wonders if the sporopollenin coat which the cysts had in common with spores/pollen might have had something to do with their comparatively successful survival. Fig. 14.11 illustrates some typical Cenozoic dinoflagellate cysts. Various authors present range charts for Cenozoic taxa in Wrenn *et al*. (1986).

A very important publication on (mostly) dinoflagellates and acritarchs of Miocene to Holocene is that edited by Head and Wrenn (1992). In that book Zippi (1992) presents some significant data on the direct application of dinocyst studies of Pleistocene sediments in the Atlantic Ocean to hydrology and climatology of theø studied interval. Waxing and waning of various taxa indicate higher and lower temperatures of the air, and or cooling or warming of the water due to circulation changes. Edwards (1992), in the same book, presents information on the use of dinocyst concentrations measured by ratios and combined percentages for detecting the presence of climatic changes in the Pliocene of offshore eastern North America.

◄

Plate 14.1 Dinoflagellate cysts from the Oligocene-Miocene of the Danish North Sea. **1.** *Pentadinium laticinctum*, DS, HF. **2.** *Cannosphaeropsis passio*, SF, DS up. **3.** *Pyxidinopsis fairhavenensis*, DS, HF. **4**. *Lingulodinium machaerophorum*, DS, HF. **5.** *Nematosphaeropsis labyrinthus*, SF. **6.** *Tuberculodinium vancampoae*, SF, oblique antapical view, **7.** same specimen as 6., HF on antapical archeopyle. **8.** *Polysphaeridium zoharyi*, antapical view, HF. **9**. *Thallasiphora pelagica*, SF, DS up. **10.** *Palaeocystodinium* sp., SF, DS up. **11.** *Wetzeliella symmetrica*, SF, DS up. **12.** *Cordosphaeridium cantharellus*, VS, HF. **13.** *Bitectatodinium*? sp. (cf. Manum et al., 1989) DS, HF. **14.** *Chiropteridium lobospinosum*, VS, HF. **15.** *Areosphaeridium diktyoplokum*, SF, VS up. **16.** *Distatodinium biffii*, SF. **17.** *Hystrichokolpoma* sp.?, SF, DS up. **18.** *Deflandrea heterophlycta,* SF, DS up. **19.** *Distatodinium tenerum*, SF. **20.** *Operculodinium tiara*, SF, LS up, cf. fig. 27. **21.** *Cerebrocysta bartonensis*, HF. **22.** *Cerebrocysta bartonensis,* DS, HF. **23.** *Amphorosphaeridium*?*almae*, SF, VS up. The arrow and notation 3" refer to an archeopyle paraplate (see Fig. 12.6). **24.** *Phthanoperidinium amoenum*, SF, DS up. **25.** *Samlandia chlamydophora*, SF, VS up. **26.** *Enneadocysta pectiniformis*, VS, HF. **27.** *Operculodinium tiara*, DS, HF, cf. fig. 20. **28.** *Heteraulacacysta porosa*, SF.**29.** *Cordosphaeridium gracile*, SF, VS up. **30.** *Spiniferella* cf. *cornuta*, LS, HF. All of the size bars are 20 μ. Meaning of acronyms: DS=dorsal surface; HF=high focus; LF=low focus; LS=left lateral surface; RS=right lateral surface; SF=sectional focus; VS=ventral surface. This plate consists of a selection of photomicrographs from almost 300 of them in 19 plates published by Poul Schiøler (2005). They are printed here by his permission and that of the Micropalaeontological Society.

Schiøler (2005) published a beautifully illustrated study of dinocysts and other microphytoplankton from the North Sea of Denmark that displays well the richness of dinoflagellate diversity in the Cenozoic. A selected group of Schiøler's dinocysts is presented here as Plate 14.1. Other elements of the microphytoplankton–the Acritarchs–are regarded by most paleopalynologists as not very significant in the Cenozoic, and hence have not been much studied, but they do occur. The above mentioned paper of Schiøler illustrates a number of prasinophyte and other microplankton forms, though their non-dinocyst assignment is not mentioned in the captions. In fact, even *Veryhachium*, which one normally thinks of as Paleozoic, does occur in the Cenozoic.

Chapter 15

Neogene Palynology

1 Introduction

The Neogene period began about 24 million years ago with the Miocene. As used in this book, it extends to present, consisting of Miocene, Pliocene and Pleistocene, and the present interglacial, usually called the Holocene. However, as often defined, the Neogene consists of Miocene and Pliocene only, with the "Quaternary" (= Pleistocene and Holocene) being separate. Much of the middle part of the Miocene was warmer than any time since the Eocene, but the general temperature decline of the Cenozoic was reasserted about 15 million years ago. The expansion of temperate deciduous trees, grasses, composites (= Asteraceae), and other herbaceous dicots, and of conifers at high altitudes and latitudes, that began about then at middle latitudes became the signature of the later Neogene. A very significant aspect of plant evolution in the Neogene has been the development of a special variant of photosynthetic pathway–C_4 photosynthesis–as opposed to C_3,"normal" photosynthesis, especially in grasses, but also in many families of dicots, such as the chenopods. C_4 photosynthesis was probably an adaptation with evolutionary advantage in warm-dry, CO_2-poor early Neogene

conditions (Sage, 2004; Fox and Koch, 2004). Palynological analysis of sediments can reveal the presence of abundant grasses and chenopods, but cannot prove the style of photosynthesis of the producing plants. That evidence comes from carbon isotope studies of carbonate sediments. Of course, if such isotope evidence indicates C_4-photosynthesis, and associated palynological evidence for abundant grasses is found, it is probable that the two data points support each other. By 20 Ma practically all angiosperm remains, including pollen, are referable to extant families, and this datum ties in (mnemonically at least) with the beginning of the Neogene (about 24 Ma). About 10 Ma, the level of close to 100% extant genera was attained (see Fig. 15.1).

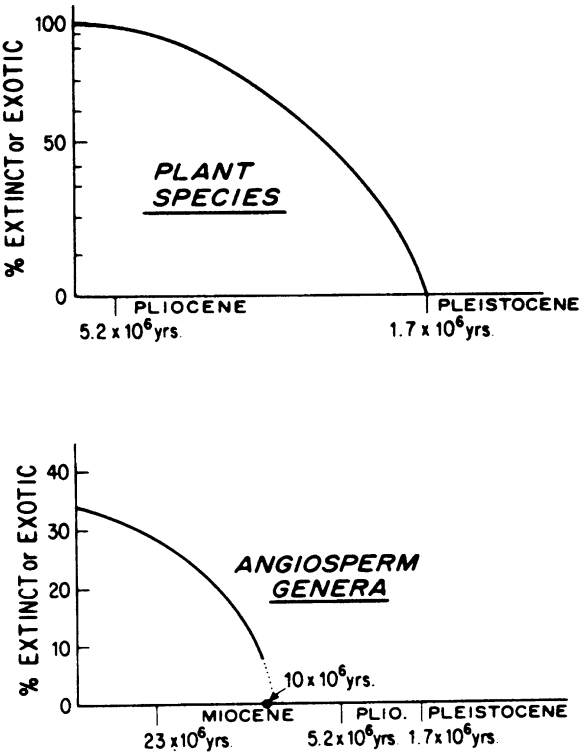

Figure 15.1 Percentage of extinct or exotic plant species in late Neogene time and of extinct or exotic angiosperm genera in North America. The data are all derived from megafossil floras. Jan Muller (in Traverse, 1982) put the level of 100% modern families at about 20 Ma. As pollen can routinely (by LM) be recognized only to genus of extant plants, this means that the same sorts of interpretations can be made from pollen analytical data for sediments 10 million years old as for those only 10,000 years old. Adapted from Reid (1920) and Barghoorn (1951).

This time also marks the formation of major Antarctic ice (glaciation may have commenced as early as 35 Ma) and the initiation in America and Eurasia of widespread steppe vegetation, dominated by grasses and by shrubby composites and chenopods. I informally refer to this 10-million-year period as the "Ultimogene" (Traverse, 1982). Its inception is based on the presence of practically 100% extant plant genera. We recognize as fossil pollen primarily genera, not species, of angiosperms. (In some cases, as grasses and sedges, we tend to identify only the *family*.) Thus, although the level of almost 100% extant species is not attained (as recognized from megafossils by Reid, 1920; see Fig. 15.1) until about the beginning of the Pleistocene (earlier in some locations; see Leopold, 1967), about 1.8 million years ago, the techniques applied in Pleistocene palynological studies are also frequently applicable in the "Ultimogene," because the studies are really based on generic identification. The use of the data is primarily for paleoclimatic and paleoecological reconstruction.

As one moves back in the pre-"Ultimogene," this procedure is riskier, because the assumption of paleoecological significance of pollen data is less supportable the greater the proportion of extinct and exotic forms. Thus, the "Ultimogene" is really palynologically different from pre-"Ultimogene," and it is not surprising that Pleistocene palynology (especially present interglacial = Holocene = "post-glacial" = Flandrian palynology) has always been quite different in approach from study of older sediments. It should be mentioned that some paleobotanists, such as the late Norman Hughes (cf. Hughes, 1994, p. 229), would be unhappy with the Ultimogene concept for the last 10 million years; he was opposed to recognizing any modern plant genera and species further back than the Pliocene/Pleistocene boundary, which is about 2 Ma.

The year 1916 is often reckoned as the beginning of palynology, with the publication of Von Post's (1916) post-glacial studies. The truth is that since that time "pollen analysis" (or "pollen statistics"), as this branch of palynology has sometimes been called, has always steered an independent course from "paleopalynology proper" (pre-Pleistocene palynology), and has been more connected to plant ecology, vegetational history, archeology, and paleoclimatology than to geology. "Pollen analysts" in this sense tend to be basically botanists, whereas most, especially applied, pre-Pleistocene palynologists tend to be geologically oriented. I am saying here that the normal boundary between the two approaches is really best set at about 10 Ma with the beginning of the "Ultimogene" (about 100% modern plant genera), not at 1.8 Ma with the beginning of the Pleistocene, or at 10,000 years ago with the inception of the "Holocene" or present interglacial. (It is sometimes useful to group the Paleocene and Eocene informally. The Oligocene and the early and middle Miocene, up to the onset of major cooling about 10 Ma can also be informally grouped for discussion of floral evolution.)

One dramatic demonstration of the profound effect of late Cenozoic cooling is in western North America, where continuing orogeny and resultant rain shadow development and other changes in climate were added to worldwide depression of

temperature. Fig. 15.2 shows such a case, the present extent of "Sierra Madrean" woodland, as contrasted with much more northerly records from earlier in the Cenozoic. Much more information on North American vegetational history, as characterized by both palynofloras and megafossil floras is to be found in the book by A. Graham (1999), and in a long series of papers by Graham and associates, such as Graham *et al.* (2001). Many of these papers deal with Neogene floras.

Some characteristic Mio-Pliocene spores/pollen from England are displayed in Fig. 15.3. All of these forms are still encountered in various parts of the Northern Hemisphere, but Pleistocene glaciation has eradicated many of the taxa from present-day Europe. Note also the use of form-generic names. In my opinion this is quite unnecessary, and even not helpful, in the "Ultimogene," for reasons already explained. (Palynologists working with Miocene-Pliocene floras customarily use many such names: see the profusely illustrated work of Nagy, 1985.)

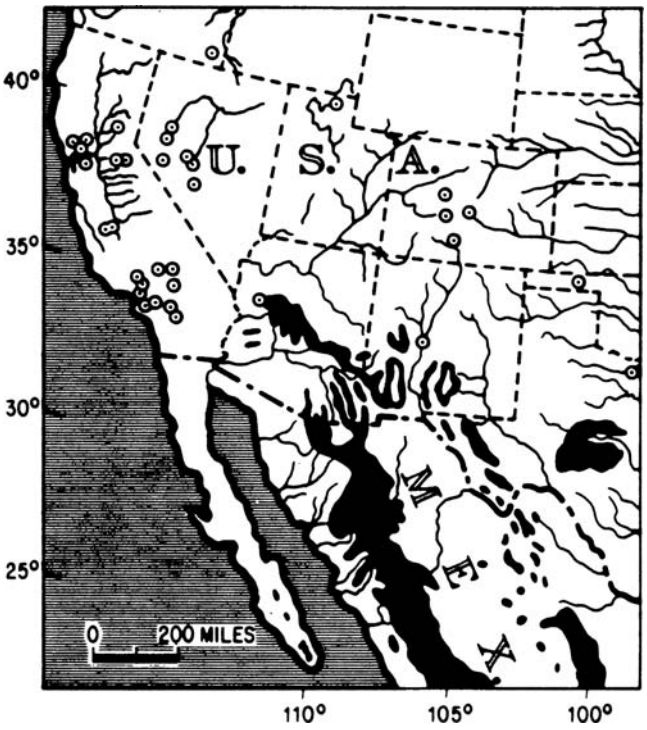

Figure 15.2 Present day "Sierra Madrean" woodland (blackened areas) vs. records of related Tertiary vegetation (circles) in southwestern North America. This retreat is a characteristic result of cooling in the Neogene in higher latitudes, plus orogenic effects. Axelrod and Raven (1985) present more information on the Madrean flora. Adapted from Axelrod (1958, fig. 9, p. 491).

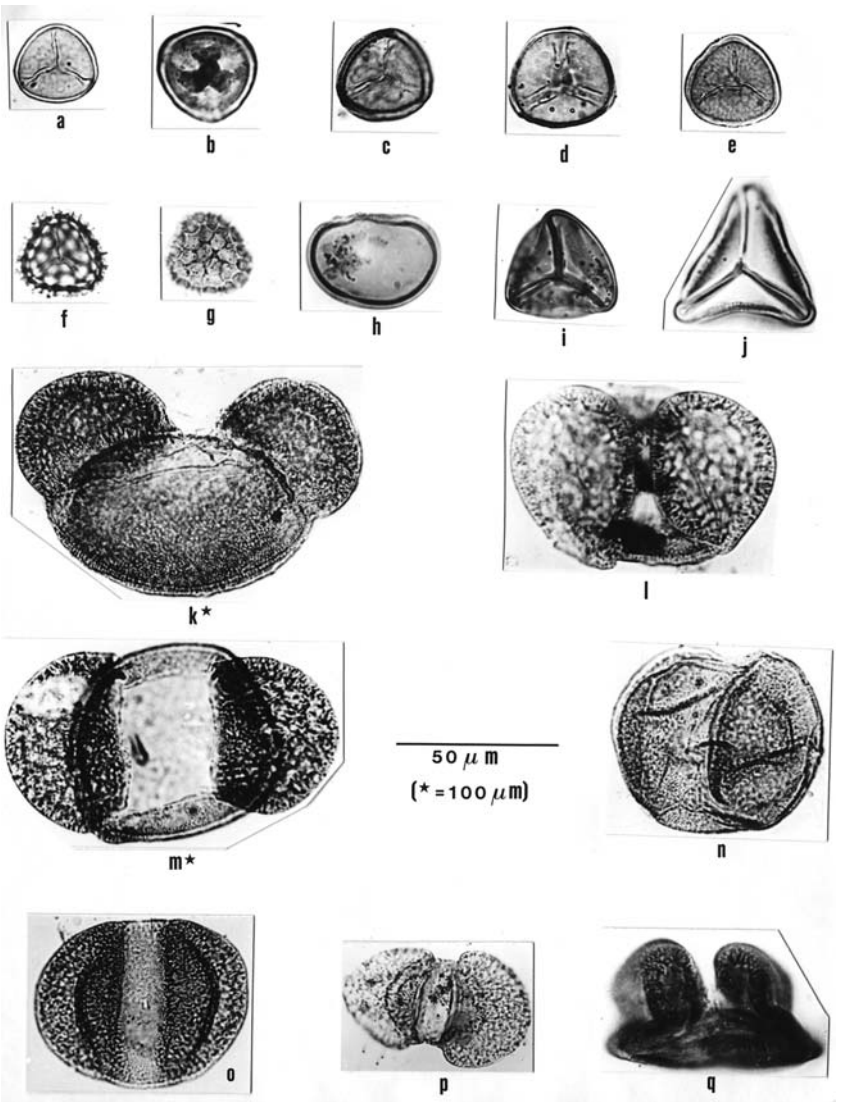

Figure 15.3 *(See caption on page 433).*

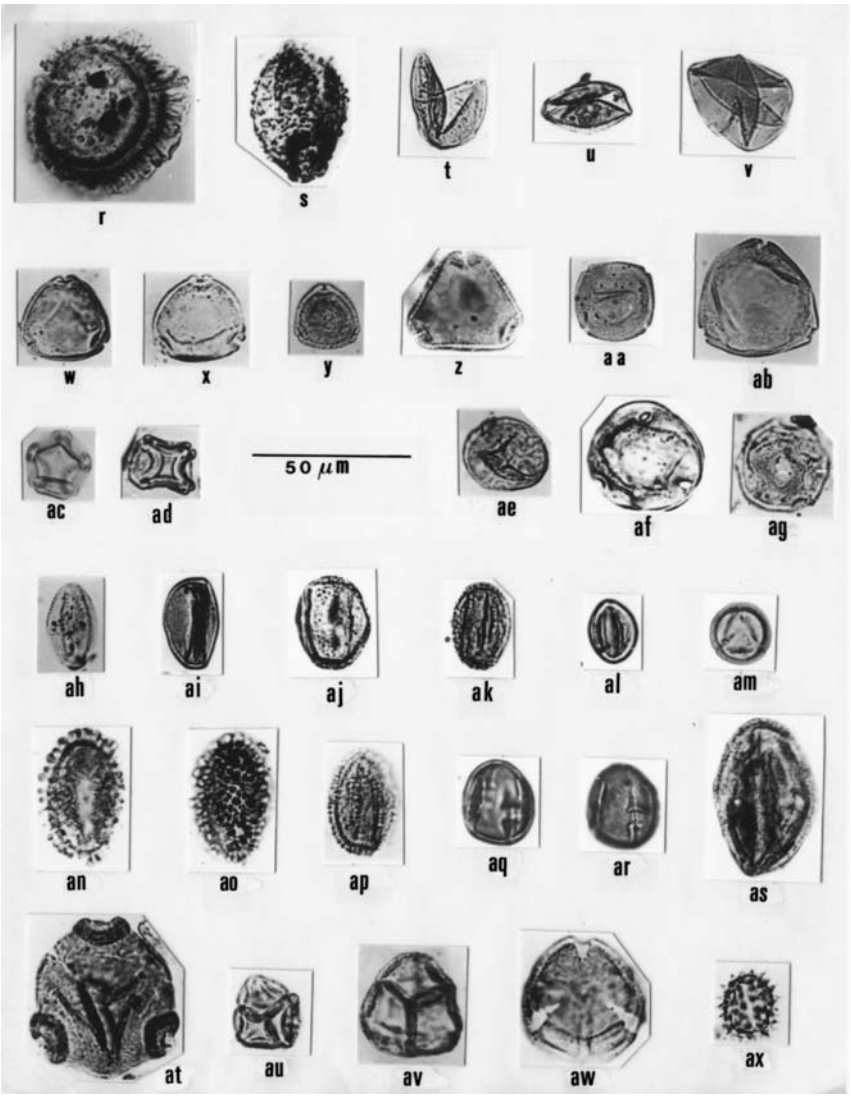
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Figure 15.3

Figure 15.3 Some characteristic late Miocene to Pliocene spores/pollen from clays in limestone sinkholes in Derbyshire, England. Similar sporomorphs occur in mid- to late Neogene sediments all over the Northern Hemisphere. As explained in the text, forms such as these, which are about five million years old were made by plants that most likely belonged to extant genera. It does not therefore seem to me that form-generic names need be used when referring to such pollen. However, if new species based on fossil pollen or spores are created, even for late Neogene material, they should be morphospecies of morphogenera [="form-genera") in recognition of the fact that the circumscription of a species of an extant genus cannot in principle be based on pollen alone. Magnification indicated by bars between (m) and (n) and under (y). (**a**) *Stereisporites stereoides* (Potonié & Venkatachala) Pflug, (see also (b)-(e)). Proximal view. Spores of this form-genus are common in some Cenozoic sediments. These are derived from the *Sphagnum* sort of moss, being one of the relatively few bryophyte spores with enough sporopollenin to be preserved. (**b**) *Stereisporites wehningensis* Krutzsch. Proximal view. The laesura has thick labiae. (**c**) *Stereisporites germanicus* Krutzsch. Proximal view. (**d**) *Stereisporites granistereoides* Krutzsch. Proximal view. A form with well-marked laesural labiae. (**e**) *Stereisporites magnoides* Krutzsch. Proximal view. (**f**) *Lycopodium* sp. Proximal view, high focus, showing somewhat sinuous laesura. The extant generic name is used for such Cenozoic spores more commonly than are other extant generic names, perhaps from the unproven view that the genus has not rapidly evolved in the Cenozoic, and because reference to *Lycopodium* seems very sure. (**g**) Same as (f). Distal view. (**h**) *Laevigatosporites haardtii* (Potonié & Venitz) Thomson & Pflug. Lateral view. Such Sa0 fern spores have a Paleozoic to present range! (**i**) *Leiotriletes wolffii* Krutzsch. Proximal view. As (h), a kind of fern spore having a not very distinctive form. (**j**) *Gleicheniidites senonicus* Ross. Proximal view. A distinctive fern spore which should eventually be referable to a particular extant genus. (**k**) *Abies* sp. Lateral view. Conifer pollen is often dominant in Miocene-Pliocene sediments of the Northern Hemisphere. (**l**) *Pinus* sp. ("sylvestris-type"). Distal view. (**m**) *Keteleeria* sp. Distal view. (**n**) *Picea* sp. Distal view. (**o**) *Pinus* sp. ("haploxylon-type"). Distal view. (**p**) *Podocarpoidites libellus* R. Potonié. Distal view, mid-focus. Podocarpaceous conifers are now confined to the Southern Hemisphere. (**q**) *Cedrus* sp. Lateral view. Distinction of *Cedrus* and *Pinus* pollen in sediments containing both is very difficult. (**r**) *Tsuga* sp. (*diversifolia* section). Shows that this extant conifer pollen is Pv1. (**s**) *Sciadopitys* sp. Shows the peculiar hollow verrucae. This taxodiaceous genus is now confined to east Asia but in the Miocene-Pliocene was widely distributed in the Northern Hemisphere. (**t**) *Inaperturopollenites hiatus* (Potonié) Thomson & Pflug. The clamshell-like opening is characteristic of extant *Taxodium* pollen. (**u**) *Cryptomeria* sp. Lateral view. *Sequoia* pollen is very similar. Note the bent papilla on top. (**v**) *Graminidites media* Cookson. The thin-walled baggy nature of such grass pollen yields folded walls on collapse. Note the single annulate pore. There is no doubt that this is a grass pollen, but genera of grasses are very difficult to separate by the pollen. Use of the morpogeneric name *Graminidites* for fossil grass pollen is a more formal, alternative way to say "grass pollen" or "Gramineae". (**w**) *Porocolpopollenites rotundus* (Potonié) Thomson & Pflug. Polar view, with short colpae as well as pores. (**x**) *Trivestibulopollenites betuloides* Thomson & Pflug. Polar view. A triporate-vestibulate form, which could also easily be referred to *Porocolpopollenites*. (**y**) *Porocolpopollenites vestibulum* (Potonié) Thomson & Pflug. Polar view. (**z**) *Porocolpopollenites* sp. Polar view. Such pollen is very similar to

2 Palynologically Significant Stratigraphic Boundaries in the "Ultimogene"

The boundaries between the Miocene and the Pliocene and between the Pliocene and Pleistocene have to be established on the basis of extension to other parts of the world of data from the type-section areas in France and Italy. Oxygen-isotope ($\delta^{18}O$) data, radiometric dating and magnetostratigraphy extended from marine cores to type sections, plus micropaleontological data (foraminifera and nannofossils, mostly), have helped make this possible. It is a stratigraphic, not a conceptual, problem. The Miocene/Pliocene boundary has been established and extended this way, with an absolute date of about 5.2 Ma. The base Calabrian of Italy, the undoubted bottom Pleistocene, has been linked with the worldwide Olduvai magnetic event. The basal Pleistocene is thus set at about 1.7–1.8 Ma.

Figure 15.3 modern *Symplocos* pollen and could be referred to, e.g., the morphogenus *Symplocoipollenites*. (**aa**) *Carpinus* sp. Polar view. P03 is a more common *Carpinus* form, and pollen of the near relative *Ostrya* is not easily distinguished from it. (**ab**) *Myrica* sp. Polar view. (**ac**) *Alnus* sp. Polar view (see also (ad)). Note characteristic arci. (**ad**) *Alnus* sp. Polar view (see also (cc)). (**ae**) *Ulmus* sp. Rugulate stephanoporate. (**af**) *Carya* sp. A triporate pollen grain with the pores characteristically located off the equator in one hemisphere. *Carya* was common in the Mio-Pliocene of Europe but did not survive the Pleistocene there. (**ag**) *Liquidambar* sp. A reticulate P0x with characteristic large pores with distinctively sculptured pore membranes. (**ah**) *Tricolpopollenites reniformis* Thomson & Pflug. Equatorial view. There are hundreds of different extant angiosperm genera making such pollen. (**ai**) *Tricolpopollenites microhenrici* (Potonié) Thomson & Pflug. Equatorial view. (**aj**),(**ak**) *Hedera* sp. Equatorial view. "English ivy" is a sensitive indicator of climatic fluctuations in the late Neogene. (**al**),(**am**) *Tricolpopollenites ipilensis* Pacltová: (**al**) equatorial view, (**am**) polar view. (It is worth emphasizing how different these are; even professional palynologists sometimes have difficulty recognizing that polar and equatorial views, e.g., of some tricolporate forms, go together.) (**an**),(**ao**) *Tricolporopollenites iliacus* (Potonié) Thomson & Pflug. Equatorial view. (**an**) mid-focus; (**ao**) high focus. Clavate sculpture is identical to that of extant *Ilex* pollen. (**ap**) *Tricolporopollenites margaritatus* (Potonié) Thomson & Pflug. Equatorial view. Clavate sculpture finer than that of (an) and (ao). (**aq**), (**ar**) *Tetracolporopollenites sapotoides* Thomson & Pflug. Equatorial view. (**aq**) mid-focus; (**ar**) high focus. This Pd4 pollen despite the specific name is not like that of sapotaceous genera. (**as**) *Tricolporopollenites edmundii* (Potonié) Thomson & Pflug. Equatorial view. (**at**) *Corsinipollenites maii* Krutzsch. Polar view. Certainly onagraceous, probably with careful SEM study referable to an extant genus. (**au**) *Empetrum* sp. Mid-focus of tetrahedral tetrad. Such *Ericaceae-Empetraceae-like* pollen is very common in Neogene sediments. (**av**) Ericaceae (?*Rhododendron*). Mid-focus of tetrahedral tetrad. (**aw**) Ericaceae (?*Erica*). High focus of tetrahedral tetrad. (**ax**) *Compositoipollenites rizophorus* Potonié. Equatorial view. Echinate Pc3 pollen certainly referable to the Asteraceae plays an increasingly important role through the Neogene. All photos courtesy of M. C. Boulter. They originally appeared in Boulter (1971a).

Fig. 15.4 shows how these pieces of stratigraphic information were applied (Hsü and Giovanoli,1979) to studies of DSDP cores in the Black Sea.

The "steppe/forest index" (SFI) is based on calculations of the ratio between pollen of major steppe indicators and major forest indicators as follows:

$$SFI = \frac{(\textit{Artemisia} + \text{Chenopodiaceae} + \text{Amaranthaceae pollen})}{(\text{the above} + \textit{Pinus} + \textit{Cedrus} + \textit{Picea} - \textit{Abies} + \textit{Quercus} + \textit{Alnus} + \text{Ulmaceae (and other tree genera) pollen})} \times 100$$

The cold peaks shown by the SFI curve are clearly glacial events, which I have called alpha, beta and gamma. This is because steppes in the Northern

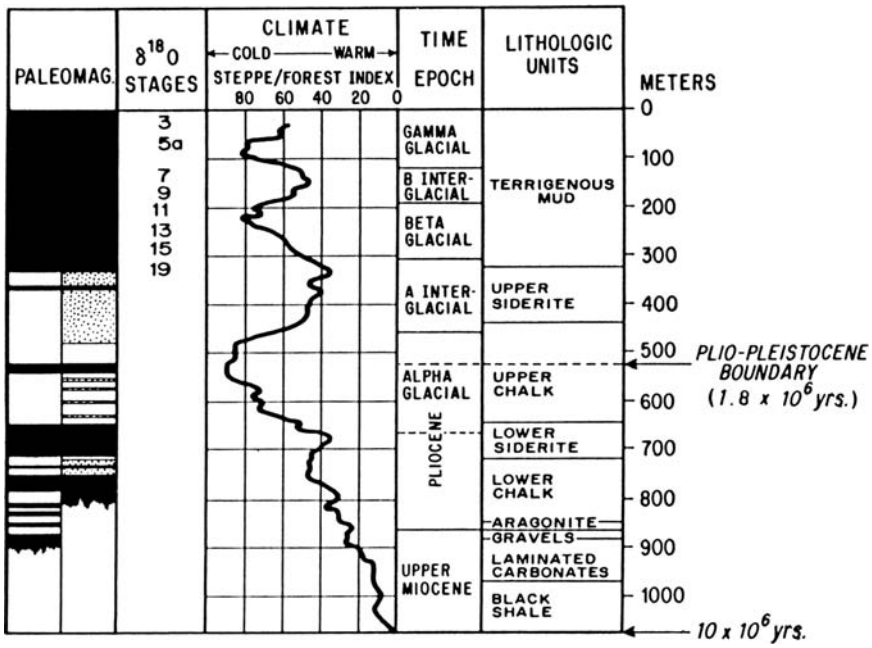


Figure 15.4 The last 10 million years in a continuous core record from the Black Sea (DSDP leg 42B, holes 380-380A). The steppe-forest index (SFI) curve represents a ratio of *Artemisia* + Chenopodiaceae plus Amaranthaceae to total pollen. The higher the SFI curve, the colder and drier the conditions indicated. There are three peaks of coldness called alpha, beta and gamma to avoid unwarranted correlation with glacial periods shown in Fig. 15.7. Interglacials are labeled A and B for the same reason (the current interglacial is C, not labeled). "Paleomag" on the left refers to paleomagnetic normal (black) and reversed (white) readings, interpreted to the left and measured to the right. Fig. originally appeared in Traverse (1982), based on data in Traverse, 1978a, 1978b, and in Hsü and Giovanoli,1979.

Hemisphere dominated by *Artemisia* and "Cheno-Ams" are located in cool, dry areas. The Olduvai magnetic event occurs in the middle of the alpha glacial, indicating that European glaciers extend back at least to the Pliocene, and that there was in the Black Sea drainage absolutely no early, non-glacial Pleistocene (as mentioned by Birks and Birks, 1980, and by others). Oxygen-isotope data support strongly the concept of late Pliocene pronounced cooling, including presumed development of continental ice sheets in Europe and North America beginning about 3.2 million years ago, but that was not the beginning of the Pleistocene, when it is defined the only way it logically can be–stratigraphically. (It should be emphasized that the curve in Fig. 15.4 is a smoothed-out curve, having the effect of grouping smaller fluctuations. Oxygen-isotope work suggests as many as 19 glaciation peaks in the Pleistocene.)

3 Miocene-Pliocene Palynology

3.1 General Remarks

Inasmuch as almost all of the spores/pollen found in rocks of the "Ultimogene" (the last 10 million years) are determinable to extant genera (in some cases only to families, rarely to species), it is not really very helpful that palynologists sometimes feel compelled to use artificial generic names (form-generic names) for the fossils studied, even though this *is* necessary for most forms pre-"Ultimogene." A compromise approach is that of Meon-Vilain (1970) for the late Miocene-Lower Pliocene of France, in which the reader is informed that "*Polyporopollenites stellatus"* is *Pterocarya*.

"*Tsugaepollenites*," however, is not identified as *Tsuga*, probably because that was thought to be obvious. "*Quercoidites"*, on the other hand, refers not only to *Quercus* pollen but in part to things such as *Q. henrici* and *Q. microhenrici*, which are likely fagalean but probably not *Quercus*, and may be forms for which a form-generic name would be appropriate. (It is likely, however, that the producing genera are extant somewhere in the world.) There is no reason, however, why form-generic names have to be coined just because it is the current vogue to do so. It is quite all right, for example, to refer chenopodiaceous pollen just to "Chenopodiaceae" or to "Cheno-Am," without feeling compelled to create a form-genus for this concept. Menke's (1976) approach for Pliocene pollen seems very reasonable: pollen recognized as certainly rubiaceous but not for sure belonging to a particular genus is referred to as "Rubiaceae". Pollen known to belong to *Myriophyllum* is so listed. Pollen probably referable to *Ulmus* but perhaps running over into *Zelkova* is "*Ulmus-habitus"* without a new taxon being formally named. Quaternary palynologists often use "*Ambrosia*-type", "cf. *Ambrosia"*, etc., to show varying degrees of closeness of match; see Birks and Birks (1980, "nomenclature of fossils"). Some forms not recognized as to extant taxon are "Pollen-6024a" and the like. In just a few instances form-generic names are used.

Givulescu's (1962) studies of Romanian Mio-Pliocene megafossil plants illustrate a couple of the palynological problems. The floral lists include many lauraceous forms. These will not produce preservable pollen if modern examples tell us anything. On my property in Pennsylvania, *Sassafras albidum* (Nutt.) Nees and *Lindera benzoin* (L.) Blume are abundant, the latter dominant in the understory, but the pollen record would be completely blank for them. On the other hand, Givulescu reports many representatives of the Fagaceae, and these would be the source of "*Quercoidites"* and "*Cupuliferoipollenites"*, forms that are characteristic of latest Miocene sediments in North America-Eurasia.

Not only do we have in the spores/pollen flora evidence of plants referable to modern genera, but in a broad way it is reasonable to draw paleoecological conclusions from them. However, it is obviously pressing the significance of a single genus too far, when it is known that various extant species of the genus have quite different ecological requirements. One must admit the limitations of palynology. Some elegant statistical approaches based on the distribution of pollen "species" may be forcing the data somewhat, because the "species" are mostly genera. Here I have reference to techniques such as Mosbrugger and Utescher's (1997) CLIMBOT, based on specific coexistence, or the method of Klotz and Pross (1999) based on pollen indicator "species." Such techniques have been proven to some extent effective, but they would certainly work better for fossils identified with confidence to plant species. Furthermore, the stratigraphic use of palynological data in the whole Neogene is difficult, because there are very few real extinctions, only local extinctions and migrations. Thus the significance of certain "tops" (last occurrences) in northwest Europe per Van der Hammen *et al.* (1971) cannot be directly expanded to include the Black Sea drainage. The use, for example, of *Engelhardia* pollen as a Miocene-Pliocene transition indicator is worrisome, because *Engelhardia* still survives in several parts of the world, although not in Europe where its local extinction can be so used. Another example is *Pterocarya*, whose disappearance in northwest Europe is a useful palynological indicator for the arrival of later Pleistocene time. It still persists in the Caspian-Black Sea drainage and cannot be so used there. Van der Hammen *et al.* (1971) and Leopold (1967) give lists of local extinctions that are useful as local stratigraphic markers. Particular plant assemblages are indicative of some of the interglacials: *Carpinus* is common in the Eemian (= Ipswichian) of northern Europe.

3.2 General Vegetational Trends Represented By Palynofloras In "Ultimogene" Time

In the Northern Hemisphere, the temperate deciduous hardwood forest was expanding while the paleotropical (= "mastixioid") flora was retreating. This gives the present-day Eurasian-American vegetation its character, as such taxa as the Poaceae (=Gramineae), the Asteraceae (=Compositae), the Chenopodiaceae, *Acer, Alnus, Betula, Carya, Pterocarya, Ulmus, Pinus, Abies, Picea, Sciadopitys,* and *Tsuga* come into importance or dominance.

Secondly, outside of the areas affected by these trends, floras also were changing in distribution. Fig. 15.2 shows from Axelrod's (1958) megafossil flora work in southwestern North America the related migrations of "Sierra Madrean" and "Lagunan" woodlands in response not only to cooling but to aridity caused by orogeny and epeirogeny. Van der Hammen *et al.*'s (1973) study of cores from the Colombian cordilleras dramatizes that, on top of the late Miocene cooling, mountain building can continuously produce new plant associations. Truswell and Harris (1982) have shown palynologically that arid-adapted plants expanded their range from Eocene onward in Australia, with grasslands developing in central Australia by late Eocene. The trend toward xerophytic vegetation accelerated in the Neogene, with *Acacia* appearing, eucalypts expanding their range, and *Nothofagus* declining (see Fig. 14.10). All of this indicates the Australian plate's northward movement into warmer zones in the Cenozoic.

Thirdly, in the Neogene, angiosperms of middle latitudes moved strongly toward deciduous and herbaceous habits:

3.2.1 Deciduous Habit

The coming to dominance of this character of trees and shrubs is linked to the progressive cooling of the Neogene. *Alnus, Acer, Ulmus, Fagus, Castanea*, and *Carya* are all deciduous. *Quercus* is instructive in that it seems to show its ancestry in the Paleogene by ranging from evergreen (*Q. virginiana* L.) to irregularly or incompletely deciduous (*Q. nigra* L.), to completely deciduous (*Q. alba* L.), but even the white oak sometimes shows poor abscission in the fall.

3.2.2 Herbaceous Habit

This character among both monocots and dicots was an obvious response to the Neogene climatic collapse and the expansion of deserts, semiarid regions, and seasonality. The Poaceae (= Gramineae, the grass family) and Asteraceae (= Compositae, the sunflower family) are primary examples of the advancing tide of herbs. In both families there are (more primitive) members that are woody plants confined to the tropics and subtropics. Pollen of both groups occurs in abundance first at the Oligocene-Miocene transition in Euramerica, but does not become really common until late Neogene. (Monoporate pollen very similar to grass pollen occurs in the not closely related, much smaller monocot family Restionaceae, and this monoporate type has been identified in Paleocene and even latest Cretaceous rocks; see Medus (1982). Because restionaceous P01 pollen is scrobiculate and grass pollen mostly scabrate, they can be distinguished.) The Chenopodiaceae and Cyperaceae have a similar history. The chenopods are prevailingly herbaceous but have many woody members such as *Atriplex* (the saltbush genus, characteristic mostly of arid and semiarid regions). They are almost strictly a Pliocene and later phenomenon, though periporate (P0x) pollen that could be related occurs much earlier. Cyperaceous pollen is also primarily a

Pliocene-Quaternary phenomenon, though 10 million year old (Miocene) cyperaceous pollen is reported by Barnosky (1984). Unlike the other characteristically herbaceous families just mentioned, there are no woody family members.

During the latest Miocene and Pliocene of North America and of Eurasia, the more warmth-demanding hardwoods, as well as some conifers, such as *Tsuga*, gradually withdrew from high latitude areas. *Tsuga, Nyssa, Juglans, Castanea, Carya*, and *Liquidambar* and other tree taxa retreat southward in North America and disappear in Europe. *Quercoidites* spp., such as *Q. henricii* and *Q. microhenricii*, and *Cyrillaceaepollenites* spp., such as *C. megaexactus* disappear in Europe and perhaps are even extinct. Planderová (1972), speaking of central Europe, notes that the following families are much more significant in the Pliocene than in the Miocene (they first appeared much earlier): Poaceae (= Gramineae), Chenopodiaceae, Apiaceae (= Umbelliferae), Onagraceae, Rhamnaceae, Ericaceae. She also points out that Taxodiaceae, Nyssaceae, Myricaceae, and the genus *Engelhardia* are practically gone by latest Miocene. *Abies* becomes important at about the same time, along with Asteraceae (composites) and Poaceae (grasses). However, Reinink-Smith and Leopold (2005) show that, at least for part of southern Alaska, the Miocene warmth persisted until quite late in the Miocene. They describe a palynoflora rich in warmth-loving angiosperm taxa and including even such surprising conifers as members of the Podocarpaceae. In the early Pliocene *Acer, Betula*, and *Alnus* begin to appear in larger percentages. The early Pliocene is very rich in taxa, as new forms come in while some of the older ones are still present.

Table 15.1 shows the stratigraphic picture for some important palynological indicators, from latest Miocene to Pleistocene in northwest Europe and central Europe. An incidental matter regarding the identifications of taxa is that flowering material in Neogene sediments can sometimes be identified to genus by the *in situ* pollen. Kohlman-Adamska *et al.* (2004) were able to name new species of a number of genera based on pollen identifications. Reading this paper made me think of my work with Barghoorn on the Brandon lignite flora. Once we found a flower that seemed to be a tiny oak flower. I macerated an anther and, sure enough, it was thrilling to observe that the pollen was undoubtedly that of *Quercus.*

Benda (1971) studied the Miocene-Pleistocene of southwest Anatolia, and the results for Mio-Pliocene are interesting to show the possibilities and difficulties of geographically extending correlation based on Neogene pollen records (see Fig. 15.5).

Black Sea DSDP cores I have studied tie in fairly well with Benda's horizons, as do the European records shown in Table 15.1: latitudinal differences were not as sharp in the Mio-Pliocene as since. However, Benda found a "top" (last occurrence) for *Arecipites* (Arecaceae = Palmae) pollen in the earliest Miocene, whereas I found rather abundant palm pollen in the latest Miocene of the DSDP cores. Van der Hammen *et al.* (1971) have palm pollen well up in the Pliocene of

Table 15.1 Stratigraphic occurrence of important floral elements in the "Ultimogene" (late Neogene) of northwestern and central Europe (names from both lists modified for ease of comparison)

Northwest Europe (from van der Hammen *et al.*, 1971)	*Germany* (from von der Brelie, in Boenigk *et al.*, 1977)
"Top" mid-Pleistocene	
Carya	
Castanea	
Juglans	
Ostrya	
Pterocarya	
Tsuga	
"Top" early Pleistocene	"Top" early Pleistocene
Fagus	*Carya*
Phellodendron	*Eucommia*
	Fagus
	Juglans
	Pterocarya
	Tsuga
"Top" about end of Pliocene	"Top" in or at end of Pliocene
Aesculus	*Castanea*
Cupuliferoidaepollenites fallax	Cupressaceae *(=Inaperturo-pollenites dubius*)
Liquidambar	*Cupuliferoidaepollenites fallax*
Nyssa	*C. quisqualis*
Sciadopitys	*Cyrillaceaepollenites exactus*
Sequoia	*Liquidambar*
Zelkova	*Nyssa*
"Top" about mid-Pliocene	*Platanus*
Eleagnus	*Taxodium*
Arecaceae (= Palmae)	*Tricolporopollenites edmundii*
Symplocos	*Sciadopitys*
Tricolporopollenites edmundii	*Sequoia-Metasequoia-Glyptostrobus*
"Top" about end of Miocene	"Top" about end of Miocene
Cupuliferoipollenites villensis	*Araliaceoipollenites euphorii*
Cyrillaceaepollenites exatus	*Betulaceoipollenites bituitus*
Engelhardtioipollenites	*Engelhardtioipollenites punctatus*
Quercoidites henrici	Arecaceae (= Palmae)
Q. microhenrici	*Quercoidites henrici*
Rhoipites pseudocingulum	*Q. microhenrici*
	Tritriopollenites myricoides

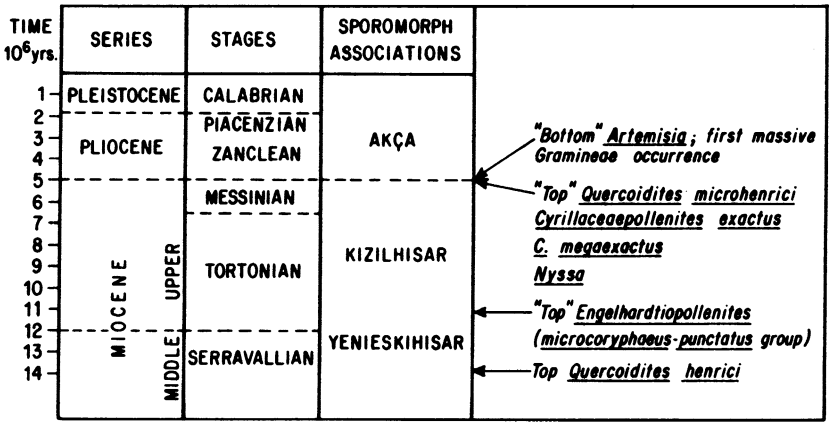


Figure 15.5 Miocene-Pliocene sporomorph associations from western Turkey. Note the influx of *Artemisia* and grasses, two of the principal steppe-indicators beginning in the Pliocene after the end (top) of many of the Miocene warmth-loving woody plants. Data from Benda and Meulenkamp (1979) and Benda (1971); the figure originally appeared in Traverse (1982).

northwest Europe, which seems discordant. Palms are, however, a tricky business, as a few species occur naturally in southernmost Europe even today. However, the frequently mentioned palms of southern England and southern Ireland are well-protected horticultural items, not native plants.

The latest Miocene did not produce really cold climates even quite near the Arctic Circle, at least not west of the continental divide. Hopkins *et al.* (1971) analyzed a flora radiometrically dated as somewhat more than 5.7 million years old, i.e. Messinian or latest Miocene, from Seward Peninsula, Alaska, latitude 65° N. The overall pollen flora includes no tundra elements. Brady and Martin (1978) report that much of Antarctica was glaciated at the beginning of the late Miocene, but that in places a rather luxuriant vegetation of Proteaceae, Fagaceae (*Nothofagus* spp.), Podocarpaceae and ferns still existed. Mercer (1973) says that even west Antarctica was glaciated by at least 3.5 Ma. The east Antarctic ice sheet is considerably older; various authors would have it in place by about 14 Ma (mid-Miocene) and the west Antarctic sheet beginning perhaps as early as 9 Ma (late Miocene), but some geologists favor considerably older, early Miocene, Antarctic glaciation. Oceanographic evidence mostly supports an approximate 10 Ma initiation of glaciation and worldwide major cooling (see Kerr, 1982). Various Soviet scientists have mentioned that extensive steppe vegetation developed in central Asia and Siberia during the late Miocene, but whether this was a modern steppe flora is not certain. Leopold (1984) and Leopold and Wright (1985) have established that in parts of western North America *Artemisia* steppe was present by late Miocene, but Leopold notes that major expansion of grasslands

and steppe west of the Rockies is a Pliocene-Pleistocene phenomenon, which would agree with palynological observations for south-central Europe (Traverse, 1982). Leopold's studies also established from modern pollen deposition that the pollen content of lake and alluvial sediments does indicate the broad vegetational type in the original area of deposition.

Most paleobotanists and palynologists who have worked in the tropical Cenozoic believe that in the lower latitudes there has been no massive change of floras at the generic level since pre-Messinian Miocene. Even at higher latitudes in Eurasia-America, profound changes of the vegetation in place in the Miocene did not begin until late Pliocene, with the arrival of continental ice sheets.

Thus, the use of pollen floras for broad-scale stratigraphy in the Miocene-Pliocene-Pleistocene is not practicable, though, within a selected area, trends may be observed and used. Van de Weerd (1979, p. 1260), for example, has cautioned:

> Uppermost Miocene and Lower Pliocene associations are rather similar and cannot be clearly separated. The morphotype distributions of *Pinus* do not provide an unambiguous boundary. . . . Pollen associations within a basin are stable over long periods. Gradual changes in the frequencies of pollen within lithological units cannot be detected. Marked differences in pollen associations are due to tectonic events. . . . Boundaries present in one basin may be absent in other basins.

3.3 The Pliocene Record

The Pliocene palynoflora of Eurasia-North America was characterized especially by conifers, though angiospermous pollen is numerically dominant (except in mountainous or high latitude areas). For example, in the Black Sea DSDP cores, when one works downward through the Pleistocene, one is struck by the abundance and diversity of conifers in the Pliocene: *Tsuga* spp., *Abies* spp., *Cedrus, Podocarpus, Pinus* spp., plus many species of Taxodiaceae such as *Taxodium, Sequoia*, and *Sciadopitys*, and Cupressaceae-Taxaceae forms. Presumably this indicates widespread cool but not yet arid climate. The first massive cooling of the late Neogene occurred in the late Pliocene, perhaps about 2.5 million years ago, whereas because of dating of the type sections the Pleistocene does not begin until about 1.8 million years ago. Suc (1980) studied sections in France and Spain that were mostly Pliocene and noted that the bases of his sections are dominated by Taxodiaceae. The middle of the sections shows a replacement of taxodiads by abietineans. Toward the top of the Pliocene, xerophytic plants are present in great numbers: grasses, chenopods, *Artemisia*, in brief, steppe-like indicators. In the Mediterranean area, *Pinus*-Taxodiaceae-Cupressaceae- *Sciadopitys* are abundant in early Pliocene, followed by *Pinus* and other conifers, then Podocarpaceae, then *Pinus-Sciadopitys*-Asteraceae at the Pliocene/Pleistocene boundary (Sauvage, 1979; Sauvage and Sebrier, 1977, studying sections in Greece). The first interglacial was characterized by *Tsuga-Sciadopitys-Carya-Pterocarya*. I also observed this flora in the Black Sea DSDP cores, after the "alpha" glaciation. Bertolani-Marchetti

et al. (1979) observed in northern Italy that *Sciadopitys* terminated near the end of the Pliocene (see Fig. 15.6).

Palynological writers have interpreted a "preglacial Pleistocene" ("Pre-Tiglian") and have drawn conclusions from this concept. This is no longer tenable, as we have seen. The "Tiglian" of the Netherlands sections belongs in the Pliocene (pre-1.8 million years). The "Tiglian warming" perhaps shows in the DSDP record just before the "alpha" glaciation (see Fig. 15.4). The Pliocene/Pleistocene boundary depends on sections in Italy for which there is marine fossil control. These sections have not been studied palynologically until comparatively recently. It would be fortuitous if a universally present and marked Pliocene/Pleistocene palynological boundary existed. Thus, the termination of *Sciadopitys* (Taxodiaceae) pollen near the boundary in Italy shown in Fig. 15.6 is not to be taken as a demonstration of an extendable datum. Nevertheless, there are observable worldwide palynological effects of the late Pliocene cooling. For example, great expansion of *Artemisia* and Poaceae (grass) pollen in the USA Gulf Coast coordinate with other signs of the event, e.g., mottled clays. Suc (1980) observed steppe-forest alternation in the Plio-Pleistocene of France.

This and related phenomena are widespread, at least in the Northern Hemisphere. Boulter (1971a, b) has shown that, given the knowledge of where such sediment occurs, even a Neogene deposit for which other stratigraphic evidence is not helpful can be palynologically dated. Boulter analyzed "pockets" of clay from sinkholes in Carboniferous limestone in Derbyshire, England, and dated the palynoflora as Miocene/Pliocene boundary (5.3 Myr). See Fig. 15.3 for examples of this flora.

4 Pleistocene Palynology

4.1 General Remarks

The Pleistocene is a time of widespread "catastrophes," that is, a time of comparatively rapid and oscillating climatic changes in many parts of the world. The steppe/forest curve in Fig. 15.4 is a smoothed-out, running-average curve, and even this curve is based on very widely spaced samples. The oscillations are really much more numerous. One can observe the same sort of rapid Pleistocene oscillations on a small scale in places in Scotland, where birch or pine forests have been killed and covered by blanket peats since the climatic optimum of a few thousand years ago (human clearing of forest has probably also played a role). The violent and frequent swings of climate in the Pleistocene are shown by detailed steppe/forest index curves in Black Sea cores (Traverse, 1978a), and by non-tree pollen vs. tree pollen (arboreal pollen) (NAP/AP) fluctuations in many other places. In areas such as Africa and southwest USA and Australia, oscillations of dry vs. moist conditions rather than temperature changes are the

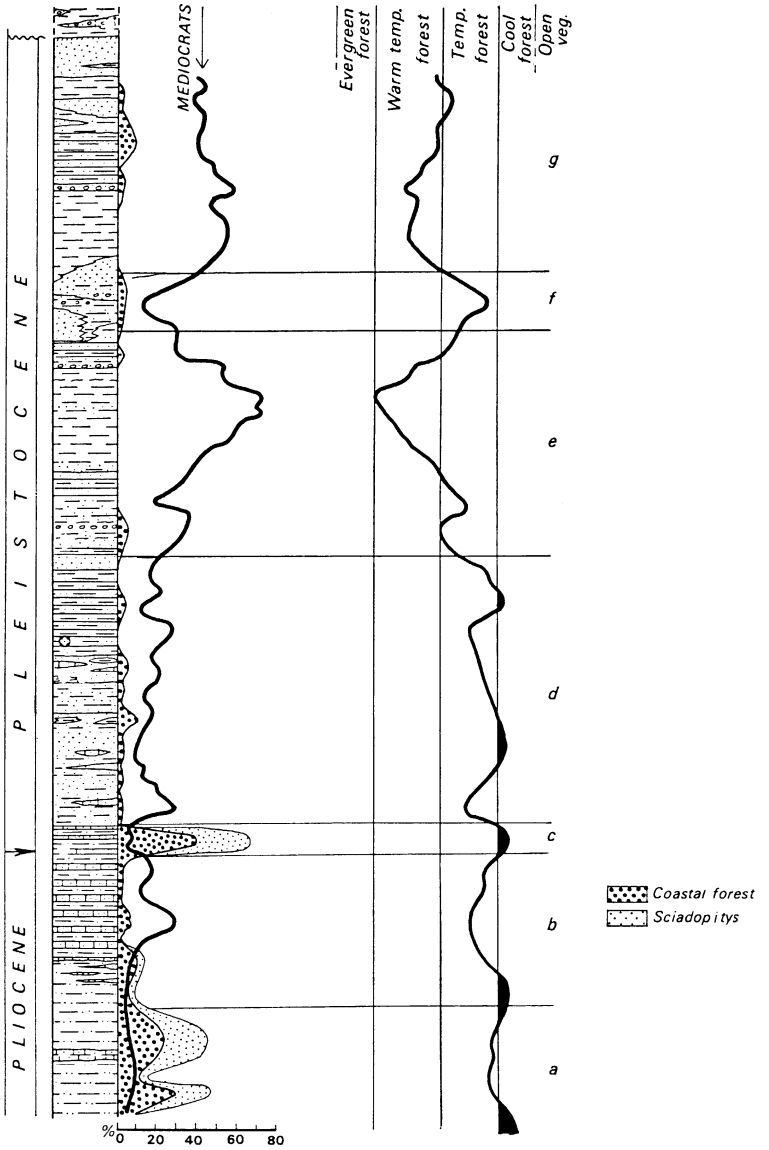


Figure 15.6 Late Pliocene to (ca.) first half of Pleistocene pollen record, Stirone River, northern Italy. Note especially the termination of *Sciadopitys* (today there is only one species, confined to Japan) soon after the end of the Pliocene, and the diminution but periodic minor reappearance of *Sequoia-Taxodium* ("coastal forest", now confined to North America) at that time. The mediocrats (see "mesocratic" in Figure 15.8) curve refers to *Quercus, Tilia, Ulmus*, and other trees/shrubs characteristic of the climatic-optimum part of interglacials. The curve on the right is climatic, indicating cooler to the right, as shown
.

important matters, whereas at high latitudes and elevations temperature swings have been important.

The rapidity of climatic swings (some quite brief) in the late Cenozoic can apparently be shown by palynological analysis of closely spaced dark and light laminations of Black Sea DSDP cores, as shown in Table 15.2. The swings in steppe/forest pollen index and accompanying chemico-physical measurements indicate very rapid changes, in the range of a century. Based on oxygen-isotope data, the light layers represent colder episodes than the dark layers. The precise causes of the climatic swings are not known, and it must be mentioned that some palynologists (Davis and Botkin, 1985) are of the opinion that, at least for cool temperate forests, short term climatic changes on the scale of a few hundred years are not picked up by the pollen record, partly because of lag time in vegetational response. There is also a problem in getting samples from very short intervals. Palynologists seldom sample sediments centimeter by centimeter; 10 cm or much wider spacing is more common. Close spaced sampling and study enables palynology to combine with isotope and other studies to pick up climatic and sedimentological changes associated with such late Pleistocene phenomena as Heinrich Events: massive release of icebergs from continental ice sheets, reflected in a layers of sediment rich in ice-rafted debris and palynomorphs of pioneer vegetation (cf. Jennerjahn *et al.*, 2004).

The conventional divisions of the Quaternary and Pleistocene are shown in Fig. 15.7. As discussed in Chapter 14, some of the primary authorities on stratigraphic nomenclature (cf. Aubry *et al.*, 2005) propose making the Tertiary and Quaternary each a sort of honorary "sub era" of the Cenozoic, and setting up the Paleogene and Neogene as a detached, parallel set of periods of the Cenozoic, with the Neogene Period comprising about the latest third of the Tertiary Sub-Era, plus all of the Quaternary Sub-Era. The Neogene would then consist of the Miocene, Pliocene, and Pleistocene/ Holocene epochs, extending to the present, with recognition that the Holocene is post-Pleistocene. Clearly, Quaternary and Holocene are concepts with a large following, based on more than logic alone. It will be interesting to see how this all plays out.

Originally, the Pleistocene was envisioned as one great glacial time, by Louis Agassiz and others. Later scientists such as Geikie (see Charlesworth, 1957) showed that there were multiple large glaciations ("polyglacialism"–see discussion by West, 1985). How many has been much disputed. Geikie suggested six. Penck and Brückner (1909), working on alpine sections of Germany and Switzerland, claimed four major alpine glaciations and named them Günz, Mindel,

Figure 15.6 by the vegetation types at the top. Patterns shown on the left are standard indications of sediment type: dots = sand and silt, lines = shale, blocks = limestone, etc. The zones a-g indicate characteristic vegetational complexes described in detail by Bertolani Marchetti *et al*., 1979, in which these diagrams first appeared.

Table 15.2 "Light"-"Dark" cycle pairs from Deep Sea Drilling Project (Leg 42B, 1975) Holes 379A and 380-380A, showing the regularly found association in "Light" samples between high SFI, high $CaCO_3$, low SiO_2 and less negative $\delta^{18}O$-isotope values; compared with "Dark" samples with lower SFI, lower $CaCO_3$, higher SiO_2 and more negative $\delta^{18}O$-isotope values. A "light" sample apparently represents the cooler part, and a "dark" sample the warmer part, of a cycle

Sample Pairs (cycles)	*I*		*Pairs I-III, 380A:51:3* *II*		*III*		*Pair IV, 379A:60:2* *IV**	
Color	Light	Dark	Light	Dark	Light	Dark	Light	Dark
Depth (cm)	76–77	75–76	110-111	109–110	116–117	115–116	10–12	6–9
SFI	54	10	70	9	72	36	55	9
$CaCO_3$†	92	46	94	81	89	53	67	45
SiO_2†	7	17	6	14	6	30	20	33
$\delta^{18}O$‡	−2.20	−3.32	−2.72	−3.25	−2.82	−3.03	−5.80	−6.19

* This pair was reported in Traverse, 1978a, and a sample residue remained for later x-ray and isotope analysis.

† X-ray analysis by J. Pika, ETH, Zürich. Values expressed in % of total crystalline inorganic matter.

‡ Isotope analysis by J. Pika, ETH, Zürich. Note: the more negative values indicate warmer. Presumably the explanation for the high readings for Pair IV is that if a pair is deposited during a generally warmer period, both "Light" and "Dark" will be more negative than are sediments laid down during a generally colder period. The darker layer of a "pair" is almost always more negative than the lighter layer. Values are expressed as relative enrichment of ^{18}O against the "PDB" standard, which is taken as 0 on the scale. ("PDB" refers to Peedee Formation belemnites, the University of Chicago standard.) This material originally appeared in Traverse, 1982.

Riss, and Würm for superimposed terraces of Danube tributaries, which are listed alphabetically. America for a time favored the concept of five great glacial episodes: Nebraskan, Kansan, Illinoian, Iowan and Wisconsinian. Under the influence of the European chronology, the Iowan was suppressed as a separate mega-glaciation, and a four-glaciation Pleistocene came to be widely accepted: Nebraskan, Kansan, Illinoian, and Wisconsinian. As can be seen in Fig. 15.7, the Riss and Würm together are now thought in Europe to be equivalent to the Wisconsinian, the Danubian to the Nebraskan, the Günz to the Kansan, and the Mindel to the Illinoian. Whereas in Europe the intervening warmer times have been traditionally labeled by the combined names of the preceding and following Alpine glacials (thus, Günz-Mindel, etc.), in North America separate names are used for the interglacials: Aftonian, Yarmouthian, and Sangamonian. In Europe the interglacials in areas away from the Alps are commonly given distinctive names: Ipswichian, Hoxnian, etc. The truth seems to be that there were multiple

GLACIAL – INTERGLACIAL SUBDIVISIONS

	CLIMATIC REGIME	NORTH AMERICA	BRITISH ISLES AND NORTHWEST EUROPE	CENTRAL EUROPE
ca. 10^4 years	Interglacial	Holocene ("Post Glacial")	Flandrian	Flandrian
PLEISTOCENE	Glacial	Wisconsinian	Devensian–Weichselian / Ipswichian=Eemian Interglacial / Wolstonian–Saalian	Würm / Riss–Würm Interglacial / Riss
	Interglacial	Sangamonian	Hoxnian–Holsteinian	Mindel–Riss
	Glacial	Illinoian	Anglian–Elsterian	Mindel
	Interglacial	Yarmouthian	Cromerian	Günz–Mindel
	Glacial	Kansan	Menapian	Günz
	Interglacial	Aftonian	Waalian	Danubian–Günz
1.8×10^6 years	Glacial	Nebraskan	Eburonian	Danubian
PLIOCENE	Interglacial	"pre-Nebraskan"	Tiglian	Biberian–Danubian
	Glacial	"pre-Nebraskan"	pre-Tiglian	Biberian (Transitional Beds)
		Reuverian		

Figure 15.7 Pleistocene subdivisions as used in North America and Europe. Redrafted from Godwin (1975) and various other sources.

cold phases, alternating with multiple warmer phases. In my work with Black Sea DSDP cores, I concluded that the most reasonable grouping of multiple oscillations was into three great glacial times, which I have called alpha, beta and gamma, to avoid confusion with the classical names (see Fig. 15.4). This broad grouping is at least as compatible with oxygen isotope data from marine cores as a four-phase or a six-phase model.

4.2 Palynology of Glacial-Interglacial Cycles

Our best information centers on studies of the last mega-glaciation (Riss + Würm = Saalian + Weichselian = Wisconsinian) and of the interglacial that preceded it (Sangamonian in North America = Mindel-Riss = Holsteinian in Europe). The terminal Wisconsinian (about 18,000 yr B.P.) seems to have been the coldest time of all (Peterson *et al,* 1979), archetypal Pleistocene. Godwin (1975), working on both of the last two European interglacials, the Ipswichian–from the American point of view, a Wisconsinian interstadial–and the Hoxnian (= Holsteinian = Sangamonian of North America) in Britain, has prepared

a palynological model for the glacial-interglacial transitions (see Fig. 15.8). Fig. 15.9 gives a pollen diagram for the Ipswichian interglacial or interstadial, and Fig. 15.10 for the Hoxnian and for what we so far have experienced of the present, Flandrian (= Holocene) interglacial. Obviously the interglacials are rather similar to each other in comparable areas. Van der Hammen *et al.* (1971) have also diagrammed these events. Their presentation emphasizes the impact of temperature on moisture. It gets cold first, then dry, in a glacial, warm first, then wet, in an interglacial.

That it is very difficult to transfer such a model directly to other parts of the world is shown by Fig. 15.8b. Heusser (1977a) finds a number of cold-warm oscillations during the last 100,000 years of the Washington State area, northwest U.S.A. The exact relation of these to the Würm-Wisconsinian, etc., is unclear. experienced of the present, Flandrian (= Holocene), interglacial. Obviously the interglacials are rather similar to each other in comparable areas. Van der Hammen *et al.* (1971) have also diagrammed these events. Their presentation emphasizes the impact of temperature on moisture. It gets cold first, then dry, in a glacial; warm first, then wet, in an interglacial. The oscillations are obviously numerous, and the great glaciations are groupings of closely spaced cold times. It is also well known that sedimentary factors (associations of palynofloras with sediment types) have a considerable bearing on a spore/pollen "signature" (the shape of a pollen analytical curve). It is therefore unreasonable to expect to find exactly the same sequences in peat from a peat bog, in silt from the center of a large lake, and in a core from offshore clayey silt, even in the same general area.

Baker (1986) describes the pollen and plant megafossil record of the last glacial-interglacial cycle from a site in Yellowstone National Park, Wyoming. The peak warm period assumed to represent the Sangamonian interglacial is represented by a flora dominated by *Pseudotsuga-Pinus* forest, and a climate considerably warmer than any Holocene climate is suggested.

The sorts of pollen on which the palynological records discussed above are based represent a relatively small list, of mostly wind-pollinated extant plants, primarily those from mid-latitudes of the Northern Hemisphere. Figs. 15.11 (mostly gymnosperms) and 15.12 (angiosperms) present illustrations of a number of such forms, comprising a large percentage of all the important taxa.

4.3 Glacials vs. Interglacials and Water Budgets: "Pluvials"?

This is a very important and vexing question to which palynology has made some contributions. The long and the short of it is that, despite exceptions and over large areas, cold means dry, and warm means wet. It was long believed that the reverse was generally true. That is to say that glacials were associated outside of the glacial areas with wet "pluvials". This does seem to be true at some places. But in Africa, for example, the colder times seem to have been prevailingly dry

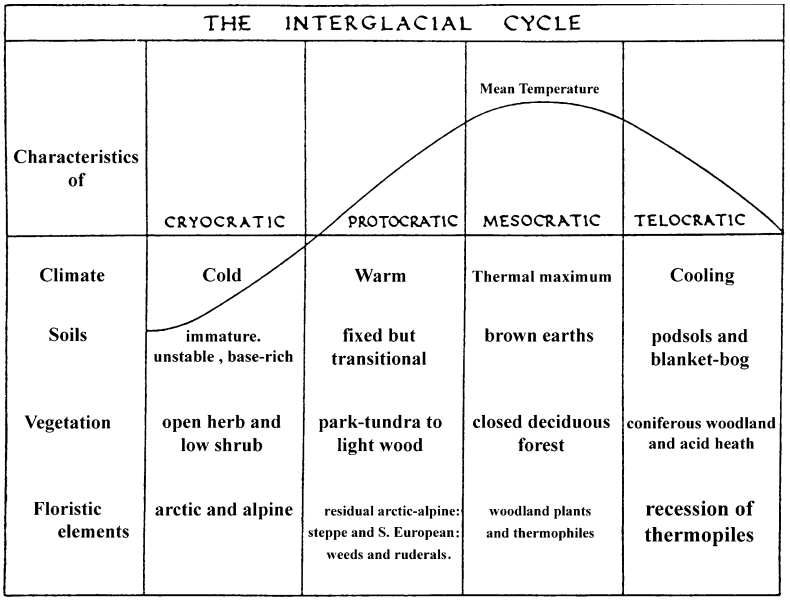


Figure 15.8 Glacial–interglacial "cycles" in perspective. (a) The formal interglacial cycle of vegetation–soil–climate alterations indicated by pollen analytical data of northwest Europe. Note measocratic is equivalent to a climatic ptimum. (b) Oxydata and ^{14}C dated.

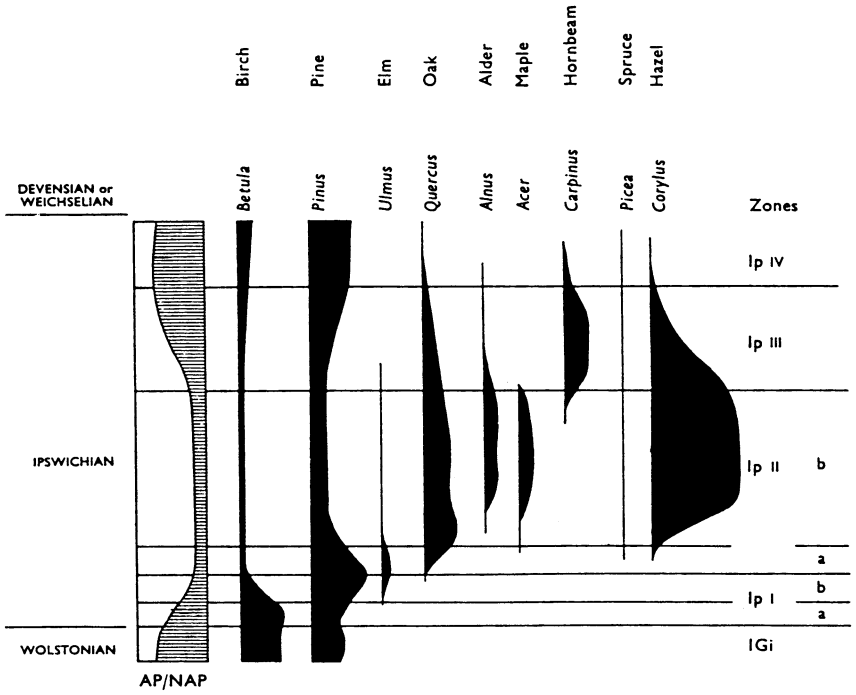


Figure 15.9 Composite pollen diagram for Ipswichian interglacial (see Fig. 15.7) of eastern England representing vegetational changes during stages of this interglacial. (An interglacial contemporaneous with the Ipswichian is not recognized as a separate interglacial in North America–it would be a late Wisconsinian interstadial.) Compare with Figure 15.10 for evidence that glacial-interglacial cycles are repetitive (in one geographic area) and that the present (Holocene) interglacial is "z normal." Diagram from Godwin, 1975; data originally from West, 1968.

periods when the Sahara has advanced. Street and Grove (1979) have shown that, in the tropics generally, high lake levels were interglacial phenomena due to increased monsoons. However, in North America, the argument about pluvials still goes on.

Figure 15.8 core from western Washington State, USA, correlated to pollen zones, with temperature estimate curve. The approximately 80,000 year record is characterized by frequent, even rather dramatic, shifts. Putting the Pleistocene record into a three or four glaciation–interglacial framework represents very considerable smoothing of the record. In fact, there have been hundreds of smaller climatic changes. (a) is from Godwin, 1975; (b) is from Heusser, 1977a.

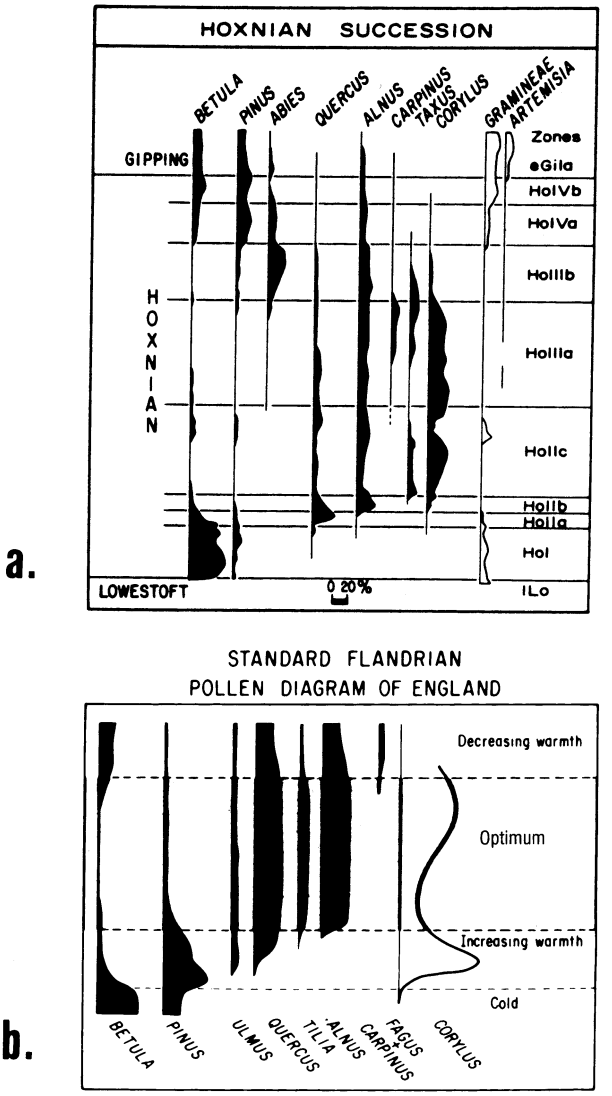


Figure 15.10 Two more interglacial pollen diagrams from England, for comparison with Figure 15.9. (**a**) The Hoxnian diagram is for the interglacial known as Sangamonian in North America, Mindel-Riss in central Europe. (**b**) The present interglacial (called the Flandrian in parts of Europe)is also known as "post-glacial" or Holocene. Compare with Figure 15.9 to show that glacials-interglacials have a repetitive character, e.g., *Betula* peaks in late glacial time, minimizes during the climatic optimum, etc. There are small characteristic differences too, e.g., *Carpinus* has a somewhat different response to local circumstances in each of these three interglacials. Redrawn from Godwin, 1975.

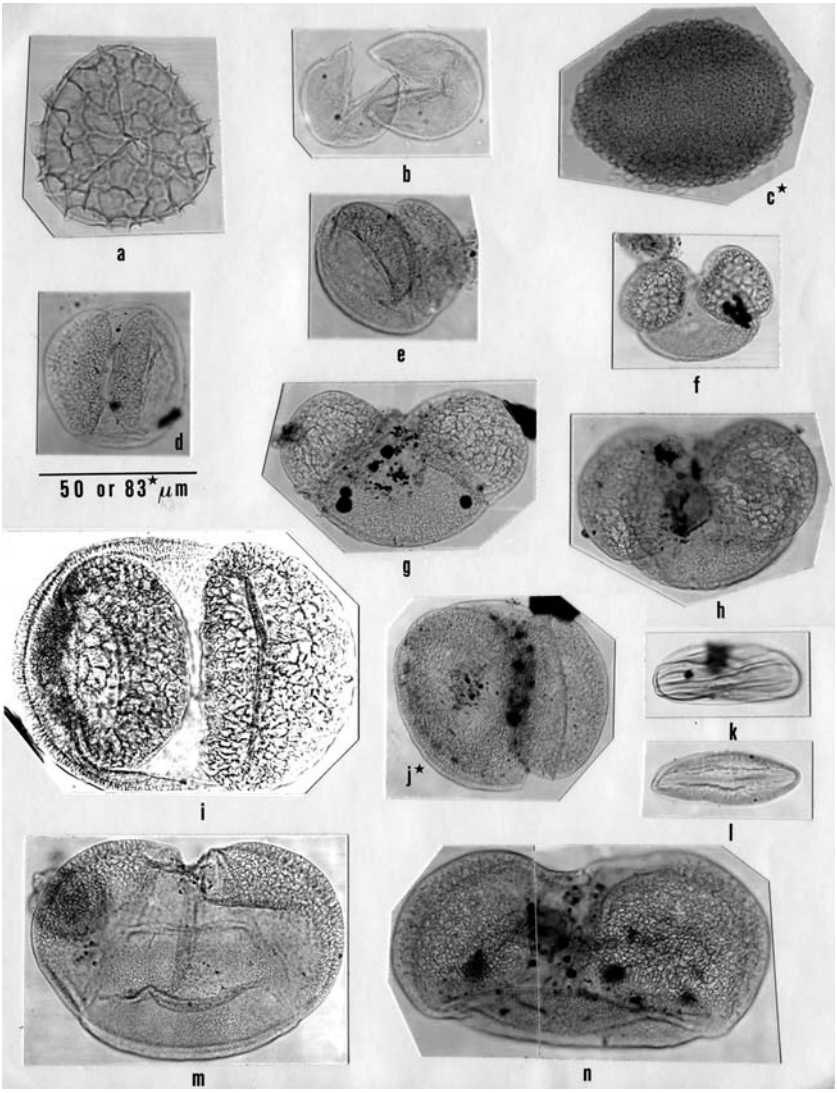


Figure 15.11 Some characteristic sporomorphs (mostly gymnosperm pollen) from the Northern Hemisphere Pleistocene, including the present interglacial (= Holocene). Some of the specimens are from a Holocene peat from New Brunswick, Canada (NB); others are from Pleistocene levels in DSDP hole 380 in the Black Sea (DSDP). The specimens from the New Brunswick peat were prepared by KOH digestion and are somewhat expanded. Magnification indicated by bar under (d). Note that specimens indicated by * have a different magnification from the others. (**a**) *Lycopodium* sp., proximal view (NB). A frequent constituent of Pleistocene samples, known amounts of *Lycopodium* spores are

Wells (1979) and Benson (1978) believe that lakes such as Lahontan and Bonneville in the central west of the USA had high stands during glacials ("pluvials"). This could, however, be due to increase in effective moisture because of lower temperature. Brakenridge (1978) showed that temperature factors alone could account for all vegetation displacement in the late Pleistocene of the western USA and also for the higher lake levels, because of lowered evaporation, not greater precipitation (see Fig. 15.13). Spaulding *et al.* (1983) emphasize that the full glacial climate of the southwest USA *was* moist. That is, it was effectively moist compared to the Holocene, because of lower temperatures and prevalence of winter precipitation, in contrast to Holocene summer precipitation, but

Figure 15.11 also added to samples by palynologists for use in calculation of the concentration of spores and pollen. Fern spores are also frequently encountered in Pleistocene work. (**b**) *Taxodium* sp. (swamp cypress). Two specimens in lateral view (DSDP) showing the "clam-shell" appearance usually presented by the split-open fossil pollen. (Other taxodiaceous pollen as well as pollen of Taxaceae and Cupressaceae pollen sometimes look much the same, so the forms are sometimes lumped under the designation "TCT," a term introduced by Martin and Gray, 1962.) (**c**) *Tsuga* sp. (hemlock). A monosaccate conifer fossil pollen with very characteristically ropy-ruffled exine (NB). (**d**)?*Cedrus* sp. Distal view (DSDP). In practice the differentiation of specimens of *Cedrus* from those of *Pinus*, where both occur, is so difficult that it is probably better to lump them as *Pinus/Cedrus*. With rare exceptions, Pinus pollen will be much more abundant. (**e**)?*Cedrus* sp. Distal-lateral view (DSDP) (see comments under (d)). (**f**) *Pinus* sp. Lateral view (DSDP). *Pinus* is a large genus, and various people have demonstrated the possibility of separating the pollen as to species or groups of species, on the basis of the morphology. However, in work with sediments such as those in the Black Sea or the Gulf of Mexico, with streams contributing sediment and pollen from a very large area, it is only practical to count "*Pinus*". (**g**) *Pinus* sp. Lateral view (DSDP). The black spots are pyrite (probably marcasite variety) crystals, a product of sulfur-bacterial activity and a feature of pollen deposited in a reducing environment. (**h**) *Pinus* sp. Distal-lateral view (DSDP) (see (f) and (g). (**i**) *Abies* sp. Distal view (DSDP). Two sorts of giant bisaccates occur commonly in Pleistocene sediments–*Abies* (fir) and *Picea* (spruce). The two genera of conifer trees are somewhat similar phenotypically. *Abies* pollen looks more like a giant pine pollen grain than does *Picea*, however (see (m) and (n)). (**j**) *Abies* sp. Distal view (DSDP). Photo at lower magnification than most others on this plate. Note, as in (i), the pine-like appearance. (**k**) *Ephedra* sp. Proximo-distal view (DSDP). A psilate form. *Ephedra* pollen is often found in the same samples as *Artemisia*, but is never as abundant. It is a polyplicate (= taeniate) pollen grain with a long fossil history (see (l)). (**l**) *Ephedra* sp. Proximo-distal view (DSDP). A species with fossulate sculpturing in addition to being polyplicate. (**m**) *Picea* sp. Lateral view (DSDP). A giant conifer bisaccate pollen with sacci that blend into the corpus and more or less continue its outline in lateral view (see *Abies*, (i) and (j)). (**n**) *Picea* sp. Lateral view of somewhat flattened specimen (DSDP). See (m).

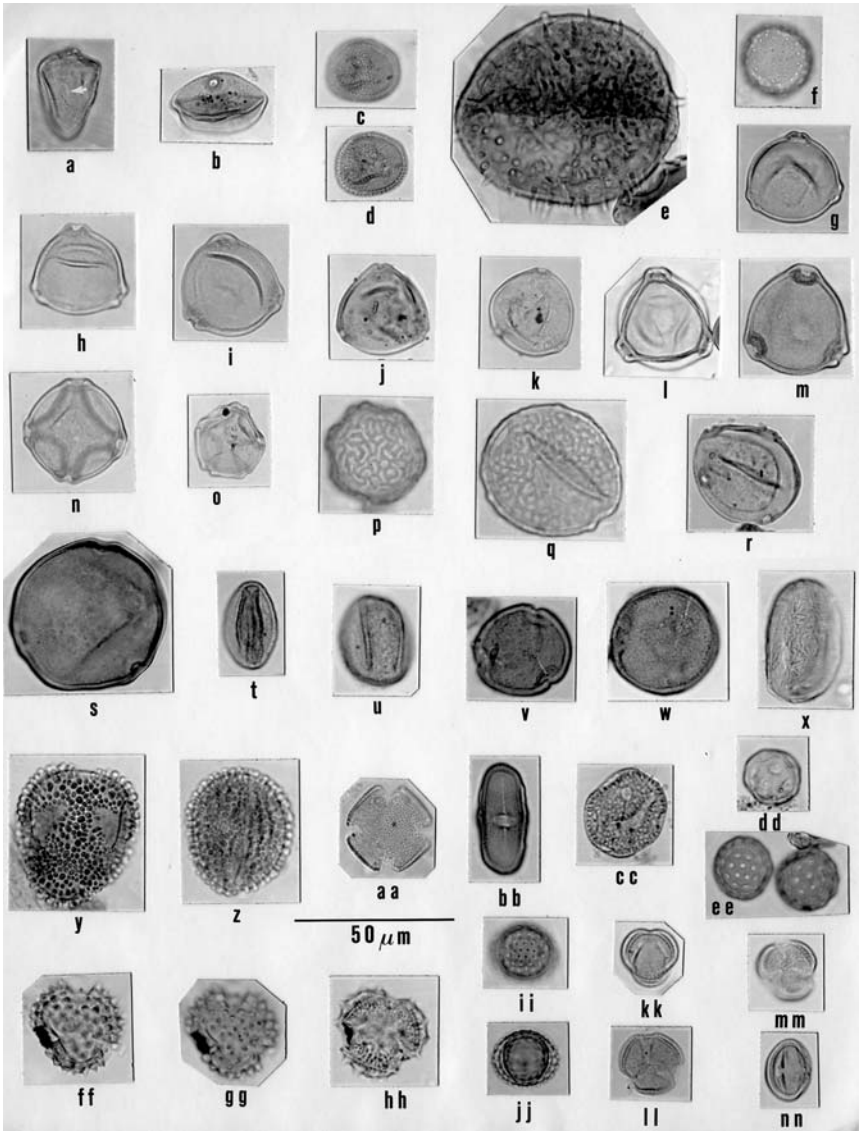


Figure 15.12 Some typical angiosperm pollen forms encountered in the Northern Hemisphere Pleistocene, and the present (Holocene) interglacial. Some of the specimens are from a Holocene peat deposit in New Brunswick, Canada (NB), some are modern pollen from water samples from Trinity River and Trinity Bay, Texas, USA (TR), some are from Pleistocene levels in DSDP hole 380, Black Sea (DSDP). NB forms were processed by KOH digestion and are somewhat enlarged. Magnification indicated by bar under (aa). (**a**) Cyperaceae (sedge). Lateral view of the typically pear-shaped pollen, showing an ulcus

Figure 15.12 at the top and one on the surface (arrow) (TR). (**b**) Poaceae (grass). Obliquely distal view showing the annulate pore with operculum, and the characteristic folded nature of most fossil grass pollen (DSDP). (**c**),(**d**) *Typha* sp. (cattail), or the closely related *Sparganium*. Two levels of focus (DSDP). *Typha* pollen is mono-ulcerate. Fresh-water indicator. (**e**) *Nuphar* sp. (pond-lily). Monosulcate echinate pollen, distal view (NB). Fresh-water indicator. (**f**) *Sagittaria* sp. (arrowhead). A weakly periporate echinate pollen of a common inhabitant of fresh-water wet places (DSDP.). (**g**) *Carpinus* sp., or *Ostrya* sp. (ironwood). Two very common betulaceous tree genera, polar view (DSDP). Separation of the many triporate pollen types in Pleistocene pollen analysis is very difficult. *Carpinus* and *Ostrya* pollen are so similar that best practice is to include them under "*Carpinus/Ostrya"*. The pore structure is relatively small and protrudes relatively little from the perimeter. (**h**) *Myrica* sp. (wax myrtle). Triporate pollen of a common shrub genus, polar view (NB). See comments under (g). The pore structure is relatively heavy but does not have a well developed vestibulum as does *Betula*. In practice, *Myrica* spp. pollen are difficult to separate from *Corylus* spp. (**i**) *Myrica* sp. (NB). See comments under (g) and (h). (**j**) *Corylus* sp. (hazelnut). Polar view (DSDP). Very similar to *Myrica*. Pore structure somewhat less pronounced, annulus not as heavy. See (g) and (h). (**k**) *Corylus* sp. Polar view (DSDP). See (g), (h), and (j). (**l**) *Betula* sp. (birch). Polar view of triporate pollen of a very common Pleistocene tree (NB). The heavy structure of the pore apparatus is characteristic, as is the large vestibulum between pore and os. The triangular figure connecting the pores represents an exine band at the equator, indicating the shape and size of the grain before KOH treatment and mounting in glycerin jelly caused swelling poleward. (**m**) *Betula* sp. See (l). Probably a different species from that of (n), though from the same preparation (NB). (**n**) *Alnus* sp. (alder). Polar view of 4-stephanoporate pollen of a very common shrub and tree genus (NB). The thickened bands (arci) connecting pore structures are characteristic. See (o). (**o**) *Alnus* sp. A 5-stephanoporate form (DSDP). See (n). The specimens (n) and (o) were probably originally about the same size, but different sedimentary history and processing technique has swollen specimen (n). (**p**) *Ulmus* sp. (elm). Polar view of 6-stephanoporate form of this common tree pollen, in high focus to demonstrate characteristic rugulate sculpture (TR). (**q**) *Ulmus* sp. A 5-stephanoporate form, (NB). See (p). (**r**) *Pterocarya* sp. Polar view of 5-stephanoporate pollen of an Old World juglandaceous tree common in Pleistocene samples of Black Sea-Mediterranean area (DSDP). (**s**) *Carya* sp. (hickory). Polar view of P03 pollen of this very common Pleistocene tree genus (DSDP). (**t**) *Quercus* sp. (oak). Equatorial view of verrucate Pc0 pollen of this very common Pleistocene tree genus (DSDP). *Quercus* is a very large genus, and pollen of at least some of the species can be distinguished by combination of light microscopy and SEM. In many Holocene sediments *Quercus* and *Pinus* combined are 50% or more of the palynoflora. (**u**) *Quercus* sp., a different form, DSDP. See (t). (**v**),(**w**) *Fagus* sp. (beech). Polar and obliquely equatorial views, respectively, of Pc3 pollen of a common Pleistocene tree genus, showing the evenly scabrate sculpture and spherical shape (DSDP). (**x**) *Acer* sp. (maple). Equatorial view of Pc0 pollen of a common Pleistocene tree; high focus to show the striate pattern of sculpture (NB). Pollen of some other plants, especially in the Rosaceae, has similar sculpture. (**y**),(**z**) *Ilex* sp. (holly). Polar and equatorial views, respectively, of Pc0 pollen of a common tree and shrub of Pleistocene, with characteristic clavate sculpture (NB). (**aa**) *Fraxinus* sp. (ash). Polar view of Pd0, reticulate pollen of a common Pleistocene tree (TR). (**bb**) Apiaceae (carrot family) pollen, equatorial view of

possibly also with higher annual precipitation than today, especially in some areas.

That the situation is very complicated is demonstrated by Jansen *et al.* (1986) in a multipronged study of ocean cores, indicating that a swing to more glacial conditions in the Northern Hemisphere 300,000-400,000 yr B.P. was correlated with a trend to more interglacial conditions in the Southern Hemisphere!

In Australia, Dodson (1977) shows that *Casuarina* plus *Eucalyptus* forests have greatly expanded in the Holocene of coastal Australia, whereas very dry open woodland dominated the same areas during full glacial time, 11,000–26,000 yr B.P.

Van Zinderen-Bakker's (1976) palynologically based diagrams for the African cold vs. warm fluctuations clearly show that warmer times are prevailingly moister (see Fig. 15.14). Flenley's (1979) extensive survey of the African equatorial rainforest in the Pleistocene supports the idea generated from palynological and other evidence that the time from 26,000 to 12,000 yr B.P. was cooler *and* drier than at present. On the other hand, a thorough review of tropical pollen analysis in Africa, South America and elsewhere, by Livingstone and Van der Hammen (1978) shows the difficulty of interpretating the as yet rather limited number of data points. Clearly, tropical climates are and have been very unstable. While

Figure 15.12 characteristic perprolate Pc3 pollen (TR). Herbaceous Apiaceae are abundant contributors of pollen to Pleistocene sediments. Pollen of many Apiaceae genera are very similar. (**cc**) Caryophyllaceae (pink family). Reticulate P0x pollen of herbaceous dicot, (DSDP). Many members of the family make similar pollen. (**dd**) Amaranthaceae (amaranth family). Micropitted P0x pollen of herbaceous dicot (DSDP). The amaranths and chenopods (ee) form a complex of periporate pollen which many palynologists lump in counting as "cheno-ams". (**ee**) Chenopodiaceae (beet family). Microreticulate P0x pollen of abundant herbaceous dicot family (DSDP). Chenopodiaceous genera are difficult to separate on pollen characters, see also comment under (dd). (**ff**), (**gg**) Asteraceae (=Compositae). Long-spined sort, polar view, high to mid-focus and high focus, respectively (DSDP). This huge family of herbs and shrubs is ubiquitous in the Pleistocene. It is difficult to separate the many genera on pollen characters in routine analysis–most of them are Pc3-echinate. (**hh**) Asteraceae. Long-spined type, mid-focus, showing the clearly expressed columellate structure (DSDP). See comments under (ff) and (gg). (**ii**), (**jj**) *Ambrosia* sp./*Iva* sp. (ragweed, Asteraceae). Equatorial view, high focus and mid-focus, respectively (TR). This herb complex is the bête noire of pollinosis, and because it is a weed also is abundant in Holocene sediments where human habitation was a factor. (**kk**)-(**nn**) *Artemisia* sp. (sagebrush, Asteraceae). Oblique-polar, polar mid-focus, polar high focus, and equatorial views, respectively, of short-spined Pc3 asteraceous pollen (DSDP). Some species ("sagebrush") of this genus thrive especially in cold, dry environments such as large areas of the modern Rocky Mountains. It is characteristically associated with chenopod pollen in pollen floras sedimented from steppe areas. (There are *Artemisia* spp. with rather different ecological significance.)

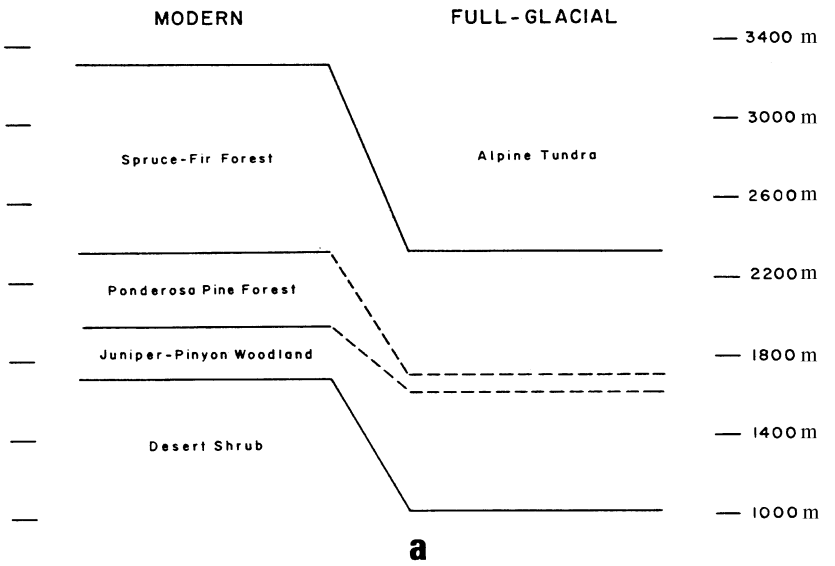
the period 20,000–12,500 yr B.P. was, in general, drier than the present in the tropics, there were exceptions.

Rossignol-Strick and Duzer (1979a) show, in a palynological study of a core from offshore Senegal (northwest Africa), very dry circumstances at the 18,000 yr B.P. glacial maximum and very moist during the mid-Holocene (sometimes called the hypsithermal, or thermal maximum). That these generalizations only work as a broad view is shown, however, by Sowunmi's (1981) work in Nigeria, where very complex oscillations of moisture-loving and xerophilic vegetation were measured palynologically. The picture agrees in general with glaciations at higher latitudes being correlated with dry conditions at low latitudes, partly because of marine regression, resulting from lower sea levels during glaciations. Primarily, however, the low latitude dryness has to do with changes in atmospheric circulation brought on by glaciation: shifts in position of trade winds, etc.

4.4 Palynological Information On Late Pleistocene Chronology and Vegetational History

Woillard's (1978) work with the long Grande Pile peat core in France (Fig. 15.15) is very important as a very complete, continuous, non-marine palynological record in western Europe. The commencement of the Eemian (= Riss-Würm = Wisconsinian interstadial) at about 130,000 yr B.P., as indicated by arboreal pollen (AP), looks good. The end of the Eemian is at the break toward colder conditions at about 125,000 yr B.P. This trend agrees well with Shackleton and Matthews (1977) 125,000 yr B.P. level for Barbados, based on oxygen isotope studies. In any event, Woillard's data and the oxygen-isotope data agree well with the Black Sea data in indicating one large, last interglacial (Riss-Würm = Sangamonian = "gamma"). Wijmstra's (1969) diagram for a long core from Macedonia looks remarkably like the Grande Pile core, with a prolonged glacial period, apparently a "gamma" (Black Sea), with interstadials toward the bottom, identified by increased AP. Delcourt (1979) has analyzed cores from Tennessee, hundreds of kilometers south of the glacial limit, representing the last 25,000 years. The late glacial maximum (LGM) at 19,000–16,300 yr B.P. is represented in Tennessee by dominance of *Picea, Abies*, and *Pinus banksiana* pollen, probably indicating cold-dry conditions. Mixed mesophytes began to appear in the pollen record at 16,300 yr B.P., and this sort of forest was replaced largely by oak-hickory forest in the mid-Holocene.

Heusser (1977b) has investigated a variety of sites in central and northwestern North America where records going back from 30,000 to more than 50,000 yr B.P. are obtainable. In northwest Alaska and most other sites, evidence of a pre-40,000 yr B.P. interstadial or interglacial shows clearly. During fully glacial times, Illinois apparently somewhat resembled present-day northwest Alaska. As is discussed later, in connection with Fig. 17.6, Delcourt (1979) was able to show,



a

PUBLISHED ESTIMATES OF FULL-GLACIAL PRECIPITATION AND EVAPORATION DEPARTURES

Location	ΔT_a (°C)	ΔT_s (°C)	ΔP (cm)	ΔE (cm)	%E	New values resulting from an assumed 8°C annual cooling: %E	ΔE (cm)	ΔP (cm)
Lake Estancia, New Mexico	−6.5	−9	+18	−38	34	42	−25	−4
Lake Lahontan, Nevada			+84		34			
Lake Lahontan, Nevada	−5	−5	+27	−41	30			
Spring Valley Lake, Nevada		−7	+21	−33	30	43?	−48	0
Llano Estacado Lakes, northern Texas	−5	−10	0	−41	27			
Llano Estacado Lakes, northern Texas	−5	−8	+39	−4	27			
Lake Estancia, New Mexico	−10.5	−10	−4.6	−51	45	38	−42.5	+2

b

Figure 15.13 Brakenridge (1978) concluded that in the American Southwest full glacial conditions caused displacement to lower altitudes of vegetation communities, as shown in (**a**). The displacement was estimated from pollen and pack rat (megafossils from middens) data. Broken lines indicate displacements based on only two sites. Brakenridge

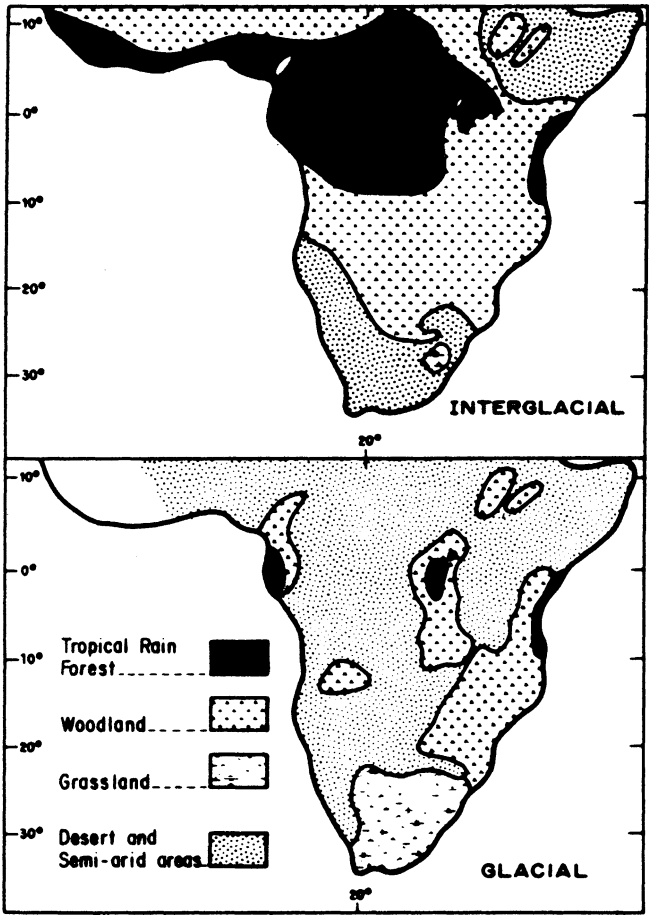


Figure 15.14 Generalized hypothetical vegetation maps of Africa south of the Sahara during glacial and interglacial maxima, based partly on palynological data. Glacial times were prevailingly drier. (On the basis of more recent information, Van Zinderen Bakker would have slightly decreased both the tropical rainforest area and the desert area for the interglacial, while increasing the woodland area concomitantly.) Much simplified from Van Zinderen Bakker (1976).

◄

Figure 15.13 also concluded (**b**) that full glacials were not "pluvials", but that the observed increase in volume of southwestern lakes during glacials resulted from decreased evaporation. ΔTa and ΔTs are changes in annual and summer temperatures, respectively. ΔP is change in annual precipitation, ΔE is change in annual evaporation; %E = ΔE/modern E. Although previous estimates had claimed much elevated precipitation during glaciations, Brakenridge's recalculations show precipitation to have been little different from present levels. From Brakenridge (1978).

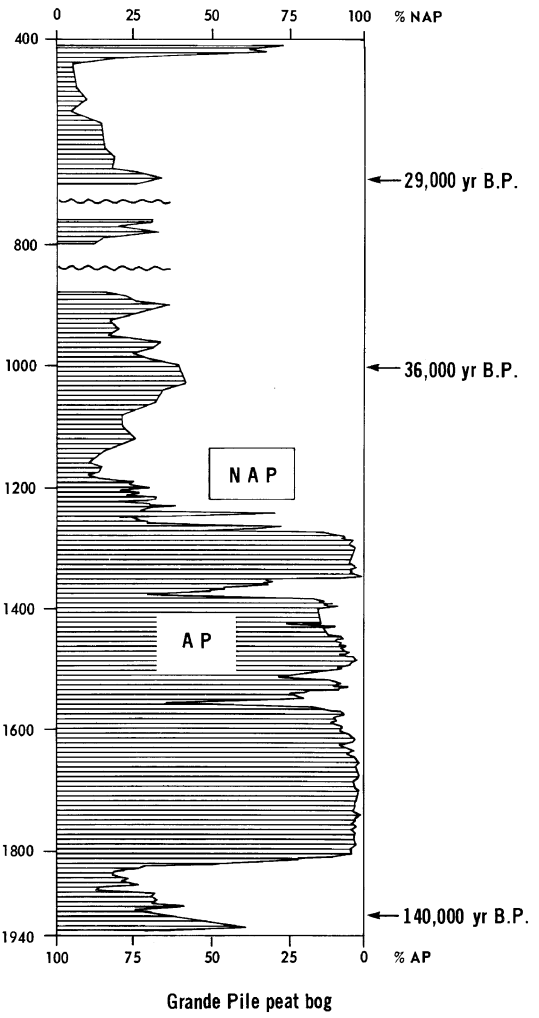


Figure 15.15 One of the longest, most nearly complete late Pleistocene pollen record in existence, Woillard's study of the Grande Pile peat bog, Vosges Mountains, northeastern France. The NAP (non-tree pollen) vs. AP (tree pollen) curve shows the last major interglacial (Eemian = Sangamonian), which Woillard subdivides into Eemian plus St. Germain I and II, but it clearly seems to be one interglacial with minor colder interludes. In any event, the AP dominance is clear. The collapse to the last full glaciation was dramatic, as forests largely gave way to steppe, tundra and grasslands in periglacial areas and NAP greatly increased. The sensitivity of NAP/AP to glacial-interglacial conditions is characteristic all over the northern parts of the Northern Hemisphere. Slightly modified from Woillard (1978).

by comparison of surface sample pollen floras with palynofloras from cores, that Tennessee at 19,000 yr B.P. had vegetation resembling today's vegetation in south-central Manitoba, Canada. There has been much discussion of evidence for plant refugia where northern or high altitude species survived the glaciations in lower altitude or southerly locations. Mexico and the southern USA are full of evidence for this concept. Tzedakis *et al.* (2002) present a detailed study of pollen records from western Greece showing that in southern Europe some such refugia may not only have permitted the survival of species but also the evolution of new forms.

There has been considerable discussion about whether glaciations toward the poles and at high elevations caused significant disruption of the vast areas of tropical rain forest in Asia, Africa and South America. Colinvaux *et al.* (1996) have shown that at least during the last big glaciation an extensive area of such forest in western South America the rain forest was not fragmented into refugia separated by grassland or savannas, but remained substantially intact.

A marvelous illustration from the late Neogene of the application of palynology to broader scientific concerns is the work of Kloosterboer-van Hoeve (2000), demonstrating from long sections in northern Greece that pollen data can be correlated with astronomical records. She found precession cycles of 21.7 yrs. to be especially well correlated.

Chapter 16

Holocene Palynology

1 Introduction

Many palynologists concerned with study of the (relatively) glacier-free time in which we live agree that aside from human disturbance of Earth systems, it is presumptuous to speak of it as a completely different epoch, the "Holocene." Also, it is too soon to presume that the Pleistocene is over, and thus "post-glacial" is likewise inappropriate. In westernmost Europe palynologists sometimes refer to the "Flandrian" as the timespan of about 11,000 years since the last major retreat of continental ice sheets. However, this term cannot readily be transferred to other parts of the world. A term such as "present interglacial" has problems too, as we do not know for sure that another glacial time follows. For the present we seem to be obliged to follow convention and say "Holocene" for the last approximately 11,000 years. There are geologists who feel that the Holocene can be defended as an epoch/series from purely geological reasoning. In any case, Holocene palynology has always had different approaches from palynology of older sediments, as we have seen. One can practically neglect the presence of extinct or grossly exotic species. Thus, floral studies based on known present plant associations and their ecological requirements, and rather precise paleoclimatological deductions, are possible.

In the pre-Holocene Neogene, pre-11,000 years ago, the same sort of approach is possible, but the *SFI* (steppe/forest index) curve in Fig. 15.4 is an illustration

of differences. The *SFI* curve is too crude for the Holocene, where more precise analytical methods are possible. On the other hand, the *SFI* curve is also progressively less good as one works back to the early Pliocene and into the Miocene, because plant communities with no modern analog were dominant in the Black Sea drainage; for example, *Artemisia* and grasses were no longer found. Palynological count data in the pre-Holocene can be mathematically analyzed with multivariate analytical techniques to pick up associations of taxa that one might not recognize in terms of modern plant associations. This is a better approach than to attempt to reconstruct pre-Holocene forest communities from the pollen-analytical results, as is possible in the Holocene, based on modern analogs. In the pre-Holocene we may be obliged to use fungal spores, acritarchs, algal colonies, wood and cuticle fragments, and especially dinoflagellate cysts to tell us things about temperature, salinity, and pH. The paleoecological approach in the Holocene has to do largely with forest history, plant-association history, and other related ecological matters. For the most part, peats and lake sediments, prevailingly autochthonous, are studied. In the pre-Holocene, we often study allochthonous sediments (though peats and lake sediments are also investigated), and we therefore look at a broader, regional picture for our environmental trends. In Holocene palynology the normal approach is very careful study of pollen-rain from the potential source plant communities and their ecological requirements. Precise pollen analytical counts of very closely spaced samples from cored sediments, and the plotting of these analyses in rather standardized "pollen diagrams," is employed, in conjunction with ^{14}C dates (see examples later in this chapter). A good example of a broad-scale pre-Holocene approach is the work of Heusser *et al*. (1980), in which modern pollen "rain" of surface samples from Alaska to California was studied, and known broad climatic indications were applied mathematically to pollen-analytical data from cores obtained in Washington State, to ascertain probable temperature and precipitation at various levels in the cores representing about the last 80,000 years–well back into the Pleistocene.

It should be emphasized that the entire Holocene has been influenced by the activities of human beings. Study of palynomorph assemblages has been widely applied to investigation of the interplay of environment and humans. I do not recognize the validity of the concept of "subfossil," which says that traces of former life in the crust of the earth are not truly fossil unless they are older than 6,000 or 10,000 yrs., depending on the opinions of the proposer of the subfossil idea. In my view, all traces of former life in sediments are fossils, regardless of age. Thus, "paleopalynology" definitely includes archaeological palynology, a subject that is well outlined by Bryant and Holloway (1996). Study of the palynology of archaeological sites is particularly important in gaining insights into the diets of ancient humans and such matters as the origins of agriculture (cf. Bryant, 2003). One fascinating aspect of such study is the palynological investigation of fossil feces (= coprolites; see summary in Sobolik, 1996). Pollen from

fossil dung of various animals such as hyrax and hyenas have been important sources of information in Pleistocene and Holocene studies (see Carrión, 2002; Carrión *et al*., 2001). Indeed, the spores of the dung fungus, *Sporomiella*, have proven, among other things, to be an important indicator of the probable extermination of large ungulates by humans, because the spores go from very abundant in some lake and wetland sediments to near zero in a geological instant, apparently coordinate with the arrival of humans in the western USA (cf. Davis, 1987, Davis *et al*., 2002). Because archaeological sites tend to be difficult for palynology for a variety of reasons, such as alkaline conditions and location in relatively pollen-free caves, human and other coprolites are some of the best sources of archaeologically significant fossil pollen. However, caves in some arid areas also produce productive archaeologically important palynofloras in their layers of sediment (cf. Carrión *et al*., 1999).

Europe was the cradle of palynological work in the late Pleistocene and Holocene, begun by Von Post, Faegri, Godwin and many other pioneer scientists. Figure 1 in Birks' (2005) summary of Quaternary pollen analysis in Fennoscandia demonstrates this clearly. I highly recommend Birks'article to get a grasp of what has been done in a century of work in this field, and his insightful view of what the next century may hold in store for more research in this field.

2 Holocene Palynological Methods

Pre-Holocene, Neogene palynologists mostly work with sedimentary materials –outcrop samples, oil well cuttings, cored intervals, side-wall cores, and the like– obtained by conventional geologic methods. Holocene (and late Pleistocene) palynologists are mostly interested in lake, swamp, and bog deposits reflecting the history of the local and to a more limited extent, the regional vegetation, and they sample the sediments in a variety of ways quite different from conventional geologic methods. The devices used include the Hiller and other sediment (especially peat) samplers (Fig. 16.1a,b). Hiller and similar samplers are devices with a chamber on the end for taking a plug or core of soft sediment from a carefully measured depth. Extension-rods enable reinsertion of the device into the sampling hole and repeated sampling to depths of 5 m or more. More commonly used now where possible, because a continuous relatively undisturbed section of core is obtained, are various sorts of piston corers (Fig. 16.1c-e). A tripod is usually used in pulling the core; chain hoists are sometimes used if the sediment is compact, but usually the corer can be pushed in and pulled out by hand, using rope or wire for attachment to the tripod. The coring device consists basically of tubing, usually aluminum, with a strengthening bit-like device on the end to penetrate the sediment, and a rubber piston inside. The tube sits on top of the sediment and maintains a partial vacuum behind the core when it is pulled, to prevent loss of the core. There are many variations on these themes, but the

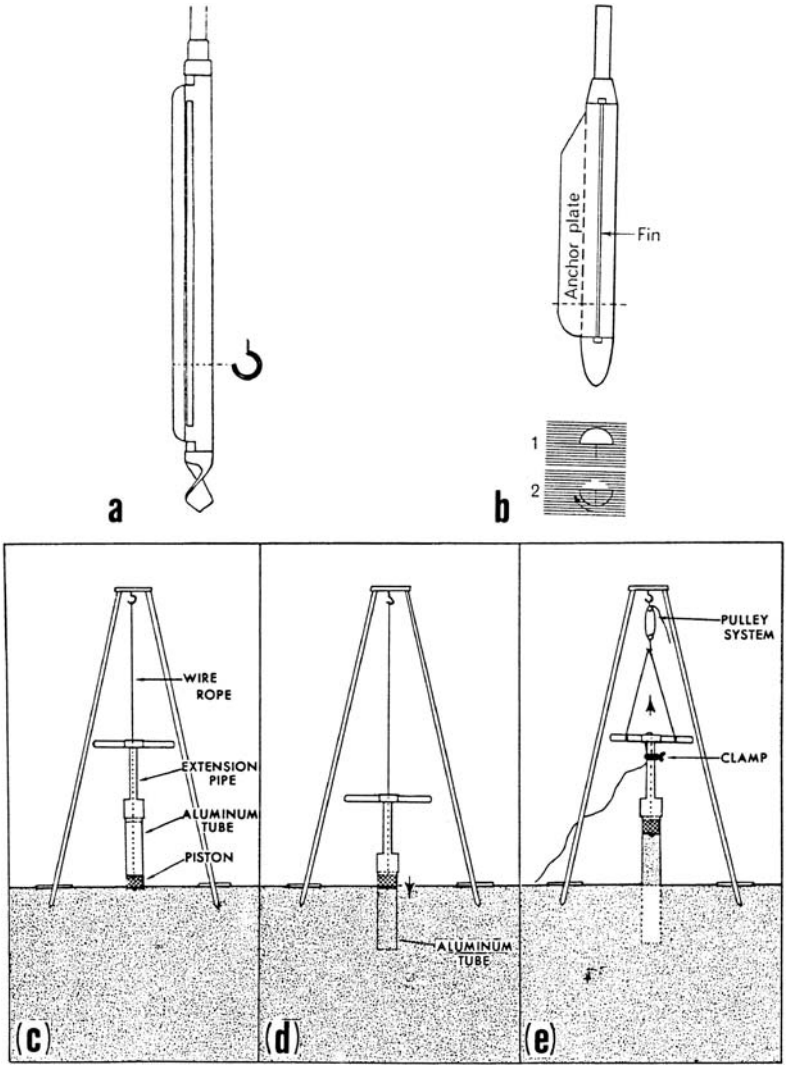


Figure 16.1 The three most common sediment-samplers in use by late Pleistocene palynologists. All are really "generic" and have variants. (**a**) The "business end" of a Hiller peat-borer, much used for sampling of fibrous peats. At the tip there is a sharp auger device which penetrates the peat as the auger is twisted into it, using a handle attached to the end of screw-together rods or pipe sections. The sampling chamber, shown also in section at right, is a cylinder within a cylinder, with an outer, flanged cutting edge, such that when the direction of turning is reversed to counterclockwise, a sample of peat is cut by the blade and taken in. Turning in the opposite direction closes the chamber, and the sampler and sample can be withdrawn. Most versions have a sample chamber about 50 cm

basic idea is the same. Piston corers can be operated in shallow water either by standing on the bottom or by using a raft or boat. When working in water, some sort of casing is necessary. The collected cores are sealed in the field, or may be extruded, described, and wrapped there. In the laboratory they can be sub-sampled by sawing open the sections of tubing lengthwise, at which time samples for other purposes can be obtained, the cores described, and photography of the relatively fresh sediments accomplished. Excellent presentations of various methods of sediment core collection from many sorts of sediment accumulations are presented by Glew and Smol (2001) and Leroy and Colman (2001) in the Last and Smol (2001) volume on study of lake sediments.

Samples for palynology are processed in various versions of the standard methods given in the Appendix, though the prevalence of peat in the samples has caused Holocene palynologists to emphasize KOH cooking and acetolysis, both

Figure 16.1 long, and many meters of peat can be cored quite accurately by repeated sampling. Unfortunately, the sample is somewhat contorted and smashed laterally, and may be contaminated superficially, though the vertical integrity is preserved. Various scientific supply houses sell these, or they can be made up by a machine shop. (**b**) The "Russian" peat sampler (sometimes called Macaulay sampler), which collects a 50 cm sample as does the Hiller, but has the advantage of not compressing the sample laterally during the sampling operation. This sampler is especially good for peat and sand. The sampler consists of a 50 cm × 5 cm half-cylinder, fixed to the sampling head, which is rotated 180° when the desired depth in the peat is reached. This encloses a half-cylinder of peat against the central anchor plate which remains stationary as the half cylinder is rotated (see sectional drawings 1 and 2). The half-cylinder sample is bisected by a fin-plate at right angles to the anchor plate. The sample is then easy to remove and is usually enclosed in plastic sheeting in the field. Unfortunately the only way to obtain such a sampler is to have one made by a machine shop. (**c**)-(**e**) One version of the piston-coring device, often called a Livingstone piston-corer or Livingstone sampler, after D. A. Livingstone, who first used such sampling devices. This sort of sampler is poor for fibrous peat but excellent for non-fibrous peat and mud. The operation sequence is: (**c**) preparatory to coring; (**d**) coring tube pushed into ground while piston is held stationary with respect to ground by wire fixed to tripod; (**e**) core withdrawn from ground while piston is held stationary with respect to core tube by clamping wire rope to extension tube pipe. The sample is brought to the surface in sections of aluminum tubing, which can be sealed, frozen if desired. The tubes can be sawed in half later in the laboratory for interval sampling. In other versions, the sampling tube for the piston is steel and permanent, and the sample is extruded from it after collection into a plastic tube for storage and study. The accuracy of piston-samplers is in general better than that of Hiller-type samplers, though compression of sample and loss of various intervals occurs with piston devices. Some of my students have used locally available materials such as irrigation pipes for collecting tubes, and trees cut down at a site for the tripod, to approximate the set-up shown here, in places such as remote areas of Honduras and Montana. (a) is from Faegri and Iversen (1975); (b) is from West (1977); (c)-(e) are from Cohen and Spackman (1972).

aimed at destruction of the abundant cellulose and cellulose derivatives in peaty sediment, and HCl/ HF digestion where siliceous minerals are abundant. The completed slides are analyzed by counting the spores and pollen and calculating spores/pollen percentages and/or concentrations per gram of sediment, or annual pollen influx per area (cm^2) of sedimentary surface (for which rate of sedimentation must be known). Sometimes known amounts of a foreign pollen (most commonly *Lycopodium* spores, *Eucalyptus* pollen, or polystyrene spherules) are added to each sample before processing, so that pollen present in the preparation can be expressed as a ratio to this foreign matter, especially as a means of determining the abundance of fossil pollen per unit of original sediment sample (see Appendix for methods of calculation). The most common approach by far is to express the amounts of various sorts of spores/pollen as percentages of either total pollen or of a "pollen sum" from which certain forms, such as aquatics, are excluded. The idea is to get a number that relates to the composition of the vegetation that produced the pollen. This concern for relationship to vegetation composition has greatly influenced Holocene and late Pleistocene palynology, because many palynologists in this specialty are ecologically based, and many sorts of pollen are well known to be over- or under-represented in comparison to the producing vegetation. However, pollen analytical data that do not directly relate to forest composition can nevertheless yield very valuable information about climatic and other changes. For example, some pollen may be reworked from older sediments and indicate from their presence erosion in the basin of deposition, caused by high precipitation levels. In some lakes and other small basins there is evidence of different rates of accumulation of palynomorphs in deeper parts of the basin than in other parts; this is often called "pollen focussing." Beaudoin and Reasoner (1992) show, however, that for at least some lakes this is not a problem, and that a single core from any place in the lakes they studied provides a reliable pollen record for the whole lake.

In many branches of palynology it has been pointed out that percentage data have a built-in bias, because the percentages must total 100%, and the percentage of pollen *A* therefore influences the percentage of pollen *B*. Palynomorphs per gram of sediment, or as a ratio to an added "constant," or per area per year (pollen influx), or per volume of sediment have been suggested as alternatives; see Fig. 16.2. The subject is more fully discussed in the next chapter. Fig. 16.2b shows an application of both pollen-influx and pollen concentration methods to a problem of change in a very short time frame. The use of pollen influx demands very good data on chronology because of dramatic differences in rate of sedimentation in different parts of the same basin.

In previous chapters the problem has been discussed that with conventional comparative microscopy, pollen and spores are seldom identifiable to the species level, if a genus has more than one species. In fact, if there were dramatic differences between the pollen of plant species, this would be strong evidence that the species were really not congeneric. In the Holocene this is especially

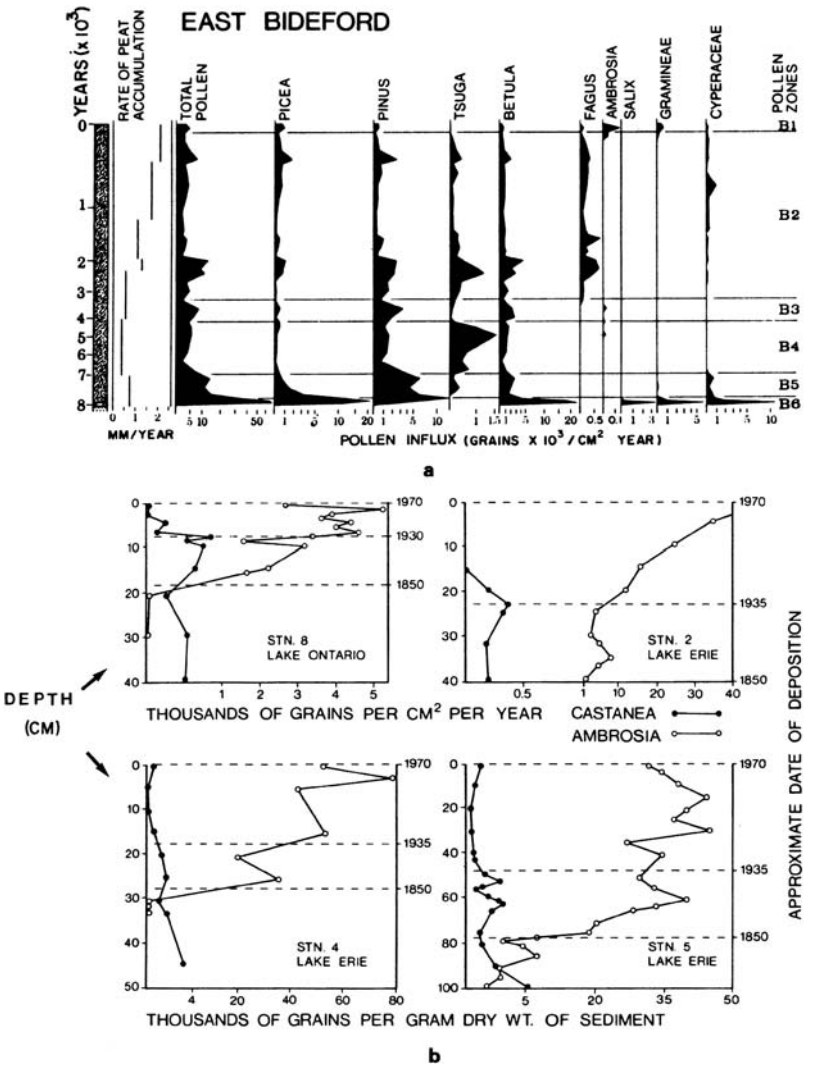


Figure 16.2 Examples of the use of pollen-influx ratios instead of percentages of either total palynomorphs or of a selected pollen sum. (**a**) East Bideford, Prince Edward Island, Canada, diagram on pollen-influx basis, for comparison with same data diagrammed on percentage basis in Figure 16.7. This method requires ^{14}C or other precise dating, so that the annual amount of sediment accumulation can be measured (see "rate of peat accumulation"). Then the number of grains per area (cm^2), per year, can be calculated. The method avoids the problems of (1) overabundant forms swamping out the percentage of other forms, and (2) the effects of changing sedimentation rates on calculations of concentrations per gram of sediment. (**b**) Use of per gram or per volume and influx pollen concentration to measure the near disappearance of *Castanea* (chestnut) and the great

troublesome, because the plant species are all extant, and specific determination would be very helpful in untangling the meaning of pollen analyses from a study area. Two techniques are proving helpful: (1) the use of scanning electron microscopy, which can be applied even to strew maceration residues, though this is a bit beyond a routine procedure–differences in exine sculpture in SEM examination frequently permits species separation not possible with conventional light microscopy; (2) detailed morphometric analyses in light microscopy of the pollen of significant species of a genus. Lindblad *et al*. (2002) have shown, for example, how this can be done by statistical analysis of measurements of 13 attributes of the three *Picea* (spruce) species of eastern North America.

3 Presentation of "Pollen Analysis" Data

Symbolic presentation of data for the various pollen types was developed quite early in the history of late-glacial/post-glacial pollen analysis. Jessen (1920) used the term "pollen spectrum," and pollen analysts thus developed a "spectral" diagram, presented in circular form. Each of the kinds of tree pollen counted was presented as a fraction of the circle; consequently a form with 10% would get 36° on the circle. The taxa were presented in the same order and in the same pattern, to make the diagrams easier to compare. However, it was not practicable to display more than a few taxa, and these "pie" diagrams are no longer used. The use of circles of different sizes on maps to demonstrate the relative abundance of a certain type of pollen or pollen associations at various localities is a related idea.

Pollen analytical results lend themselves to representation in diagrams in which the depths of the samples are displayed on the ordinate (= y or vertical) axis, and the percentages or other indication of amount of pollen are shown on the abscissa (= x or horizontal) axis. Frequently the concentrations are expressed logarithmically or to different scales. An early idea was to connect the points and identify them by using symbols for each sort of spores/pollen, e.g., solid circles for *Pinus*. Fig. 16.3 shows a modern pollen diagram employing such symbols for a few taxa. The system of symbols originally introduced by Erdtman is shown to the right.

Line-and-symbol diagrams are sometimes difficult to read; diagrams displaying more than five or six taxa are practically indecipherable. The symbols are not

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Figure 16.2 expansion of *Ambrosia* (ragweed) in the time of human population explosion in the eastern Great Lakes area of North America. Note that in this particular case, as in many, concentration per gram of sediment, a much less expensive procedure, yields acceptable results. The methods of calculation are explained elsewhere in this book–see especially the section on pollen per gram, etc., in Chapter 17. Diagrams are from Anderson (1974, 1980).

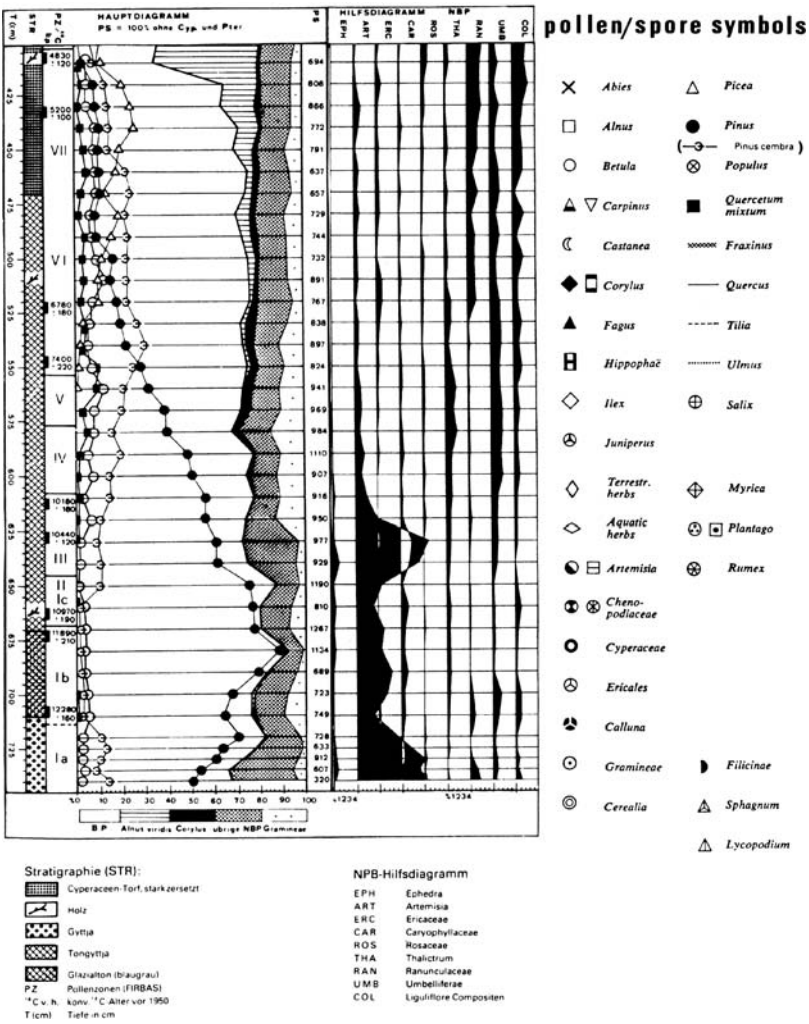

Figure 16.3 The use of symbols for pollen and spore types in Pleistocene palynological diagrams. The example, from the German literature, is a late glacial to hypsithermal record from Sass de La Golp, southern Switzerland. In the Hauptdiagramm (main diagram) on the left of the figure, PZ = pollen zones (Firbas zones–see Fig. 16.4); in its legend, BP = AP. In the Hilfsdiagramm (supplementary diagram) in the center of the figure, NBP = NAP; in its legend, Compositen = Asteraceae. Shown on the right of the figure are pollen and spore symbols commonly used in Europe, with one parenthetical additional type, *Pinus cembra*, because it occurs in this particular analysis. Note high *Artemisia* in the late glacial (before 10,000 yr B.P.) and the decline of *Pinus* in the Holocene. The use of the symbols is not common outside of Europe. Symbols are from Faegri and Iversen (1975); the pollen diagram is by Burga, as presented by Hantke (1983).

always consistently used. Hence, line + symbol diagrams were mostly displaced by simple, labeled line "sawblade" diagrams, of which the center (supplemental) diagram in Fig. 16.3 is an example; another example is Fig. 16.2a.. Such diagrams make it possible to display not only the sorts of tree pollen (= arboreal pollen = AP) but also non-tree pollen (NAP) and aquatic pollen (AqP). Some authors have used bar graphs in the same way. Because it could be argued that the points measured really represent separate "events," not a connected curve, bar graphs have some conceptual advantages. Nevertheless, easier to read "sawblades" are usually preferred. I feel strongly that most late glacial/Holocene pollen analytical diagrams could be improved by standardization and simplification. Units for which the counts are probably too small to be statistically significant should be listed in a table. In fact, I believe that the great majority of publications would be improved by giving much of the raw data (counts) in tables and diagramming only the major or most significant taxa preferably by composite summary, and smoothed-out curves. Unfortunately, the trend has been in the other direction. The literature is full of pollen analytical fold-out diagrams, some with several folds and /or diagrams with sawblades for taxa not even mentioned in the text. A few simple diagrams of the major points would be more useful, more readable, and more likely to be consulted and understood.

Another problem with glacial-Holocene palynological diagrams is that the taxa are often presented in no standardized order, but according to "dealer's choice". One prominent Quaternary palynologist wrote me:

> You asked if there is any convention in the ordering of genera in Quaternary pollen diagrams. Authors vary greatly, and there is no generally accepted discipline. The Minnesota practice, which I...think best is to place genera in order of time of appearance, so the order will differ between diagrams. It is also usual to divide the diagram into sections for trees/shrubs/woody vines/herbs (including the pteridophytes, usually grouped together) and obligate aquatics.... The modern practice is to have a percentage pollen sum calculated on everything, excluding only obligate aquatics such as waterlilies. Pollen sums based on trees alone are increasingly unusual. It is also unusual now to exclude the pteridophytes from the pollen sum. (W. A. Watts personal communication, 1980, quoted with permission.)

The quotation from Watts also makes the point that the basis for calculation varies somewhat from author to author. In addition to the pollen sum and percentage methods, one must be alert for less common calculations based on neither, but on pollen per gram of sediment, or pollen influx based on calculations of pollen sedimentation per unit surface area or per volume of sediment.

4 Holocene Chronology

Typical transition to the Holocene in northern Europe features decrease of *Artemisia* and increase of *Betula, Juniperus*, and *Salix* at the end of the Weichselian (= Würm = Wisconsin). The "Alleröd interstadial," generally viewed as

occurring just before the end of the last glaciation, could perhaps just as well be taken as the beginning of the Holocene, although it was followed by renewed glaciation. It should also be noted that the Holocene is in a sense a relative chronological unit, beginning at different times in different places, although we use 11,000 yr B.P. as a sort of convenient average. (In central Greenland, one could argue that it is not yet fully Holocene. Similarly, in a sense, northern Scandinavia is now about Dryas I or earlier.) The names of the stratigraphic chronological terms usually used are shown in Fig. 16.4. The divisions are based on northern Europe, where the work began, and are now time-stratigraphic, based on ^{14}C dating. In northeastern North America, where Holocene research also has a long history, these units have little applicability. The "Two Creeks interstadial" in North America, for example, is probably not directly equivalent to the Alleröd interstadial. On the other hand, Holocene diagrams from Japan, though based on quite different taxa, have the same general shape as those of Europe (see Tsukada, 1957, 1958).

The pollen diagram of the British Flandrian (= Holocene) is so well known that standardized versions of it have even been used as a logo (by the American Association of Stratigraphic Palynologists for several conventions). Fig. 15.10b shows a simplified, caricature version. The diagram shows the termination of the latest glacial and the earliest Flandrian. *Betula-Pinus* dominance in the early Holocene is replaced by interglacial-type dominance of *Quercus-Alnus-Ulmus-Tilia* in the middle Holocene. This dominance characterized the warmest part of the Flandrian, the "climatic optimum" (sometimes called "hypsithermal"), about 9,000 to 2,000 yr B.P.

(The warmest middle part of this period is sometimes called the "altithermal," about 7,500–4,000 yr B.P.) During the last 2,000 years it has not been so equable in western Europe; birch, for example, has re-expanded its range in northern Europe. Some northern forest lands have reverted to scrub. In various places, all or part of this post-hypsithermal is known as the "little ice age." An interesting comparison of ocean (mostly dinocyst) data and nearby land records in Nova Scotia, Canada, by Levac (2001) show that the climatic optimum on land starts about 2000 years later, but lasts longer, than the optimum at sea. It is clearly too soon to conclude that the au courant apparently human-conditioned "global warming" will overcome the long range tendency, if the rest of the Pleistocene/Holocene is used as a gauge, which should be toward colder conditions.

Fig. 16.5 shows the application of Firbas (F) and Overbeck (O) schemes in Germany in particular, with the forest equivalents given in Fig. 16.5b. The Bölling interstadial is omitted in many diagrams. The original German has been left on the figure, as the German terms were given great currency by Firbas and by Overbeck, and because from Von Post (1916) until after 1945, Scandinavian palynologists frequently wrote in German, so students will encounter the terms. The numbers applied to the late glacial and interglacial "times" comprise a classification named for Blytt and Sernander, Scandinavian botanists-geologists

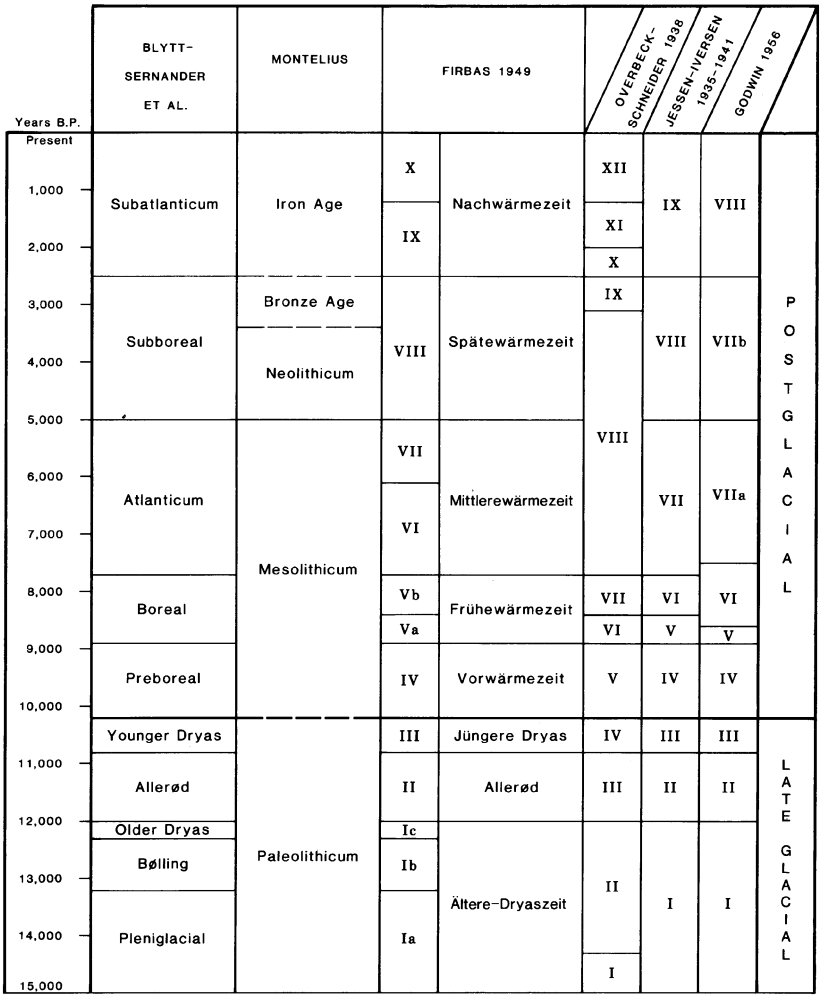

Figure 16.4 Various schemes for pollen zonation of the late glacial (Weichselian) and post-glacial or Holocene) of Europe, along with the vegetation zones of Blytt-Sernander, and the pre-historical designations of Montelius. Compare with Figure 15.7. Modified slightly from Janssen (1974).

of about a century ago, who noticed evidence for post-glacial floral change and suggested in outline a model for the post-glacial fluctuations upon which Von Post, Firbas, Jessen, Overbeck, and Godwin, among others, later built. Firbas' 10 "times" have been mostly replaced by Overbeck's 12 "times." Others have used still different numbers. This is unfortunate because now "IX" in some papers does not mean the same as "IX" in other contributions.

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Figure 16.4a (**1**) Sir Harry Godwin (1901–1985), one of the nestors of pollen analysis and thus of what came to be called palynology. His pioneer research on Pleistocene and Holocene vegetational history of the British Isles via pollen analysis led eventually to creation of the Sub-department of Quaternary Research at Cambridge University.

The "chronology" applies only in northern and central Europe, and even there it is time-transgressive. Parts of central Europe are now in the Sub-Atlantic, but much of Scandinavia is not, if *Fagus* is the signature. (One can define the Firbas, etc., zones radiometrically with arbitrary dates, and then they are not, of course, time-transgressive.) Fig. 16.6 shows a typical sawblade-style pollen diagram for Germany. The vegetational history can vary considerably even in a rather small region, especially if there are considerable altitudinal differences between sites studied.

The palynologically-botanically based chronology has been very useful as a reference, and before radiocarbon even for dating. In northern Europe it was long ago observed that at about the beginning of the Iron Age, 500–600 B.C.E., the nature of the peat in raised bogs changed abruptly–a "Grenz Horizont"–what is probably the same thing shows in some places as the lower boundary of Godwin zone VIII (= bottom of Firbas IX) (see Fig. 16.4; obviously at other times elsewhere). Another example of direct application of the European Flandrian (Holocene) chronology is the demonstration of "isostatic rebound" in Oslofjord, Norway, by pollen analysis, as is discussed below (see Fig. 16.13). When Von Post introduced pollen analysis as a practical tool in 1916 he considered it primarily of geochronological usefulness (Faegri, 1974). However, with the advent of direct, absolute ^{14}C radiometry, this aspect of pollen-analysis (in Holocene palynology) has taken a back seat to the use of it for investigation of vegetational change.

An attempt has been made in eastern North America to establish a Blytt-Sernander type division of the Holocene. A classification analogous to the Blytt-Sernander one was introduced by Deevey (1949) (see Fig. 16.7a).

Mostly because North America is too large and too diverse for such a scheme to work over any very large area, Deevey's or similar schematic subdivisions have not been widely adopted. The pollen zones are clearly local and time-transgressive. "C3," for example, cannot be applied as a dateline in both Ohio and Nova Scotia. It does seem to be true that a three-fold division of the "post-glacial"

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Figure 16.4a I attended his lectures on pollen analysis as it applied to Pleistocene/Holocene vegetation history of the UK at Cambridge in 1946–47 and applied what I learned to my doctoral research in palynology at Harvard, beginning in the autumn of 1947. This picture was taken in August, 1964, at the time of the 10th International Botanical Congress in Edinburgh, of which Godwin was president, published here by permission of the Hunt Institute for Botanical Documentation, Carnegie-Mellon University, Pittsburgh, PA. (**2**) Professor Knut Faegri and Alfred Traverse, in front of Faegri's laboratory building, Bergen, Norway, November, 1955. (See Fig. 1.5 for a much later photograph of Faegri.) In my entire palynological career I have never learned so much about how to study palynomorphs in such a short time as I did that week in Bergen from Faegri and his student and associate, Ulf Hafsten. Photo by the author (with self-timer!).

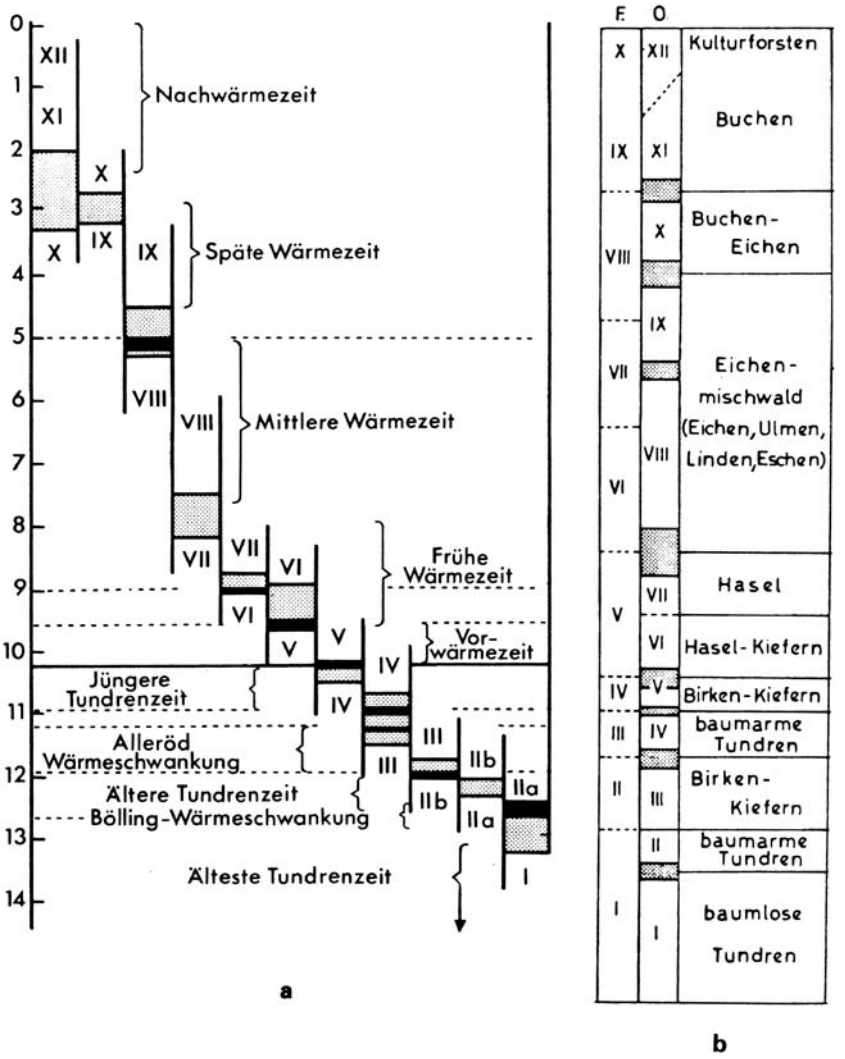

Figure 16.5 (**a**) Summary of relationship between ^{14}C dates (scale on the left, in years B.P.) and Overbeck Holocene subdivisions for western Europe from a series of overlapping European records. The stippled areas between Roman numerals represent range of ages, black bands signify zones of especially numerous dates. (**b**) Firbas ("F") and Overbeck ("O") zonation compared for Germany, with the vegetational history indicated by pollen analyses (see Fig. 16.4). Original German terminology retained because much of it has been widely used in Holocene palynology. Nachwärmezeit = Sub-Atlantic, or post-climatic optimum; Späte Wärmezeit = Subboreal; Mittlere Wärmezeit = Atlantic; Frühe Wärmezeit = Boreal; Vorwärmezeit = Preboreal; Jüngere Tundrenzeit = younger tundra period (later Sub-Arctic); Alleröd Wärmeschwankung = Alleröd warm oscillation;

in the northeast USA is a reality. Fig. 16.7b shows that, when Holocene pollen zones are used in North America, they are usually described in such a manner as to make clear that the zones are purely local in significance. With the widespread use of radiocarbon dating, the palynological zones are mostly of historical significance, no longer of chronological significance.

5 Some Characteristic Holocene Pollen Analyses

5.1 Europe

In a "classic" British Flandrian pollen analysis of the sort on which the caricature in Fig. 15.10b is based, there is a *Corylus* maximum in VI, *Betula* decline beginning in VI, and *Ulmus* decline at VIIA–VIIB. (Numbers are in the Godwin sequence, per Fig. 16.4; see also Fig. 16.4a.) The diagram lacks the continental *Fagus-Carpinus* "signature" of the Sub-Atlantic (see Fig. 16.6). It has been shown (Birks, 1973) that this diagram cannot be directly applied outside of England, not even in Scotland. Fig. 16.6 is a characteristic continental diagram. Note especially the climatic optimum (Wärmezeit) and the *Ulmus* decline (later than in England). Note also the grain grasses as evidence of human activity in the Sub-Atlantic. Swiss lake diagrams show abundant steppe pollen (*Artemisia*-Chenopodiaceae-grasses) in the late glacial, and sometimes *Juglans* pollen to show introduction by Roman settlers of walnuts about 2,000 B.P., an interesting example of human activity. In the Mediterranean very different Holocene diagrams are obtained. Mixed oak forest is present from the beginning of the Holocene. *Pistacia*, not seen in central or northern Europe, is a characteristic form. The decline of steppe pollen begins much earlier in this area than farther north.

Students should consult the very useful series of pollen maps of Europe by Huntley and Birks (1983), covering the last 13,000 years. These maps show for Europe the history of vegetational changes as revealed by pollen analysis, in a most dramatic way. (Birks, 2005, cites many publications that update the maps just cited.)

Figure 16.5 Ältere Tundrenzeit = older tundra period (earlier Subarctic); Bölling Wärmeschwankung = Bölling warm oscillation; Älteste Tundrenzeit = oldest tundra period (Arctic); Kulturforsten = cultivated forests; Buchen = *Fagus* (beech); Eichen =*Quercus* (oak); Eichenmischwald = *Quercetum mixtum* (mixed oak forest); Ulmen = *Ulmus* (elm); Eschen = *Fraxinus* (ash); Hasel = *Corylus* (hazel); Kiefern = *Pinus* (pine); Birken = *Betula* (birch); baumarme Tundren = tree-poor tundra; baumlose Tundren = treeless tundra. Both diagrams are modified from Straka (1975).

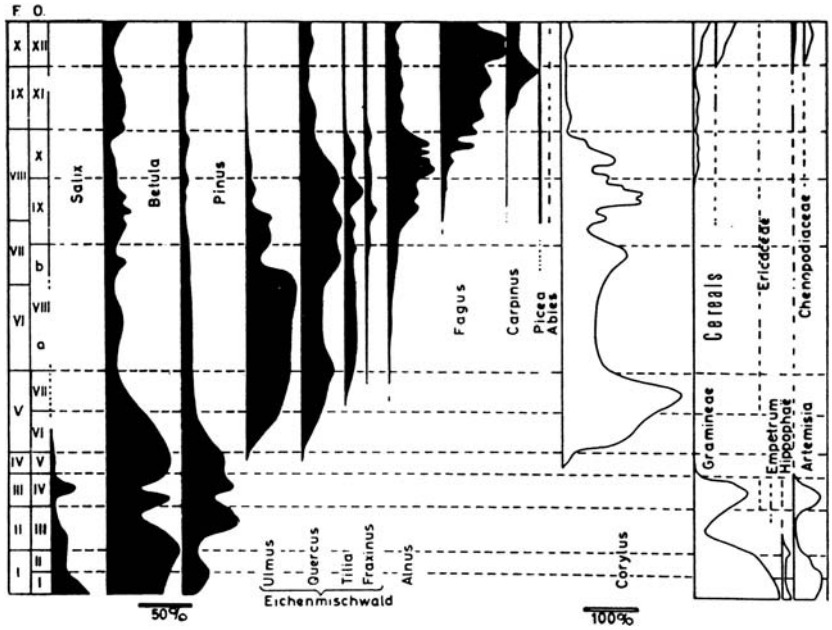

Figure 16.6 Schematic latest Pleistocene pollen diagram from near Göttingen, Germany. Black curves = AP, white curves = NAP. Only the most significant NAP are shown. See Figures 16.4 and 16.5 for orientation. F = Firbas, O = Overbeck. Eichenmischwald = *Quercetum mixtum* (mixed oak forest). Note that this association is the "signature" of the hypsithermal in Europe. From Straka (1975).

5.2 North America

This continent is too vast and vegetation too variable to produce the sort of common thread that pollen diagrams for northwest Europe have had. This is certainly one reason why North American Holocene studies have lagged behind European, though research was already under way in the 1920s. During the 1930s and 1940s "friends of pollen analysis" published a *Pollen and Spore Circular*, mostly under the auspices of Paul Sears at Yale, later at Oberlin. Many scientists, especially Pleistocene geologists, saw the potential importance of pollen analysis in America and encouraged it. Kirk Bryan, geomorphologist at Harvard, and R. F. Flint, Pleistocene geologist at Yale, are examples. (It was in the *Pollen and Spore Circular* that Hyde and Williams, 1944, introduced the word "palynology".) The thinness of the coverage is dramatized by the presence in Pennsylvania (about 650 km wide) of only a handful of Holocene pollen analyses.

The pollen diagram for a locality in Prince Edward Island in the Atlantic provinces of Canada (Fig. 16.7b) shows that replacement of *Picea* by *Pinus*,

a

Pollen zone	Pollen description	Zone Age (years B.P.)
C-3	Return of spruce and fir	0 ± 80 - 1600 ± 100
C-2	Hemlock minimum; pine, beech, oak, and birch maxima	1600 ± 100 - 4000 ± 120
C-1	Hemlock maximum; pine minimum	4000 ± 120 - 7250 ± 175
B	Pine maximum at about 8500 ± 180 years B.P.	7250 ± 175 - 9300 ± 200
A	Spruce and fir	9300 ± 200 - 10,500 ± 200

b

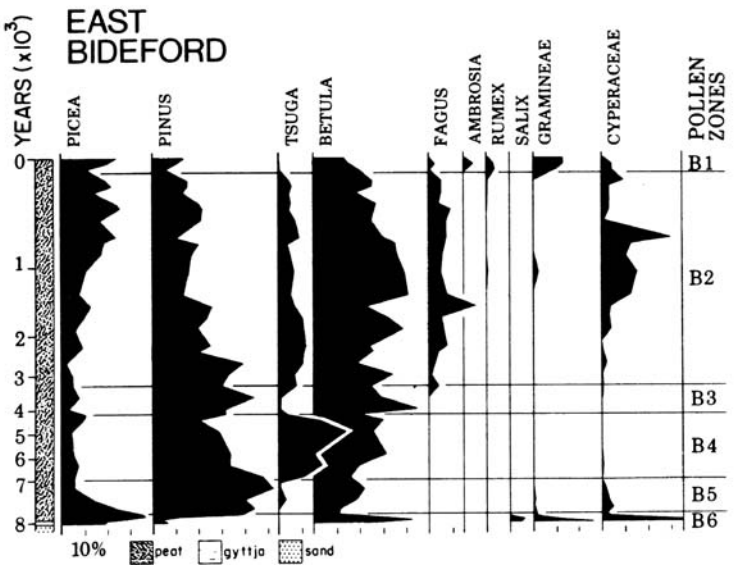

Figure 16.7 Holocene palynological zonation in North America. (**a**) An attempt was made to establish a Blytt-Sernander type division of the "post-glacial" for North America, and this has been applied by various palynologists since. Shown here is such a zonation by McDowell *et al*., 1971, for Bugbee Bog, Vermont, along with radiocarbon dates. The A–C-3 zones came originally from Deevey, 1949. The hypsithermal (climatic optimum), consisting of approximately B–C-2, was originally published by Deevey and Flint, 1957. The hypsithermal was originally defined as having time-significance, but the climatic signal is actually time-transgressive, occurring at different times in different localities. The scheme is now mostly of historical significance; (**b**) Other palynologists recognize only local pollen zones and thus use arbitrary letters, partly to avoid confusion with the Deevey zones. In this diagram by Anderson, 1980, of a site in Prince Edward Island, Canada, the "B" notation for the zones refers only to the site name (East Bideford). Compare this diagram with that in Fig. 16.2, for the same data plotted as pollen influx ratios. (a) is reproduced from McDowell *et al*., 1971; (b) is from Anderson, 1980.

characteristic of northeastern USA diagrams, has only partially occurred in Prince Edward Island, and the subsequent rise in oak pollen seen in the presumed climatic optimum of New England has not happened at all this far north. This sort of phenomenon is called a migration lag.

The fact that a climatic optimum warmer than present existed in the Holocene of northeastern USA is dramatically demonstrated by Davis *et al*. (1980) from studies in the White Mountains of New Hampshire, where pollen and megafossils show that *Pinus strobus* and *Tsuga canadensis* trees grew at elevations hundreds of meters higher than their present limits for thousands of years of the Holocene.

In Appalachian parts of North America the glaciations caused withdrawal of vegetation types southward into a somewhat larger continent, as world sea-level fell. Fig. 16.8 presents a West Virginia diagram by Watts (1979); he published pollen diagrams from a number of previously poorly covered areas south of the glaciated parts of eastern North America. As would be expected, events are well ahead of those in New England. In all of these diagrams the biggest changes in vegetation coincide with the end of the Wisconsinian glaciation. (This sort of change is, however, not synchronous across the USA.) Nothing else approaches this in magnitude. In South Carolina there is practically no *Picea* record. *Nyssa* and *Liquidambar* invaded South Carolina about 9,500 yr B.P. The refugium was probably well down in Florida (Watts, 1980). The change in vegetation occasioned in north central North America by retreat and disappearance of the glacial ice was profound and affected Pleistocene animal populations directly (Whitehead *et al*., 1982).

In the western USA, various diagrams show that we are in a position to map the migration of some taxa during the Holocene. Fig. 16.9 shows that in New Mexico a big change occurred at the end of glacial time with massive decline of *Artemisia* ("sagebrush") and grasses. *Pinus* greatly expands post-11,000 yr B.P. and has been more than 80% of all tree pollen for thousands of years. In some western diagrams ash-falls are very significant as marker-horizons for dating purposes. Fig. 16.9a also demonstrates the very frequent use of vernacular names for taxa on diagrams. In scientific literature this should probably be avoided, though in presenting talks, review papers, or newspaper articles to laymen, one can scarcely get around it. "Sagebrush" is a good example of the technical problems: although "sagebrush" is usually restricted to various species of *Artemisia*, "sage" commonly means dozens of species in at least four different genera, in different families! In Fig. 16.9 "sagebrush" means *Artemisia*, "ragweed" is *Ambrosia, et al*., greasewood is *Sarcobatus*, and the other vernacular names are unequivocal. In the southwestern USA and Mexico generally, the comparative dearth of sediments that can be cored (natural lakes or wetlands) has hampered the rapid expansion of the database, though much work has been done, even, for example, on pack rat middens. Pollen studies in the southwest USA are especially important because they tie in with archeological and dendrochronological studies, as has been abundantly

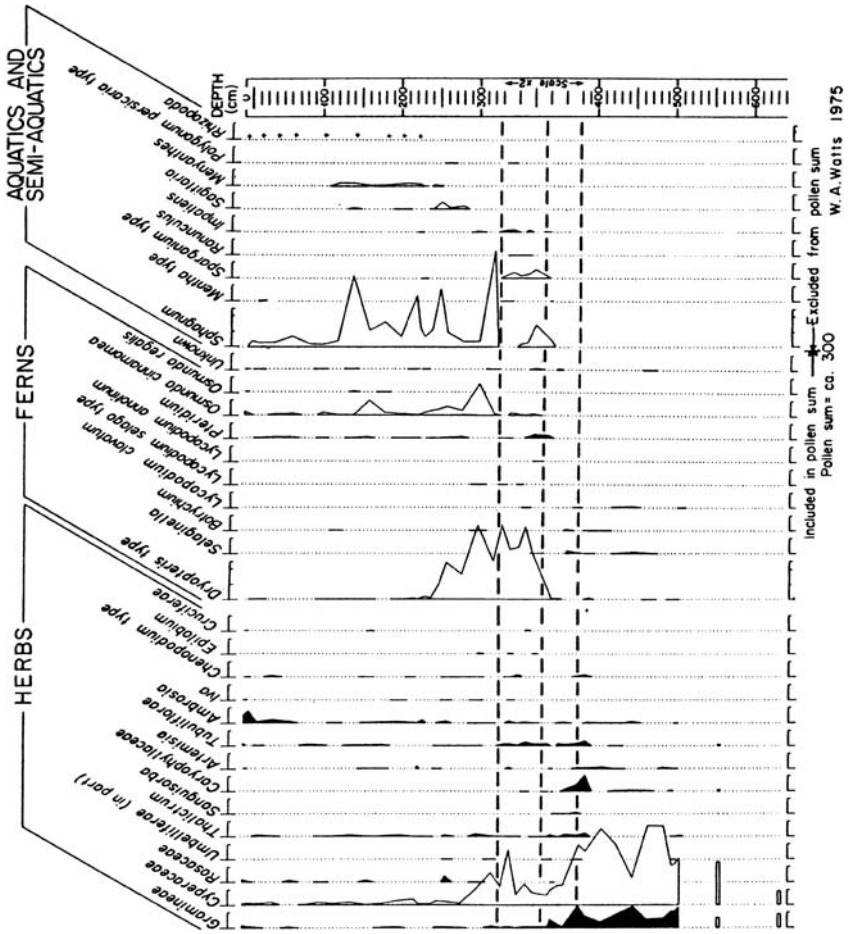

Figure 16.8 *(See caption on page 484)*

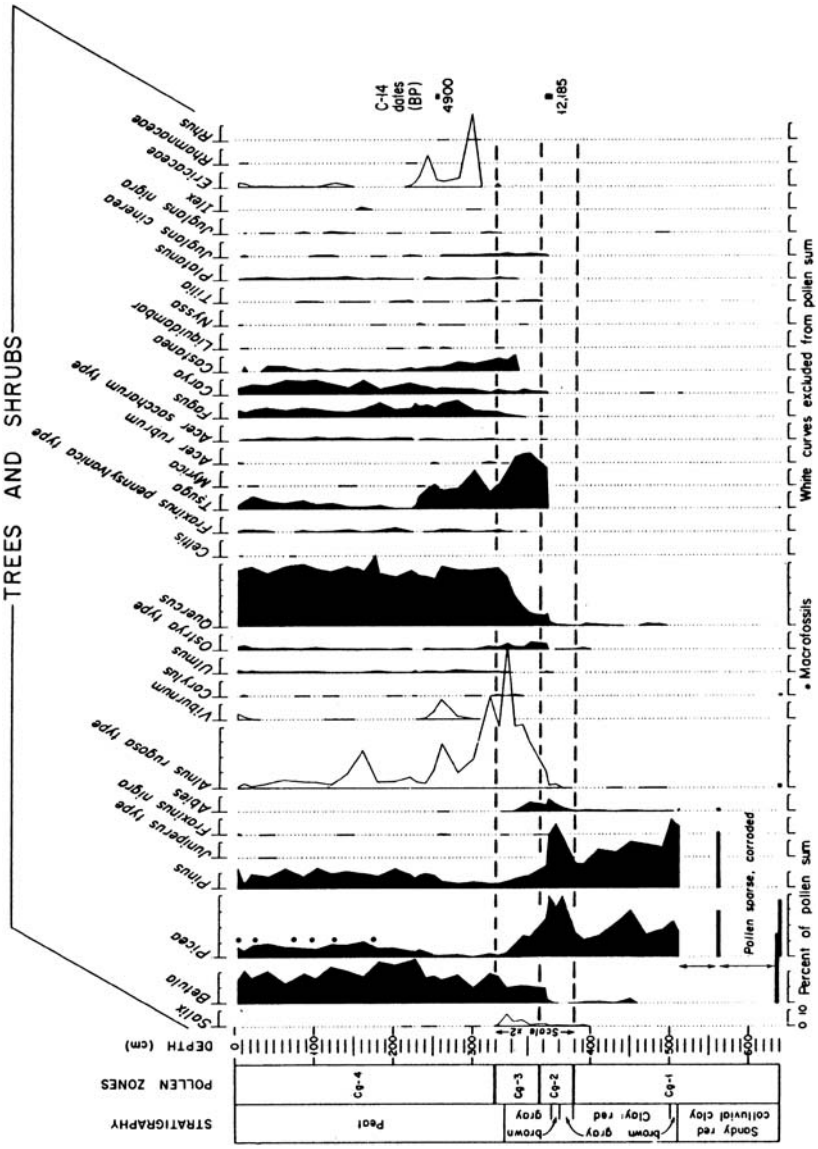

Figure 16.8 *(See caption on page 484)*

demonstrated by the work of Bryant and coworkers in Texas and vicinity (see Bryant and Holloway, 1985).

From the western USA, Fig. 16.10 presents pollen analytical data from California and Colorado. The decline of *Artemisia* and Poaceae post 7,000 yr B.P. plus expansion of *Abies* is notable in the California diagram, which also illustrates the value of showing macrofossil data in association with pollen stratigraphy. Charcoal influx presumably indicates human activity as well as natural fires. The diagram from Colorado is given to show an interesting graphical technique, stressing concomitant *AP* expansion and *Picea* decline in the post 7,000 yr B.P. part of the record.

Fig. 16.11 presents diagrams from Iowa in the central USA. The Lake Okoboji diagram illustrates use of key taxa to typify "stratigraphic zones" in the record. Here *NAP expands* in post-glacial time! This reflects prairie expansion, with increasing grass and composite pollen. Climatic factors favoring grassland expansion, perhaps combined with grazing pressure of bison herds, may have been at work. The generalized composite diagram to the right is also shown for Iowa, to illustrate this very useful method of dramatizing the data. Such diagrams are perhaps better than detailed diagrams, with the supporting data to be presented in tables. The overall Holocene vegetational history of the north-central USA is now reasonably well understood from many pollen analyses coupled with radiocarbon dates (Webb *et al*., 1983).

Fig. 16.12 illustrates diagrams from north-central and northwestern North America. In the Yukon and Alaska, steppe taxa decline post-9,000 yr B.P., and most tree genera (*Picea, Pinus, Betula, Alnus*) greatly expand soon thereafter. *Picea* declines in Saskatchewan post 8,000 yr B.P., however. The summers became too hot and total effective precipitation too low, presumably. Fig. 16.12c is also an excellent illustration of the desirability of generalized, smoothed-out, composite summary diagrams that make it easier for the reader to grasp the main points. (More detailed information can be made available in tabular form.)

◄

Figure 16.8 A complete late glacial to Holocene pollen diagram from central Appalachians, USA. Note the post-12,000 yr B.P. dramatic decline of spruce and increase of oak. This sort of diagram is an effort to combine the complete data-recovery given in a table with graphic presentation. This is the opposite of a composite diagram (see Figs. 16.11 and 16.12) and requires two pages or a foldout unless greatly reduced as here. Note that the pollen sum from which percentages are calculated includes no aquatics, and also excludes some other locally abundant herbs and woody plants, but includes many herbaceous types. "Common" (vernacular) names are not used here although they are found in diagrams in many palynological papers. Proper (Latin) scientific names are greatly to be preferred for all scientific literature. Reproduced from Watts, 1979.

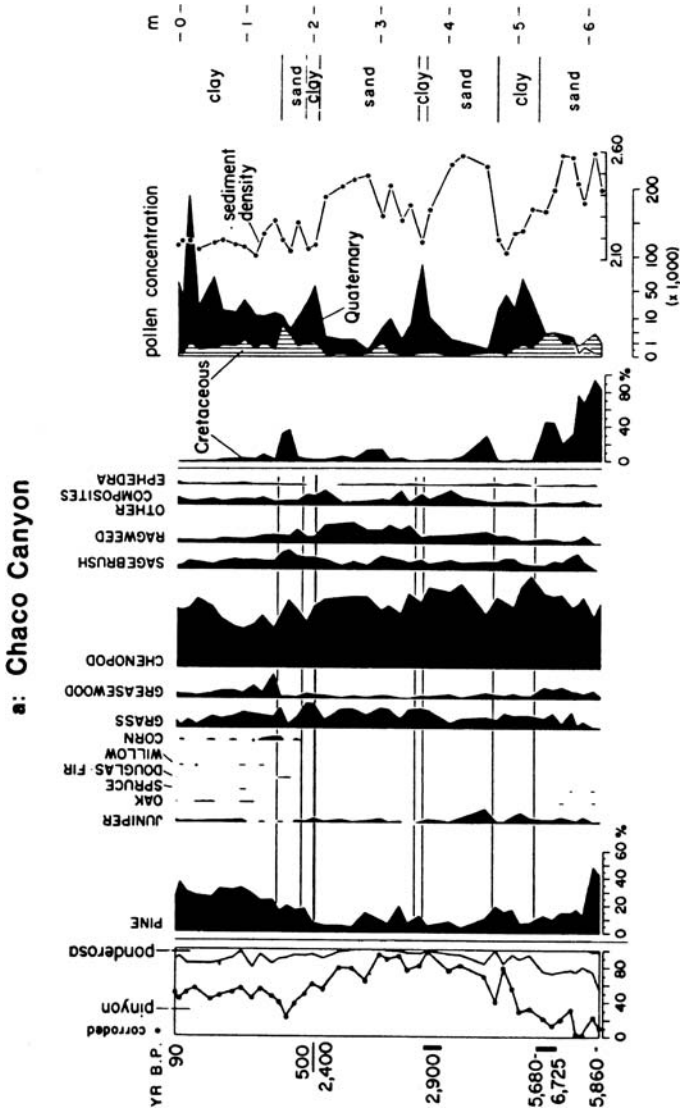

Figure 16.9 *(See caption on page 487)*

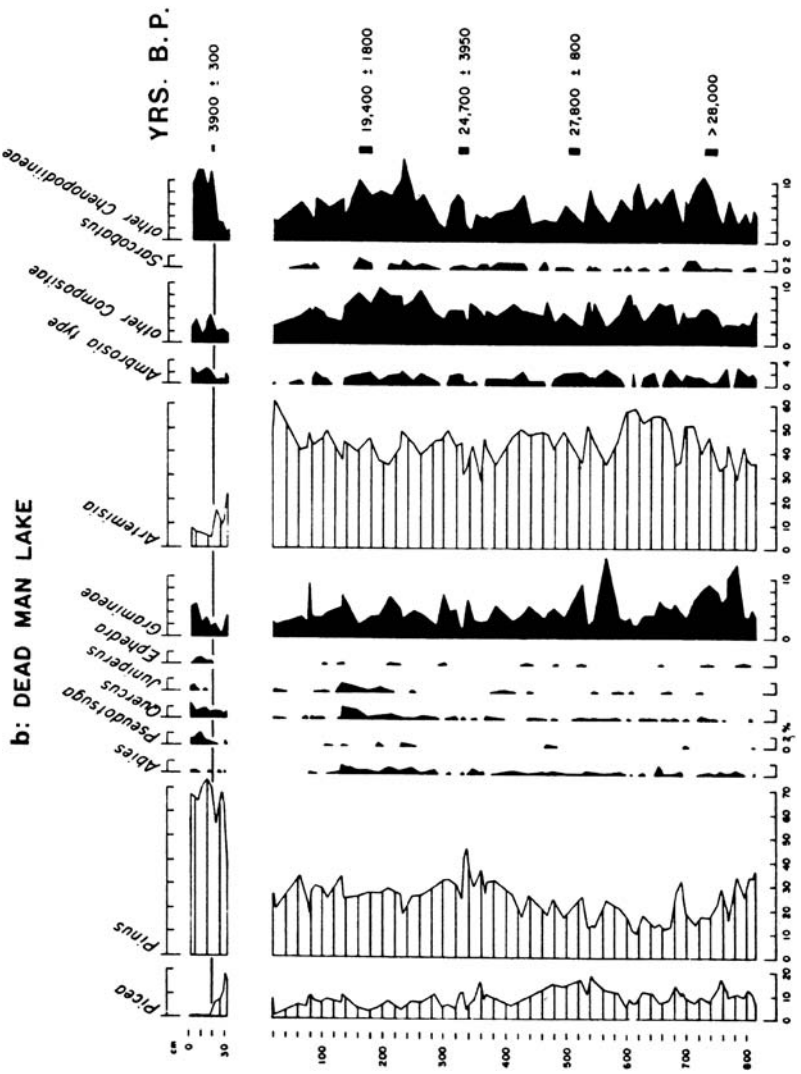

Figure 16.9 *(See caption on page 487)*

6 Applications of Holocene Palynology

One of the first applications of pollen analysis was to archeology. The Iron Age was linked to the beginning of the Sub-Atlantic (Firbas zone IX) of central Europe. The onset of agriculture was marked by the first abundant occurrence of pollen of human-introduced weeds. The spreading of heath in Scotland from clearing and grazing activities (Birks, 1973), the clearing of forests for field crops, and the coming in of cereal grains and walnuts are all shown in pollen analyses in Europe. Van Geel (1972) was able to show the advent of field cropping to a section of western Germany about 700 B.C. and *Secale* pollen commencing about 50 B.C. A pollen study of the sediments associated with a Neanderthal burial is credited with showing that an individual who died some 50,000 years ago was buried in or on a bed of flowers (Leroi-Gourhan, 1975). Palynologists have studied the stomach contents of a late glacial musk ox (Benninghoff and Hibbard, 1961) and of burial vases (Rue, 1982), with interesting and significant results. A very interesting and important contribution to early Holocene palynology is the discovery of O. K. Davis (2003; see also Kerr, 2003) that the spores of the fungus *Sporomiella*, a dung fungus, can track the population of large, presumably grazing animals. The waning of this spore is some of the important evidence for the collapse of megafaunal populations over much of North America about the time of the retreat of the last glaciers.

Pollen analysis continues to be important to archeology, but the problems encountered are often considerable. For example, sediments from cave sites are often studied, but such samples are in my experience usually very poor in spores/pollen, I would guess because of the restricted air circulation in caves, plus

◄

Figure 16.9 Two pollen diagrams for (**a**) middle to late Holocene, and (**b**) last full glacial and middle Holocene, of New Mexico, USA. Note the importance of Gramineae (=Poaceae=grass) and Chenopodiaceae plus *Artemisia* (= sagebrush), the signature of Northern Hemisphere steppes, in the record right down to the present, though more abundant in the full glacial. These diagrams also illustrate several other points. Note the separation of pine species into *P. ponderosa, P. edulis* and corroded pine at the left in (a), and also the plotting of Cretaceous reworked (also called secondary) palynomorphs at the right. Pollen concentration represents grains per gram of sediment. The ages indicated at the left would have to be more closely spaced to permit calculation of pollen influx accurately, but the Chaco Canyon record is from fluvial sections. for which pollen influx is not as significant as for lakes, ponds and bogs. Students should note from these and other diagrams that Pleistocene palynologists are not consistent in the use of Latin versus vernacular plant names ("Douglas fir" = *Pseudotsuga,* etc.), nor is there any firm convention as to the order of presentation of taxa, e.g., *Quercus* (oak) is before *Juniperus* (juniper) in (b) but not in (a). Clearly Pleistocene palynologists tend to plot the taxa as the "sawblade" graphs fit best on the diagram. Some sort of convention would be preferable. Diagrams from Hall,1985.

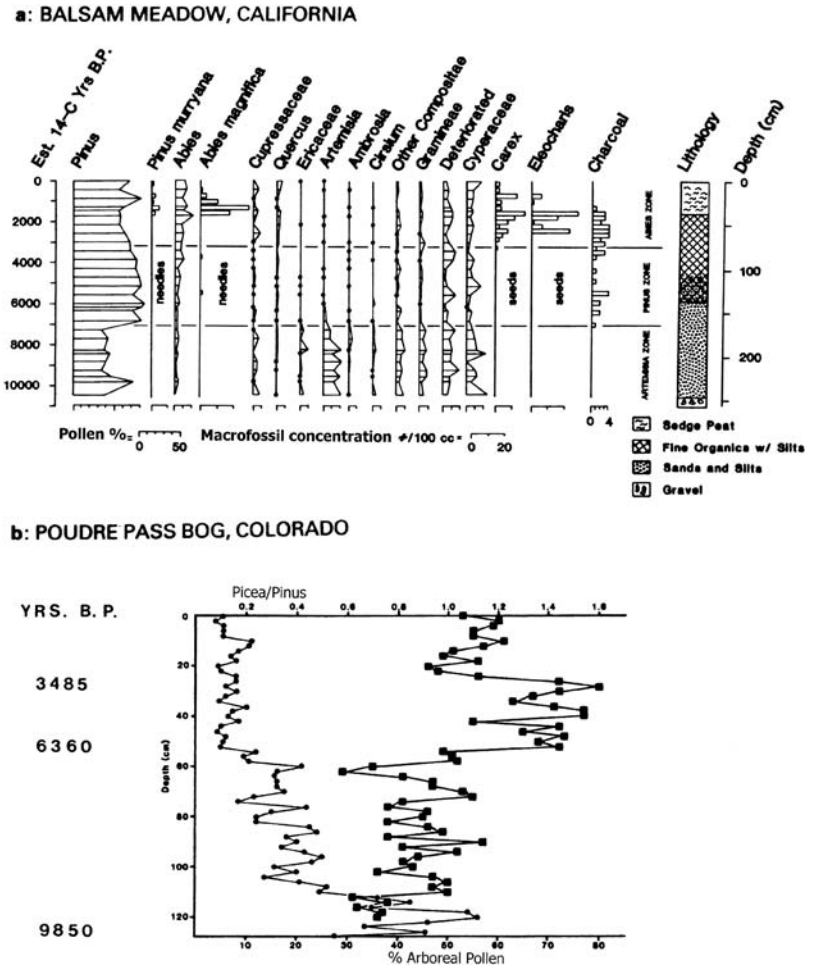

Figure 16.10 Pollen analytical data from the western USA, also illustrating some graphical techniques. (**a**) In this diagram from California, note the decline of *Artemisia* and Gramineae (= Poaceae) and increase in *Pinus* since 6500 B.P. Also note that megafossil (= macrofossil) elements are plotted and are much more abundant in the last few thousand years, also reflecting change in the abundance of vegetation. Charcoal abundance indicates forest fires and is probably related to human activities. The pollen percentages in this case are based not on total pollen but on a pollen sum of all non-aquatic plants. (**b**) This diagram from Colorado shows another technique for presenting AP vs. NAP, plus the relative abundance within AP of *Picea* vs. *Pinus*. The relative decrease in *Picea* probably bespeaks warming. (a) is from Anderson *et al.* (1985); (b) is from Short (1985).

post-depositional oxidation and disturbance of sediment. Furthermore, the pollen that is found is often introduced or badly mixed up by sedimentary and biogenic processes in the cave. However, I would say, based on experience with one deposit of bat guano in Texas, that cores of such deposits are quite promising. Others have also noted this since the first edition of this book (cf. Maher, 1991). Samples from other sorts of archeological digs (soils, garbage dumps) are often very much weathered and for that reason pollen-poor or (usually) barren. Various techniques may be employed to increase the number of palynomorphs recovered, especially starting out with very large samples, then using physical dispersion techniques, and float-sink, panning, and re-screening methods. In these ways it is sometimes possible to overcome the worst problem of archeological palynology, which is the derivation of conclusions from the study of very small numbers of palynomorphs. A special case is the study of pollen in fossil human feces. These coprolites are often comparatively rich in pollen, and their study can be very revealing as to

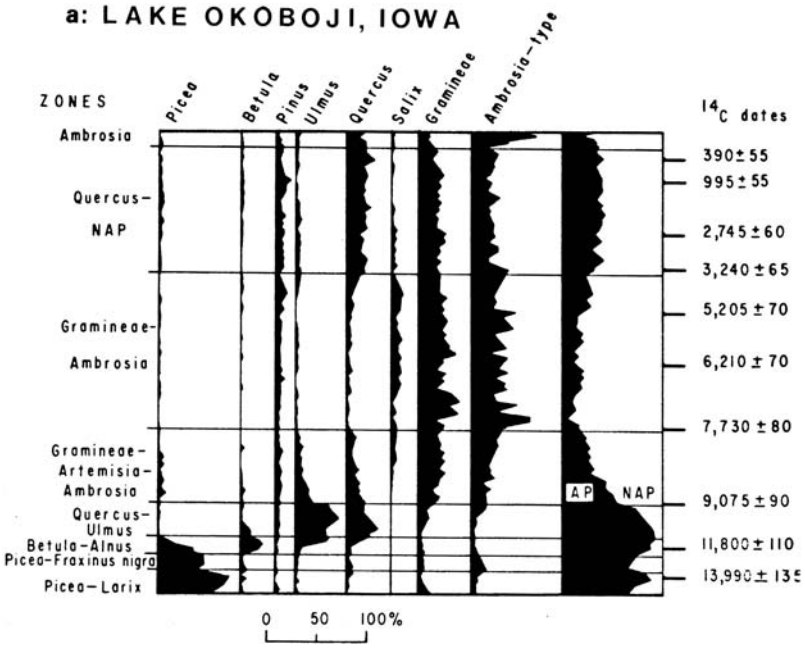

Figure 16.11a Diagram of Wisconsin glacial to Holocene time, Iowa, central USA. (**a**) A diagram from a large lake in Iowa, showing the use of dominant genera as names for pollen zones. Obviously the diagram is of selected forms only, as several of the typifying genera for zones (*Artemisia, Fraxinus*, and others) are not on the diagram. The increase of NAP from about 9,000 to 3,000 yr B.P. clearly represents increase in Gramineae (=Poaceae) and Compositae (Asteraceae), reflecting the expansion of prairie.

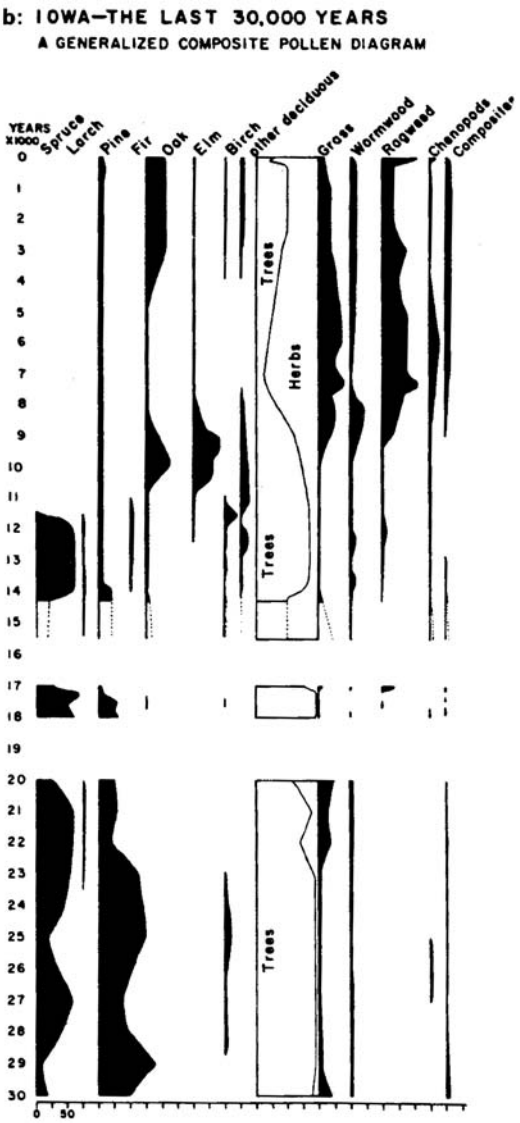

Figure 16.11b (**b**) A composite, generalized, smoothed out diagram for the past 30,000 years, based in part on the same information as in (a). Generalized diagrams have much to recommend them, and they can now be computer-generated from the pollen counts. Purely objective, all-inclusive, diagrams tend to be printed too small to read, or they appear as bulky foldouts. (a) is from Holloway and Bryant (1985), redrawn from Van Zant (1979); (b) is from Baker and Waln (1985).

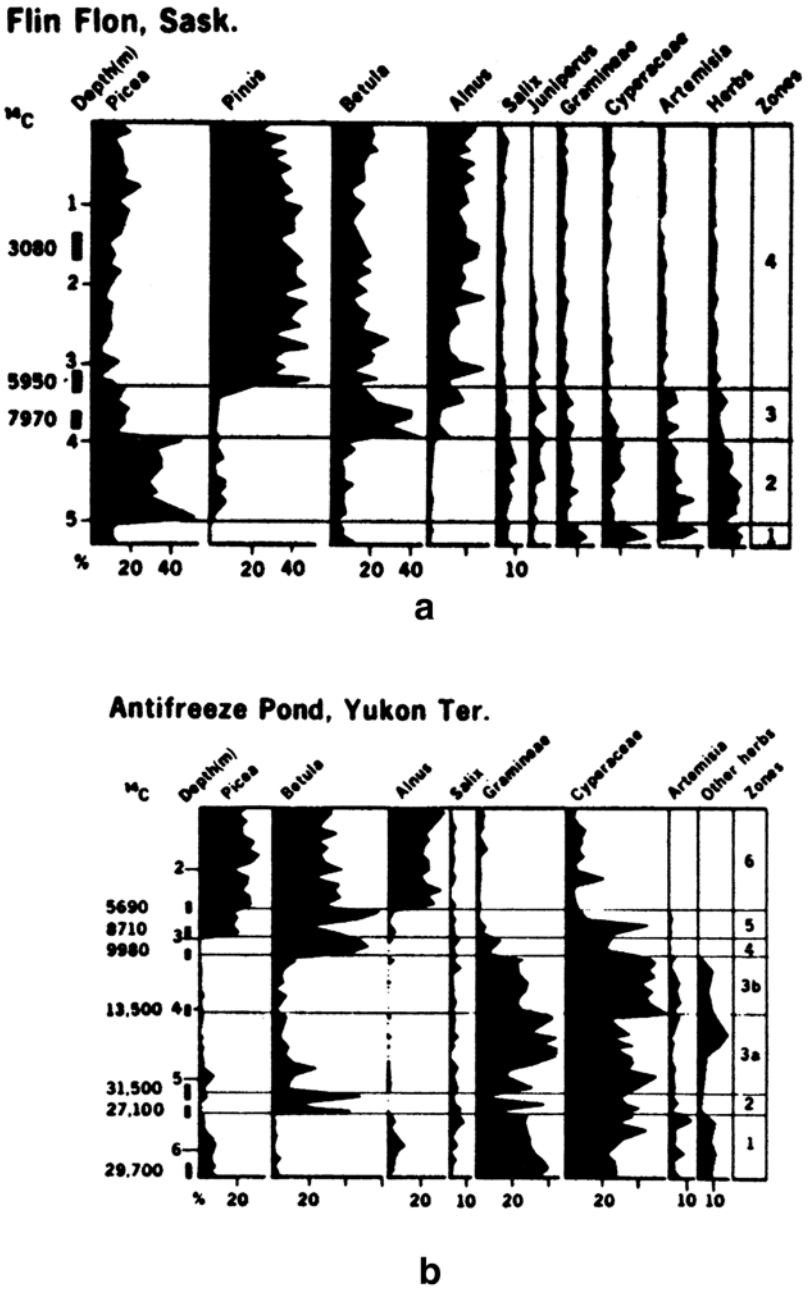
Flin Flon, Sask.
Depth(m)
Picea
Pinus
Betula
Alnus
Salix
Juniperus
Gramineae
Cyperaceae
Artemisia
Herbs
Zones
14C
3080
5950
7970
%
20 40
20 40
20 40
10
a
Antifreeze Pond, Yukon Ter.
14C
Depth(m)
Picea
Betula
Alnus
Salix
Gramineae
Cyperaceae
Artemisia
Other herbs
Zones
5690
8710
9980
13,500
31,500
27,100
29,700
%
20
20
20
10
20
20
10 10
b

Figure 16.12

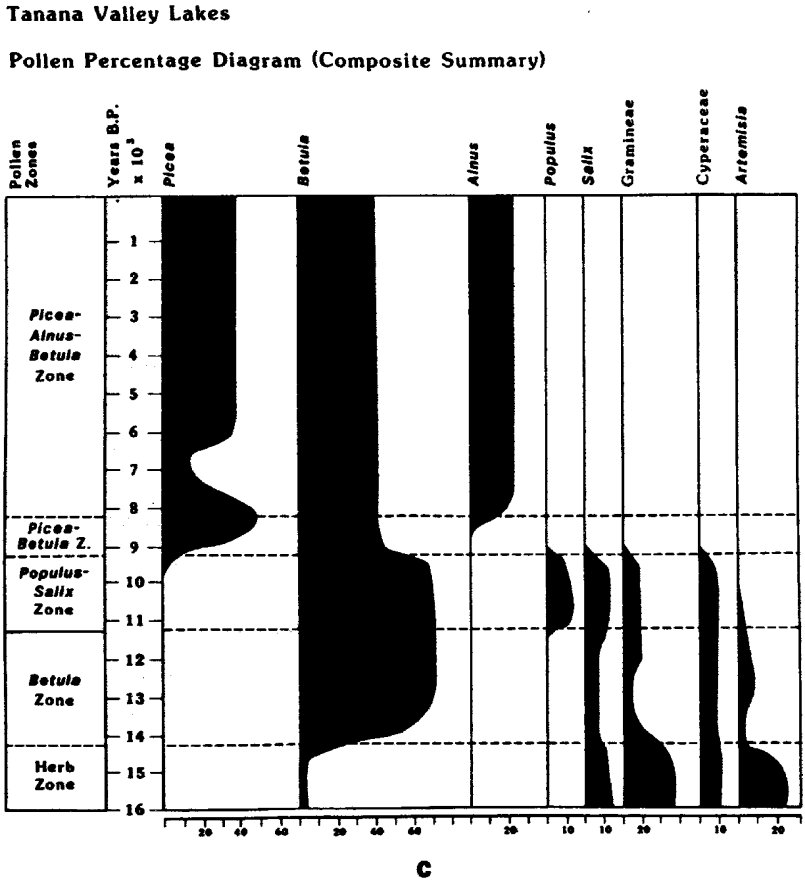

Figure 16.12 Pollen diagrams from (**a**) northern Saskatchewan, (**b**) Yukon Territory in northwestern Canada, and (**c**) central Alaska. Diagrams (a) and (b) are clearly of selected pollen, while diagram (c) is a composite summary, smoothed-out diagram (see caption for Fig. 16.11). Note that the Yukon and Alaska diagrams are very similar for the 16,000 years they have in common: decline of steppe taxa such as *Artemisia* and Poaceae post-9,000 yr B.P., along with expansion a little later of *Alnus* and *Picea*. (The author of the diagram notes that one ^{14}C date for Antifreeze Pond is apparently out of sequence.) The Saskatchewan diagram shows decline of steppe taxa and NAP generally and expansion of *Pinus* 2,000 years later (at about 6,000 yr B.P.). (a) and (b) are from Ritchie 1985; (c) is from Ager and Brubaker 1985.

the diet of the humans who made them, and the climatic conditions at the time of production (see Martin and Sharrock, 1964; Bryant, 1974a,b). Dimbleby (1985) has summarized the available information about archeological palynology in a text that describes the possibilities and pitfalls. (The subject is also discussed in the preceding chapter of this book–see also Bryant and Holloway, 1996.)

A beautifully illustrated example of direct connection of palynological diagrams and anthropology is to be found in the work of Empson *et al.* (2002) in New Zealand. Their pollen diagram (too big to be reproduced here) shows a fascinating coordinated explosion of charcoal fragments and *Pteridium* (a typical weed fern of clearings) spores, and the decimation of *Agathis* conifers, some 600 yrs. ago, with the explosion of the Maori population.

Holocene palynology has contributed to an understanding of the autecology of certain plants. For example, Davis (1980) has called attention to the dramatic drop in pollen counts of *Tsuga canadensis* (= hemlock) pollen in eastern North America 4,000–5,000 yr B.P. She believes that this is best explained by massive attack on *Tsuga* by a plant disease. There is a model in historic time: the near extinction by disease of *Castanea dentata* (= chestnut) in the eastern USA since 1900. Fig. 16.2 shows palynological evidence for the disappearance from its former range of this once dominant tree.

A direct contribution of Holocene pollen analysis to tectonics is the palynological evidence for "isostatic rebound," the elastic rise in the Holocene of land masses once covered and weighed down by ice (see Fig. 16.13). Hafsten (1956) showed such a case from Oslofjord in Norway. Sediment samples recognized as originally deposited at sea level at various localities, now found at various elevations above present sea level, were dated palynologically according to Jessen's (see Fig. 16.4) numbering scheme for the Holocene. The data show that since the early preboreal (Jessen IV), about 10,000 yr B.P., isostatic rebound of 220 m (= 2.2 cm/yr) has occurred.

Bernabo and Webb (1977) demonstrated the possibility from the analyses available of constructing isopollen (= "isopoll") lines for selected genera and plant associations at various times during the late glacial and Holocene. Sensitive ecological markers, such as the conifer-hardwood/prairie border, can reveal much about what would happen in certain areas if temperature and/or moisture factors changed a little.

The *Handbook of Holocene Palaeoecology and Palaeohydrology*, edited by Berglund (1986), contains very useful sections on all of the field and laboratory techniques, as well as on statistical (numerical) methods and other matters relating to Holocene palynology.

7 "Theory of Pollen Analysis"

The question of how pollen, spores, and other palynomorphs get into sediments is in general a matter of processes of rivers and oceans. That subject is dealt with

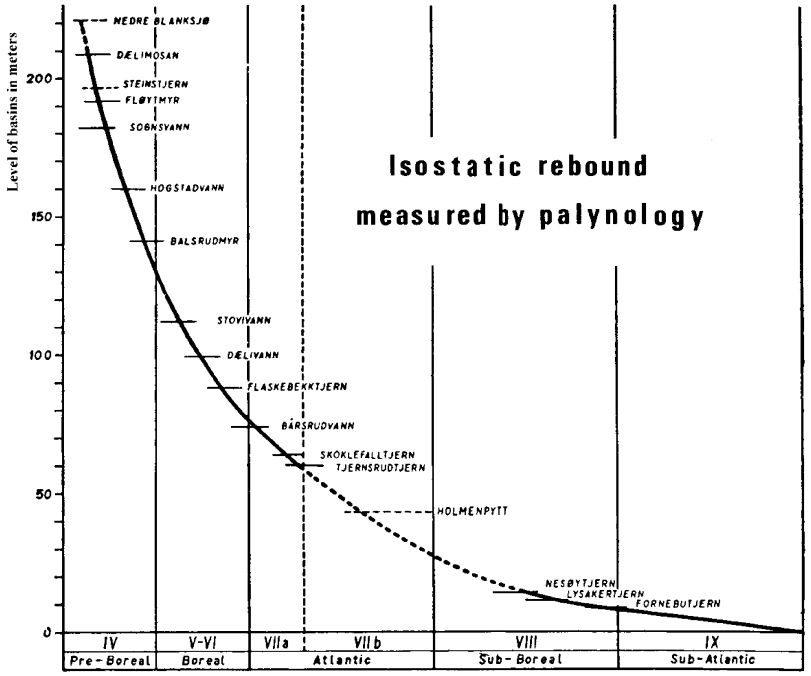

Figure 16.13 An interesting application by Hafsten (1956) of palynologically based chronology that had been correlated with varved-clay studies before common application of radiocarbon dating. (Hafsten has more recently applied radiocarbon dating to these localities, but there are technical difficulties that have made absolute dating so far impossible.) Each of the named levels refers to a small basin in the Oslofjord area, southeastern Norway. Hafsten found the marine-lake contact in cores of the sediment in each basin and then placed the pollen flora of that interval in the appropriate pollen analysis zone. (Hafsten used Jessen's scheme for southern Scandinavia; see Fig. 16.4.) The present elevation of the basins is shown on the left in meters. The 220 m elevation at Nedre Blanksjo, with a pollen flora of early Preboreal (Firbas IV; see Fig. 16.4) age (10,000 yr B.P.) indicates isostatic rebound of 2.2 cm/yr.

in Chapter 17. The subject of sedimentation of organic particles is of great importance to all geological oriented palynologists. However, palynologists studying Pleistocene/Holocene records, in the tradition of Lagerheim, Von Post, Erdtman, Godwin and countless others, focus mainly on the changing patterns of vegetation as revealed by pollen analysis. They have some special concerns with the sedimentation of sporomorphs out of the atmosphere. Their subject depends largely on study of sediments from ponds, bogs, and other small basins of deposition. While the palynomorphs found in such sediments reach their final destination via water, that part of their history is seldom as significant as how the pollen and spores got to the locality in the first place, which is an interplay between atmosphere and

vegetation. The questions of the importance of local meteorological conditions, the degree to which and how regional pollen rain penetrates the local pollen rain, and related concerns, have been thoroughly studied, resulting in some rather complex mathematical models. This subject is sometimes called the "theory of pollen analysis" and goes well beyond what is presented in this book.

Birks (2005) summarizes the literature on this subject, as it pertains to Scandinavia and nearby countries, where pollen analysis originated. The publication is a good resource for persons who need introductory information on this complex topic. Davis (2000) summarizes the literature on modeling of the relationship between vegetation and pollen records and the interplay of locally and regionally derived pollen in pollen analysis. Jackson and Lyford (1999) present a valuable detailed survey of various studies of pollen sedimentation out of air. They emphasize that pollen dispersal, and its sedimentation from the atmosphere tends to be somewhat chaotic ("...most pollen dispersal takes place in unstable atmospheric conditions...."). I find this a valuable insight, to prevent us from taking the very elegant equations and graphs presented in this area of palynology too literally.

Chapter 17

Production, Dispersal, Sedimentation and Taphonomy of Spores/Pollen in Relation to the Interpretation of Palynofloras

1 Introduction

The production and subsequent distribution of spores/pollen has been much studied from modern models, and the information transferred back to older sediments. In order to understand sedimentation of palynomorphs in the fossil record, this is the most obvious approach, but it is not without shortcomings. For example, the organic productivity of angiosperms is much greater than that of older groups of embryophytes, and it is very likely that this applies also to pollen/spore abundance. It is also probably too facile to presume that extinct forms of pteridophyte spores and gymnosperm pollen were transported and preserved in the same way that ragweed pollen is. Nevertheless, the actualistic approach yields information that is applicable to older sediments.

2 Spores/Pollen as Sedimentary Particles

As produced by the source plants, spores/pollen are solid bodies of low specific gravity. They have a resistant, organic outer coat or shell, an inner cellulosic wall, and a protoplasmic interior which is destroyed rather quickly by bacteria, fungi, oxidation, and hydrolysis upon falling to the ground or into water. A spore/pollen grain ready for fossilization is therefore a more or less hollow, more or less spherical body consisting of the sporopolleninous outer shell of the grain (which flattens to a double-layered micro-pancake in sediments). Such particles, along with other sedimented plant products are sometimes referred to as sapropel if they are a major constituent of the sediment. More specifically, various plant products including spore/pollen exines in sediment, are sometimes termed "type III kerogen" (Batten, 1981a).

2.1 Production of Spores/Pollen

It is now axiomatic that wind-pollinated seed plants, and some spore-producing plants such as *Lycopodium, Pteridium* and *Sphagnum*, produce prodigious quantities of spores/pollen. Straka (1975), in discussing a series of measurements in Darmstadt, Germany, says that a single measured cubic meter of space yielded during the whole year 12.5 million spores/pollen! In east Texas, I harvested the pollen from a few branches of *Pinus taeda* and extrapolated to show that an uncrowded 15 m tree could produce about 5 liters of pollen per year. A modest 100 hectare woodlot of such trees would produce in the spring something like 250,000 liters of pine pollen–a large railroad carload. I once measured the pollen output of single *Zea mays* plants as of the order of 25 cm^3 per plant. At this rate a corn field could therefore produce about 500 liters of *Zea* pollen per hectare. *Lycopodium* produces isospores in such large amounts that they have long been harvested commercially and sold by the kilogram for various purposes. Textbooks have frequently quoted data originally from Pohl (1937a,b) on pollen productivity of plants. The data are certainly all right as to order of magnitude, and are displayed here in Table 17.1. Some species produce much more spores/pollen than others, and a large wind-pollinated tree produces far more pollen per year than an herb, even if the herb is one like *Rumex*, with huge productivity per inflorescence. I would "guesstimate" that the average hectare of woodland in eastern North America produces at least 3,000 liters of pollen per year, though the amount will vary greatly depending on specific composition of the forest. It is obvious that wind-pollinated trees are the major producers. *Acer* (maple), *Pyrus* (apple), and *Tilia* (basswood, linden), all partly or wholly insect-pollinated, are not in a pollen-productivity class with strictly anemophilous genera such as *Alnus* (alder), *Corylus* (hazel) and *Pinus* (see Table 17.1). Some zoophilous plants such as the Orchidaceae and certain Asclepiadaceae produce large pollinia in which all

Table 17.1 Pollen production, per flower (or male cone) and inflorescence (or group of male cones on one branchlet). The numbers are rounded to nearest thousand. *Vallisneria* is an aquatic plant, as an illustration of low pollen productivity. Some plants produce relatively small flowers but large inflorescences, e.g., *Polygonum*. The super-producers per branchlet on the list, indicated by asterisks, are either large trees or else shrubs and herbs of sorts that grow in dense stands, so that the immensity of the productivity is relatively much greater than indicated. Data abstracted from Birks and Birks (1980) and Wijmstra (1978); original source is Pohl (1937a,b)

Species	*Pollen production per flower (or male cone)*	*Pollen production per inflorescence*
Vallisneria spiralis	70	140
*Polygonum bistorta**	6,000	2,860,000
Sanguisorba officinalis	11,000	–
Fagus sylvatica	12,000	174,000
Calluna vulgaris	18,000	–
*Betula verrucosa**	20,000	5,453,000
Fraxinus excelsior	25,000	1,606,000
Carpinus betula	28,000	–
Quercus robur	41,000	555,000
Tilia cordata	44,000	200,000
*Secale cereale**	57,000	4,241,000
*Pinus sylvestris**	158,000	5,770,000
Aesculus hippocastanum	180,000	765,000
Picea excelsa	590,000	–
*Pinus nigra**	1,480,000	–
*Populus canadensis**	–	5,800,000
*Alnus glutinosa**	–	4,445,000

* Super-producers

the pollen of one pollen chamber is shed as a cemented-together unit. Such plants are so adapted to pollination by animal vectors that they are very economical in pollen production, and thus their occurrence as fossil sporomorphs is minimal! The production of flowering plant pollen is a seasonal phenomenon, with certain plants favoring cool, moist weather for flower and pollen maturation (such as spring in Switzerland–see Fig. 17.1), while others favor drier, warmer conditions. In areas with alternation of dry and wet seasons, most but not all angiosperms flower in the moist season.

2.2 Preservability in Sediment and the Taphonomy of Palynomorphs

The propensity of spores/pollen to be preserved in sediments depends largely on the amount of sporopollenin in the exine, which is partly a function of

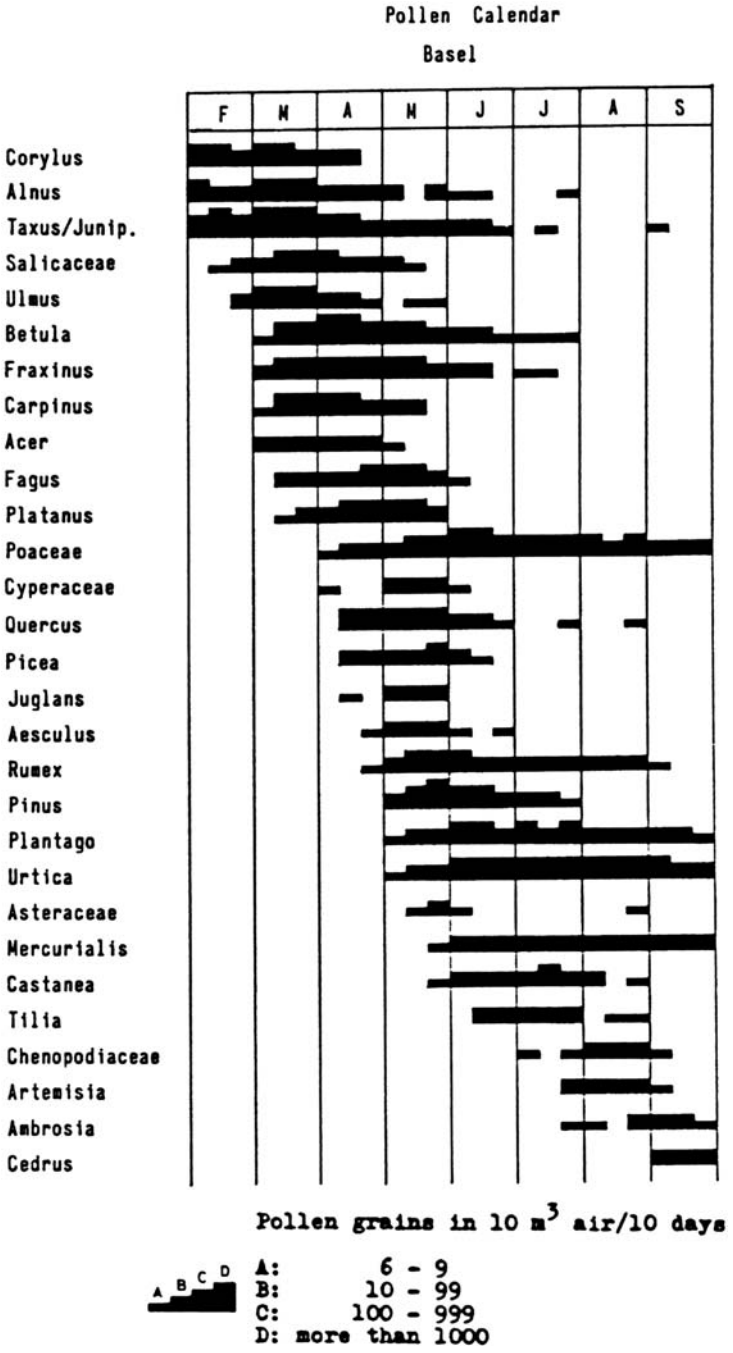
Pollen Calendar
Basel
F
M
A
M
J
J
A
S
Corylus
Alnus
Taxus/Junip.
Salicaceae
Ulmus
Betula
Fraxinus
Carpinus
Acer
Fagus
Platanus
Poaceae
Cyperaceae
Quercus
Picea
Juglans
Aesculus
Rumex
Pinus
Plantago
Urtica
Asteraceae
Mercurialis
Castanea
Tilia
Chenopodiaceae
Artemisia
Ambrosia
Cedrus
Pollen grains in 10 m3 air/10 days
A B C D
A: 6 - 9
B: 10 - 99
C: 100 - 999
D: more than 1000

Figure 17.1

the thickness of the exine, and of the division of the exine between endexine and ektexine (the more ektexine, the more sporopollenin), and partly due to other factors. It is clear that exines of *Equisetum* spores and *Populus* pollen are less likely to be preserved as sedimentary particles than are other exines, because of relatively low sporopollenin content. *Pinus*, on the other hand, is not only abundantly produced and relatively buoyant, but is also very rich in sporopollenin. The character of the sporopollenin in individual taxa is also apparently significant. *Beta vulgaris* (and presumably other chenopodiaceous pollen, such as *Atriplex* and *Salicornia*) has moderately high sporopollenin content (about 17%–see Table 3.2), and the exines are extraordinarily durable. I have cooked a sample of *Beta* pollen for many hours in successive treatments of HCl, KOH, and various organic solvents without affecting the integrity of the exines. On the other hand, the family Lauraceae as a whole is characterized by very low sporopollenin content in the exine. Acetolysis of pollen of this family produces only fragments of very thin exine. Had this "lauraceous tendency" ever become prevalent in the angiosperms, Cenozoic palynology would be even more of a dinoflagellate story than it is! Hopkins and McCarthy (2001) have shown by experimental oxidation of dinoflagellate cysts that they are also not uniformly provided with resistant dinosporin. They found that peridinioid (proximate) cysts were destroyed more readily than chorate forms (those with processes), which would thereby be enriched in sediments subject to oxidation. They also observed that pollen was more resistant to experimental oxidation than dinocysts and that bisaccate conifer pollen was the most resistant of all forms studied. This sort of "taphonomic effect" can obviously affect relative abundances and can even cause absence of some palynomorphs that were originally present.

As is stressed elsewhere, the sedimentary situation into which palynomorphs are deposited also has very great control over the likelihood of preservation: acid environments preserve better than alkaline, reducing environments better than oxidizing, and quiet sedimentary situations better than very energetic ones. The exclusion of oxygen is especially important. However, even some seemingly unlikely sites of deposition such as soils can preserve pollen, though preservation in soils is erratic and usually poor, and thus the records are probably biased toward resistant types. Furthermore, in soils, downwashing and redistribution by

Figure 17.1 Pollen rain in Basel, Switzerland, 1969–79, as measured by collecting pollen with a Burkhard pollen-trap located on a building in that city. The collections also include considerable fungal spores and industrial dust particles, not graphed here. These continue through the fall and winter months, October-January, but relatively small amounts of pollen are trapped then. Note that readings of more than 1000 pollen grains of one taxon per 10 cubic meters of air collected over a ten day period occur, e.g., *Betula* in April. Reproduced from Leuschner and Boehm, 1981.

vectors such as earthworms must be allowed for. Spores/pollen spectra of soils often permit drawing of conclusions about vegetational history during soil genesis (Dimbleby, 1961).

However, Cushing (1966) has shown that preservability of spores/pollen in sediment is the result of complex factors, not just sporopollenin content alone. Furthermore, the destruction of exines follows various pathways in various situations: degraded exines in which the structure is generally altered are common in silty sediments, whereas superficial corrosion (pitting, etc.) is more likely to be encountered in peat, and crumpling is characteristic of copropels (caused by processing in animal guts). Also, Cushing's studies showed that in some situations a seemingly delicate pollen such as *Populus* can outlast apparently tough forms such as *Alnus*.

The whole subject of the various processes that affect palynomorphs from their shedding by the producing organism to their incorporation in sediment and on through lithification of the enclosing sediment, and even its later thermal history in the rock so formed, is all part of *taphonomy*. The study of palynomorph taphonomy is a subject with a considerable history, though the pertinent studies have seldom been so identified. There is also room for much more study of the matter. It is also true that paleopalynologists need to be familiar with the impact that patterns of sedimentation have had on the production of the rock matrix from which the palynomorphs studied are derived. For example, the degree of sorting to which the sediment in a turbiditic shale has been subjected is very different from that of an associated gravititic mudstone, and this is very likely to account for at least part of the palynofloral character of samples from these rocks. An insightful and well-illustrated publication on the various taphonomic exigencies to which palynomorphs in rocks are subject is that of Tiwari *et al.*, 1994. A table of the effects of carbonization, oxidation, pyrite crystallization, etc., is included.

2.3 "Pollen Rain"

This refers to pollen sedimentation from the air. Pine and other pollen occurs in sediment at the Mid-Atlantic Ridge and other places far removed from the source. Erdtman's (1954) vacuum-cleaner experiments on board a passenger ship in the Atlantic were enough to show this, though the observation has often been repeated in other ways. Maher (1964), for example, showed that *Ephedra* and *Sarcobatus* pollen were transported many hundreds of kilometers from western North America to the Great Lakes region. Scott and Van Zinderen Bakker (1985) report that on Marion Island, southern Indian Ocean, exotic pollen comprises more than 1% of pollen spectra from surface samples. Most of the forms come about 2,000 km from southern Africa, but some are from more distant South America. They are transported by the prevailing winds and perhaps by ocean currents.

As spores/pollen are silt-sized, or very fine sand-sized particles (see Fig. 17.2) and are low in specific gravity, they obviously can get into the upper atmosphere when the air is turbulent, and there is certainly every reason to assume that some such grains can and do circle the Earth in the same way as volcanic dust. However, almost all pollen falls out of the air very near the producing plant. This is evident from the sinking rates reported in Table 17.2. Data for three species of saccate conifer pollen, based on sophisticated modern techniques, yielded an average rate of 2.7 cm/s (Niklas, 1984). An average sinking rate of 3 cm/s is nearly 2 m/min, and it is quite clear both from this theoretical consideration and from many observations that most pollen, even pollen from a large tree, reaches the ground a few tens of meters from the tree unless the air is turbulent at the time of pollen dispersal. Clearly pollen from tall trees will spread farther laterally while settling than pollen from shrubs and herbs, other things being equal. More solid data based on marked pollen would be desirable, but I think it is clear from many studies already made that at least 95% of all pollen has normally settled down within a kilometer of the source plant. An incidental indication of the limited range of airborne pollen is provided by the study by Knapp *et al.* (2001), showing that for a species of *Quercus* (oak), thinning of the trees by humans had potentially disastrous effect on acorn set by the remaining trees when they were 60 m apart. Lange *et al.* (2002) likewise expressed concern about the genetic viability of *Taxus baccata* (yew) in central Europe because human activities have left individual trees too far apart for efficient pollination. On theoretical grounds, Tauber (1965) calculated that most pollen, even from an elevated source, would be on the ground within 2,700 m. Tsukada (1982) reports that 90% of pollen of *Pseudotsuga menziesii* (northwest USA) falls within 100 m of the source trees.

Various palynologists have pointed out that, in a forest, the canopy of trees is a controlling factor. Thus, the autumn leaf fall provides one peak in "pollen rain" that is entirely secondary–the pollen trapped on leaves then finally reaches the ground and gets into streams (Loeb, 1984). Fig. 17.3a shows Tauber's (1967) model and Fig. 17.3b presents Jacobson and Bradshaw's (1981) model for the general scheme of the early stages in pollen's journey from tree to sediment.

Since the first edition of this book, much more research has been done on pollen dispersal in the air in relation to its eventual deposition, with special reference to deposition along with other sediment in bodies of water such as lakes. Two illuminating studies are those of Jackson and Lyford (1999) and Davis (2001). Jackson and Lyford summarize the basic literature, starting with Stokes' Law, discussed elsewhere in this book in relation to the behavior of palynomorphs in water. Prentice's (1985) and Sugita's (1994) elegant mathematically based methods produce models for relating pollen analysis to vegetation that work well for ponds and very small lakes but are not readily applicable to pollen analysis/vegetation relations in larger lakes, to say nothing of really large bodies of water, where the limitation to airborne pollen is fatal. Davis's analysis particularly

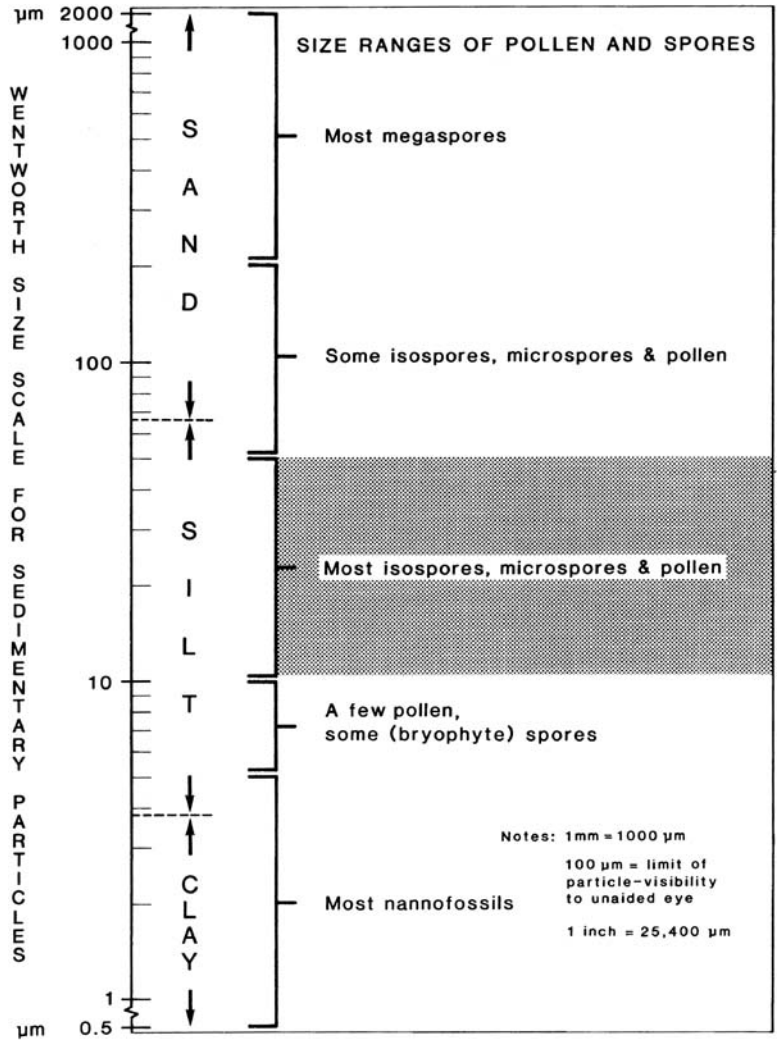

Figure 17.2 Size ranges of pollen and spores in comparison to clastic particles, per the Wentworth scale, plotted logarithmically. Most spores and pollen are silt-sized, although a few are fine sand-sized, and megaspores are practically all sand-sized. As the specific gravity of sporopollenin (about 1.4) is less than that of mineral clastic particles (about 2.5), and because palynomorphs are not solid, they will tend to sort in sedimentation in a mineral class of somewhat smaller particles than themselves (see Stanley, 1969).

Table 17.2 Sinking speed in air, measured and predicted from Stokes' law, of various wind-pollinated pollen and Lycopodium spores. There are some surprises. Grass pollen (Zea, Secale) despite being wind-pollinated, is quite dense and sinks rapidly. Lycopodium spores and Taxus pollen, rather dense-looking, are very "light". Data from Straka (1975) and Firbas (1949)

Species	*Sinking speed (cm/s) Measured*	*Calculated from Stoke's law*
Zea mays	24–30	13
Abies alba	12–39	–
Larix spp.	10–22	–
Picea spp	6–9	6
Secale cereale	6–9	–
Fagus sylvatica	6	5
Pinus spp.	3–5	3
Corylus avellana	2–3	2
Alnus spp.	2–3	2
Cannabis sativa	2–3	2
Taxus baccata	1–2	1
Lycopodium	2	–

emphasizes the different contributions of pollen local to the area of deposition and pollen from the general region. Palynologists will benefit from study of the Davis, and the Jackson and Lyford summaries. They should also read Crane (1986), which stresses the importance of the "Reynolds Number (Re)," relating to the interaction of bodies in the size range of pollen with moving air. The essence of the matter is that pollen has a very low Reynolds Number (0.1), and as a result is not easily picked up or moved very far at the velocities of air movement normally encountered. In reality the behavior of the atmosphere, and of palynomorphs in it, are very chaotic and are not easily reduced to simple laws that apply across the board. It is interesting in this connection that even the absence of prevailing wind is predicated as an assumption for the Prentice/Sugita models.

One reason why some intuitively tend to doubt the generalization that most pollen drops near the source vegetation is that pollen is found in well reported aerobiological counts of spores/pollen in the air in all sorts of places, even within a city. (See Fig. 17.1 for a pollen "calendar" for a location in western Europe. Note that $10\,m^3$ is a lot of air, and that the counts were made for 10-day segments of time.) The anecdotal impression of pollen abundance in the air is intensified by the incredible sensitivity of human sufferers from pollinosis to even tiny amounts of pollen. Five or even fewer pollen grains of an offending species can make a sensitive person ill. Thus, hyper-allergic persons may pick up enough pollen from an open window of an urban building to make them ill,

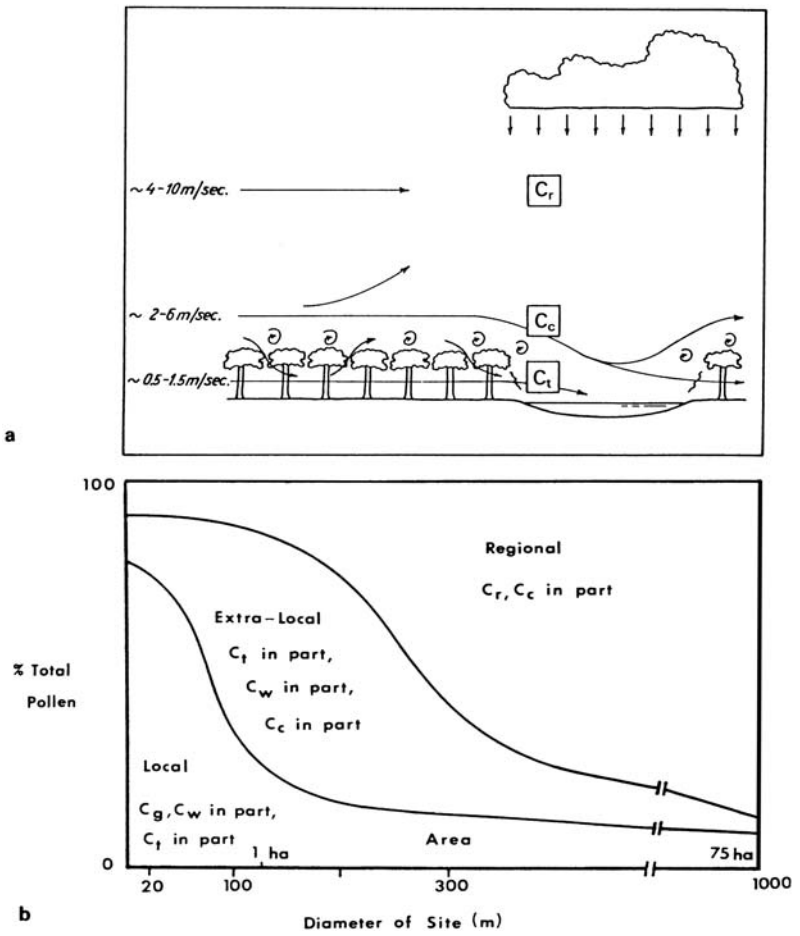

Figure 17.3 Local distribution of pollen and spores by wind and water. (**a**) Tauber's (1967) model for pollen dispersal by wind in a forested area. Pollen is shown as moved by three routes, of which the total transport is a composite. Cr = pollen brought down by rain, Cc = pollen carried above the forest canopy, and Ct = pollen carried through the trunk space in the forest. When passing over a lake the air currents bend down. However, most pollen reaching a lake does so by the lower route of Ct. (**b**) Jacobson and Bradshaw, 1981, presented a more complete model by including Cw (= surface runoff) and Cg, a gravity component for pollen dropped directly at the site of deposition. For other symbols see (a). "Regional" refers to pollen from more than several hundred meters from the basin of deposition, "Extra-local" means pollen from plants 20 m to several hundred meters from the basin, and "Local" indicates plants from within 20 m. In both models, the activities of streams entering the basin are not taken into account. (a) reproduced from Tauber, 1967; (b) reproduced from Jacobson and Bradshaw, 1981.

but the amount of pollen is very small. Mandrioli *et al.* (1982) report that they collected at various atmospheric levels up to 800 m above sea level in northern Italy significant amounts (up to 12 grains/m^3) of tree (*Quercus farnetto, Fagus* sp., *Ostrya carpinifolia*) pollen that judging from the meteorological conditions and species composition apparently had crossed the Adriatic from the Balkan area. But even these amounts are not large when compared to the total production of spores/pollen, much of which is eventually washed into streams and into basins of deposition.

One of the best illustrations of airborne pollen versus water-borne pollen in the literature is Muller's (1959) study of the Orinoco Delta. *Podocarpus* pollen, a bisaccate, was present in the sediment and from the distribution of the trees was obviously airborne to the sediment, but it was numerically overwhelmed by that reaching the basin of deposition in the streams. Thus, in measuring the "pollen rain," one must be aware that a number of conflicting mechanisms are at work.

Various devices are used to trap and measure airborne pollen. The typical apparatus is a sophisticated mechanical device for passing air over sticky slides. These devices are often located on tops of buildings. Pollen rain has also been measured over long terms from stationary traps on the ground, or the spore/pollen content of moss polsters and other surface litter may be analyzed, as may surface sediments from lakes. Palynologists have also measured the pollen in the atmosphere at various levels using pollen traps. From a geological point of view, however, perhaps the most significant data are from studies of spores/pollen in the water of streams of various sizes, and we have so far very few data of this sort.

The specific gravity of whole pollen is a tricky matter. Wodehouse (1935) and others have shown that the protoplasmic content of spores/pollen picks up moisture from the atmosphere. The specific gravity of *Zea mays* pollen, given in Firbas (1949), as 0.35, will obviously approach 1.0 if the pollen has taken up enough moisture. The specific gravity of pollen is also dependent on air spaces within the grain. Bisaccates such as *Pinus* have much trapped air in the sacci. The specific gravity of pollen exine itself is well above unity–about 1.4. Therefore, fossil exines devoid of air and protoplasmic contents sink in water but float in a $ZnCl_2$ or $ZnBr_2$ solution with specific gravity about 2.0; this is the basis of one of the laboratory techniques for concentrating fossil palynomorphs. Some sorts of pollen, especially bisaccates, will float for long periods in water. Most of the large numbers of *Pinus silvestris* pollen grains I once put in large beakers of water were still floating a year later. Those still floating when mounted in water on a microslide showed air bubbles filling the sacci. The grains that had sunk did not show these air bubbles; the sacci were "wet." When the exines are completely filled with water, the specific gravity of the sporopollenin (1.4) governs, and the exines sink. (See also later field evidence for long-term floating of pollen in the Bahamas.)

Barriers to transportation of spores/pollen in the air are many, even if there are strong winds and the air is turbulent. Fig. 17.3a shows that pollen well above the tree canopy of a forest travels nearly an order of magnitude faster in the wind than does pollen near the ground, where it is impeded by tree trunks and shrubs. Once spores/pollen reach the ground, further movement is mostly by water, except in open areas such as grassland or desert, where repeated deflation is likely. Trees that are wind-pollinated apparently have had to adapt to the exigencies of too little pollen reaching the area of the female gametophyte. Niklas (1984) has shown that female cones of coniferous trees are constructed in a way that incidental air currents are directed in a manner that maximizes the probability of pollen capture.

It is precisely because spores/pollen mostly sink to the ground quickly that the pollen rain of an area tends to be characteristic, that is, rather constant from year to year. ("Iatropalynology," the application of medical methods to the alleviation of pollinosis, assumes the relative predictability of spores/pollen in the air in a given area at a given time.) Studies of pollen in surface sediment have shown that several widely dispersed collecting stations in about the same latitude and altitude will yield a rather similar pollen "signature," if the vegetation is similar.

However, the extent to which pollen rain in surface sediment presents a picture from which the source vegetation can be "reconstructed" is a complex matter. For one thing, there is allochthonous or "outside" pollen, despite the prevailingly local character of the pollen rain. "Outside pollen" ranges from 100% on Antarctic or Greenland glaciers to near zero in a wooded peat swamp–this is why, as noted by Nichols (2005), that the vegetation that produced peat and coals derived from it can be so well characterized by paleopalynology. McAndrews (1984) showed that ice from a glacier on Devon Island, Arctic Canada, contains pollen from sources more than 1,000 km away. When the ice melts the pollen can be reworked into glacially derived sediments. On the Isle of Skye, Birks (1973) has shown that surface samples from some environments yield mostly local pollen, e.g., a woodland that produces plenty of pollen itself and the trees of which impede penetration of pollen rain from outside. Sub-alpine grassland, scrub, and alpine vegetation have as much as 40% outside pollen. Mack and Bryant (1974) note that in steppe communities of the Columbia Basin, Washington State, USA, pine pollen may equal 50% of pollen in surface samples, though collected 10 km from pine forests. Mack *et al.* (1978) showed that, although in general the pollen flora of surface samples from Washington and Idaho could be related, with corrective factors, to the surrounding vegetation, samples from grass-dominated areas in the sub-alpine zone contain much tree pollen from nearby forests. Markgraf (1974) has shown that areas above the timberline in mountains produce very little pollen–at least an order of magnitude less than lower in the same mountains–and thus the pollen that comes in with regional winds is relatively prevalent above the timberline, as in marine sediments from far offshore (see also Fig. 17.4x).

a

Dominant trees in vicinity of sample	Percent pollen in sample				
	Pinus	Picea	Fagus	Carpinus	Quercus
Pinus	85.7	1.2	0.5	1.1	1.9
Picea	54.0	29.0	---	---	1.5
Fagus	51.1	2.1	22.0	1.3	6.1
Carpinus	68.0	1.0	1.0	13.0	2.0
Quercus	68.7	3.0	1.0	1.3	9.3

b

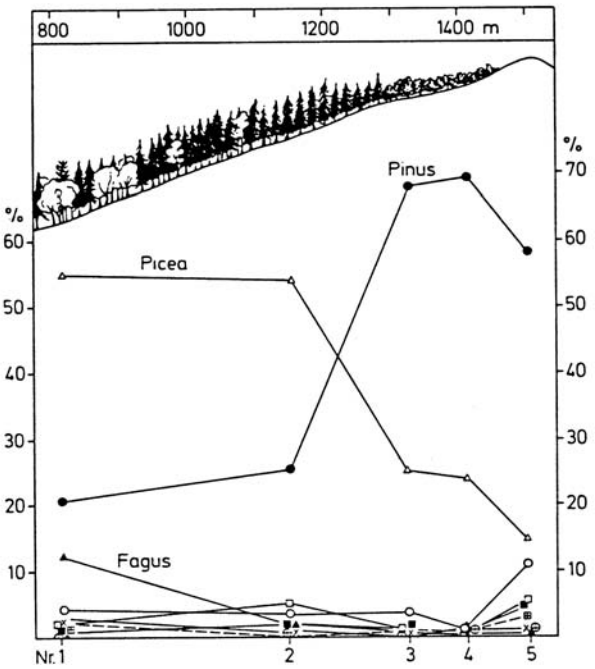

Figure 17.4 Pollen rain as a reflection of standing vegetation. (**a**) Pollen in surface samples from a locality in Germany. The data here and from many other places have shown that pollen of a given tree taxon is most abundant in surface sediment from areas where the taxon is dominant. Thus, *Carpinus* pollen is most abundant in soil from *Carpinus*-dominated woods. However, wind-pollinated taxa which produce large amounts of pollen, such as *Pinus* in this case, tend to overwhelm pollen of other taxa, even in their own areas. Samples do not total 100%, because of minor constituents not listed. (**b**) Pollen rain in comparison with forest composition in a mountainous area of central Europe. Sample No. 1 came from a *Picea-Fagus* forest, No. 2 from a *Picea* forest, No. 3 from a boundary zone for dwarf *Pinus*, No. 4 from the dwarf-*Pinus* zone, and No. 5 from above the timberline. *Pinus* pollen is abundant (20%) at Nos. 1 and 2, where there are no pine trees. At No. 5, easily airborne *Pinus* pollen dominates in the total absence of trees, but pollen of other

The altitudinal diminution in pollen rain is matched by a latitudinal decrease in Arctic areas, from Boreal forest to tundra to ice field, something like an order of magnitude in each case (see Birks *et al.*, 1975). Jacobson and Bradshaw (1981) have shown that when pollen is deposited in a small basin, such as a lake with no inflowing streams, the proportion of autochthonous (locally produced) pollen varies inversely with the size of the basin. The effective "pollen rain" of an area is a product of three factors: (a) what is produced locally (some species are much over-represented), (b) what is preserved (no *Sassafras*, little *Populus*), (c) what comes in from outside. Heusser (1978) has shown that off the Pacific coast of North America the general pollen rain is 100–1,000 grains/m^2 per year.

A study by Grindrod (1985) of mangrove vegetation on a prograding shore in Queensland, Australia, demonstrated that pollen analysis can be employed to create models for plant successions even in such highly mobile, unstable environments.

2.4 Spores/Pollen/Other Palynomorphs in Water

Not nearly enough work has been done on the behavior of spores/pollen and other palynomorphs as sedimentary particles in water, especially in major streams. (Unfortunately, we are running out of undammed major streams to study!) Fig. 17.4x presents the sort of data that are currently available. Fedorova (1952) studied the Volga River and showed that the amount of spores/pollen in the water varied from about 23,000 to about 45,000 per 100 liters of water.

Her laboratory technique consisted of allowing the pollen to settle from the water by gravity. She did not study the water of different levels in the river. Groot and Groot (1966) used continuous centrifugation and measured 50,000-800,000 spores/pollen per 100 liters of water in the estuary of the Delaware River. Using shipboard continuous centrifugation on the Great Bahama Bank, Traverse and Ginsburg (1966) found pollen (mostly *Pinus*) of the order of 1,000 per 100 liters of water. In 1960-62 I studied the Trinity River, Texas, near its mouth, and Trinity/Galveston Bay, into which it empties. The Trinity River at the time was relatively unaffected by dams and culture generally. I sampled water at various stations in the lower river, the delta, and in the bay on a monthly basis for about a year. Using a pumping apparatus mounted in a small boat, I sampled surface, mid-depth, and near-bottom water. The entire sample (20 liters) was evaporated in the laboratory to obtain a sludge which was then centrifuged, and processed

Figure 17.4 species from the mixed forest is also blown in to a smaller extent (symbols species are those given in Fig. 16.3). The relationship of vegetation to pollen rain is clearly complex. Reproduced from Straka, 1975.

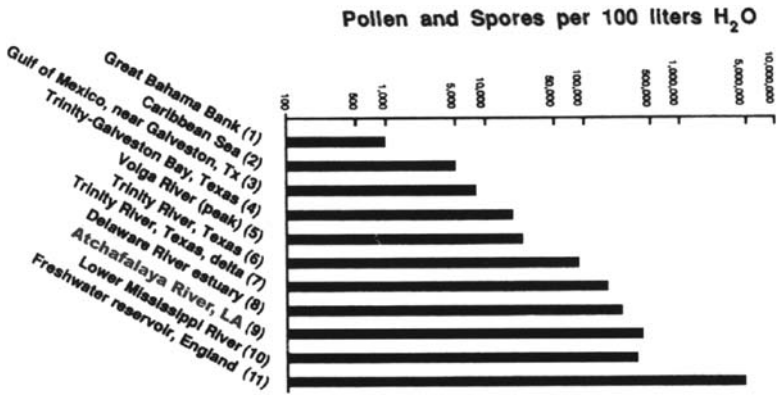

Figure 17.4x Pollen and spores in the water in various sedimentary situations. The concentration of palynomorphs per volume of water varies considerably from season to season and in response to storms and other factors. Therefore, all of the data with the exception of (5) are estimated averages for multiple measurements. Pollen and spores are expressed per 100 liters of water, rather than per liter, as the numbers so generated are then similar to that for data for palynomorphs per gram of sediment (see Fig. 18.6). The data are plotted logarithmically. Water from mid-ocean localities would presumably contain at least an order of magnitude less per 100 liters than even the water of Great Bahama Bank. The reading of 5,000,000 per l00 liters of water for a small reservoir in England (11) is an indication of the high density that can be obtained in water with limited influx, closely surrounded by pollen-producing vegetation. Sources for data: (1) Traverse and Ginsburg, 1966; (2) Farley, 1987; (3, 4, 6,7) Traverse, 1990; (5) Fedorova, 1952; (8) Groot, 1966; (9) Campbell and Chmura, 1994 (10) Chmura and Liu, 1990 (11) Peck, 1973.

by ordinary palynological techniques. Practically 100% recovery was assured by this technique. A great variety of pollen, spores, and other palynomorphs was obtained. Some of them are illustrated in Plate 17.1.

The average numbers obtained were about 90,000/100 liters of water in the river some miles upstream, about 180,000/100 liters in delta river water, and about 20,000/ 100 liters in Trinity Bay, and about 8,000/100 liters in the Gulf of Mexico off Galveston. (See Fig. 17.4x; the detailed results were reported in Traverse, 1990.) There was much seasonal variation, depending on a variety of factors, especially flowering seasons and rainfall. The range of values for all depths and all stations was 10,000–500,000 per 100 liters of water. One of the interesting sidelights of this work was the frequent appearance of *Engelhardia* pollen, obviously reworked from Tertiary rocks far upstream, probably from the Eocene, about 300 km northwest. Frequent appearance of this reworked form apparently was directly related to periods of heavy precipitation in upstream areas. The palynoflora of the water was very diverse and overwhelmingly well

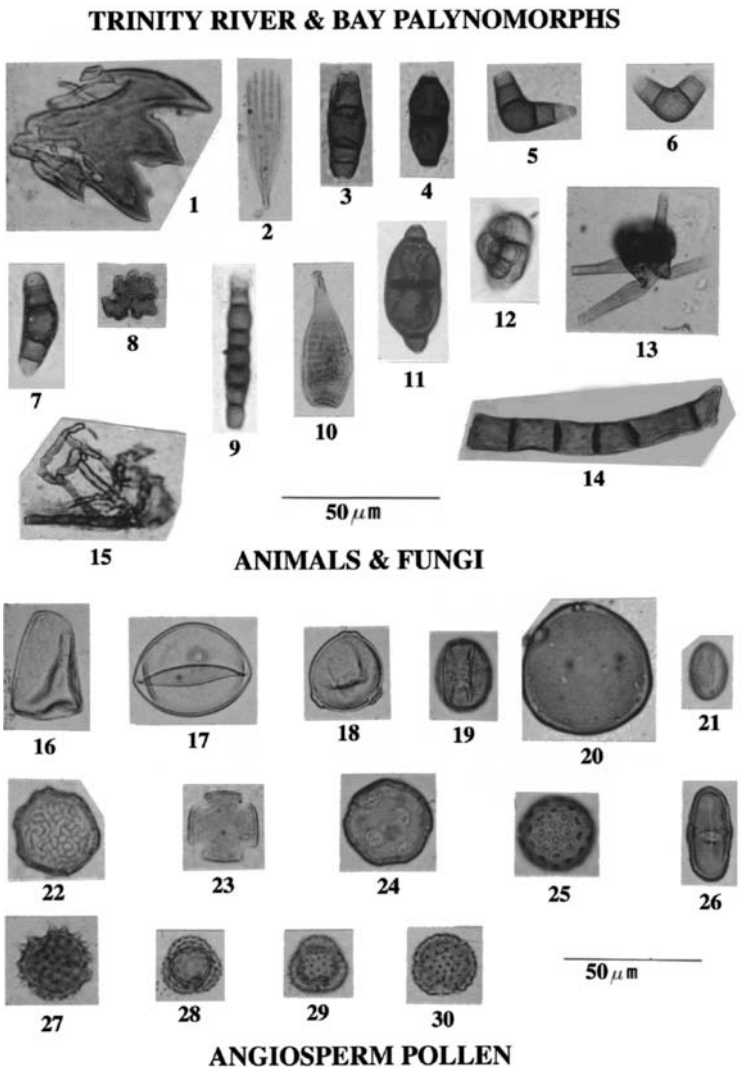

Plate 17.1 Animal and fungal palynomorphs, and angiosperm pollen from Trinity River water, Texas. Pteridophyte spores, conifer pollen, and algal palynomorphs, such as *Pediastrum* spp. coenobia and *Pseudoschizaea* spores, were also found to be abundant in the water.**1**. Chitinous mouth part, probably of polychaete worm. **2**. Chitinous lepidopteran wing scale. **3.-9**. Fungal spores (8 is a sporeling–germinated spore). **10**. Either a fungal spore or, more probably , a tintinnid test. **11**. Fungal spore. **12. -14**. Fungal spore bodies. **15**. Fungal mycelia. 16.-30. Pollen. **16**. Cyperaceae (Pu1). **17**. Poaceae (P01). **18**. *Myrica,* polar view (P03) . **19**. *Quercus*, equatorial view (Pc0). **20**. *Carya*, probably pecan, polar view (P03). **21**. *Salix,* equatorial view (Pc0). **22**. *Ulmus*, polar view (P0f). **23**. *Fraxinus*,

preserved: pollen, spores, animal and fungal particles and a variety of abundant algal micro-remains such as *Pseudoschizaea* and several species of *Pediastrum* coenobia (cf. Plate 17.1).

In 1985–86, sampling was repeated, using the same techniques as in 1960–62, at the same stations. By this time damming upstream had produced Lake Livingstone, and it acted as a settling basin, greatly reducing the palynomorph load of the downstream river and accumulating it in the lake (cf. Traverse, 1990, 1992). Significant information about the relationship of the Texas coastal vegetation to the palynomorph load of the river and bay are presented in Traverse (1994a).

Chmura and Liu (1990) studied the palynomorphs in water of the Lower Mississippi, finding palynomorph counts per volume of water somewhat larger than I did in the relatively small Trinity River (see Fig. 17.4x). Very unlike the situation in the Trinity River and Bay, however, much of the palynoflora was observed to be highly corroded and/or abraded, indicating (probably repeated) recycling in its course down the river. Campbell and Chmura (1994) report the highest palynomorph counts per volume of water for a river of which I am aware (350,000/100 l; see Fig. 17.4x), in a study of the Atchafalaya River, Louisiana, a culturally much modified distributary of the Lower Mississippi. As in the Mississippi, reworked pollen was a factor, but the grains were not as much corroded as in the Mississippi.

3 Vegetational Analysis From Pollen Analytical Results, "*R* Values," Etc.

The principal paleoecological purpose for study of the pollen rain that produced a palynoflora is to relate it to the source vegetation, partly with the hope of relating a known fossil pollen spectrum to the unknown vegetation that produced it. Tracing the changing composition or distribution of vegetation through time enables one to draw conclusions about the past climate and about environmental changes of other sorts. For example, maps can be produced based on isopolls (see Fig. 17.5) showing lines connecting points with the same percentage of spores/pollen of particular taxa.

Clearly, despite over- and under-representation of taxa and other detracting factors, these isopoll maps do really represent changes in vegetation and thus of climates. Even a single taxon can show much. Iversen (1944), for example, studied *Hedera*, showing the presence or absence of freezing weather, and *Hippophae*

◄

Plate 17.1 polar view (Pd0) (also common as Pc0). **24**. *Liquidambar* (P0x). **25**. Chenopodiaceae (P0x). **26**. Apiaceae, equatorial view (Pc3). **27**. Asteraceae, long-spine, polar view (Pc3). **28**. *Ambrosia* (ragweed), a low-spine Asteraceae, polar view (Pc3), low-focus. **29**. same as 28., high-focus. **30**. Asteraceae, low-spine, (Pc3), polar view.

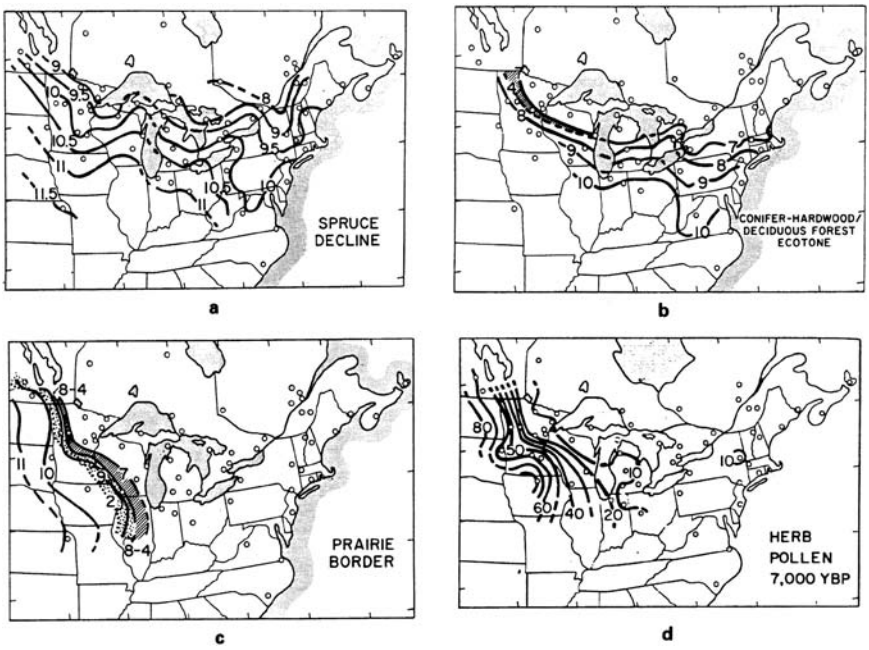

Figure 17.5 Extrapolation of pollen analytical data for graphical interpretation of vegetation distribution in the North American Holocene. Preparation of such maps is based on isopollen lines (see Fig. 17.6). (**a**) *Picea* (spruce) decline. The lines are isochrones showing how many thousands of years B.P. *Picea* pollen analytical values fell below 15%. (**b**) Conifer/hardwood deciduous forest ecotone (= transition between the two vegetational types), showing where this zone was 10,000, 9,000, 8,000, and 7,000 yr B.P., based on pollen analyses. For Minnesota, the situation is confused by the prairie expanding eastward post-8,000 yr B.P., then moving westward again after 4,000 yr B.P. (**c**) The location of the prairie border is shown by isochrones for 11,000, 10,000, 9,000, 8,000 and 7,000 yr B.P., based on herb (= NAP) isopolls. Shaded areas refer to the region over which the prairie retreated after reaching maximum Holocene extent at 7,000 yr B.P. (**d**) Isopolls can show the concentration of high counts for given pollen types at a selected time, in this case for herb (= NAP) pollen at 7,000 yr B.P. This shows that the prairie border in (c) is based on the 30% herbaceous pollen isopoll. From Bernabo and Webb, 1977.

pollen in northwestern Europe (Straka, 1975) indicates pioneer colonization of deglaciated areas. However, the aim of pollen rain investigations is usually to seek a model for interpretation of pollen diagrams, but over-, under-, and non-representation prevent direct translation of even Holocene pollen analyses into vegetation reconstructions. Cross (1984) has shown that in an arid environment, for example, pollen floras of surface samples reflect the vegetation very poorly. In an investigated part of Baja California, surface samples had *Opuntia* pollen where

no *Opuntia* plants were present, whereas *Lycium* and *Larrea*, the dominant shrubs, were not represented by pollen in the surface sediment samples. In tropical rainforest areas, surface samples are dominated by wind-pollinated plants, such as grasses, composites, and chenopods, with very small amounts of (animal-pollinated) pollen from the dominant trees (Rue, 1986). Early in the history of Holocene pollen analysis correction factors were suggested. For example, it was proposed (Faegri and Iversen, 1975 edition; the idea goes back at least to the 1940s) that in northwest Europe *Betula* and *Corylus* counts should be divided by 4 to correct for over-representation of birch and hazel pollen–one unit of *Betula* or *Corylus* plants was interpreted as producing four units of pollen. Davis (1965, 1973) has published sophisticated arithmetic methods for calculating analogous ratios. "R_m" is the ratio determined from comparison of the pollen rain with the actual vegetation. Davis' R_m is based on the same idea as division by 4 for *Betula* and *Corylus*, as cited above. An R_m of 4 means that the fossil pollen percentage is divided by 4 to get the corresponding density (percentage) of the taxon in the vegetation. Davis (1963a, b) showed that the use of an "*R* ratio" to correct the fossil pollen counts in a subsurface sample yields a modified "percentage" which is close to the presumed composition of the fossil (i.e., theoretical) forest. However, it is clear that Davis' method would not help if the forest had large amounts of *Persea*, *Lindera* or *Sassafras*, of which no pollen is preserved, and probably would not work for forests rich in *Populus* or *Liriodendron*, of which relatively little pollen would be found. It also would not work in tropical rainforest areas with enormous number of species represented by very few individual trees. However, Davis has shown that the method does work in a small and thoroughly studied environment. Janssen (1967) demonstrated that *R* values can vary tremendously even in the same general area, with the same vegetational patterns throughout, e.g., *Betula* from 0.5 to 15. The *R* ratios tend to be locally too large when the taxon really is rare to absent in the actual very local vegetation, and too small when the taxon is correspondingly locally abundant. Parsons and Prentice (1981) have examined the mathematics of the *R* value method in detail and have suggested computer-based multivariate and other statistical methods, designed to counter the problems encountered in application of *R* value techniques for vegetation reconstruction from pollen data.

Webb *et al.* (1981) used regression analytical techniques with a rather simple formula for converting pollen-analysis data to estimates of relative abundances of taxa in forests. The basic formula is

$$p_{ij} = v_{ij} r_j + p_{oj} \tag{17.1}$$

where p_{ij} is the percentage of taxon j at site i in the pollen assemblage, v_{ij} is the percent abundance of taxon j at site i in the forest vegetation, r_j is a representation coefficient for species j (comes from pollen productivity), and p_{oj} is the percentage of taxon j at site i in the pollen assemblage, but derived from outside the local area (regional background pollen influx). (The equation can be further corrected by factors for error in measurements.)

In a study of 1,684 modern pollen (surface sample) samples in comparison to forest-inventory summaries for eastern North America, Delcourt and Delcourt (1985b) state that taxon calibration based on known pollen production and dispersal data are the best available means for reconstructing forest history. Pollen percentages (P_a) are transformed into preliminary vegetation values (V_a) using geometric-mean linear regression equations:

$$V_a = \frac{P_a - P_o}{r} \text{ where } P_a \geq P_o \tag{17.2}$$

where P_o is the y-intercept of the regression line, and r is the slope of the regression line. The resulting V_a values must be corrected based on the sum of all V_a values at a specified time, in order to represent the paleovegetation values based on 100% recalculated vegetation (V_c):

$$V_c = \frac{V_a}{\sum V_a} \times 100 \tag{17.3}$$

Solomon and Webb (1985), noting that pollen data integrate information from 50–3,000 km^2 around the basin of deposition, have discussed the subject of modeling of vegetation on the basis of pollen analyses and use of forest-stand simulation models (JABOWA, FORET). Computer-based manipulation of the two sorts of data offer potential for an integrated approach.

Overpeck *et al.* (1985) have demonstrated how dissimilarity coefficients, measuring the difference between multivariate samples, can be used to identify modern analogs for fossil pollen samples. The mathematics of this and other analog techniques based on multivariate analysis are complex and should be studied in the original papers or in Birks and Gordon (1985), a specialist text on mathematical approaches in pollen analysis.

Delcourt and Delcourt (1985a) have shown that data on relative abundance of different sorts of pollen in present day surface sediment of eastern North America can be compared directly with forestry data on the abundance of trees of the same species in forests close to the surface sediment sources (see Fig. 17.6a–e). From such and other plant-distribution data it is possible (Fig. 17.6f,g; Delcourt, 1979) to plot areas in eastern North America where the present-day vegetation best matches the environmental requirements of dominant species at various levels of a late Pleistocene core in Tennessee. The level dated 19,000 yr B.P. ("19"), for example, finds its closest analog today in Manitoba.

Prentice et al. (1996) suggest an interesting approach for translating pollen data into vegetation maps with the "biome"concept. Plant taxa represented in a sample's palynoflora are assigned to plant functional types, and the whole flora of the sample is assigned to one of a series of pre-determined biomes with which it has the highest affinity. This establishes a point for the preparation of a vegetation map of that stratigraphic level for the area studied.

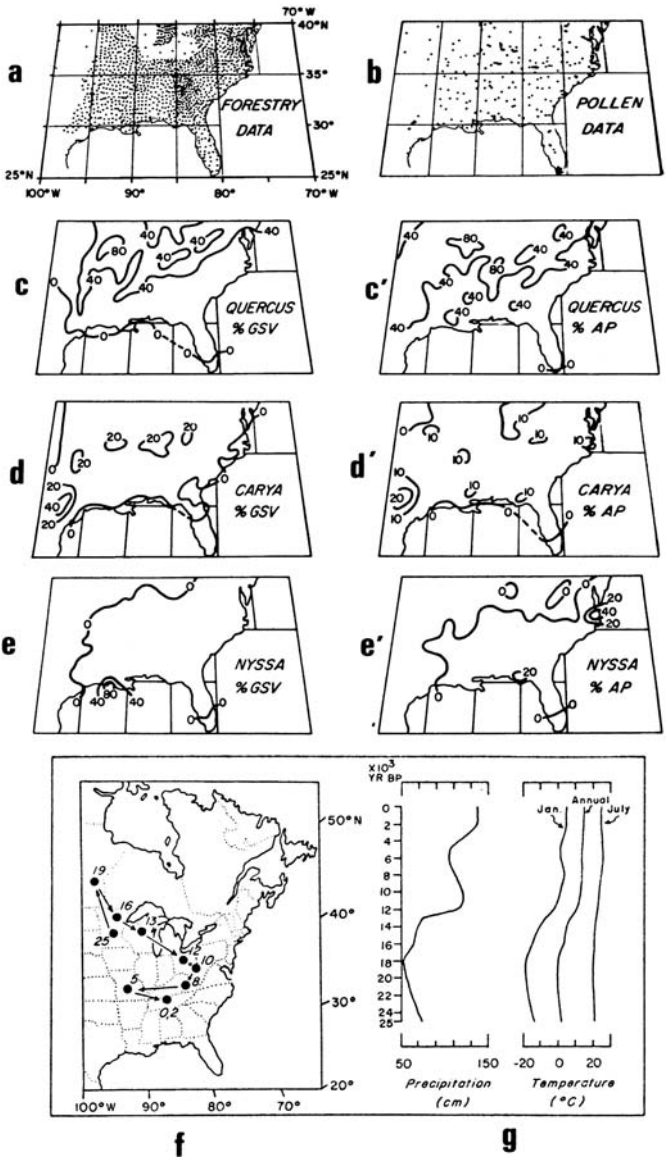

Figure 17.6 Use of pollen data for interpretation of Pleistocene-Holocene plant distribution and paleoclimates. (a)-(e) The relationship between present-day forestry data on relative dominance of tree taxa in commercial forests, and the contribution of pollen from these taxa to surface sediment: (**a**) and (**b**) indicate geographical sources for data; (**c**) shows the isophytes of *Quercus* (oak) abundance as a percentage growing stock volume), from forestry data; (**c'**) shows isopolls for the of GSV

4 Pollen Per Gram, Pollen Influx, Etc.

From the beginning of pollen analysis, the most frequently used method of data presentation has been by percentage of each important taxon. Often the total palynoflora to which the percentages are related is modified from the actual total counted by eliminating certain forms; the modified total is the "pollen sum." The present trend is to use pollen sums that include nearly all land plant spores/pollen. In any event, there are clearly difficulties with the percentage approach. For example, if the palynoflora consists overwhelmingly of *Pinus* and *Quercus* pollen, an increase in *Quercus* pollen will cause a decrease in *Pinus* percentage, even if the absolute numbers of *Pinus* remain about the same. A number of suggestions have been made to correct for this difficulty. One is to express spore/pollen concentration as a ratio to a common fossil that is not usually part of the spore/pollen analysis, such as fungal spores, but fungal spores are not themselves constant.

As noted in the previous chapter, foreign spores/pollen (usually *Lycopodium* spores, but *Eucalyptus* and other pollen or even silicious microspheres have sometimes been used) can be added to samples before processing, and the fossil palynomorphs can then be expressed as a ratio to the added spores. The foreign sporomorphs added are sometimes called "the stick."

This technique yields not only such a ratio, but by simple calculation also gives the approximate total number of fossil palynomorphs in the sample processed. If the weight or volume of the original sediment sample was measured, the concentration of palynomorphs per gram or volume of sediment sample can then easily be calculated (Stockmarr, 1971). This Stockmarr technique depends on

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Figure 17.6 pollen percentage, as a percentage of total AP (tree pollen) in surface sediment; (**d**) and (**d'**) presents the comparable data for *Carya* (hickory), and (**e**) and (**e'**) for *Nyssa* (tupelo, black gum). Oak and hickory pollen show a close relationship between isophyte and isopoll data, as is the case for most wind-pollinated tree genera, which allows quantitative calibration from pollen data for reconstructing changes in forest dominance in time. However, *Nyssa*'s abundance in the forests and the percentage of AP shown by its pollen in surface sediment are rather widely different. This is presumably a product of the local nature of production and the durability of *Nyssa* pollen, as well as the rather local abundance of *Nyssa* trees, primarily in swamp-forest situations, and the similarly patchy distribution of surface-pollen samples. (f) and (g) Applications of the known environmental requirements of plants dominant at various levels of sediment cored at Anderson Pond, Tennessee; (**f**) represents location of modern pollen samples in North America with composition equivalent to pollen samples from various levels in the cores, from 25,000 yr B.P. ("25") to just before present ("0"); (**g**) shows the precipitation and temperature changes inferred from weather-station data at the location of modern analogs for the fossil-pollen assemblages. (a)-(e) are from Delcourt and Delcourt, 1985a; (f) and (g) are from Delcourt, 1979.

tablets of *Lycopodium* spores held together by $CaCO_3$ and water-soluble organics. Five tablets contain $105,000 \pm 3000$ spores. If five tablets are added to the sediment sample before processing, then

$$\frac{105,000 \times \text{palynomorphs counted on a slide}}{\text{number of } \textit{Lycopodium} \text{ spores counted}} = \text{number of palynomorphs in sediment sample} \tag{17.4}$$

The method has the advantage that not all the palynomorphs on a slide need to be counted to make the calculation.

I have always used a more direct method involving no additives:

(1) Weigh the original sample.
(2) Weigh the final maceration residue plus mountant (glycerin jelly in our laboratory).
(3) Weigh the slide and coverslip before and after adding the drop of residue and mountant.
(4) Count fossils on the slide (or a carefully measured fraction, if it is very dense) and calculate fossils per gram as follows:

$$X = \frac{BD}{CA} \tag{17.5}$$

where $X =$ microfossils per gram of sediment, $A =$ grams of rock sample, $B =$ grams of maceration residue plus mountant, $C =$ grams of residue plus glycerin jelly on slide, $D =$ microfossils counted on whole slide. My method requires a microbalance for weighing of the slides, but has some advantages–no intentional contamination of the samples, and especially no tedious counting of hundreds or thousands of the "stick" spores. I showed by experiments years ago that such repetitive counting numbs the counting senses and makes for inaccurate counts. Another factor is that *Lycopodium* pills necessary for the technique are not always easy to obtain. In my method it is possible to count a fraction, such as 1/4, of the total slide, by ruling the coverslip with ink, and then multiplying the palynomorph counts by 4.

As is discussed elsewhere, the total numbers of spores/pollen per gram in a sample is interesting from a sedimentological point of view. The amount of a particular pollen type per gram is in some ways more significant than the percentage, as it is related to a non-pollen datum and is not affected by fluctuations in the amounts of other pollen types.

However, spores/pollen per gram *is* affected by fluctuation in the sedimentation rate. From the fact that total pollen per gram of sediment in the Great Bahama Bank is on the order of 1,000/g or so, in silts from a river delta on the order of 50,000/g or so, and in silts from the Gulf of Mexico on the order of 10,000/g,

it is obvious, that spores/pollen per gram cannot be directly compared from one environment to another. Even in one place, if sedimentation of mineral matter goes up significantly, the amount of pollen per gram of sediment must go down if pollen delivery to the basin of deposition remains constant. To compensate for the difficulty of differing sedimentation rates, Davis (1967) developed methods for calculating a "pollen accumulation rate" or "pollen influx" (Davis *et al.*, 1973). In effect this is done by correcting data for pollen/volume of sediment by a factor depending on sedimentation rate, so that the data are expressed as pollen/cm^2 (surface) per year. Obviously, this elegant method depends on ^{14}C or other dates in sufficient number to ascertain that sedimentation rate has remained constant, or to what degree and when it has fluctuated. Pollen influx, then, is the amount of total spores/pollen, or of a particular spore/pollen type, falling on a unit area of the basin of sedimentation per year. The calculation is as follows:

$$\text{pollen-influx } (PI) = \text{spores/pollen per cm}^2 = \frac{\text{spores/pollen per cm}^3}{\text{years for deposition of 1 cm (vertical) of sediment}} \tag{17.6}$$

The amount of spores/pollen per cm^3 of sediment can be calculated by correcting data for spores/pollen per gram by the specific gravity of the sediment. It can be calculated directly, of course, by adding known amounts of foreign spores/pollen to measured volume, as in the Stockmarr method, or by my weighing technique, both described above.

Figure 16.2b shows an application of the pollen influx approach to a problem in the eastern Great Lakes of North America. This illustration also shows that concentration per gram of sediment, a less complicated and less expensive procedure (no ^{14}C dates needed), gives acceptable results, at least in some cases. Where sedimentation rates are very variable, however, there will clearly be a problem.

Pollen influx studies have been used other than in connection with efforts to reconstruct vegetation. If the average pollen-influx in an area is known, this estimate of the number of spores/pollen incorporated into sediments per unit surface area per unit-time (usually per cm^2 per year) can be used to detect very rapid changes in sedimentation rate, such as occur in an ash fall, or to estimate the length of time during which the ash fell (see Mehringer *et al.*, 1977). (The pollen deposition rate (*PDR*) of some authors is a measurement essentially equivalent to *PI*.)

Another approach that can be objective is the use of ratios between counts of various taxa, to show regional paleoclimatic trends. Firbas *et al.* (1939) long ago showed that the ratio between *Picea* and *Fagus* pollen in surface and subsurface

samples from the Oberharz region of Germany can be revealing. Samples from a number of different locations in Flandrian zone IX, the "beech time," yielded consistent *Picea/Fagus* ratios of 0.3–0.4, whereas surface samples from the same areas show the present pollen rain to yield a *Picea/Fagus* ratio of 7.0 –14.0. Firbas related the sets of ratios to the respective climatic regimes.

A ratio such as

$$\frac{\text{spores/pollen}}{\text{total palynomorphs}} \tag{17.7}$$

can yield an indication of the relative contribution of land-based flora to total palynoflora, and

$$\frac{\text{phytoplankton}}{\text{total palynoflora}} \tag{17.8}$$

can indicate the "marine influence," if the dinocysts and acritarchs are known to be marine. Manum (1976a, b) shows, in a study of palynomorphs in DSDP cores from the Norwegian Greenland Sea, that the ratio between marine and non-marine palynomorphs can be displayed graphically to advantage.

Birks and Birks (1980) have shown very clearly that sophisticated mathematical methods such as factor analysis, cluster analysis, principal components analysis and other matrix algebra based, computer programmed techniques offer great possibilities for detecting from the data the existence of significant patterns. For example, cluster analysis dendrograms can show unsuspected similarity between samples, as can principal components analysis, but principal components analysis can also reveal clearly associations between many more types of pollen than can be conveniently shown in a dendrogram. The example in Fig. 17.7 of the application of principal components analysis shows that pollen-spectra sometimes sort out on the basis of linkage of high and low analytical values, related to environment. Fig. 17.8 shows an interesting application of factor analysis, demonstrating linkage between groups of taxa and geographic distribution. It would be almost impossible to make the necessary calculations of such association without this mathematical tool.

All of these multivariate mathematical methods demonstrate association, but not what the association means. The methods have also been applied to older sediments, and the older they are, the more difficult it is to interpret the displayed associations. Palynologists in practice are best advised to visit statisticians and computer specialists at a university or elsewhere for help in the necessary programming and analysis of their data.

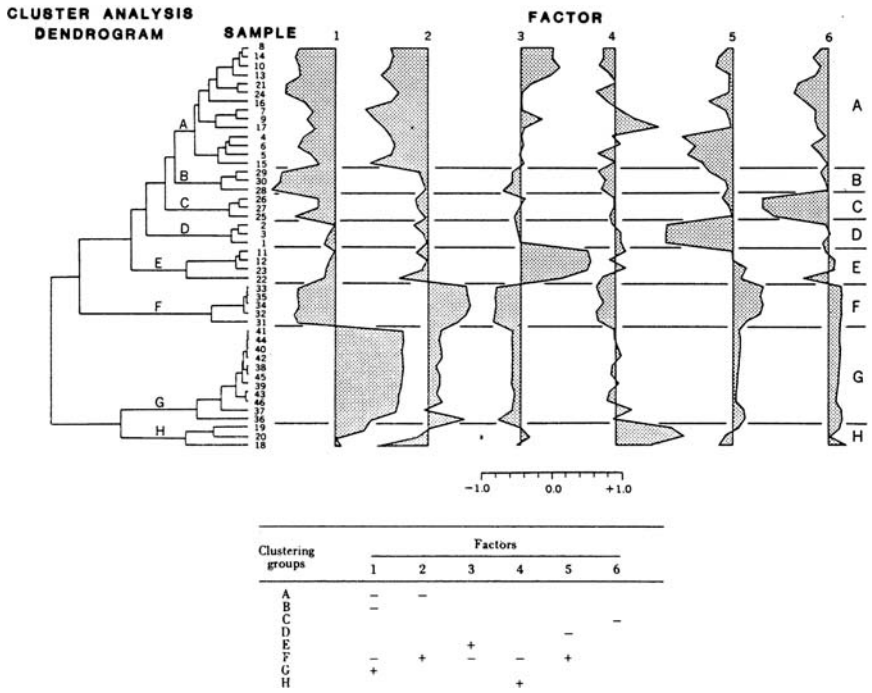

Figure 17.7 Palynological application of principal components and cluster analyses. These two multivariate statistical methods are used to detect and describe patterns in pollen data. If there are *m* samples and *n* pollen types, the data can be regarded as a set of *m* points in *n*-dimensional space. Cluster analysis produces a dendogram or clustering tree in which the samples are grouped with other samples, on the basis of similarity to each other. Principal components analysis produces a set of variants that are linear combinations of the data from the pollen samples, and are uncorrelated to each other. The method is useful in reducing the dimensionality of data sets and in clarifying patterns in the data. These and other statistical methods are applied to a palynologist's data with the aid of computer programs, and the average palynologist is best advised to read Birks and Gordon, 1985, and papers that use multivariate analytical techniques, and then seek help and guidance from computer science and statistics specialists. The pollen analytical data presented here are from Osgood Swamp, California, representing about the last 12,000 years. The sample numbers (1-46) are for samples ranging from surface (1) to 440 cm (46), but the samples are not presented in stratigraphic sequence, but rather in the order of their clustering, though most of the clusters are themselves stratigraphic subsets. The clustering is on the basis of pollen types in common. The principal components analysis depends on a series of complex pollen analytical factors. Factor 1, for example, is related to high *Artemisia* values and low *Pinus, Abies* and *Isöetes* values. This factor is highly positive at the glacial/post-glacial interface of cluster G, highly negative in clusters representing the higher levels of the core. From Adam, 1974.

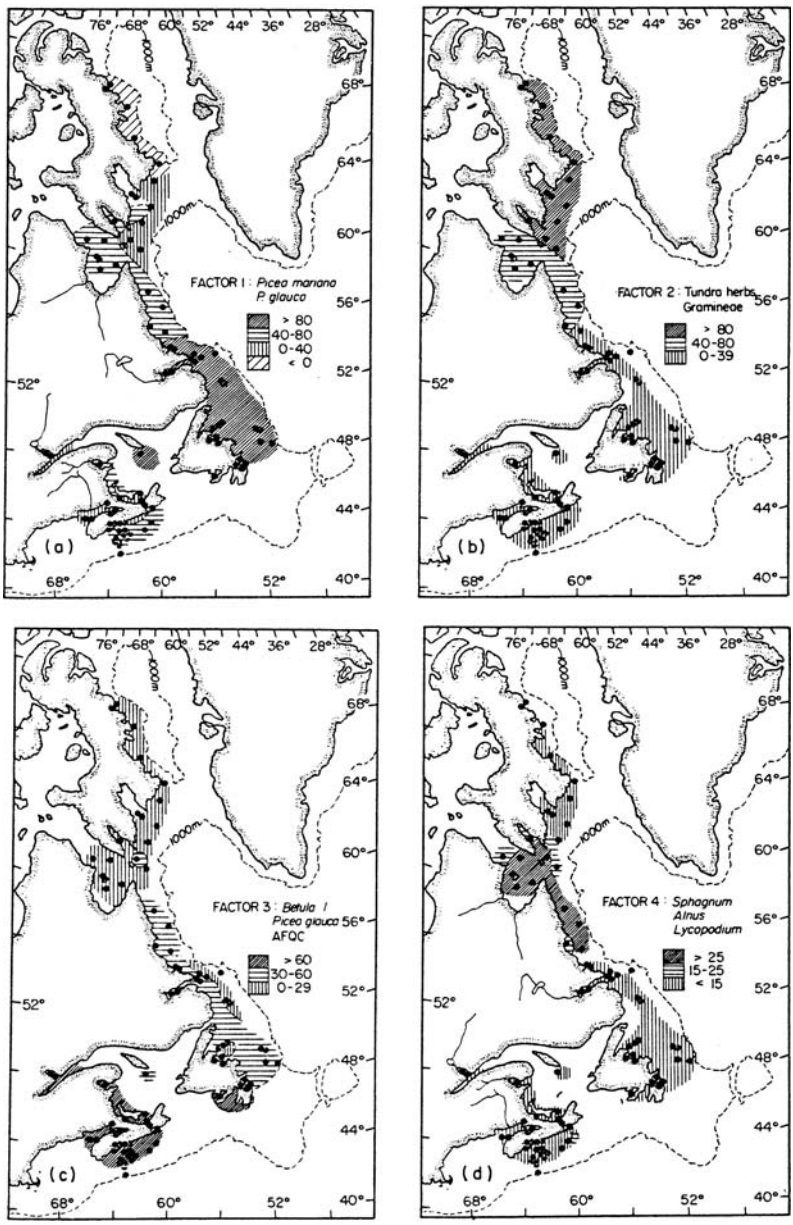

Figure 17.8 Geographic plots of factor analysis data for pollen in recent marine sediments, eastern Canada. Factor analysis is a multivariate technique in which large matrices of variable data are simplified by grouping the taxa into coherent assemblages which co-vary in a similar fashion. Factor 4, for example, is a sub-arctic assemblage, with a geographic

5 Sedimentation of Spores/Pollen and Other Palynomorphs

Spores/pollen exines (and other palynomorphs such as dinoflagellate cysts and fungal spores) when occurring in water are technically, from their size, silt or very fine sand particles (see Fig. 17.2), which behave in water according to the same principles as govern other clasts. The low specific gravity (about 1.4) of palynomorphs, the fact that they contain internal space, their tendency after initial stages of preservation to be tiny disks rather than spheres, and other factors give them somewhat different settling characteristics from mineral particles (specific gravity equal to or greater than 2.4) of the same maximum size. As is true for sedimentary particles generally, the settling speed in water in general follows Stokes law, a formula devised for expressing the settling rates of spherical bodies (which palynomorphs usually are not):

$$w = \left(\frac{(\rho_s - \rho)g}{18\mu} \right) d^2 \tag{17.9}$$

where $(\rho_s - \rho)$ is the density difference between the particle (ρ_s) and the fluid (ρ), g is the acceleration due to gravity, μ is the dynamic viscosity of the fluid, d is the diameter of the particle, and w is the settling or fall velocity (from Blatt *et al.*, 1972).

Palynomorphs are more or less hollow and variously wrinkled as soon as the protoplasts are destroyed (or after excystment for dinocysts). They also often have external processes or other sculpturing and are usually more or less flattened to tiny disks. Laboratory measurements I have made show that speeds of sinking in water for acetolyzed modern pollen (substantially like fossil pollen, except not flattened) are generally slower than the calculated speed, often 50% slower. According to Muller (1959) an average pollen exine should sink at the rate of 4 cm/h, but Muller's measured rate is a bit higher, of the order of 7–17 cm/h, about like that for fine silt (4–8 cm/h). Stanley (1965) observed that palynomorphs usually sort out in a mineral silt fraction one class smaller than would be expected from the palynomorph size, which is another way of saying that they do not settle as fast as mineral particles of the same maximum dimension. The relative proportion of various classes of palynomorphs (spores/pollen, dinoflagellates, acritarchs) in sediments is a function of distance from shore and depth of water, as can be seen in Fig. 17.9.

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Figure 17.8 distribution favoring the 56°–60° latitudes. The four factors displayed here, and two others (5: *Pinus banksiana* + *Tsuga canadensis*; 6: Gramineae (=Poaceae) + *Picea mariana*) account for 95% of the variance in the samples studied. Note that a taxon can occur in more than one factor, e.g., *Picea glauca* in factors 1 and 3. From Mudie, 1982.

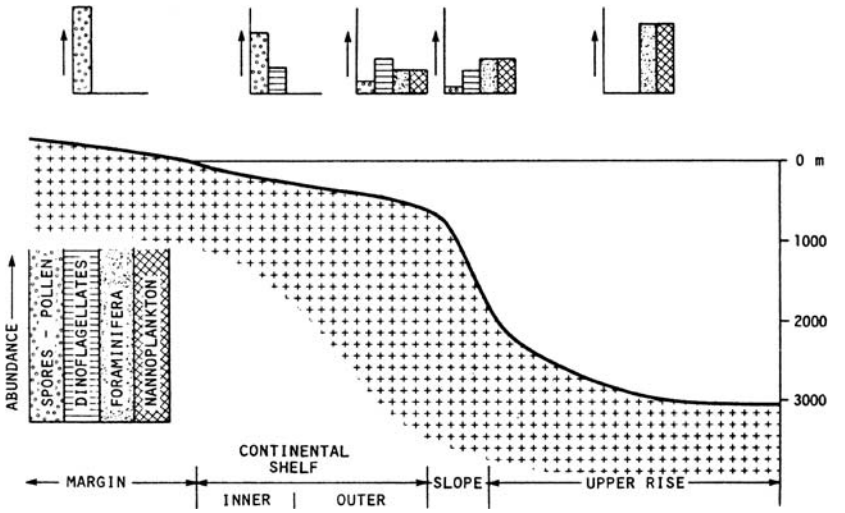

Figure 17.9 Distribution of various microfossil groups in sediments of marine or near-marine sedimentary environments. Spores/pollen are shown as a constituent of all environments except deep sea (more than 3000 m), in decreasing abundance toward the open ocean. Actually, even deep sea sediments contain some pollen, especially bisaccate conifer pollen, but the amounts are about 50/g, only about 0.01 times as abundant as in average shelf deposits (Melia, 1982). Only spores/pollen provide a link between terrestrial and truly marine environments. The marginal and inner continental shelf environments contain only palynomorphs: spores/pollen, dinoflagellate cysts and (not shown) acritarchs. Acritarchs have about the same distribution as dinoflagellate cysts. Freshwater environments lack foraminifera and nannoplankton. Relatively exceptional freshwater dinoflagellates, plus a suite of freshwater acritarchs are found in totally non-marine environments, along with pollen and spores. From Stover and Williams, 1982.

5.1 The Hoffmeister Patent Statement

Until the mid-1950s most palynologists assumed that those spores/pollen which enter the fossil record owe their distribution primarily to the atmosphere, especially to wind patterns. Thus, spores/pollen should as easily be found in sands as in silts, inasmuch as they would fall out of the air into all sorts of depositional environments.

It turns out that only palynofloras from sediment of small ponds, soils and swamp-generated peat contain mostly autochthonous spores/pollen that dropped out of the air in the neighborhood of the site of deposition. Most fossil spores/pollen in sediments have been transported, sometimes very long distances, by streams and by ocean currents. The spore/pollen flora of the Mississippi River Delta, for example, contains spores/pollen from the vegetation of North Dakota,

Pennsylvania, Minnesota, and all areas between those states and Louisiana, carried by the various tributaries of the Mississippi. There are also reworked sporomorphs from early Paleozoic to Holocene, and variously sorted and reworked, as well as more or less contemporary dinoflagellate cysts, some formed in the present Gulf of Mexico, in short, a potpourri, the understanding of which depends partly on sedimentology. Peck (1973) has shown that even in a very small catchment basin in Yorkshire about 97% of the spores/pollen in the sediment reaches its destination in the small stream and runoff, not in the air. As late as the mid-1950s, however, the prevailing idea still was that pollen and spores reach sites of deposition mostly by air.

W. S. Hoffmeister, of the oil company (Standard Oil of New Jersey) which is now part of Exxon Mobil (the Mobil part was formerly Standard Oil Company of New York), startled the palynological world in 1954 by obtaining a U.S. patent for virtually the whole field of paleopalynology, especially as it applies to paleoecology (Hoffmeister, 1954). Later (1955) Hoffmeister dedicated his patent to the public, and explained (to me) that his only purpose in getting the patent was to prevent others from patenting the method and preventing its free use. (Perhaps this was also the reasoning of R. A. Jones (1996), who with the University of Sheffield applied for and were granted a patent for a method of palynological HF maceration of rocks with a microwave device.)

Of much more palynological significance than the patent itself was the announcement it made that Hoffmeister's palynological group in Tulsa had discovered that spores/pollen are distributed in sediments according to principles that are basically sedimentological. Hoffmeister noted that the abundance of spores and pollen in sediment decreases sharply (more or less logarithmically) as one moves offshore. He also noted that there is a marked sorting among fossil spores/pollen, with smaller forms being relatively more abundant than larger forms, as one samples further offshore. Hoffmeister stated that in samples of shale:

(1) proximity of an ancient shoreline (of potential importance for oil exploration) is indicated where the ratio

$$\frac{\text{large (70–120}\,\mu\text{m) spores/pollen}}{\text{small (20–50}\mu\text{m) spores/pollen}} \simeq 0.25 \qquad (17.10)$$

(2) proximity of an ancient shoreline is indicated where the concentration of spores/pollen is about 7,500 per gram of sediment.

However, various investigators have since stressed that, while palynomorph concentration decreases with distance from shore in a general way, in sediment from far offshore other factors are more important: sediment size and bottom morphology. Palynomorphs are much more abundant in sediment offshore

from stream mouths than where no such drainage is nearby. The Hoffmeister large/small palynomorph ratio, indicating distance from land, has been presumed to derive from sedimentary sorting, based on size of the particles. However, Moss *et al.* (2002), who studied palynomorph sedimentation in Australia, found no support for such sorting, and the matter needs to be revisited. Heusser (1983) and Heusser and Balsam (1977) have shown that total palynomorph concentration tends to be lower on the continental shelf, and higher on the slope and rise. In the western North Atlantic they found 10 grains/g on the abyssal plain and as high as 230,000/g on the slope, a product of the deposition of palynomorph-rich sediment on the slope.

5.2 Muller's Orinoco Delta Work

About the same time as Hoffmeister's patent statement, Jan Muller, a Royal Dutch/Shell employee, accompanied the Van Andel expedition to the Orinoco Delta of South America, sponsored by the Netherlands government. Muller's (1959) pioneer palynological work showed that the total spores/pollen of surface sediment followed in a very general way Hoffmeister's outline, but that the picture is much more complicated than the Hoffmeister patent statement said. As can be seen in Fig. 17.10, the concentration of fossils per gram of sediment in the Orinoco Delta-Gulf of Paria (map in Fig. 17.10a) is about 7,500/g only in a few places where the conditions are "normal." In areas of little water turbulence ("low energy"), the concentration is much greater than 7,500/g, e.g., south of the Peninsula of Paria (see Fig. 17.10b). In "higher energy" areas, such as just west of Trinidad, the concentration per gram is considerably less. *Rhizophora* (red mangrove) pollen is very small in size and it does generally increase in percent of total pollen as one moves offshore, though the situation is complicated by current patterns (see Fig. 17.10c). *Rhizophora*, although a mangrove, also grows along stream banks well upstream. The pollen is found in deltaic sediments. *Avicennia*, the black mangrove, must have salt water, and the pollen is found almost exclusively offshore (see Fig. 17.10d). *Polypodium*, a fern, as do many ferns, produces spores that look heavy but are light, and are found not only on the delta but in considerable numbers well out to sea (see Fig. 17.10e). Dinoflagellate cysts (= Muller's "Hystrix"; such chorate cysts were not recognized as dinoflagellates at the time), of the same general size as spores/pollen, and apparently of approximately the same chemical composition, are distributed quite differently from spores/pollen in the sediment (see Fig. 17.10h). Their distribution, unlike that of land-originating spores/pollen, is a thanatocoenosis, apparently primarily a product of nutrient availability for the dinoflagellates and only secondarily to later operative sedimentological factors. Fossil fungal spores (see Fig. 17.10g), consisting of chitin, were found hardly at all in the marine environment but in enormous quantity in all non-marine parts of the delta. (By contrast, Wang *et al.* (1982) and others have shown that halophyte pollen, such as *Salicornia*, occurs

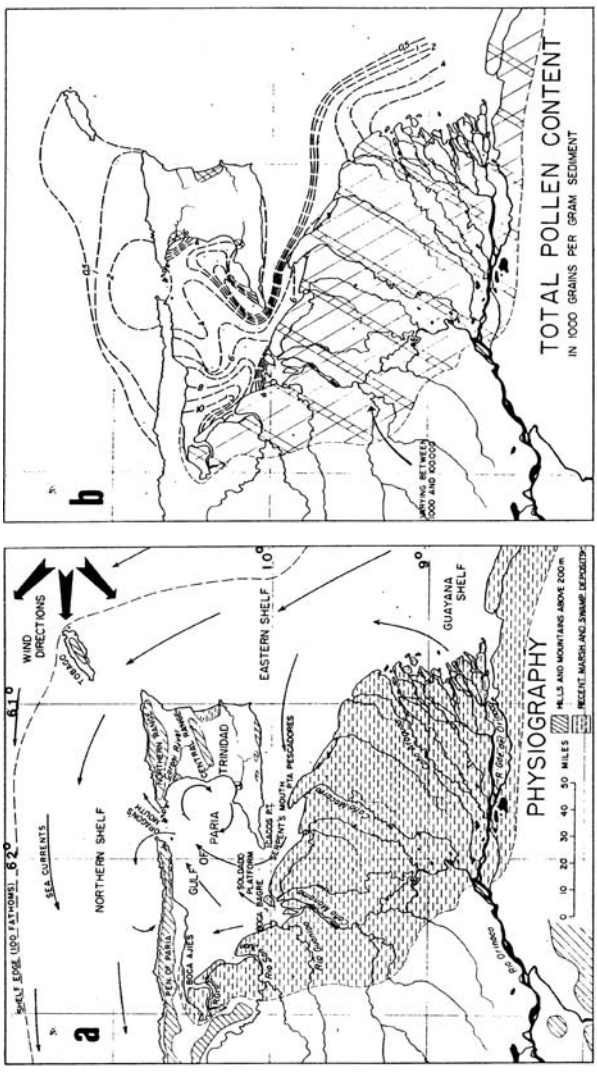

Figure 17.10ab Muller's pioneering study of palynomorph sedimentation in the Orinoco Delta. (a) General layout of the Delta in northern South America, about 10 degrees north of the Equator. Note prevailing eastern winds and sea currents. (b) Total pollen content in grains/g of sediment. Note a general decrease in amount offshore, but that water trubulence and current and current are very important. Highest concentrations are in quiet embayments and on the western Gulf of Paria. Hoffmeister's "7,500/g" for shoreline is approximately correct only for some places along the delta. Off Trinidad and the Paria Peninsula, concentrations are much less.

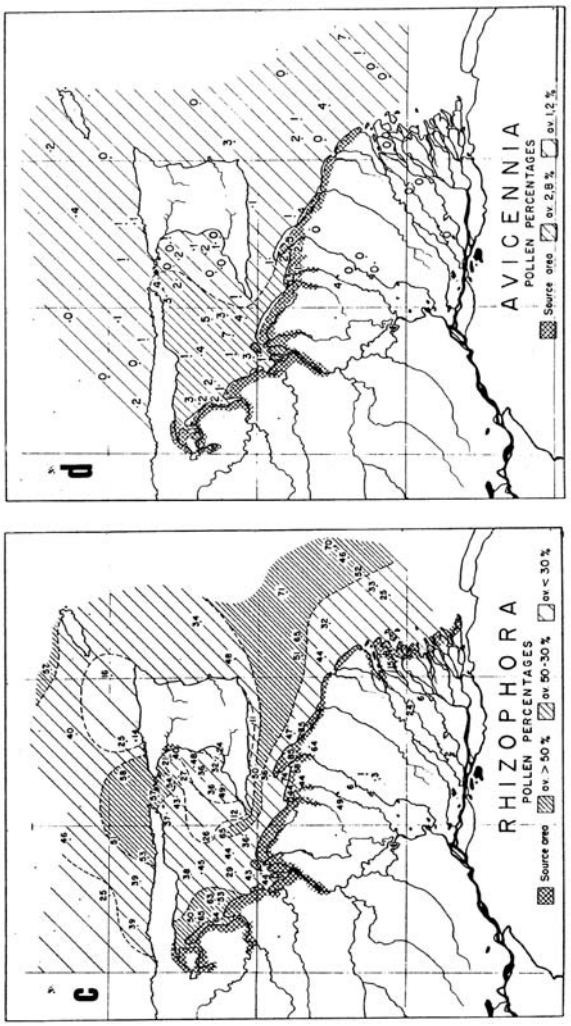

Figure 17.10cd (c) *Rhizophora* (red mangrove), a very small, smooth, thin-walled pollen grain, is carried easily by the water, actually increasing in percentage in some far offshore locations. (d) *Avicennia* (black mangrove), an insect pollinated, moderately heavily sculptured, medium sized pollen grain, is never abundant and mostly drops out of the water close to sources of the producing plants.

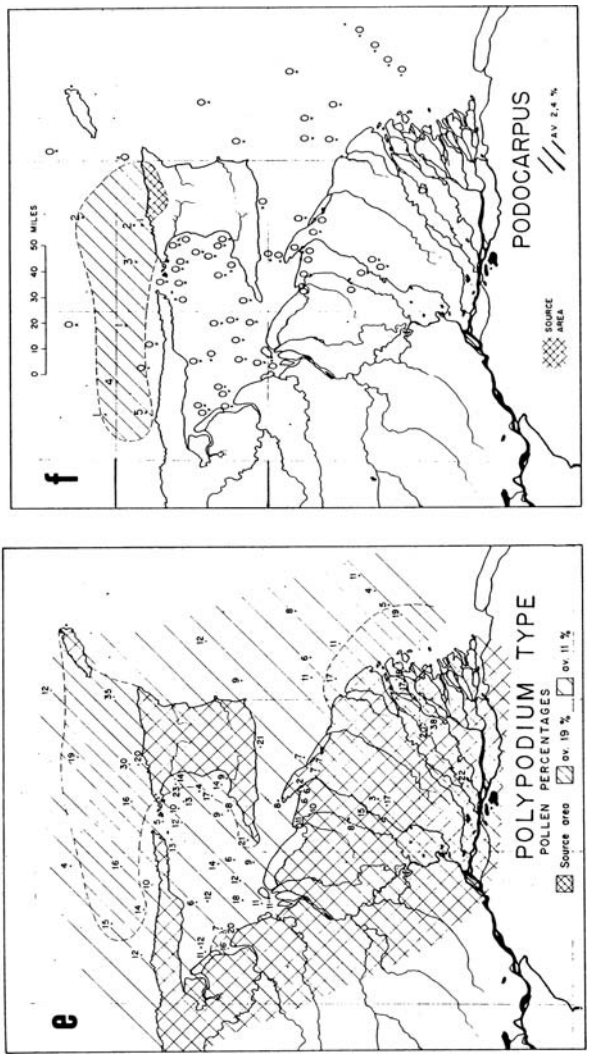

Figure 17.10ef (e)*Polypodium*-type fern spores, although heavy walled, are apparently buoyant and are found in sizable percentages far off-shore in agreement with observations for some fossil fern spores. (f) *Podocarpus* pollen encountered west of Trinidad clearly are dropped there as wind-borne grains.

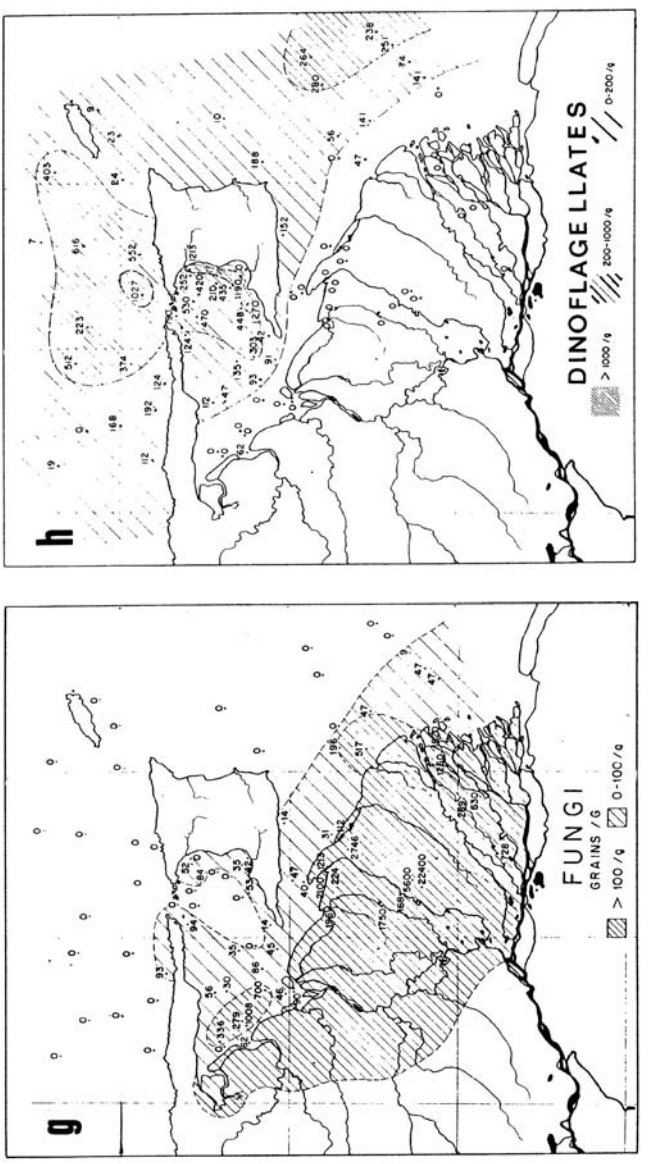

Figure 17.10gh (**g**) Fungal spores are a deltaic phenomenon; the sharp drop-out of fungal spores offshore is dramatic, presumably related to the specific gravity of the spores. (**h**) Dinoflagellate cysts show a distribution related partly to sedimentary factors (note that concentration in the Gulf of Paria west of Trinidad parallels pollen concentration-see area marked 1190), and partly to nutrient availability-see sizable numbers at some offshore locations, such as the small area marked 1027 north of Trinidad, and total lack of specimens near influx of fresh after. Modified from Muller, 1959, especially by addition of shading, emphasis of the highest numbers, and outlining of land masses in the dinoflagellate illustration.

practically exclusively offshore, in the marine parts of the Yangtze River delta of China, not in the upriver, fresh-water parts of the delta.)

Muller's work established the importance of clastic sedimentation to fossil palynomorph distribution. The significance of local "energy level" (water turbulence) was demonstrated. That wind distribution plays some role even in marine sediments was shown by bisaccate pollen of *Podocarpus* (Fig. 17.10f), blown in small amounts in a northwest arc from upland source areas in Trinidad. Long-distance transport by water was shown by sedimentation offshore of very small amounts of *Alnus* pollen, originating hundreds of kilometers upstream and in a direction opposite the prevailing wind. In a follow up to Muller's work, Hofmann (2002) studied sediments of several different environments on the Orinoco delta, and found that pollen in samples of the sediment reflected in a general way the vegetation of the area from which the sample came, but that 36–78% of the pollen sums were either fully allochthonous or not strictly autochthonous. Floods bring in allochthonous pollen from upstream, and this is especially a factor in the sediment from areas with diverse vegetation rather than in areas with solid stands of one to a few taxa.

5.3 Palynomorph Sedimentation in the Bahamas: a Non-Clastic Model

Soon after Muller's work in the Orinoco area, Traverse and Ginsburg (1966), working for Shell Oil Company on sedimentation in the Bahamas, applied palynological techniques to that totally non-clastic environment, which also has no streams. The Great Bahama Bank is a drowned Pleistocene island with mostly very shallow water, relatively little current flow and a series of low islands (see Fig. 17.11a). The sediment is mostly of two types, (a) carbonate "sand", consisting of shells and shell fragments of small animals, and of fecal pellets, and (b) silt-size carbonate "mud." The concentration of pollen is typified by pine pollen per gram of sediment (Fig. 17.11b). Very small amounts of, or no pine pollen is found in samples from the sandy areas where the water is comparatively turbulent. In areas of quieter water, in the lee of Andros and Eleuthera Islands, comparatively great peaks of abundance of pine pollen were found, in the "muddy" (silt-sized) sediment. The line of demarcation between high concentrations and low (or zero) concentrations of pine pollen is very sharp, tested by very close sampling. Fig. 17.11d shows the close association of pine pollen concentration with sediment type for a transect off Eleuthera Island. Relatively high pollen concentration is a phenomenon of silt-sized sediment, as would be expected. It is also worth noting that the concentration of spores/pollen per gram in carbonate mud is one to two orders of magnitude less than is found in most clastic silts: more or less 100–1,000/g as against more or less 1,000–100,000/g (or more). Shipboard continuous centrifugation of water west of Andros Island showed comparatively large amounts of pine pollen in the water at localities where small amounts were found in the sediment, and conversely (Fig. 17.11c).

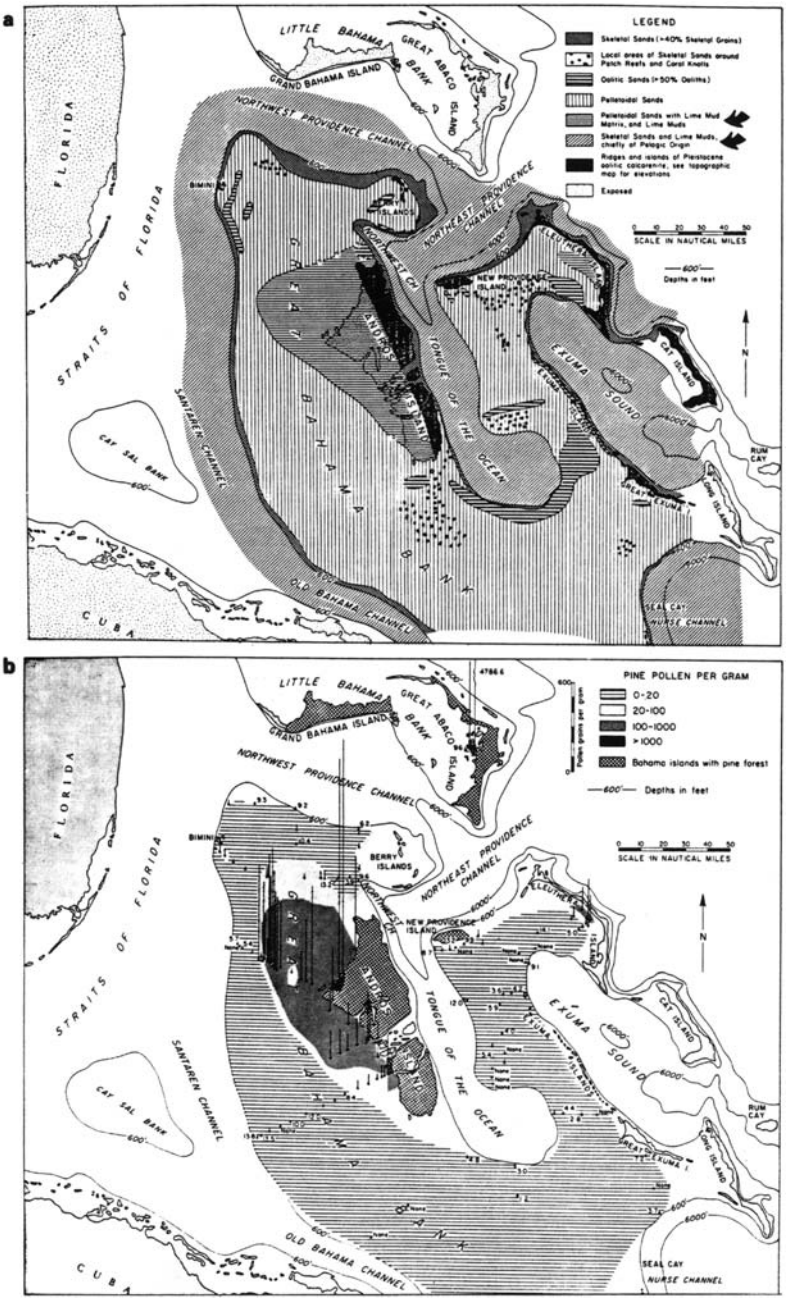

Figure 17.11 *(See caption on page 536)*

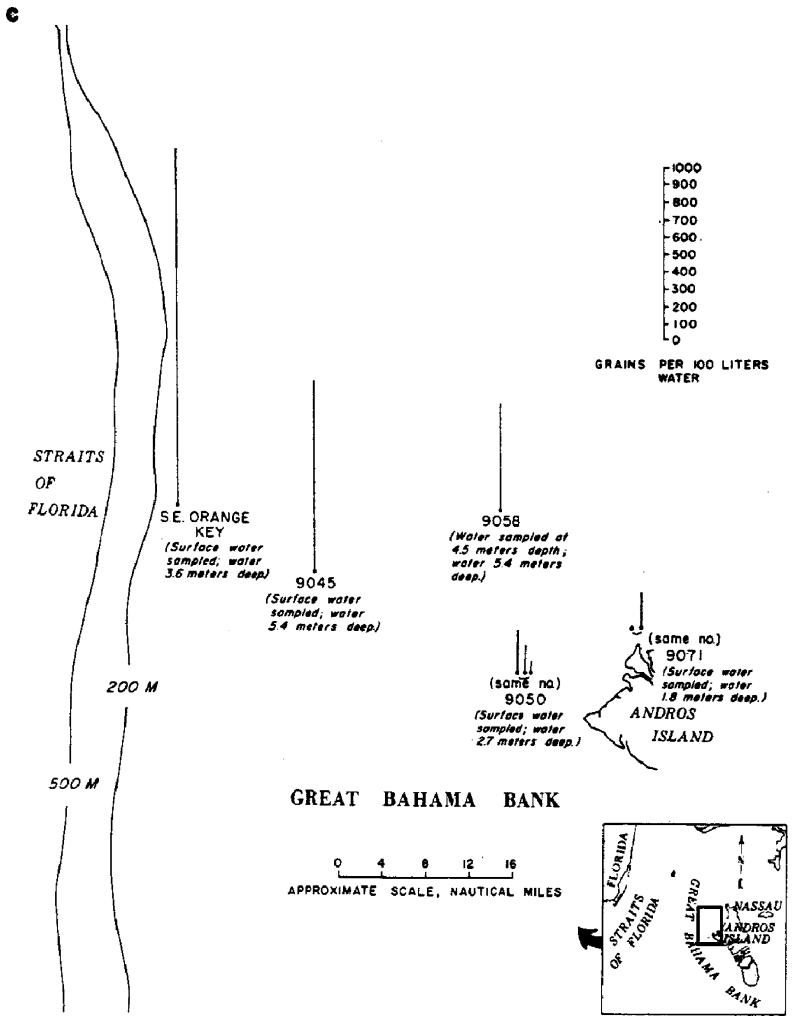
c
STRAITS
OF
FLORIDA
200 M
500 M
S.E. ORANGE
KEY
(Surface water
sampled; water
3.6 meters deep)
9045
(Surface water
sampled; water
5.4 meters deep.)
9058
(Water sampled at
4.5 meters depth;
water 5.4 meters
deep.)
(same no.)
9050
(Surface water
sampled; water
2.7 meters deep.)
(same no.)
9071
(Surface water
sampled; water
1.8 meters deep.)
ANDROS
ISLAND
GREAT BAHAMA BANK
0 4 8 12 16
APPROXIMATE SCALE, NAUTICAL MILES
1000
900
800
700
600
500
400
300
200
100
0
GRAINS PER 100 LITERS
WATER
FLORIDA
STRAITS OF FLORIDA
GREAT BAHAMA BANK
NASSAU
ANDROS ISLAND

Figure 17.11

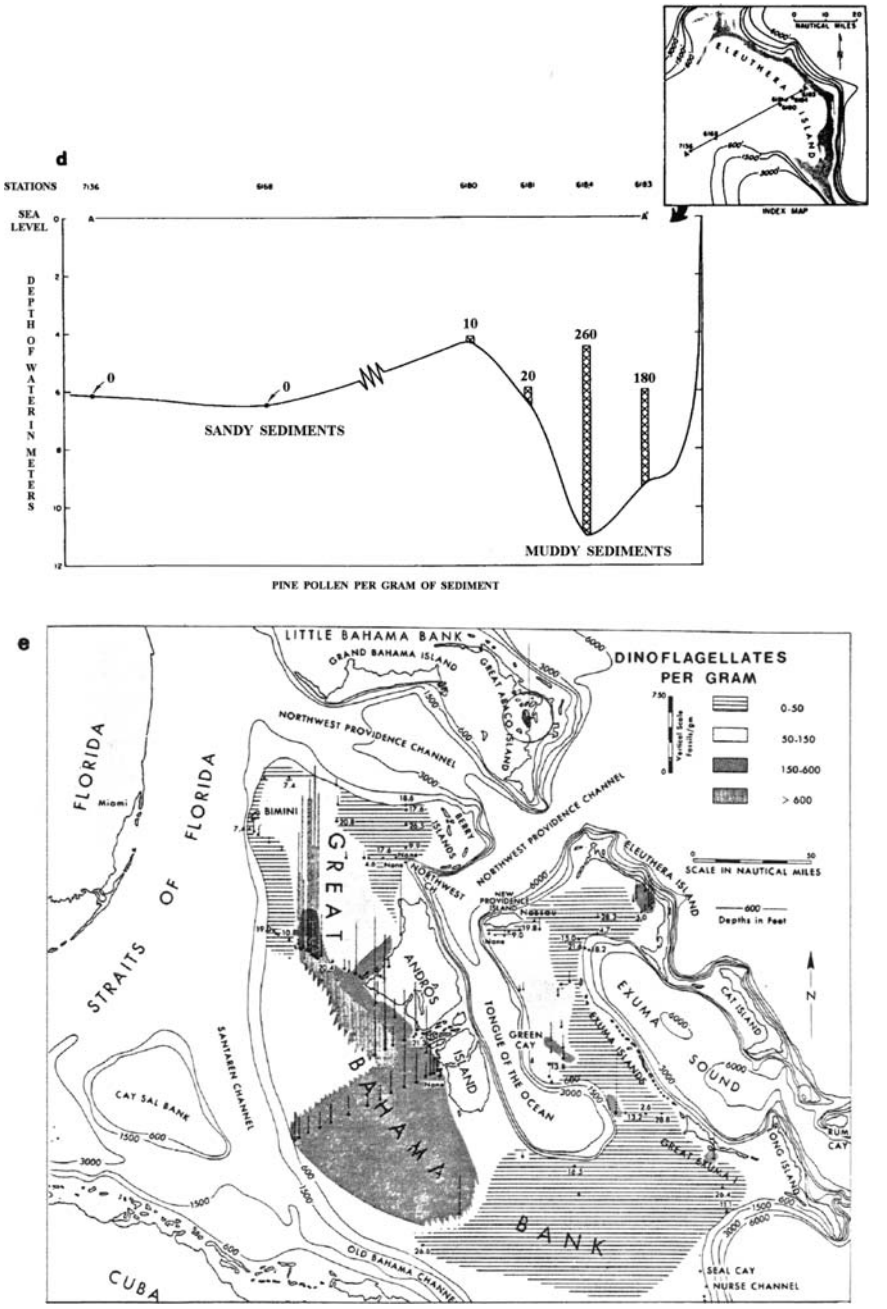

Figure 17.11 *(See caption on page 536)*

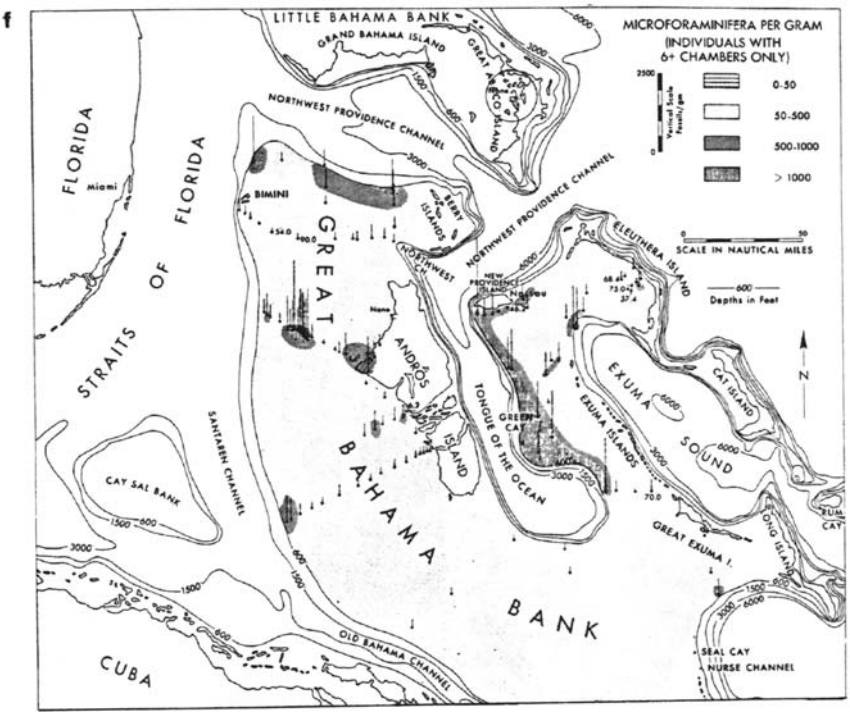

Figure 17.11 Palynomorph sedimentation on the Great Bahama Bank, a carbonate environment with no streams and no clastic sedimentation. The Bank is a drowned Pleistocene island with mostly very shallow water, over which currents drift in a generally northwestward direction. Prevailing winds are also toward the northwest. Palynomorph sedimentation here thus has provided an interesting comparison with sedimentation in clastic environments (see Figs. 17.9 and 17.10). (**a**) Sedimentary types of surface sediment. Note especially (arrows in legend) the lime mud areas in the lee of Andros and Eleuthera Islands, and the general prevalence of pelletoidal sand over much of the Bank. (**b**) Pine pollen per gram of sediment. Note the prevalence of high values in the lee of large islands, closely agreeing with location of lime mud. Sediment from areas of pelletoidal sands is practically devoid of pine pollen. Evidently, pine pollen floats for considerable periods over the Bank, eventually being trapped in areas of relatively low energy. (**c**) Pollen in the water off of Andros Island has a reciprocal distribution to that in the sediment: the areas with high pollen in sediment have low pollen in the water and vice versa (see (b)). (**d**) A traverse off Eleuthera specifically confirms the relationship of pollen highs to mud, and pollen lows to sand, as would be expected from the silt-to-finest-sand size of pine pollen. Because of relatively low specific gravity (about 1.4), and because it is not solid, pollen sorts with mineral particles (specific gravity about 2.5) a bit smaller than pollen (see Stanley, 1969). (**e**) Dinoflagellate cysts display a distribution that is partly a result of sedimentary factors (some were encountered in the water studies of (c)) and partly a product of nutrient availability. (**f**) Foraminiferal chitinous inner tests

It seems clear that pine pollen containing trapped air floats on Bahama Bank water for long periods of time, and then is sedimented out when it finally is wet and reaches a quiet water area that acts as a "pollen trap." (cf. Fig. 17.11d). The buoyancy of bisaccate pollen in water, plus its well-known very resistant sporopollenin exine, are probably primarily responsible for its occurrence in deep-sea sediments where little else occurs.

It should be noted that Koreneva (1964) observed that some sorts of fern spores are apparently also buoyant (air trapped in the perispore?) and occur in sediment in remote oceanic locations. Davis (1968, 1973) has demonstrated a similar "pollen-trap effect" in a small lake with no stream influx. Funkhouser and Evitt (1959) published a laboratory technique for concentrating and cleaning palynomorph preparations by agitation in watch-glasses, and Tschudy (1960) once designed an apparatus for separating spores/pollen types by vibration induced in a perforated tube. Both of these laboratory techniques depend on the same sensitive flotation properties of spores/pollen as observed in the field in the Bahamas. More recently, Wang *et al.* (1982) have shown in the Yangtze River Delta area that pine pollen as a percentage of total pollen is higher in most of their offshore stations than on land, bespeaking the ready transportability of pine pollen.

Dinoflagellate cysts (Fig. 17.11e) and foraminiferal chitinous inner tests ("microforaminifera;" Fig. 17.11f) found in the Bahamas sediment represent thanatocoenoses of remains which are not primarily distributed according to sedimentary environment, but apparently in response to biological factors, mostly the availability of nutrients to the living organisms, such as in upwelling areas near the Tongue of the Ocean. Melia (1984) has made a similar observation about distribution of dinoflagellate cysts and microforaminifera off the coast of West Africa.

Farley (1982) has pointed out that the relative paucity of spores/pollen in my study of the non-clastic, carbonate sediment of the Bahamas, in contrast to sediments of clastic environments, is a confirmation of the water-transport source of most fossil sporomorphs, which travel in water as clastic particles. If air-transport were of major importance, Bahamas surface sediment would be as rich as is ordinary silt formed in such an environment, which it is not, by at least an order of magnitude. That the distribution of palynomorphs in sediment is primarily a product of sea currents in the basin of deposition has been repeatedly demonstrated, but Melia (1984), working in northwest Africa, noted that spores/pollen distribution in sediment there reflected both oceanic transport mechanisms and the relatively strong offshore African wind patterns. Onshore vegetational complexes were also traceable in the marine sediments.

◄

Figure 17.11 ("microforaminifera") show a distribution entirely different from palynomorphs-proper, presumably because the foram fossils are a thanatocoenosis, related primarily to factors encouraging the development of foraminiferal populations. Reproduced from Traverse and Ginsburg, 1966.

5.4 Further Contributions to Spore/Pollen Sedimentation

Cross *et al.* (1966) have shown that palynomorph sedimentation in the Gulf of California agrees in general with patterns suggested by the above models (see Fig. 17.12). They showed in addition the importance of bottom morphology. Lower Gulf fine sediments are comparatively rich in palynomorphs, and upper

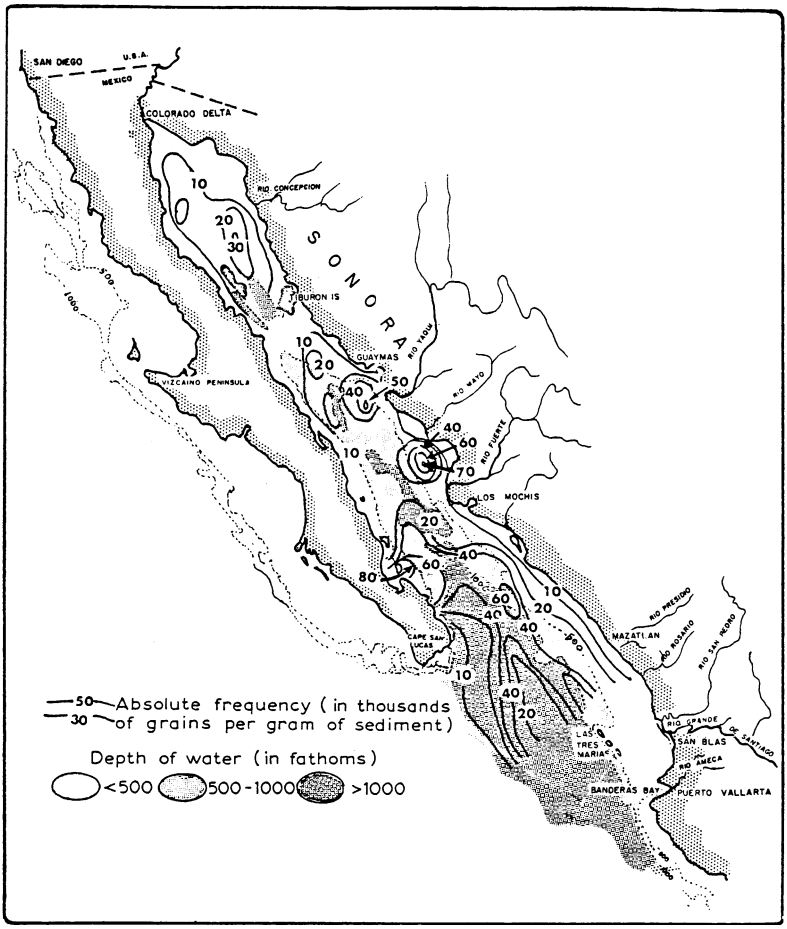

Figure 17.12 Palynomorph sedimentation in the Gulf of California. In this complex of clastic sedimentary environments in a semiarid climatic zone, the sedimentation of pollen and spores is correspondingly complex. However, in general, palynomorphs are more abundant in offshore silts and near delta mouths and in some submarine channels. Coarse sediments nearshore are poor in palynomorphs, but the transition to silt beyond these sands can be abrupt. Most forms decrease in absolute abundance with distance from shore, but pine and mangrove increase in relative abundance. Reproduced from Cross *et al.*, 1966.

Gulf sediments are coarser and relatively poor in palynomorphs. But the Gulf of California sediment contains considerable reworked palynomorphs from older sediment, and these are comparatively abundant. Some of the concentrations of palynomorphs are influenced by nearness to mouths of source streams. Smaller variations represent turbulence patterns, e.g., near the tip of Baja California. Pine pollen from trees on shore is transported to the Gulf of California by water currents, against the direction of the wind.

Stanley (1965), working on U.S. Atlantic coastal shelf deposits, and Heusser (1978), investigating the U.S.-Canada Pacific Northwest, also have shown that palynomorph concentration on a continental shelf reflects the presence of streams, among other factors. In this connection, Mudie's (1982) work demonstrates for eastern Canada that the estuaries of major rivers yield sediment with proportionately higher palynomorph levels than is true for areas with only small streams. Chowdhury (1982) shows that in the German Bay (southeast North Sea), marine current systems play a large role in distribution of palynomorphs, though the rivers (Elbe, Weser, Ems, Rhine) are the major source of pollen. In sequences of riverine sediments such as the Catskill magnafacies, New York-Pennsylvania, overbank deposits are barren or nearly so of palynomorphs, whereas channel sediments may be richly productive (Traverse *et al.*, 1984). Elsik and Jarzen (1984) present similar results from recent overbank deposits of Zambia.

Koreneva (1971) found very low concentrations of spores/pollen in surface sediment of the Mediterranean, mostly less than 10/g (Melia, 1984, found less than 50/g in deep ocean basins). The concentrations seem in general to agree with the concept of pollen settling out in quiet areas or catchment basins (such as the northern Adriatic), and for apparent concentration of palynomorphs to be greatest where general mineral sedimentation rate is lowest. Koreneva (1966) also demonstrated that spores/pollen of land plants occur in small amounts, hundreds of kilometers from the source vegetation in the Pacific, and the types found occur there primarily because of the physical characteristics of the particular spores/pollen types. Koreneva also made interesting observations in the Sea of Okhotsk and elsewhere that link the concentration of spores/pollen in sediment to the particle size of the enclosing sediment, and to the characteristics of the ocean floor: depressions act as pollen traps, as in the Bahamas (see Fig. 17.11d). Darrell (1973) and Darrell and Hart (1970) have shown by statistical analysis of sporomorph complexes of Mississippi River Delta sediments that various onshore depositional environments (marshes, levees, etc.) differ markedly in palynomorph concentration from offshore environments of the same system (mouth bars, prodelta). The same studies showed significant differences in pollen spectra between the various onshore environments, but not between various offshore environments. Surprisingly, 87% of the palynomorph taxa identified were sedimented independently of environment, just as likely to be sedimented

in one as in another. The other 13% were facies-dependent and their preferred sites of deposition were

(1) reworked forms (levees, channels and offshore),
(2) bisaccates (offshore),
(3) tree pollen (channels, levees and offshore),
(4) marsh pollen (marshes).

Groot and Groot (1971) and, in much more detail, Heusser (1983) and Sarro *et al.* (1984), have pointed out that the spore/pollen content of sediment depends to a considerable extent on the productivity of vegetation in nearby source continents, as well as on distance from that source.

The relative abundance of reworked forms increases with distance from the source continent. Stanley (1969) has in this connection cautioned against too facile interpretation of past continental climates from pollen spectra of deep-sea cores obtained far from shore, especially because of reworking. Heusser (1983) has figures that well illustrate the total situation. Total pollen concentration is affected by stream systems, as shown by lobes of higher concentration associated with major streams of eastern North America. Concentration is also affected by bottom geometry. Palynomorph abundance is low on the outer continental shelf, and relatively high on the slope analyses (maximum value 23,000 grains/g). Heusser's study also showed that vegetation types on the nearby continents are reflected in the pollen load of shelf and slope. On a much smaller scale, in Lake Turkana, Kenya, Vincèns (1984) has shown that deltaic sediments contain pollen derived from the regional montane vegetation, whereas the strictly lacustrine sediments yielded mostly pollen from the local steppe vegetation.

Wang *et al.* (1982), working in the area of the Yangtze River Delta, China, have shown that the amount of palynomorphs per unit of sediment varies with the environment of deposition, as Muller found in the Orinoco Delta. Wang *et al.* also emphasized that sediments from the mouth of the Yangtze had lower values than either upstream or offshore stations. I would attribute this to turbulence and would expect that measurements of the water itself would reveal high values at the mouth.

Williams (1971) demonstrated that in marine environments generally the distribution of dinoflagellate cysts is a product primarily of the organic productivity of the superficial water. This result agrees well with earlier studies of limited areas (see Figs. 17.11e and 17.10h). Dinoflagellate cysts offer some possibilities for paleoecologic interpretation that spores/pollen in marine sediments do not. The source for dinoflagellates is limited as to range of required environmental characters. Dinoflagellate cysts can be directly tied to oceanic temperature, nutrient supply, and currents. Various authors, e.g., Scott (1982), have suggested that smooth cysts (dinoflagellate and acritarch) are characteristic of

nearshore, high-energy, turbid environments, whereas spiny cysts suggest deeper, low-energy, cleaner water. Dinoflagellate presence or absence can sometimes be used to differentiate marine from non-marine sediments, but this is tricky because freshwater or brackish water dinoflagellates can be very abundant in non-marine sediments. Dinoflagellate diversity is a good measure of the "marineness" of sediments in which their cysts occur (cf. Fig. 17.13). Dorning (2005) has made a somewhat different observation regarding diversity of early Paleozoic microplankton (acritarchs plus prasinophyte algal spores), with diversity greatest in open marine shelf areas and less diversity in sediments from both the open ocean and near shore.

Reworked sporomorphs often demonstrate the effectiveness of long-distance transport in rivers; e.g., Stanley (1969) showed that Cretaceous sporomorphs in Pleistocene sediments of the Gulf of Mexico probably traveled over 2,000 km from the Great Plains, by way of fluviatile transport. Reworking can be a major factor in palynomorph sedimentation. (See discussion of the topic in the next chapter.) Bonny (1976, 1978) has shown that, even in small lakes, as much as 85% of the pollen in the sediment reaches its destination by the stream(s) feeding

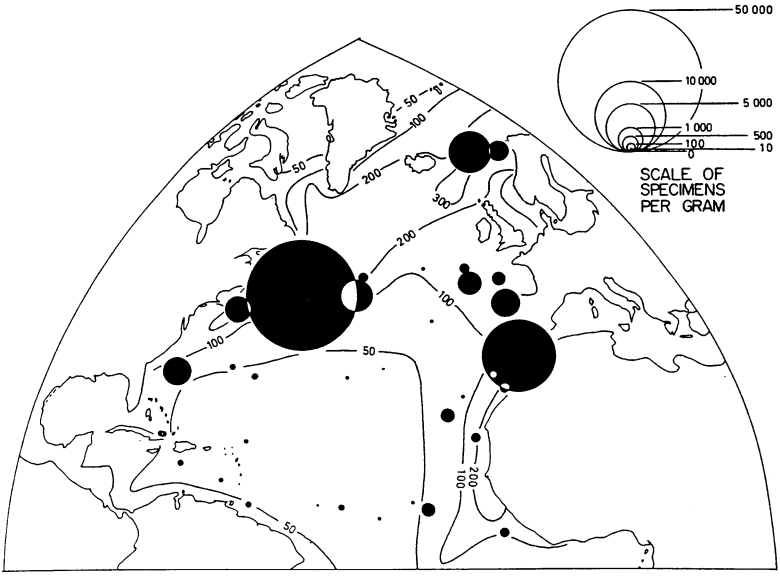

Figure 17.13 Dinoflagellate cyst concentration in marine sediments (see also Figs. 17.10 and 17.11). Dinoflagellate cysts are not abundant in situations far from continental margins, but they tend to abound in regions in continental shelf areas where, presumably, circumstances favor both dinoflagellate populations in general and encystment in particular. In Black Sea cores, I have studied a few, probably brackish water, Pleistocene samples containing several million dinoflagellate cysts per gram! From Williams, 1971.

the lake. On the other hand, Hooghiemstra and Agwu (1986) and Dupont and Agwu (1991) have shown that, in the Atlantic off northwest Africa, the trade winds and African Easterly Jet (Saharan Air Layer) make the atmosphere in this exceptional situation the main suppliers of pollen to the sediment, despite the greater significance of water transport in most sedimentary basins. The northwest Africa dominance of wind-dispersal would presumably be expected in any arid area with very few stream sources for sediment and considerable wind ablation of mineral dust. There are, of course, exceptional sediments that were partly or mostly deposited directly out of the air. Loess is the best known example. Paez and Prieto (1993) have shown that in Argentinian loess deposits analysis of the sporomorph content of the sediment reveals the wind direction from which the loess dust came, based on the palynofloral relationship to the vegetation of source areas.

Chapter 18

Differential Sorting of Palynomorphs into Sediments: Palynofacies, Palynodebris, Discordant Palynomorphs

1 Introduction: Palynofacies and Related Matters

One of the areas of paleopalynology that has expanded greatly since the publication of the first edition of this book is the subject of *palynofacies*, and its interpretation and significance in various practical connections. Palynofacies are associations of palynological matter (PM) in sediments, considered primarily in terms of the reasons for the association, which is usually geological, but may be connected to the biological origin of the particles. Spores, pollen, dinocysts, acritarchs and all other palynomorphs are of course included in a palynofacies, but so are all other visible organic particles in the palynological size range (roughly 2–250 μm) that occur in palynological maceration residues. Such non-palynomorph PM is often referred to collectively as *palynodebris*. Examples of palynodebris are shown in Fig. 18.4 and (along with palynomorphs) in the variety of palynofacies displayed in Fig. 18.5a and Plates 18.1–18.3.

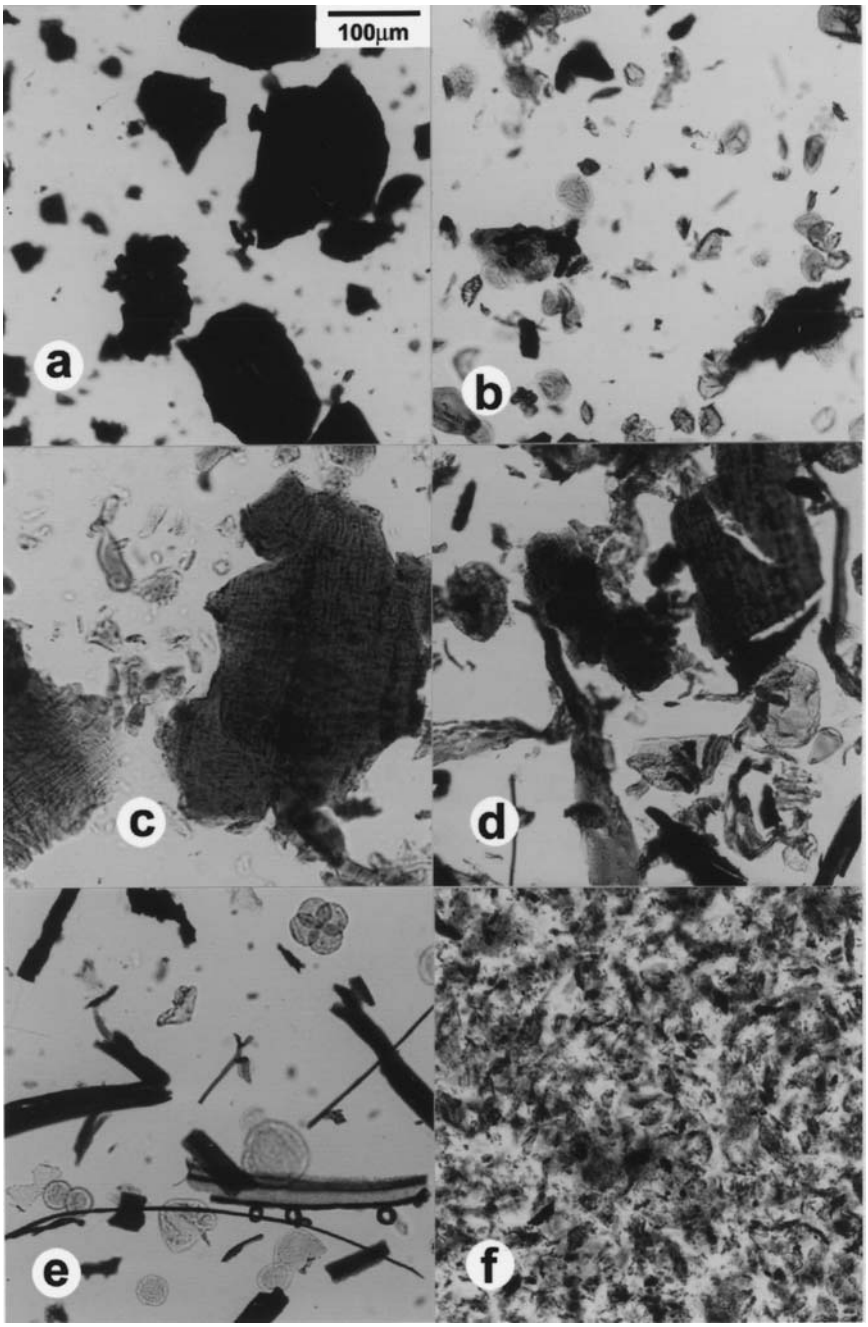

Plate 18.1

There have been at least two books published since the first edition of *Paleopalynology* that deal in large part with this subject: Tyson (1995) and Traverse (1994b). Tyson in 1993 published a pioneering contribution in the area of palynofacies analysis. Furthermore, the third volume of Jansonius and McGregor's (1996) compendium of palynology includes two chapters (Batten, 1996, 1996a) with succinct and profusely illustrated summaries and exposition of the subject, including its application to petroleum exploration.

In an older sense, "palynofacies" may connote the palynomorph load of a sedimentary rock, seldom including any of the palynodebris, in which palynomorphs of a particular species or several species of producing organisms, for example, chenopod pollen or dinocysts, or an extinct sporomorph taxon such as *Classopollis,* are enriched in concentration. Such enrichment can be explained biologically: derivation from an ecotope of the producing organism, or circumstances differentially destroying other forms. I call this a *palynobiofacie*s, to contrast it with the more recently emphasized and now dominant usage for palynofacies, which is for particular assortments of PM, including both palynomorphs and palynodebris that are associated with an environment of deposition for prevailingly non-biologic reasons. I have suggested calling this sort of palynofacies a *palynolithofacies* (Traverse, 1999) to emphasize that the concept is primarily geological not biological, although all constituents of the palynofacies are of biological origin. These matters are discussed in Traverse (1994b, Introduction). In this chapter various aspects of PM deposition that result from sedimentological processes working on organic sedimentary particles in the palynomorph size range of about 2–250 μm are examined.

Plate 18.1 Various sorts of palynofacies assemblages (part 1). Scale bar represents 100 μm for all photomicrographs. (**a**) Carboniferous coal, Midland Valley, Scotland. Organic matter dominated by vitrinite particles that are predominantly opaque (black) when unoxidized (see also c); (**b**) Carboniferous non-marine shale, northern England. Palynofacies dominated by *Lycospora*, with brown woody debris, other plant tissues and a few megaspores (not shown); (**c**) Jurassic coal, northeast Scotland. Organic matter dominated by vitrinite that has been laboratory-oxidized by nitric acid (cf. a) and is therefore brown and reveals some structure; (**d**) Jurassic non-marine shale, southern Sweden, dominated by brown wood, with some black and brown-striped tracheidal debris, other plant tissues, spores and gymnosperm pollen grains in association; (**e**) Lowermost Cretaceous lagoonal mudstone, southern England; dominated by gymnosperm pollen grains, especially numerous *Classopollis,* often in tetrads. Much of the associated organic matter is charcoalified tracheids; **(f)** Lowermost Cretaceous lacustrine mudstone, southern England; palynofacies dominated by fibrous amorphous organic matter, probably of degraded algae (AOMA-cf. Table 18.1). This plate was prepared for the author by David J. Batten.

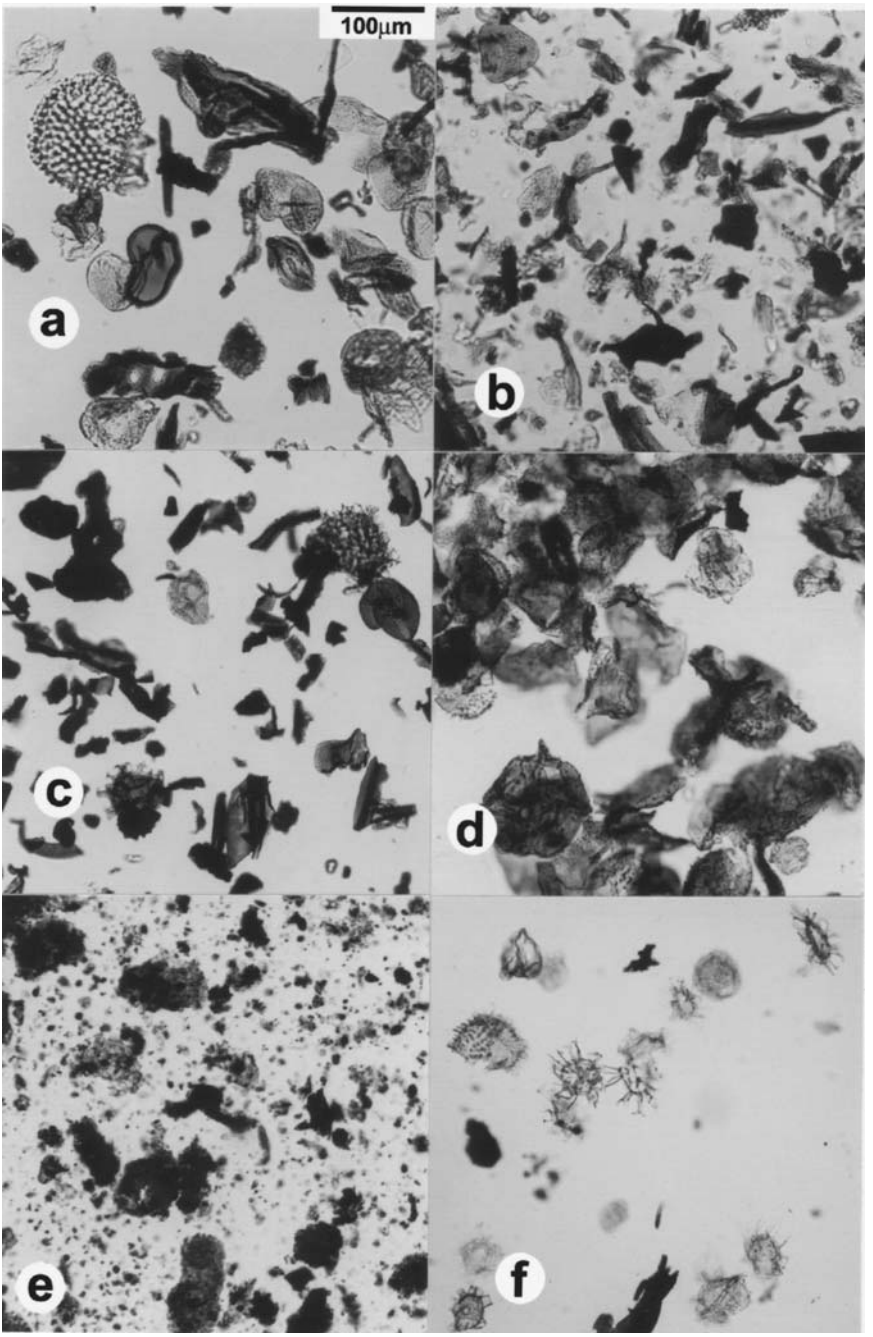

Plate 18.2

2 Sorting of Spores/Pollen per Sediment Type

In previous chapters I discussed the fact that palynomorphs are silt- and finest sand-sized clasts and therefore are mostly fellow travelers of fine silt, as they sort out along with slightly smaller mineral particles. Well-sorted claystones and well-sorted coarse sandstones will not ordinarily contain more than a trace of fossil palynomorphs. Carbonate sediments are prevailingly non-clastic. Most of them are palynomorph- poor, although some can and do contain some beautifully preserved palynomorphs (Scott *et al*., 1985b). Coal balls of Europe and North America are also calcareous sediments, in which palynomorphs are frequently very well preserved. Permineralizations such as these examples are, however, very atypical sedimentary rock. Coals are a special case. Although peats are formed even at high latitudes and such peats can and have become layers of coal, most extensive deposits of coal were formed in warm temperate to subtropical swamps. Many contain abundant spores/pollen (if attrital coal-macerals predominate), nearly all of which were autochthonous. However, vitrinitic coals, consisting largely of wood and other tissues, are often very poor in spores/pollen. Coal-derived palynofloras, being locally derived, tend to be less diverse than those from associated clastic sediments, which receive sporomorphs from a much broader area.

Various studies have shown that, when one considers broad characters of palynofloras instead of the individual taxa, palynofloras of quite different age can be grouped according to sediment-type (see Fig. 18.1).

The general composition of the palynoflora (proportion of monosaccates and bisaccates–conifers, fern-spores, etc.) from a Lower Jurassic marine sediment is often more like that of an Upper Jurassic marine sediment than it is like that

Plate 18.2 Various sorts of palynofacies assemblages (part 2). Scale bar represents 100 μm for all photomicrographs. (**a**) Lower Cretaceous non-marine shale, southern North Sea Basin. Dominated by spores, with some brown wood and freshwater algal bodies (*Schizosporis*); (**b**) Lower Cretaceous channel-fill mudstone, southern England. Some black but mostly brown woody matter and other tissue fragments dominant. Sporomorphs subordinate but generally well preserved; **(c)** Lower Cretaceous marine mudstone, southern North Sea Basin; many associated marine dinoflagellate cysts but abundant land-plant debris and spores indicate significant freshwater influence on the depositional environment; (**d**) Lower Cretaceous marine mudstone, southern North Sea Basin. Dinoflagellate cysts (especially *Cribroperidinium*) dominant, indirectly reflecting a dinoflagellate "bloom.;" (**e**) Lower Upper Cretaceous bituminous marl, northern Germany. Granular AOMA dominant, reflecting a restricted marine environment; (**f**) Lower Upper Cretaceous very pale gray chalk, southern England. Diverse dinoflagellate cyst assemblage, with subordinate black and brownish black woody detritus, indicates an open marine depositional environment. This plate was prepared for the author by David J. Batten.

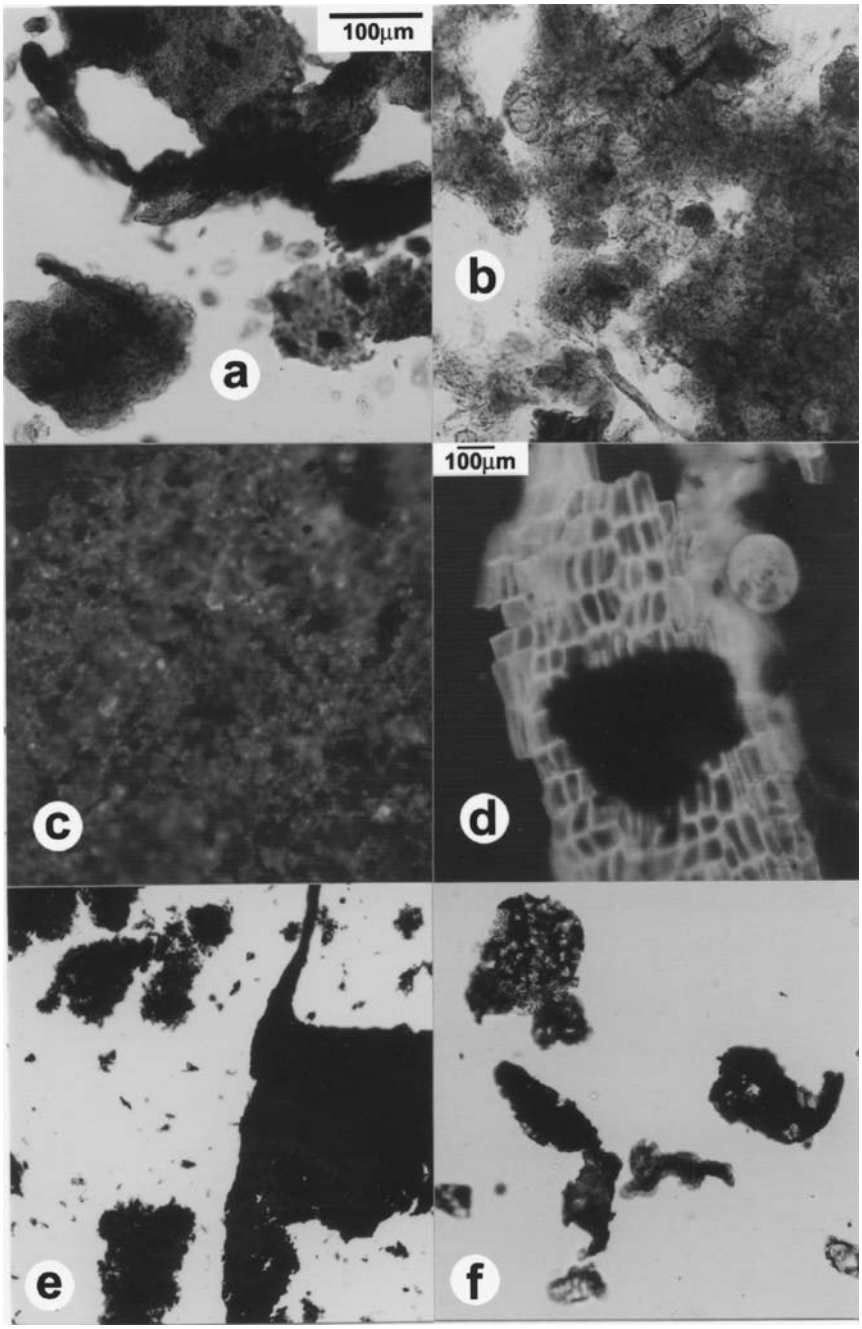

Plate 18.3

of a Lower Jurassic siltstone. In many instances, the interpretation of a fossil palynoflora depends on sedimentological environment rather than on autecology of the source plants. For example, as pointed out by Chaloner and Muir (1968), prevalence of saccate pollen in marine Carboniferous sediment usually does not demonstrate dominant Pv2-producers near the basin of deposition, but quite the opposite: deposition at considerable distance from shore because of greater amounts of bisaccate pollen being transported by air and water to that site. Chaloner and Muir called this the "Neves effect," from the work of R. Neves, which they interpreted as supporting the theory (see Fig. 18.1a).

Extant models certainly suggest that this could be possible. For example, high percentages of *Rhizophora* pollen in the Gulf of Paria (Fig. 17.10c) are explained not by nearby mangrove vegetation, but by deposition at some distance from shore, where the comparatively great transportability of the very small *Rhizophora* pollen is operative. Fig. 18.2 presents a model for the Neves effect and related phenomena.

An interesting corollary is provided by the work of Brückner-Röhling and Heunisch (2004), in which Middle Triassic Muschelkalk sediments were found to have been deposited in very high saline waters in which microphytoplankton could not live, and the palynoflora consists entirely of pollen of land plants coming in from some distance. Streel and Richelot (1994) point out that effects similar to the "Neves Effect" can occur as a result of upland pollen and spores being delivered to the marine platform by the water of flood events rather than by wind dispersal.

Interpretation of fossil palynofloras must always take sedimentary factors into consideration (see Fig. 18.3). For example, the occurrence in latest Triassic-early Jurassic (Rhaeto-Liassic) sediments of layers dominated by tremendous quantities

Plate 18.3 Various sorts of palynofacies assemblages (part 3). (**a**) Eocene dark gray lacustrine shale. Dominated by massive granular AOMA. Messel Oil Shale, near Darmstadt, Germany; (**b**) diatomaceous earth. Dominated by AOMA, but with pollen grains and *Botryococcus* (not shown). Discarded unnumbered museum specimen, labelled "Quaternary diatomaceous earth," locality unknown; (**c**) Fluorescence microscopy of granular AOMA from dark gray marine shale. Upper Jurassic, central England, demonstrating moderate fluorescence; (**d**) Strongly fluorescing cuticle (partly covered by a fragment of reworked black wood and a prasinophyte phycoma), Pleistocene biogenic mud; (**e**) Over-mature AOMA and graptolite fragments (part of an opaque sicula comprises most of the right side of photo), from very dark gray marine shale, reflecting deep water, euxinic conditions, Ordovician of southern Scotland; (**f**) Very poorly preserved prasinophyte phycomata (tasmanitids) dominate this taxonomically impoverished, over-mature, marginal marine palynofacies, Devonian of Western Australia. This plate was prepared for the author by David J. Batten.

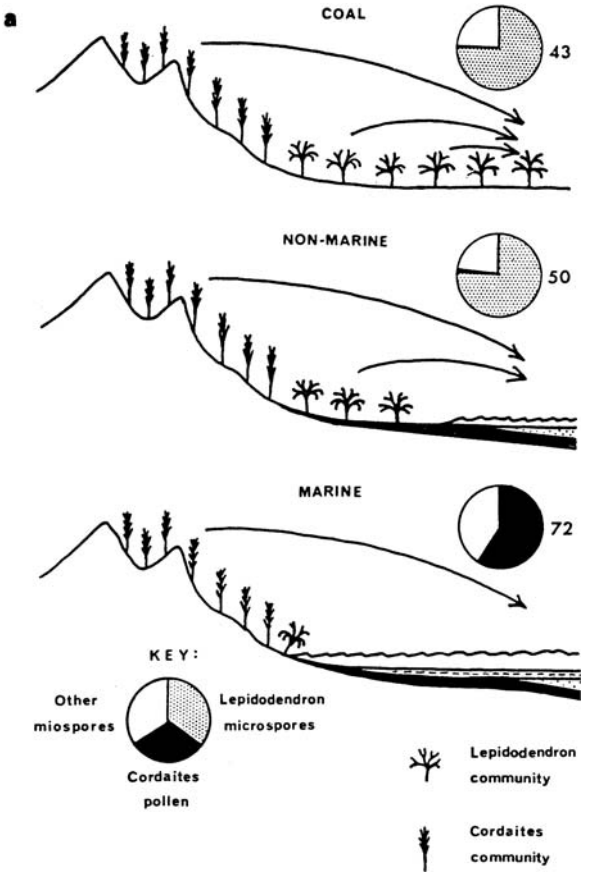

Figure 18.1 Two classic demonstrations of the fact that spores and pollen produced contemporaneously are selectively sorted by sedimentation factors into different environments. *Fig. 18.1a*. The "Neves effect:" saccate pollen (*Florinites*) of *Cordaites* trees are carried by both wind and water into marine environments, whereas microspores of *Lepidodendron* (*Lycospora*) are produced in swamps and are not so transported out of the swamps. Some other taxa of miospores are produced in other environments and do float reasonably well, and are carried seaward. In the coal swamps the locally produced *Lepidodendron* spores completely overwhelm the relatively few *Florinites* pollen grains that come in. In the non-marine, non-swamp situation there are more *Florinites* but not proportionately so many as offshore. On the other hand, Hughes (1976) has demonstrated that some Mesozoic coals produced in conifer swamps are dominated by bisaccate conifer pollen, whereas another conifer pollen, *Classopollis*, behaves as the "Neves effect" would predict: it is dominant in contemporaneous shales and limestones produced offshore from the coal swamp. Pollen and spores of coal are more a reflection of the local vegetation than of sedimentary factors. Reproduced from Chaloner and Muir, 1968.

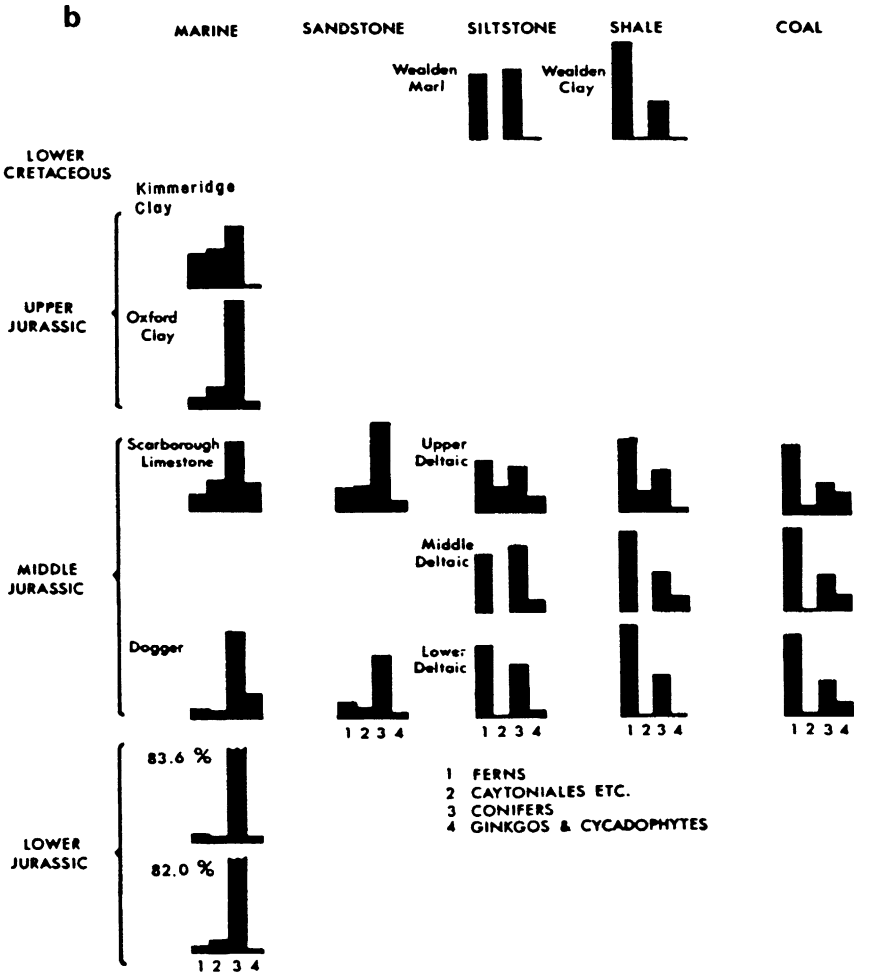

Figure 18.1b Spore assemblages of British Jurassic and Lower Cretaceous rocks of different lithology. The general palynological composition clearly depends heavily on the environment of deposition, as reflected by lithology, even over a large timespan. Sorting according to sedimentological effects is obviously at least partly responsible, although spores and pollen produced in a coal swamp reflect the immediately local vegetation and have little chance of being carried out of the swamp. Reproduced from Chaloner (1968b).

of *Classopollis* pollen obviously means presence somewhere of large numbers of cheirolepidiaceous shrubs and/or trees that produced this pollen type.

(Cheirolepidiaceae is the family of Mesozoic conifers which includes *Hirmerella*, formerly called *Cheirolepis*.) However, whether the pollen dominance

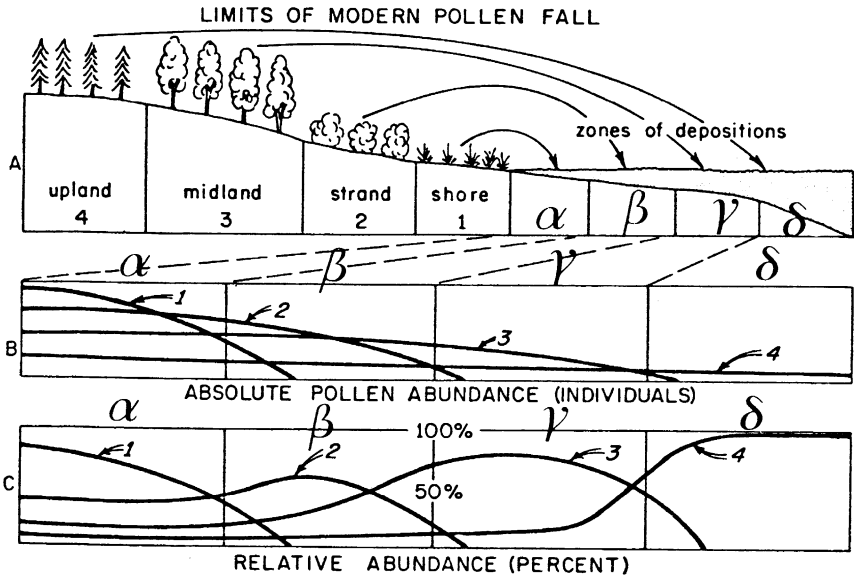

Figure 18.2 Neves effect (see also Fig. 18.1a) and related phenomena graphically displayed for a hypothetical coastal environment. Coniferous vegetation in upland zone 4 produces pollen that arrives in about equal small amounts (= absolute abundance) in depositional zones α, β, γ, and δ. This is somewhat less true of midland vegetational zone 3, because the pollen in this zone tends not to be as buoyant as conifer pollen, but is produced copiously per unit area and so starts out abundant in depositional zone α but tails off at the beginning of depositional zone δ. Strand (2) and shore (1) vegetational zones produce abundant but (in the case displayed!) typically heavy pollen which is therefore abundant only in the relatively near vicinity of production (depositional zones α and β). Note that when plotted by percentage, the upland (buoyant, gymnosperm) pollen attains 100% in depositional zone δ, though its *absolute* amount remains approximately constant from zone α to zone δ. However, compare with information in Fig. 17.10c for an example of shoreline vegetation (red mangrove) which produces small, buoyant pollen which would show quite a different distribution (more like an upland coniferous pollen in this example). Each depositional situation is a little different, but the basic analysis of the sedimentological factors follows the same "laws". Modified slightly from Wilson, 1976. See text for some alternate explanations of this sort of data.

was because the *Classopollis*-producing plants were coastal organisms like mangrove or swamp-cypress today, or whether the plants were upland shrubs/trees and the pollen blooms resulted from sedimentary sorting, can be debated. It has been noted (Hughes, 1976), for example, that *Classopollis* pollen usually is an order of magnitude more abundant in shales than in associated coals, which is an example of a palynobiofacies.

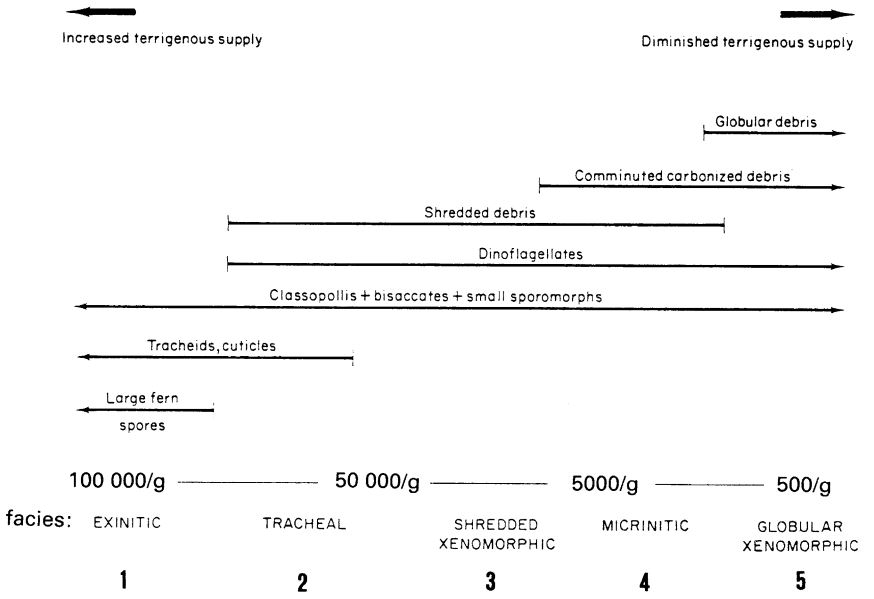

Figure 18.3 Habib's classification of "palynodebris," the dispersed organic matter found in palynological preparations, including palynomorphs but other organic (mostly plant) matter as well. This (Habib 1979, 1982a,b) classification of associations of palynodebris as "palynofacies" encountered at levels in sediment corresponding to various distances from land is paleoecological, dividing all palynodebris into: (**1**) the exinitic facies (nearest to shore), including almost no dinoflagellates; (**2**) the tracheal facies, containing derivatives of wood and leaves, the palynomorph content dominated by bisaccates and other more or less sorted pollen of kinds likely to be transported long distances, plus dinoflagellate cysts; (**3**) the shredded xenomorphic facies, dominated by shredded organic debris of uncertain origin, plus dinoflagellates and varying amounts of pollen; (**4**) the micrinitic facies, representing far offshore black clays with much black, carbonized plant debris and few palynomorphs; and (**5**) the globular xenomorphic facies (farthest offshore) with very few palynomorphs, and globular organic debris of marine origin, probably zoöplanktonic fecal pellets. Example used by Habib was Cretaceous, hence the mention of *Classopollis* pollen. Abundance of palynodebris fragments decreases from the exinitic (100,000/g) to globular xenomorphic (500/g), providing another parameter for identification of the constituent facies. Diagram from Habib (1982b). See also Table 18.1, which presents a classification based on more recent analyses, representing efforts to make the classification generally applicable to all sedimentary rocks.

In some Carboniferous coal-bearing sequences it has been observed by Smith (1962) and others that *Densosporites* spores (lycopod-derived) trend toward dominance at the top of coal beds and in the roof-shales (see Phillips *et al.*, 1974; Chaloner and Muir, 1968). Scott and King (1981) showed a similar sequence with

lycopod-derived megaspores such as *Zonalessporites*, which are megaspores of plants that produced densospore microspores. Such a situation, presumably edaphically controlled, would appear to be plant-successional, because coal palynofloras are practically 100% autochthonous. Densospore producers perhaps succeeded swamp trees as the water deepened and became more marine-influenced. On the other hand, the situation could theoretically be sedimentological, with densospores perhaps coming in with invading marine water. Chaloner and Muir called the plant-successional model the "Smith effect," from the work of A.H.V. Smith, which demonstrated it. (A regionally climatically controlled succession, such as the typical Euramerican Holocene pollen diagram, was called the "Von Post effect" by Chaloner and Muir.) The sedimentological "natural history" of spores/pollen is an advantage to their biostratigraphic use because they themselves are relatively free of purely local phenomena such as water temperature or salinity (coastal plants such as mangroves are clearly exceptions). The fact that the sedimentological history of palynomorphs makes them likely to produce palynofacies has many uses in the interpretation of the sedimentary history of rock sequences, and thus to sequence stratigraphy.

2.1 Biological "Sorting:" Marine Palynomorphs

Some palynomorphs originate in the water of the basin of deposition, e.g., those derived from marine animals or protists such as chitinozoans, copepod eggs, tintinnids, scolecodonts, and microforams, as well as acritarchs, presumably derived from mostly marine algae, and dinoflagellate cysts, which are produced by a unique, separate group of flagellate protists. For fossils that originate in the water, one must be aware of ecological factors affecting production and dispersal. In the modern Gulf of Mexico-Caribbean area, for example, "microforams" (chitinous foraminiferal linings) are abundant in the calcareous sediment of the Bahamas and Yucatan Peninsula areas, but are rare in the clastic sediments of the northern Gulf, e.g., the Mississippi Delta or Trinity-Galveston Bay. As already observed, it has been suggested that spiny acritarchs and dinocysts are more common in deeper water, and relatively non-ornamented forms are more common in shallower, higher energy situations where there may also be more brackish water. In the Bahamas, high concentrations of dinoflagellate cysts and microforams generally are strongly correlated with the presence of nutrient-rich water. (Melia, 1984, has made a similar observation in Africa.) For microphytoplankton (acritarchs and dinocysts primarily), it has also been suggested that low taxon diversity indicates nearshore deposition. However, Dorning (l981), in a study of British Silurian sediments, notes a peak in generic diversity of phytoplankton in open shelf environments with less diversity both toward the shore and toward deeper water. He also found that more highly ornamented forms dominate in shelf areas, whereas less ornamented forms and sphaeromorphs dominate in

nearshore localities and to some extent also in deeper water environments beyond the shelf. In an extensive systematic study of dinoflagellate cysts in the North and South Atlantic, Wall *et al*. (1977) found that the distribution of fossil dinocysts is a thanatocoenosis (a death assemblage) that parallels reasonably well the distribution of the corresponding living dinoflagellate species. They also noted that there are two major trends in distribution, one correlative with distance offshore (environmental), the other with latitude (climatic). Both species diversity and cyst density tend to increase seaward, as a result primarily of sedimentological factors. Biologically, the dinoflagellates that produce fossil cysts are, as a class, adapted to unstable environments in shallow water situations along continental margins, and around oceanic island groups, prevailingly in tropical regions (Wall *et al*., 1977). Individual species, however, tend to be adapted to the most stable sectors within these unstable environments.

2.2 Classifications of Organic Particles in Sediment

Palynologists have long noted that maceration residues prepared from sedimentary rocks contain a wide range of organic particles in addition to palynomorphs. This is especially true of marine shales. Manum (1976a) suggested the term "palynodebris" for such non-palynomorph organic particles, whether carbonized or not. Some examples of palynodebris are shown in Figures 18.4 and (along with palynomorphs) in 18.5a. A number of palynologists have made an effort to put study of such particles on a systematic basis, with the hope that such study could contribute to understanding of the total sedimentological picture. As Bujak *et al*. (1977) stressed, the range of kinds of organic particles in sedimentary rocks also controls to some extent the production of hydrocarbons from the rock during thermal maturation. Bujak *et al*. termed the four principal kinds of organic particles: (1) amorphogen (amorphous: structureless organic matter); (2) phryogen (non-woody plant material, including palynomorphs); (3) hylogen (from woody material); and (4) melanogen (opaque organic matter). Amorphogen and phryogen are more likely to produce liquid hydrocarbons in time than is hylogen, and melanogen is least likely to be productive. Manum and Throndsen (1978) found that, in the Spitsbergen Tertiary, phryogen is usually dominant in marginal marine sediments, amorphogen is high in offshore marine sediments, and hylogen is most common in non-marine deposits (melanogen was not common in any samples). Those particles which originally were fragments of plants are sometimes called "phytoclasts."

Masran and Pocock (1981) devised a classification for phytoclasts based largely on botanical and coal petrological classification of particulate palynodebris. The classification emphasized the sorts of original tissues represented, and the categories of coal macerals these become, and depends partly on experimental disaggregation of plant material, producing artificial "phytoclasts". Masran (1984)

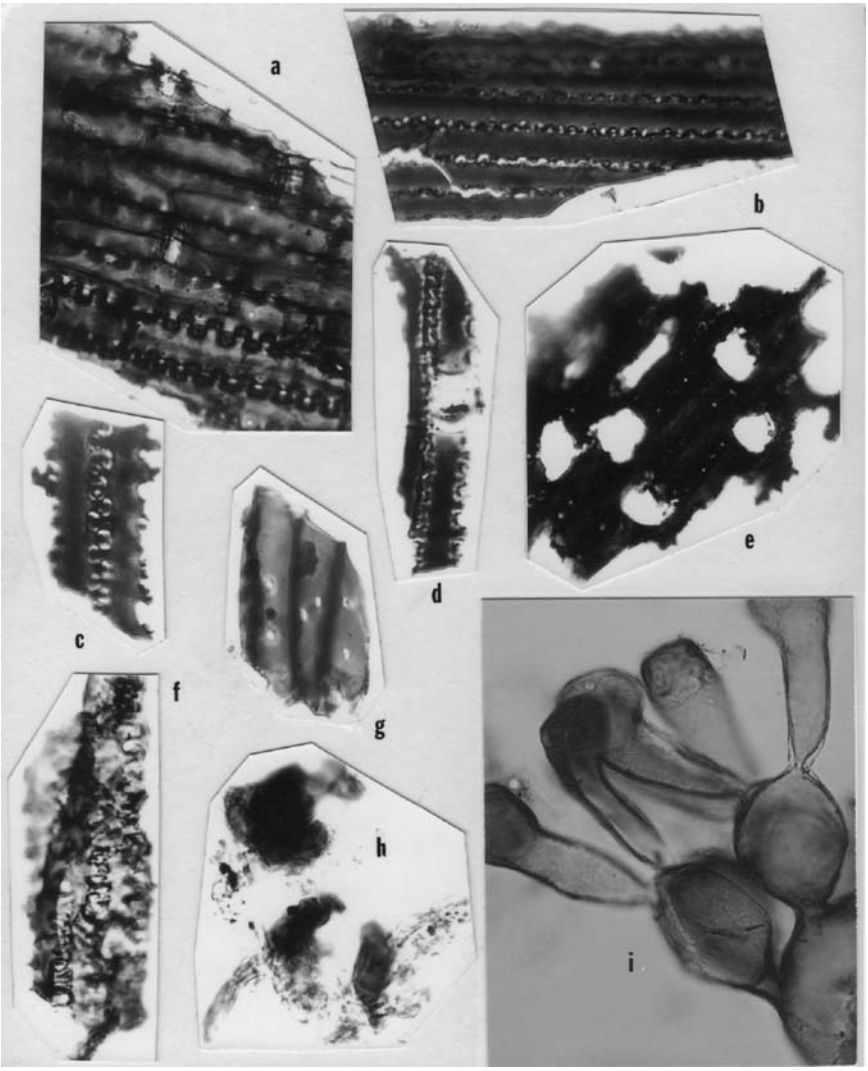

Figure 18.4 *(See caption on page 558)*

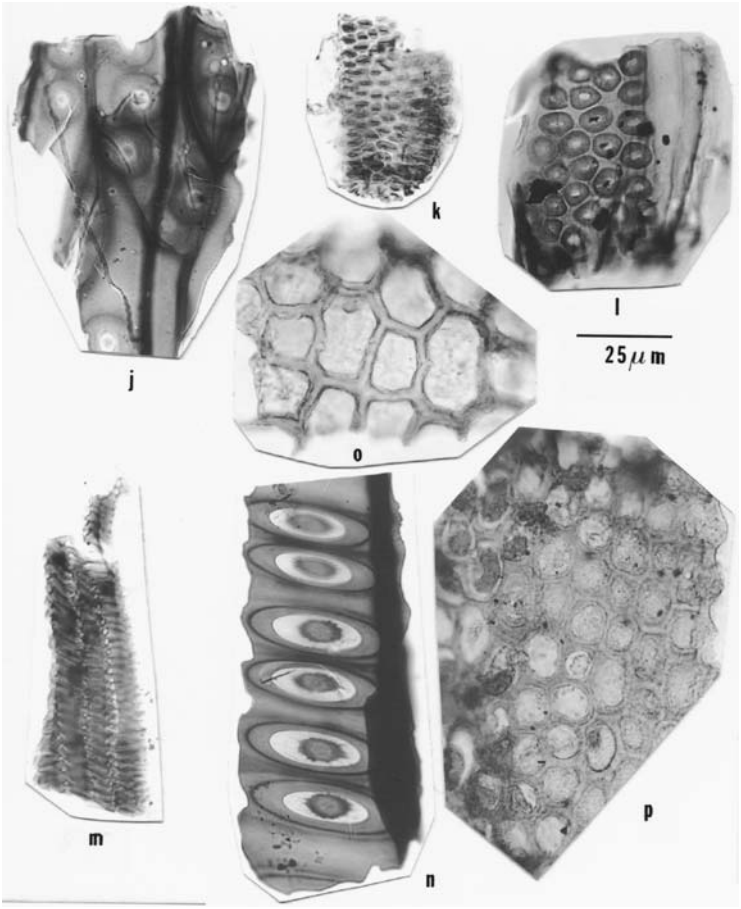

Figure 18.4 *(See caption on page 558)*

has shown the efficacy of the method in a study of North Atlantic Jurassic-Cretaceous sediment from DSDP cores.

The organic sediments could be classified as marine or non-marine in origin and conclusions could be drawn about the post-depositional history of the sediment. However, more recently different classifications of dispersed "palynological matter" (=PM) have been introduced and are in wider use (cf. Table 18.1) than those based on the Masran and Pocock, and Bujak classifications, though the latter remain important conceptually.

Habib (1979, 1982a) has classified the organic particles in palynological residues from a somewhat different point of view. The overall character of the palynologic residue from a given sample is termed its palynofacies, and they are separated into five categories (cf. Fig. 18.3): (1) exinitic, (2) tracheal, (3) shredded xenomorphic, (4) micrinitic, and (5) globular xenomorphic. Exinitic and tracheal residues typically occur in sediments that were rapidly deposited. They are comparatively rich in total organic matter. Micrinitic residues are typical of more slowly deposited sediments. Habib's system thus classifies each sample as either 1, 2, 3, 4, or 5 (see Fig. 18.3). For comparison, a micrinitic sample in the Habib scheme might be 20% melanogen, 40% amorphogen and 20% phryogen in the Bujak *et al*. scheme described above.

The study and use of palynofacies in various lines of geologic research, especially in sequence stratigraphy and in hydrocarbon exploration, has expanded greatly since the publication of the first edition of this book, and is still developing. As a result, the classification of organic particles that make up the subject matter of palynofacies research has also evolved. A significant conference on organic

Figure 18.4 Commonly encountered palynodebris from various Neogene sediments. Most of this palynodebris consists of plant fragments ("phytoclasts") and would fall in Habib's tracheid and cuticle category of the exinitic and tracheal facies (see Fig. 18.3), and in Masran and Pocock's (1981) structural terrestrial (telinite) and biodegraded terrestrial categories. There are also many more or less amorphous sorts of palynodebris (see Plates 18.1–18.3). Magnification shown by bar under (l). (**a**)-(**f**) Fragments of seed plant cuticle, Pliocene sediment of Black Sea: (**e**) shows a quite carbonized cuticular fragment in which entire stomatal apparatuses are missing, leaving lacunae and (**f**) is a very much degraded fragment, still recognizable as cuticular. (**g**) Seed plant wood fragment showing portions of several tracheids with bordered pits, Pliocene sediment of Black Sea. (**h**) Characteristic degraded, indeterminable, organic debris of palynological preparations, Pliocene sediment of Black Sea. (**i**) Probably chitinous animal (or fungal?) material, Recent sediment of Black Sea. (**j**) Portions of conifer tracheids with circular bordered pits, Pleistocene sediment, Black Sea. (**k**),(**l**) Portions of vessel elements with pitting, Pleistocene sediment of Black Sea. (**m**) Plant tracheary material, much degraded, Pleistocene sediment of Black Sea. (**n**) Portion of one coniferous tracheid with bordered pits, Pleistocene sediment of Black Sea. (**o**)-(**p**) Portions of sheets of probably chitinous cellular tissue, perhaps animal, Recent sediment of Gulf of Mexico.

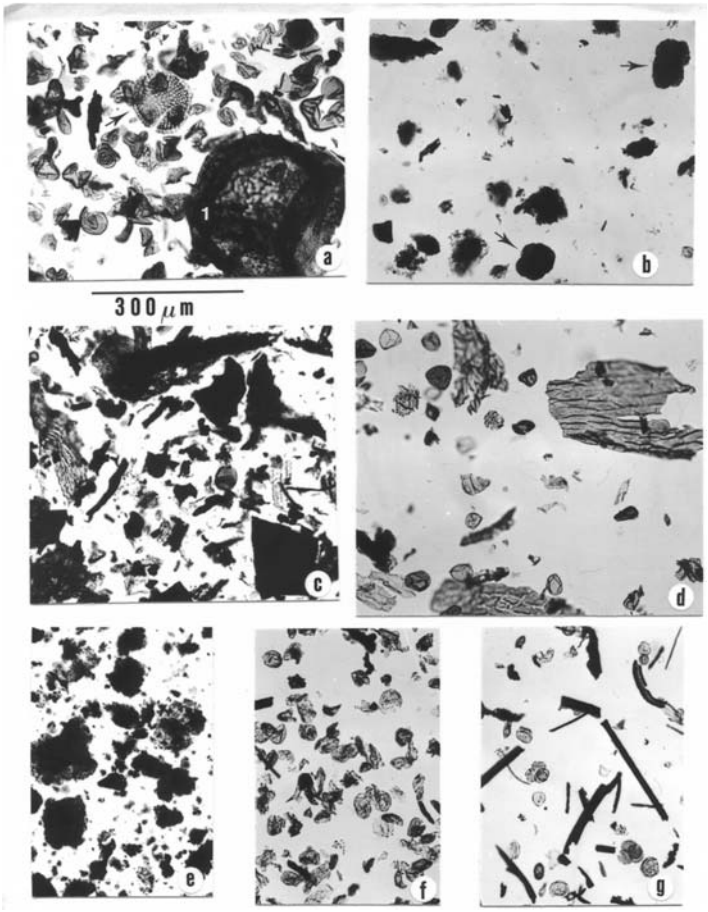

Figure 18.5a "Palynofacies" or palynologic assemblage types, as varying complexes of palynomorphs and "palynodebris," as observed in black and white photomicrography. This concept was introduced by Batten (1973, 1980, 1981a, 1982), and is useful in understanding the general origin of sediment and its propensity to be associated with hydrocarbons. In Batten's (1973) formally described assemblage types each type has a key palynological character, which is usually a palynomorph but may be a kind of palynodebris ("brown wood") or a general palynological character ("diverse miospore content"). Illustrated here are various palynofacies in Batten's sense, as seen under the microscope at low power. Magnification indicated by bar under (a). (**a**) Facies from channel-fill siltstone, containing abundant trilete spores and megaspores: *Minerisporites* sp.(lower right, indicated by white "1"), and *Schizosporis reticulatus* Cookson & Dettmann (upper left, indicated by arrow). Lower Cretaceous, England. (**b**) Facies mainly consisting of fluffy amorphous organic matter, probably of algal origin, and *Botryococcus* colonies (arrows), from a mudstone of probable freshwater origin. These colonies are thick-walled, hence appear dense. Lower Cretaceous, England. (**c**) Facies from a non-marine channel-fill siltstone dominated by

matter classification held in Amsterdam in 1991 is often cited as a benchmark event in this direction.

The classification presented below in Table 18.1 draws some inspiration from that of Lorente and van Bergen (1990), as presented in the workbook for the abovementioned conference (Lorente and Ran, 1991). A similar summary classification has been published by both Traverse (1994-Introduction) and Batten (1996). This classification is intended to cover all sorts of palynomorphs (PP)–sporomorphs, dinocysts, acritarchs, even somewhat rare forms such as lepidopteran wing scales (under IE4, "insect discrete exoskeleton parts"). It also includes all sorts of palynodebris (PD), from wood particles (under STOM) to amorphous organic matter (AOM). The aim of this classification is to provide inclusive coverage of what is encountered in palynological rock-macerations, in order to permit diverse possibilities for the use of palynofacies studies in connection with research on all sorts of sedimentary rock. I have added the acronym (F) in some parts of the table to underline the fact that fluorescence microscopy is a useful adjunct to white light microscopy for the interpretation of the indicated sorts of PM, although white light conventional microscopy can normally be used as a stand-alone method for palynofacies research.

Note that palynomorphs are by definition in the ca. 5–500 μm size range, but for palynodebris the upper size limit is more flexible, although some upper and lower size limits must be specified in reporting counts of, say, charcoal (oxidized plant vascular tissues), or the statistics will not be easily interpreted. However, it is clearly wrong to exclude from palynodebris most particles in the palynomorph size range, and thus to limit it to particles larger than 200 μm, as proposed by Highton *et al*. (1991). It should also be emphasized, as Batten (1999) points out, that a list such as that of Table 18.1 classifies only robust SOM–matter that survives palynological preparation techniques. This is palynological matter=PM.

Figure 18.5a abundant vascular plant remains, woody and membraneous, with a few miospores. Lower Cretaceous, England. (**d**) Facies with abundant plant cuticle and *Densoisporites* sp., non-marine gray shale. Mid-Jurassic, North Sea. (**e**) Facies from a marine "black shale" dominated by amorphous organic matter, a sort of facies that is likely to be associated with hydrocarbon generation, given sufficient thermal maturation. Upper Cretaceous, Helgoland, Germany. (**f**) Facies from a mudstone containing numerous specimens of a single species of peridinioid dinoflagellate cyst. The sediment was deposited in a brackish water mudplain environment. Lower Cretaceous, England. (**g**) Facies dominated by fusinite-inertinite (carbonized plant remains), and conifer pollen, especially *Classopollis*, of which two tetrads are visible here. From a calcareous mudstone deposited in a basin-margin environment. Uppermost Jurassic, England. Illustrations courtesy of D. J. Batten, as published in the first edition of this book. Compare with color photomicrographs in Plates 18.1–18.3. Further instructive color photomicrographs are to be found in Li and Batten, 1995.

Figure 18.5b David J. Batten, born 26 April, 1943, in Watford, UK. Educated partly in Canada, partly in UK, he was employed first by Robertson Research and BP Int. He began his teaching career at Aberdeen University and continued at the University of Wales, Aberystwyth, where he has been emeritus professor since 2002. He has also been, since 2004, Honorary Research Professor at the University of Manchester. Dr. Batten's publications cover a wide variety of paleopalynological subjects, with heavy emphasis on Cretaceous miospores and on all aspects of the sedimentation (palynofacies studies especially) and subsequent alteration of palynomorphs (thermal alteration, etc.) in the host rocks. His contributions to the first edition of this book, and even more to the second edition, are obvious.

Much organic matter is destroyed in standard palynological maceration of rock. The classification also does not include solvent-extractable organic matter.

The literature now provides many examples of detailed description of palynodebris from all parts of the world. The most difficult to characterize is clearly the amorphous category (AOM). Such matter varies almost infinitely in color and consistency, and the differences are clearly related to environmental factors. Oboh (1992), for example, working with Miocene material from the Niger delta, concluded that abundant yellowish gel-like AOM probably indicated terrestrial origin, whereas gray AOM has been interpreted as marine in origin by various other authors. Oboh (1995) also noted a clear relationship between

Table 18.1 Classification of microscopic sedimentary organic matter (SOM) encountered in palynological preparations = palynological matter (PM)

I. Palynomorphs-proper (PP)
  A. Plant-related remains
    1. Spores (F)
      a. Megaspores ($> 200\,\mu m$)
      b. Small spores ($\leq 200\,\mu m$)
    2. Pollen (F)
    3. Green algae (F)
      a. Hydrodictyaceae coenobia
      b. Zygnemataceae zygotic spores
      c. Prasinophyceae zoospores
  B. Acritarchs (F)
  C. Dinoflagellate cysts (F)
  D. Cyanobacteria (rare as palynomorphs)
  E. Animal-related remains (= "zoomorphs")
    1. Foraminiferal chitinous linings
    2. Chitinozoans
    3. Scolecodonts
    4. Insect discrete exoskeleton parts
    5. Tintinnids, other miscellaneous animal groups
  F. Fungal spores and sclerotia
  G. Indeterminate and opaque palynomorphs

II. Palynodebris (PD)
  A. Structured organic matter (STOM) = ca. Particulate organic matter (POM)
    1. Phytoclasts
      a. Wood
      b. Cork and bark
      c. Charcoal
      d. Cuticles (F)
      e. Other plant tissues
      f. Coal maceral fragments, including vitrinite
    2. Zooclasts: fragments of arthropod exoskeletons, etc.
  B. Unstructured (= without structure) organic matter (USTOM)
    1. Amorphous organic matter (AOM)
      a. Of terrestrial origin (AOMT)
      b. Of aquatic origin (AOMA) (F)
      c. Undifferentiated gelified matter
    2. Unstructured with identifiable characteristics
      a. Resin, including amber (F)
      b. Bitumen

AOM = amorphous organic matter; POM = particulate organic matter; SOM = sedimentary organic matter; USTOM = unstructured organic matter; PD = palynodebris; PP = palynomorphs-proper, and (F), an indication that fluorescence microscopy is useful for

certain geological lithofacies and particular sorts of palynodebris, indicating correlation between environments of deposition and both lithofacies and palynofacies. Kumar *et al*. (2001), working with Cenozoic sediments of India, diagrams an interesting use of palynodebris distribution in an oil well, as an adjunct to sporomorph stratigraphy for a zonation scheme. The palynodebris categories used, such as gray-amorphous and "black debris," are employed directly, without designation of specific palynofacies.

Publications on palynofacies are encountered, in which what is essentially identical to what is termed in this book PM is called "total kerogen" or just "kerogen" (cf. Davies *et al*., 1991; Schiøler *et al*., 2002). This term has been widely used by geochemically-oriented scientists for organic matter in rocks, but not in a consistently or easily defined manner. I believe that Batten's (1996a) brief discussion of kerogen classifications, that attempts to establish a meaningful translation of sorts of "kerogen" into PM terms will not be scientifically productive. I have the same opinion, therefore, of Tyson's (1993;1995, pp.16–23) discussion of "kerogen" in connection with palynofacies. The existing "kerogen" classifications need to be redefined and given new designations to reflect more clearly the actual substances present, if they are to be meaningful in terms of palynofacies. In the meantime, I regard "kerogen" as a confused term that should be avoided in palynological work.

3 Palynofacies

3.1 Nature and Applications of Their Study

When I was writing the first edition of this book in the mid-1980s, it was already known that study of what we now call total PM (palynological matter) of sedimentary rocks was potentially a very important adjunct of basic paleopalynology. Batten (1973, 1980, 1981a, 1982) had proposed palynofacies as assemblage types of PM in palynological maceration residues. Combaz (1964) had even earlier defined the palynofacies concept, as the general aspect of the organic matter in our preparations. This fundamentally geologic concept did not completely replace the use of "palynofacies" in a biological sense of a palynoflora dominated by a certain taxon or by taxa of palynomorphs. However, the more geological concept of palynofacies as consisting of the total palynological matter

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(Table 18.1, contd.) interpretation of that category of microscopic organic matter. Color can be used as an additional identifying character, as "dark brown wood" under IIA1a, for example. Conflated and expanded from Traverse, 1994b–Introduction, and Batten, 1996. Acronyms mostly from Batten, 1999. Note: PM is called "POM" by some authors; POM should be reserved for particulate organic matter.

(PM–see Table 18.1) of a rock sample is now more general. I (Traverse, 1994b-Introduction, 1999) have suggested distinguishing these two kinds of palynofacies. As explained in the introduction to this chapter, I would call the kind now more commonly used in geosciences, dealing with the organic load of sedimentary rock as particles with certain characteristics, rather than as biologic entities, *palynolithofacies*. Palynofacies in which the emphasis is on the fact that they are dominated by certain taxa of palynomorphs representing particular organisms I would call *palynobiofacies*. Even when palynomorph or phytoclast taxa are mentioned by name or used to name a palynolithofacies, it is still not necessarily a biological palynofacies, in the sense of one that carries ecological or other biological information about the environment of deposition.

In the early history of palynofacies research, many made contributions to the study of palynofacies, even though the word may not appear in the publications. Caratini *et al.* (1983) emphasized the significance of the agents and conditions of transportation to the assortment of what we call here PM in a sediment, and introduced useful methods for diagrammatically representing the color and size of the particles. Leopold *et al*. (1982) showed that a palynofacies does not necessarily reflect the biologic environment of the area near the basin of deposition but instead can be produced by a variety of geological and geochemical taphonomic processes associated with sedimentation. This sort of palynofacies is a product of the total sedimentary environment and is unlikely to be a palynobiofacies.

It is characteristic of the palynofacies concept, as noted by Batten (1996) that the mix of PM classified in Table 18.1 can be almost infinitely variable, in response to a great variety of geological/geochemical factors. This makes the study of palynofacies very challenging, and also potentially very rich in information yielded. The reader would do well to use Tyson (1995) and Batten (1996 and 1996a) to get a more complete grasp of the subject than this part of one chapter can present here. It is obvious that evolution of life forms has a huge impact on the sort of palynofacies to be expected in sedimentary rocks. In the Cambrian and Ordovician, for example, the rocks may yield massive amounts of AOM based on acritarchs and marine algae, but the continents were devoid of vegetation or nearly so, and POM phytoclasts of terrestrial origin are a zero factor.

3.2 Methods of Study and Presentation of Data

Batten (1996) and Batten and Stead (2005) have pointed out that it is more true even than it is for other aspects of palynology that processing methods for palynofacies investigations must be carefully controlled for uniformity, to prevent processing from creating subtle differences in apparent PM content. Batten has also pointed out in the same connection that raw, unoxidized, "uncleaned" residues should be used for palynofacies research, unlike the preparations that one would

normally use for palynomorph description. Batten also cautions against over-interpretation of what is really semi-quantitative data. He thinks that multivariate statistics of various sorts should be employed with caution in palynofacies studies for this reason–artificial groupings of data points are too easily generated. The classification and terminology of PM has still not completely jelled, although there is much progress in that direction.

Some palynologists designate their palynofacies categories largely on the basis of the dominant palynomorph taxon, even though the facies are not biological in their meaning (cf. Turnau and Racki, 1999), and PM is still being classified by some in terms of "kerogen" sub-divisions, even though, as pointed out earlier, "kerogen" is a very slippery term. Jäger (2002), in contrast, uses in part coal-petrographic terminology (cutinite, vitrinite, inertinite) in subdividing PM of his palynofacies. Hooker *et al*. (1995) do a fine palynofacies analysis without ever referring to it as such. It clearly will help in the application of of palynofacies studies to geologic problems to move toward uniform methodology and uniform classification. It is also remarkable that the literature contains so few examples of efforts to graph palynofacies occurrences in at least a semi-quantitative manner. Instead, most palynofacies publications simply present descriptions, note maximal and minimal occurrence and present the information in verbal, tabular form. A fine example of what could be done is a figure from Vigran *et al*. (1998), which is displayed here in abbreviated form as Fig. 18.6. Another excellent example of palynofacies graphical display is to be found in Mørk *et al*. (1999).

Palynofacies research is one of the best examples of which I am aware, of applied taphonomy research, as the processes by which the fossil raw materials reach the rocks, and the condition in which they get there, are all aspects of the post-life chemical, physical and spatial changes affecting the final assemblage. In the case of many dinocysts and other marine-origin palynomorphs, their contribution to a palynofacies is often also a thanatocoenosis–a death assemblage of fossils found more or less where the producing organisms lived. Although it does not deal specifically with paleopalynology, the article by Holz and Simões (2005) is valuable reading, in connecting taphonomy to sequence stratigraphic analysis, one of the main applications of palynofacies studies.

3.3 Examples of Applications to Geological Problems

3.3.1 Stratigraphy

Batten and Stead (2005) point out that a carefully analyzed palynofacies is shown to represent a particular environment of deposition, based on the original organic matter of the fossil matter and on all of the taphonomic factors that have impacted them. The palynofacies produced, if well defined, can be recognized in sections of sedimentary rock and used as a stratigraphic marker. Jäger (2002) shows, for a Mississippian section in Germany, that characteristic palynofacies permit

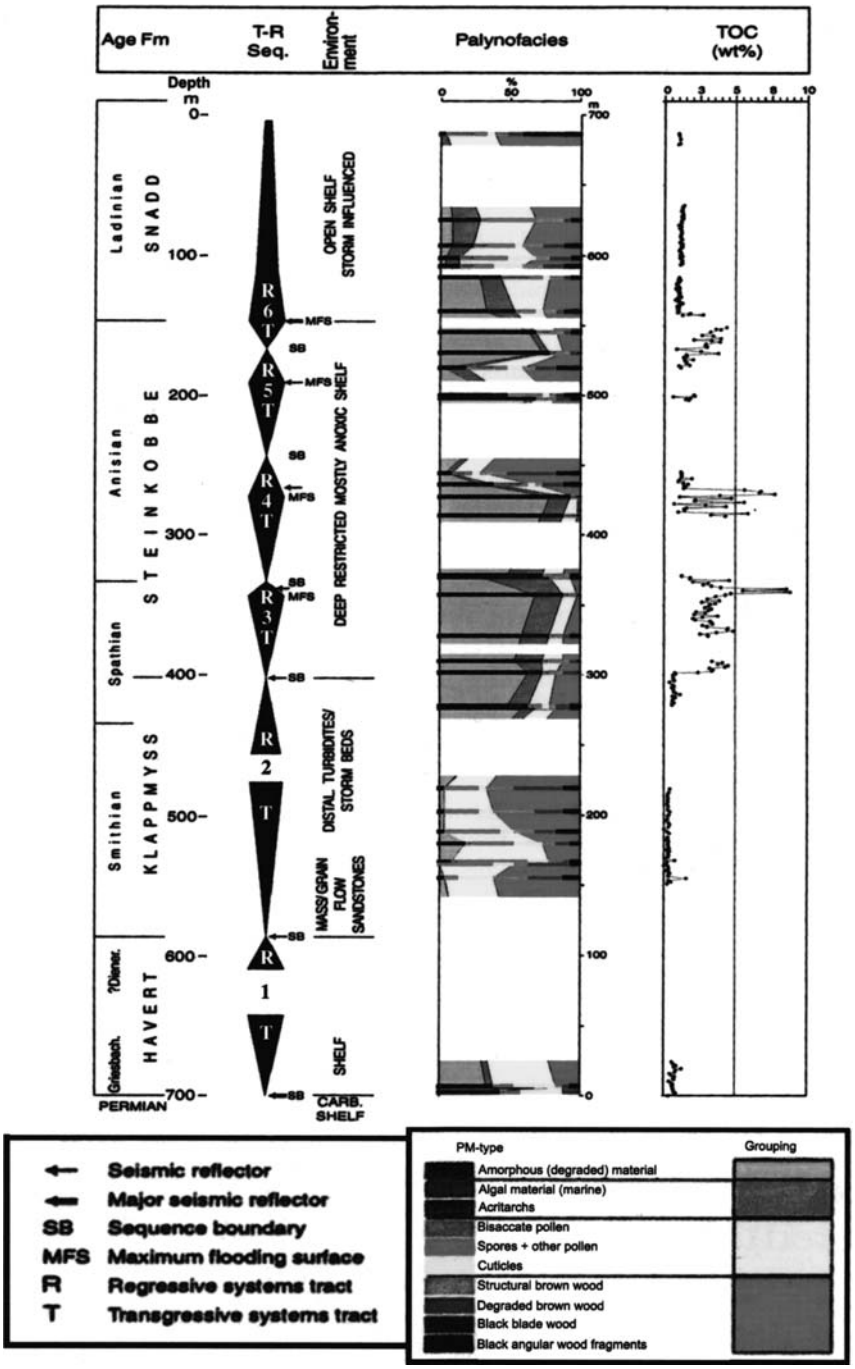
Age Fm
T-R Seq.
Environment
Palynofacies
TOC (wt%)
Depth m
Ladinian
SNADD
Anisian
STEINKOBBE
Spathian
Smithian
KLAPPMYSS
?Olenek.
Griesbach.
HAVERT
PERMIAN
OPEN SHELF STORM INFLUENCED
DEEP RESTRICTED MOSTLY ANOXIC SHELF
DISTAL TURBIDITES/ STORM BEDS
MASS/GRAIN FLOW SANDSTONES
SHELF
CARB. SHELF
MFS
SB
Seismic reflector
Major seismic reflector
Sequence boundary
Maximum flooding surface
Regressive systems tract
Transgressive systems tract
PM-type
Grouping
Amorphous (degraded) material
Algal material (marine)
Acritarchs
Bisaccate pollen
Spores + other pollen
Cuticles
Structural brown wood
Degraded brown wood
Black blade wood
Black angular wood fragments

Figure 18.6

relatively easy recognition of significant parts of the section, in various parts of the area, sometimes aided by information based on the known ranges of palynomorphs from the PP part of the PM. Palynofacies can also play a role in recognition for stratigraphic purposes of correlatable transgression and regression levels in sequence stratigraphy (see discussion below). Several authors have sought to correlate palynofacies oscillations with astronomically based Milankovitch orbital forcing cycles (cf. Marshall, 2000; Waterhouse, 1995, 1999). Waterhouse indicates that the palynofacies cycles can be detected even when lithological data for the same sections do not show them.

3.3.2 Environmental Factors

Roncaglia (2004), working on sediments in the Faroe Islands, has shown that palynofacies analysis can be used to indicate the oxygen content of water in which the PM was deposited. AOM was found to be a negative proxy for oxygen content. That is, high AOM indicates relatively low oxygen and high nutrient values in the original water at the time of deposition. Nutrient abundance is also related to abundance of dinocysts in the PP. Oboh (1992), working in the Niger Delta region, found significant correlation of palynofacies and original sedimentary types, but it is clear that does not mean that one can automatically link particular sedimentary environments, as reflected by lithology, with specific "species" of palynofacies, from one region or one time-frame to others. Gastaldo *et al*. (1996) and Gastaldo and Staub (1997) showed in a modern Sarawak delta that a variety of geological lithofacies and palynofacies did not dependably correlate with each other, from one location to another. However, Tyson and Follows (2000) found in Upper Cretaceous sediments of Spain that palynofacies characteristics could be used to show the distance of the deposition site from the sediment source, based not on counts of particular sorts of PM, but on sophisticated measurements of the constituent particles as to size, shape and state of preservation. Perhaps future research will show that such precise measurement is an essential part of palynofacies study.

Figure 18.6 An example of the diagraming of palynofacies as color plots. The colors show the categories of palynomorphs and palynodebris, per Table 18.1. T-R diagrams to the left show the sequence stratigraphic classifications of the sediment penetrated by the core. Environmental classification related to the sequence stratigraphy is also displayed on the left. TOC (total organic carbon) at the right represents the most critical information for petroleum source rock potential. Lowest Triassic (Griesbachian) is shown at the bottom and upper Middle Triassic (Ladinian) at the top of the 700 m core. Fm = formation. The basic diagram from which this illustration was abstracted is from Vigran *et al*., 1998, and is printed here with permission of the authors and of the Amer. Assoc. Strat. Palynol. Foundation.

3.3.3 Use in Sequence Stratigraphy

Sequence stratigraphy is based on recognition of correlatable transgressive (flooding) and regressive surfaces in sedimentary sequences. In general (Haq *et al*., 1987) such surfaces are related to worldwide eustatic change in sea level, but some similar phenomena have been attributed in some places as to local tectonic activity.

A succinct, readable summary of the origin and significance of sequence stratigraphy was published when most palynologists had hardly heard of it by Sloss (1988). I would strongly recommend the reading of Jones *et al*. (1993) for a very good summary of sequence stratigraphic concepts in connection with sedimentology and paleontology, including palynology. Tyson's (1995) chapter 24 is also good basic reading for an understanding of the linkage between palynofacies and sequence stratigraphy in general.

Palynofacies have proven very useful in identifying the various sequence tract surfaces. This was recognized by Jones *et al*. (1993), in which the palynological characteristics of system tracts are explained. Schiøler *et al*. (2002), for example, used palynofacies studies to good advantage in following sequences of sea level changes in New Zealand, even though they do not correlate well with the standard Haq worldwide cycles and seem instead to be tectonically controlled. Oboh-Ikuenobe *et al*. (2005), working in the Niger Delta area of west Africa, used palynofacies in conjunction with lithology and sedimentary structures to identify environments of deposition that characterize various sequence surfaces. Batten (1999) similarly urges the integration of palynofacies information with all possible geological data, which would include geochemical (TOC–total organic carbon and HI–hydrogen index) and geophysical (electric log) measurements, in identifying sequence stratigraphic surfaces. Batten and Stead (2005), in a concise but informative presentation on palynofacies and sequence stratigraphy, note that lowstand system tracts (LST) are typically indicated by palynofacies with large phytoclasts and partly oxidized sporomorphs. Transgressive system tracts contain palynofacies with more dinocysts, and highstand system tracts (HST) have palynofacies with much AOM and abundant dinocysts. Vigran *et al*. (1998), working in the Triassic of Norway, also emphasize that transgressive tracts mostly have palynofacies with very high AOM. They found that their palynofacies correlated poorly with specific tracts on a one-to-one basis, but that they correlated very well with TOC concentrations and therefore with petroleum potential (see also the next sub-section). It is interesting that Molyneux (2005), working in the Early to Middle Ordovician, finds that transgressions/highstands show microphytoplankton diversity maxima on the platforms, but that in regressions the diversity maxima apparently retreat to the continental margins. At that time there was little or no continental vegetation. Batten and Stead (2005) illustrate their paper with diagrams from the literature, showing kinds of POM and palynomorphs and other data associated with sequence tract identity for a well

in the Cretaceous of Ecuador. Abbink (1998) and Abbink *et al*. (2004a, 2004b) illustrate and describe an extensive study in the Jurassic of the Netherlands North Sea of the interplay between vegetation, as indicated by palynology of an exploration well, and sequence stratigraphic stands of sea-level. The summary diagram for this work is shown here as Fig. 18.7.

3.3.4 Applicability to Petroleum Source-rock Exploration

Batten (1999) points out that palynofacies information is very useful in identifying potential source rocks for petroleum exploration. He notes that correlating palynofacies data along with TOC (total organic carbon) and HI (hydrogen index) information is a good approach for evaluating the total effect of processes that result in hydrocarbon accumulation in sediments. TOC is especially important for source rock formation–most are in the 2–10% range. Sediments with less than 2% TOC are usually found to be barren or contain only gaseous hydrocarbons. (It is interesting in this connection that Nichols (2005) reports a connection between certain kinds of fossil pollen and gas-prone rock types.) On the other hand, TOC of more than 10% is a rare phenomenon in extensive sequences (Batten, 1996a). Mehrota, *et al*. (2002) point out that high total carbon does not necessarily mean high petroleum source potential, as the carbon could consist of dark woody material, which is very poor indicator for oil. A small percent of TOC consisting of AOM of marine algal origin is a much better indicator. Tyson (1996) concluded that the best source rock coincides with the maximum flooding surfaces identified in sequence stratigraphy.

Al-Ameri and Batten (1997) found that platform environments with a palynofacies containing more than 50% AOM are indicative of high petroleum potential, and Al-Ameri *et al*. (2001) also note the high potential of platform sediments, i.e., high water sediments. It is significant (cf. Batten, 1996) that AOM is dominant in palynofacies accumulating in anoxic situations. Vigran *et al*. (1998) found that their transgressive levels were mostly high in AOM and in TOC and are potential source rocks. Their levels with high sporomorphs and STOM are low in TOC and poor in source rock potential. Batten (1996) says that high amounts of structural matter (STOM) such as phytoclasts and sporomorphs are poor indicators for source rocks, and brown-black woody matter and evidence of reworking in the palynofacies of non-marine sediments are very negative indicators.

4 Amounts of Palynomorphs in Sediments

The concentration of palynomorphs in sedimentary rock is extremely variable. It is near zero in well-sorted sandstones (even if the sandstone contains much black organic matter–often it consists of sand-size particles of the coal maceral vitrinite) and claystones. “Dirty,” that is poorly sorted, claystones and sandstones are often rich in palynomorphs. The concentration can reach 5 million(!) per gram

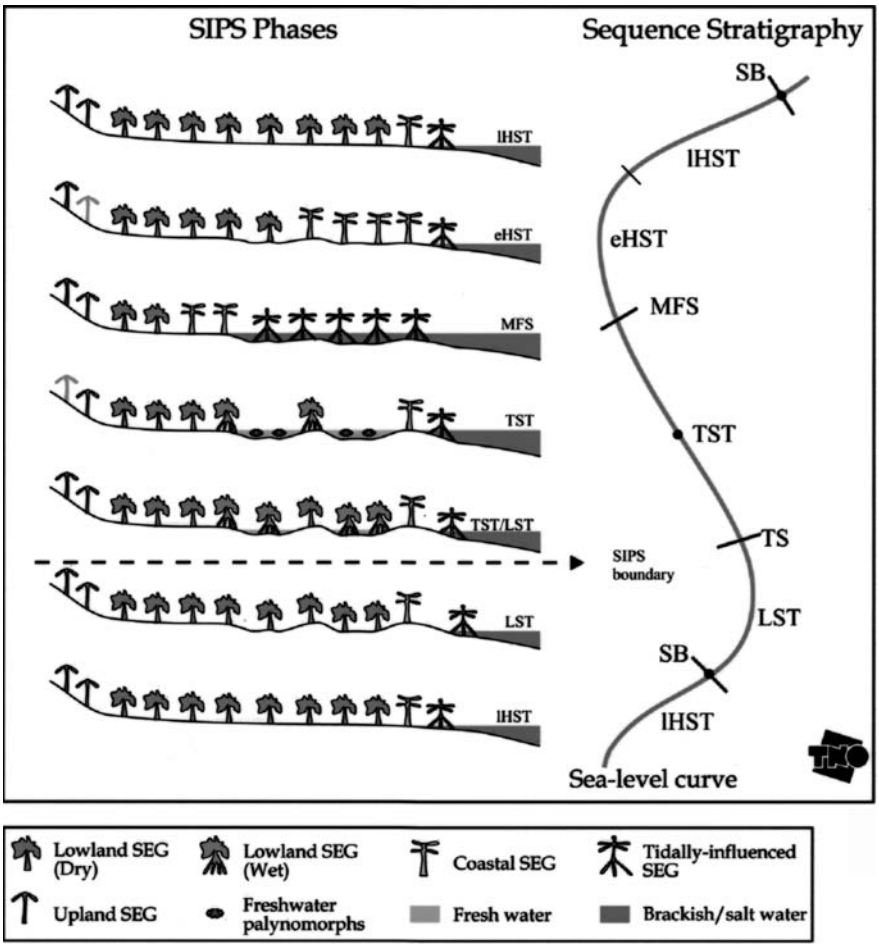

Figure 18.7 Diagrammatic summary of the SEG (Sporomorph Eco Groups) phases within a sequence stratigraphic framework recognized by Abbink (1998) and Abbink et al. (2004a, 2004b). The framework is that of Jurassic sediments of the Netherlands North Sea area, as related to sequence stratigraphic sea-level stands. Each of the SEG phases represents a distribution of vegetation as represented by the palynomorph content of the sediment produced over the area represented by the exploration well studied. Lowland SEG: lowland communities representing fresh water swamps or plains, periodically flooded, but with little or no salt water influence; Coastal SEG: vegetation of the coast, constantly subject to salt spray; Tidally influenced SEG, tidally influenced vegetation, regularly submerged; Upland SEG: vegetation of higher terrain, never flooded. Other acronyms on the diagram: SIPS = sea-level induced palynomorph successions; SB = sequence boundary; lHST = late highland systems tract; eHST = early highland systems tract; MFS = maximum flooding surface; TST = transgressive systems tract; TS = transgressive surface; LST = lowland

of sediment (or rarely even more) in some sorts of coal and some organic marine sediments (about 5 million dinoflagellates per gram in some cores of Black Sea sediment; see Fig. 18.8). Reinhard *et al*. (2006) report millions per gram, for example 6.7 million per gram of the one species, *Zea mays*, in human coprolites of individuals who had obviously been consuming pollen as a food. An average figure for a productive siltstone is about 10,000/g. M. B. Farley (personal communication) calculates mathematically that, with perfect packing, a 30 μm spore (flattened), with walls 2 μm thick, could theoretically attain a density of about 170×10^6/g, about an order of magnitude more than is ever observed in nature.

Concentrations of 100,000/g are common in some deltaic shales-siltstones: Habib (1982a) estimates 40,000-100,000/g for carbonaceous clays and silty clays. Bahamas Bank calcareous silts ("muds"), on the other hand, contain of the order of 1,000/g or less. Koreneva (1971) found only a few hundred or less per gram in most Mediterranean surface sediment. Melia (1982,1984) reported only 2,000/g in ocean sediment off the west coast of Africa and only 50/g in deep ocean basins. Most limestones contain very few palynomorphs; dolomites are almost always barren, probably because of secondary recrystallization effects.

This statement about dolomites is based largely on an (unpublished) experiment I did about 1960, when I was working for Shell Development in Houston, Texas. I processed something like 40 samples of dolomites from various continents, rocks selected for relatively high organic content, and got not one palynomorph other than obvious atmospheric contaminant modern pollen. Spores/pollen have been obtained from bedded salt (Klaus, 1955), but saltdome salt, presumably transported, is normally barren. Spores/pollen have been reported from petroleum, especially in China and the former Soviet Union (Jiang and Yang, 1980; Yang and Jiang, 1981, Jiang, 1991 and 1996, McGregor, 1996), but the concentration is extremely low, less than 0.1/g (!). Despite the very small numbers of specimens, recovered from large samples of oil, studies of palynomorphs in petroleum have potential importance for tracing the paths of petroleum to and from source rocks. In addition to the publications just cited, Jankauskas and Sarjeant (2001) report that B. V. Timofeyev of the (former) USSR pointed out as early as 1953 that petroleum often contains palynomorphs older than the rocks from which the oil was obtained. Because oxidation destroys sporopollenin and chitin, soils and redbed sedimentary rocks, regardless of particle size, are almost always barren.

Weathered outcrops are also likely to be barren, even if the same rocks are productive from material cored nearby. Kuyl *et al*. (1955) reported tropical areas in which outcrops were weathered and barren to a depth of over 10 m. (Weathering

◄

Figure 18.7 systems tract. Figure reproduced here from Fig. 11 of Abbink (1998), by permission of O. A. Abbink, and of his co-authors in the 2004 papers cited above: J. H. A. Van Konijnenburg-Van Cittert, H. Visscher, and C. J. Van der Zwan.

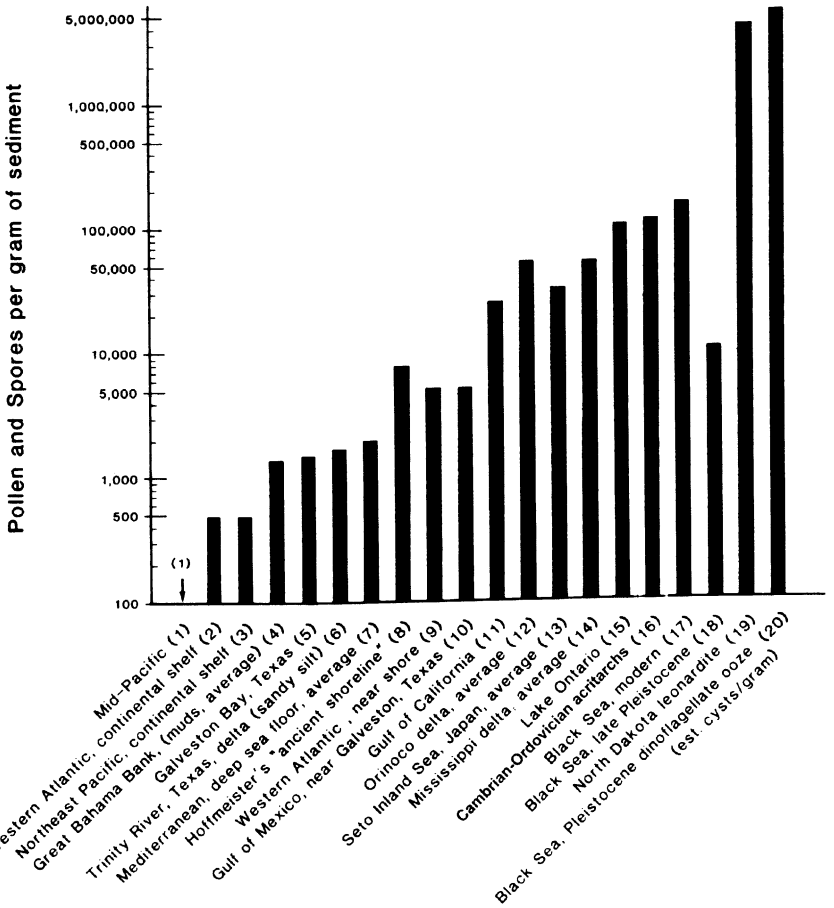

Figure 18.8 Concentration of pollen and spores per gram of sediment in various situations, plotted logarithmically. Deep oceanic sediments are practically barren. Nearshore sediments range around 1,000–5,000/g, being higher near river discharges. Lakes and inland seas are about an order of magnitude higher. Comparison of Black Sea modern sediment with late Pleistocene sediment from the same locations (see data bars 16 and 17) is instructive. With current high stand of the Black Sea, rivers are bringing relatively less mineral sediment than in the Pleistocene when water level was lower and the streams rejuvenated. Thus, if one assumes delivery of spores/pollen to the feeder streams to have remained relatively constant, we can explain the fact that the numbers of palynomorphs per gram of sediment are much higher now than in the late Pleistocene. The maximum concentration of palynomorphs per gram, found in some fossil "oozes" and in some coals, is in the 5,000,000/g range. Sources for data: (1) Koreneva (1964); (2) Stanley (1965); (3) Heusser and Balsam (1977); (4) Traverse and Ginsburg (1966); (5 and 6) Traverse, unpublished data; (7) Rossignol-Strick (1973); (8) Hoffmeister (1954); (9) Heusser (1983), Mudie (1982); (l0) Traverse, unpublished data; (ll) Cross *et al.* (1966); (12) Muller (1959);

is one source of difficulty for palynology of archeological materials, which are often soils or soil-like. The concentration of spores/pollen is usually abysmally low. Special preparation techniques start with samples much larger than normal, yet even so, much archeological palynology seems to depend on disturbingly small numbers of palynomorphs.

Outcrop samples of shale are frequently barren or have only poorly preserved palynomorphs because of oxidation-weathering, whereas cores taken nearby of the same horizon yield abundant, well-preserved palynomorphs. Because of the carbonization of chitin and sporopollenin by temperatures greater than 200 °C, palynofloras that will permit study are not obtained from rocks cooked by lava flows or intrusions. Similarly, the geothermal gradient results in very carbonized (dark) palynomorphs in deeply buried sediments, and no well preserved spores/pollen occur below about 5,500 m, even in areas with very low tectonic activity. Rock metamorphism of all kinds progressively destroys palynomorphs, so that low-volatile bituminous and anthracitic coals are barren, while closely associated high-volatile bituminous coal from the same stratigraphic level has abundant spores/pollen. Evidence of folding and faulting such as slickensides are nearly always contrary indicators, as also are evidence of cleat, cleavage, induration, and recrystallization in rocks.

5 Reworking, Recycling, "Stratigraphic Leak" and Other Instances of Discordant Palynomorphs

The splendid toughness of chitin and sporopollenin make for some perhaps unexpected problems, as well as opportunities in paleopalynology. Reworking, even recycling several times in geological history is characteristic of palynomorphs. This is one of the most important aspects of taphonomy, and it is the more significant, the more robust to the chemical and physical processes in nature the fossil group is. Weathering and erosion of siltstones release massive amounts of spores/pollen and other palynomorphs by simple disaggregation of the sediments. Sediment samples from off the Mississippi River delta contain not only spores/pollen from extant vegetation of the whole Ohio River-Missouri River-Mississippi River drainage but a grand assortment of reworked spores/pollen and other palynomorphs from Devonian on up. Kemp (1972) has noted the presence in sediment of the West Ice Shelf, east Antarctica area, of abundant spores/pollen and microplankton of Permian, Cretaceous, and Paleogene age. Rao (2005) describes

◄

Figure 18.8 (13) Matsushita (1982); (14) Darrell and Hart (1970); (l5) McAndrews and Power (1973); (16) Dorning (2005), who notes a drop of ca. two orders of magnitude in the Silurian; (17) Traverse (1974b); (18) Traverse (1974a); (19) Traverse *et al.* (1961), (20) Traverse, unpublished data.

reworking of Permian and Cretaceous sporomorphs into Miocene sediments of India, yielding rock with pollen and spores of three Eras. A very curious example of "catastrophic" reworking is that of Edwards and Powars (2003), who reported that the Chesapeake Bay bolide of Late Eocene time in coastal Virginia spewed Cretaceous, Paleocene and Eocene rock over a wide area that is now covered by post-Eocene sediments. Presumably many bolides have done the same thing in other places at other times.

Collinson *et al*. (1985) have described the reworking of Paleozoic and Mesozoic megaspores into Paleocene deposits of southern England, along with Cenozoic megaspores belonging to the time of deposition. Obviously the sediment included a fraction with clastics in the sand-size range, and the megaspores of various ages were sorted into this fraction.

There are numerous illustrations of the seriousness of the reworking problem. Chowdhury (1982) noted that up to 30% of the surface spores/pollen in German North Sea sediments are redeposited forms, as old as Carboniferous. It is easy to recognize a reworked Pennsylvanian *Densosporites* in a modern sediment as recycled, but a *Carya* pollen grain reworked from an interglacial Pleistocene terrace or from the Pliocene, is a different matter. Utting *et al.* (2004) present especially unsettling examples of reworking in many northern circumpolar areas, in which Devonian, Carboniferous, and Permian palynomorphs are found reworked into Triassic sediments on a large scale. Utting *et al*. even suggest that some formally named Triassic sporomorphs are actually reworked Devonian forms! Spores/pollen are capable of repeated "recycling," though more than one cycle lessens the relative abundance of reworked fossils and also corrodes the fossils more, so that they are easily recognizable as redeposited. Wilson (1976) documents a case from the Pennsylvanian of Oklahoma in which recycled forms of Ordovician-Mississippian ages, and from both marine and non-marine environments are regularly present. As Muir (1967) has pointed out, spores weathered and eroded from sedimentary rock are usually (but not always!) more carbonized than fresh palynomorphs and hence may be chemically more resistant to oxidation during processing, but also much more brittle. The percentage of reworked fossils is usually smaller than that of contemporaneously produced spores/pollen. Reworking in peat–hence in coals–is practically non-existent; nearly all of the spores/pollen come from the vegetation where the peat was produced. The palynoflora is therefore characteristically autochthonous. However, some interesting studies have been made of spores carried within pieces of coal into younger sediments. For example, Bartlett (1929) studied megaspores from pieces of Pennsylvanian coal reworked into Pleistocene glacial drift in Michigan.

Muller (1959) found in the recent sediments of the Orinoco delta that reworked forms are normally a small percentage of total palynomorphs in shelf sediment, but may be very high in delta levees. However, reworked spores/pollen can sometimes be a high percentage of the total palynoflora. I once studied a sample

of siltstone from upper levels of sediments of the Gulf of Mexico which was more than 90% reworked: the sediment was Holocene, but the palynomorphs were Paleogene. The sample probably consisted mostly of a pebble of Paleogene shale saltated into the recent sediment. Reworked palynomorphs have provided clues as to direction of stream-transport and sediment source, e.g. for a Cretaceous conglomerate, determined from Mississippian spores/pollen in certain of the conglomeratic clasts. Fleming reports that Cretaceous pollen in Pliocene formations of southern California supports the contention that the Grand Canyon was mostly cut in the Pliocene, rather than earlier in the Cenozoic, and it must have been much wetter in the Pliocene than it is today. Needham *et al*. (1969) reported use of reworked Carboniferous palynomorphs as tracers of sedimentation patterns in the northwest Atlantic. In the Black Sea, reworked spores/pollen are much more abundant in surface sediment formed during the last glaciation than they are now, presumably because streams rejuvenated by glacial drop of sea-level delivered far more sediment derived from weathered and eroded sedimentary rock than is now the case (Traverse 1974b; see Fig. 18.9). Riding (2005) has reported that glacial periods in the UK also caused rejuvenation of streams and much erosion and coincident reworking of palynomorphs from the prevailingly palyniferous sedimentary rocks of the UK. This makes it possible to trace the sediment provenance of Pleistocene rocks, for example in East Anglia.

When palynomorphs of discordant age occur in sediments, the usual situation is reworking of older material into younger: the discordant forms are the older. However, sometimes one finds discordant forms that are younger than the associated rock. This is called "stratigraphic leak" and can be caused in several ways:

(a) Artificial contamination: For example (Traverse *et al*., 1961), drilling muds are frequently composed partially of partly oxidized coals such as the naturally occurring leonardite (Paleocene, North and South Dakota). Drill cores and well rock-cutting fragments where such "mud" was used will be coated with, and cracks partly filled with, mud, which may be difficult to remove before processing. Thus, a Triassic core can be heavily charged with Paleocene spores/pollen, as leonardite, for example, may contain 5 million spores/pollen per gram! In addition to drilling mud additives, the circulating drilling mud also includes a mixture of particles from horizons stratigraphically above the drill bit, and these can also occur in drilled samples, just as does the drilling mud additive. These are reasons why sidewall cores are preferable to drill cuttings for paleopalynology.
(b) Natural percolation of weathered-out spores/pollen from superficial rock.
(c) Deposition in karst topography: One of the first examples of this to be observed was a Devonian miospore palynoflora from fissure fillings in a Silurian limestone reef in Illinois discovered by Guennel (1963). Another example of this sort of stratigraphic leak is the Independence Shale of

Iowa (Urban 1971), in which Mississippian and reworked Devonian spores were deposited in Mississippian time in caves in Devonian limestone, producing shales with a partially Mississippian palynoflora, occurring within the Devonian limestone sequence. A younger case is that of a Jurassic palynoflora found in Carboniferous limestones of Ireland (Higgs and Beese, 1986), indicating karst formation in the older limestone, in Jurassic time.

Discordant palynofloral elements may result from mass movement of sediment, of which the best example is the intrusion of saltdomes into sediment above. Often large amounts of sediment are thereby intruded. Ecke and Löffler (1985) for example, described a situation in Germany in which Zechstein (Upper Permian) evaporite penetrated and mixed with Röt (Lower Triassic) evaporite, resulting in a mixture of Permian with Triassic palynomorphs. Similarly, a melange rock can contain blocks of sedimentary rock of quite disparate age picked up in the course of the tectonic processes that produced the Franciscan Melange of California, for example (Traverse, 1972). In both this case and in a conglomerate, careful sampling can separate the rock fragments producing disparate palynofloras, so the palynofloras are not really mixed as they are when reworking represents weathered and eroded material.

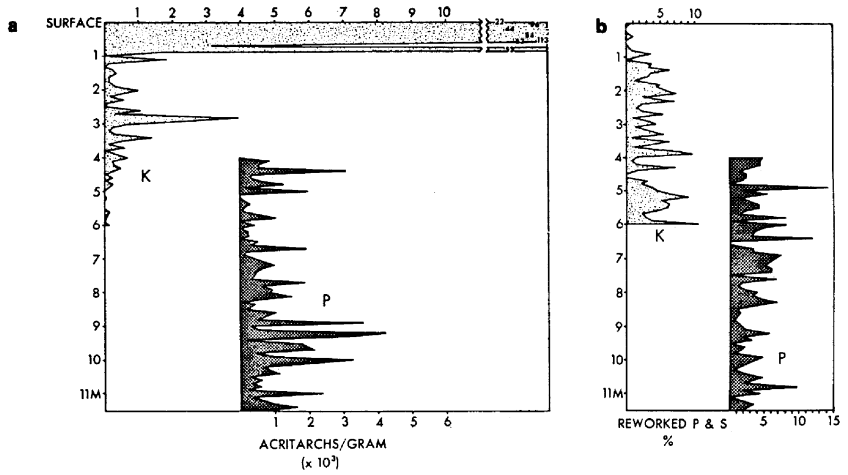

Figure 18.9 Reworked (recycled) palynomorphs, because of the toughness of sporopollenin and chitin, are a very frequent occurrence in paleopalynology. At times, they even are revealing as to the source of sediment in a rock, or in other ways. (**a**), (**b**) Palynomorph counts from overlapping sediment cores (K and P) from the Black Sea, representing about the last 25,000 years of sedimentation. As the Black Sea now is connected to the

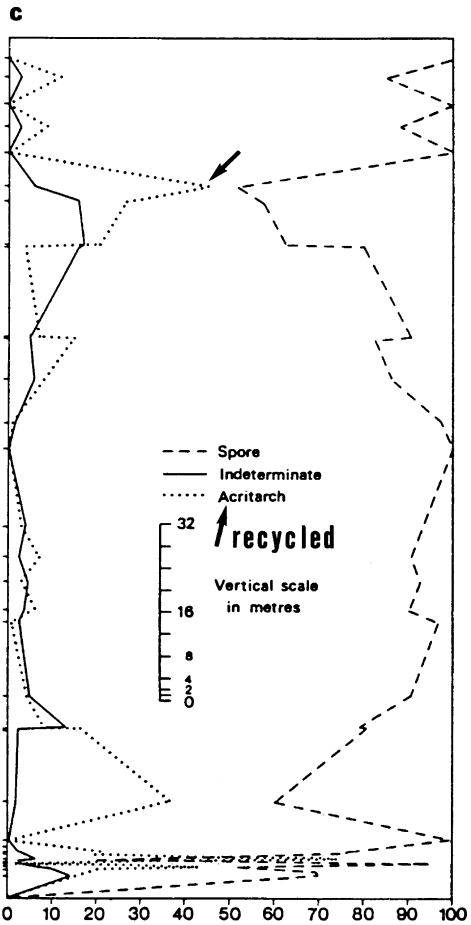

Figure 18.9 Mediterranean because of Holocene high sea level, amounts of palynomorphs per gram of sediment are very high–less sediment increases the concentration of fossil palynomorphs per gram of sediment (see acritarchs per gram in (a)). Before the present high sea level was reached, the streams in the basin were more actively bringing in sediment, and the large amount of sediment caused palynomorphs per gram to be less than is now the case. At the same time, as shown in (b), the percentage of reworked forms has markedly dropped in the late Holocene, because lower erosional rates are coupled with lower amounts of recycled palynomorphs. (**c**) In a study of non-marine Lower Devonian spores in England, Richardson and Rasul (1978) found abundant Ordovician and Silurian acritarchs, clearly reworked on the basis of both age and original environment. Because of differences in carbonization level, it was demonstrable that the Devonian streams providing sediment for the Lower Red Sandstone eroded source rocks of at least four different ages. Note toward the top (arrow) a level at which reworked acritarchs are about 50%. (a) and (b) are from Traverse, 1974b; (c) is reproduced from Richardson and Rasul, 1978.

Detection of reworked forms varies from exceedingly easy to very difficult. The detection depends fundamentally on incongruence/discordance.

5.1 Preservation Discordance

Reworked palynomorphs are usually (but not always!) more poorly preserved than the palynomorphs that came into the basin of deposition from contemporaneous vegetation. This can be picked up from corroded, ragged or thin walls, or a different natural color. Stanley (1966) noted that reworked palynomorphs often stain differently and proposed the practical use of this detection method: he used safranin-O and showed that reworked forms could stain either more or less intensely, and showed that reworked forms have ektexine vs. endexine staining characteristics differing from those of the non-reworked forms. Presumably this is a reflection of oxidation- alteration during weathering. Staining often works, but it is tricky to apply with certainty, especially where the problem of detection is most severe, with, say, Pliocene into Pleistocene. Fluorescence microscopy can sometimes demonstrate a difference in fluorescence-level between "native" and reworked palynomorphs. Drilling mud palynomorphs–"artificially reworked"–are often much better preserved than the "native" fossils. For example, abundant late Cretaceous spores/pollen in Triassic well-cuttings may stand out because the "native" Triassic forms are carbonized darkish brown whereas the probable drilling-mud forms are yellowish and much better preserved. Richardson and Rasul (1978) were able to use carbonization (TAI) differences to indicate different sources for Ordovician-Silurian acritarchs reworked into Devonian sediment (see Fig. 18.9), but Legault and Norris (1982) found that Devonian spores/pollen reworked into Cretaceous sediments were more damaged by the experience than were Devonian acritarchs associated with them. Utting (1994) records abundant reworking of Permian into Triassic in the Canadian Arctic but notes (personal communication) that TAI differences between reworked and *in situ* palynomorphs were only sometimes useful. In other instances there was no significant difference in this character between reworked and *in situ* fossils. Whether this is a universal situation is not known. On the other hand, reworked dinoflagellate cysts in some Cenozoic Arctic palynofloras are reported to be sometimes better preserved than the "native" palynomorphs. Abundant Cretaceous pollen and spores more than 70 million years old found in Pleistocene/Holocene deposits in New Jersey by Rue and Traverse (1997) are much better preserved than the palynomorphs derived from plants at the time of deposition of the sediment a few thousand years ago. The reworked Cretaceous sporomorphs were somewhat carbonized in the rocks where they originally occurred and were therefore more resistant to corrosion than the fresh grass and other modern pollen with which they were sedimented. However, it should be noted that Utting (1994) observes that such a situation can be the result of the reworked material reaching the site of sedimentation in

small rock clasts, in which case the reworked palynomorphs are protected from corrosion during lithification. Wood *et al*. (1992) reported an extensive study of the impact of reworking in a number of sections in South America and Asia. They found that reflectance studies of vitrinite in the samples sometimes show a bipolar distribution, indicating vitrinite with different thermal histories and thus showing reworking. The indications from the palynodebris agreed with palynomorphs of different ages, a matter of concern in the following section.

5.2 Stratigraphic or Ecological Discordance

Pennsylvanian or Devonian spores/pollen in a Cretaceous sediment will usually stand out like a sore thumb. However, for some generalized forms, e.g., psilate or scabrate trilete spores, this is not the case. Marine dinoflagellates in a non-marine sediment is another case of reworking which is easy to detect. In other instances, e.g., well-preserved recycled Cretaceous spores in the Neogene of Black Sea cores, it is much trickier. There are examples of palynologists being fooled by such a combination into suggesting an intermediate age! It should also be emphasized that reworking can be complicated by multiple episodes of recycling. Legault and Norris (1982) studied a Pleistocene-Cretaceous-Devonian sequence in which Devonian palynomorphs were reworked into the Cretaceous, and, later on, Cretaceous and Devonian together reworked into Pleistocene.

Chapter 19

Some Factors Affecting Practical Applications of Paleopalynology

1 Post-depositional Alteration of Palynomorphs: Thermal Maturation (= "Carbonization")

Although sporopollenin and chitin are very tough materials, they are not indestructible. Post-depositional oxidation (weathering) can corrode or even destroy palynomorphs. Furthermore, post-depositional heating causes chemical changes. These are of the same sort as affect organic matter generally, e.g., in coal beds. Just as the coal series proceeds from peat to anthracite by grades, with loss of H and O and concomitant enrichment of C and molecular condensation, the same occurs with dispersed sporopollenin, though apparently not as fast as it does with other organic substances (see Fig. 19.1a). Dispersed organic matter taken as a whole, however, coalifies at about the same rate as associated coal beds. The process of coalification of dispersed organic matter in sedimentary rock by thermal alteration can be called catagenesis (Dow, 1977). If one wishs more precision, one may follow Hayes *et al.* (1983) in referring to thermal change up to 50° C as diagenesis (R_o up to 0.5), that in the 50°–150° C range as catagenesis (R_o:0.5–2.0), that in the 150°–250° C range as metagenesis (R_o:2.0–4), and that above

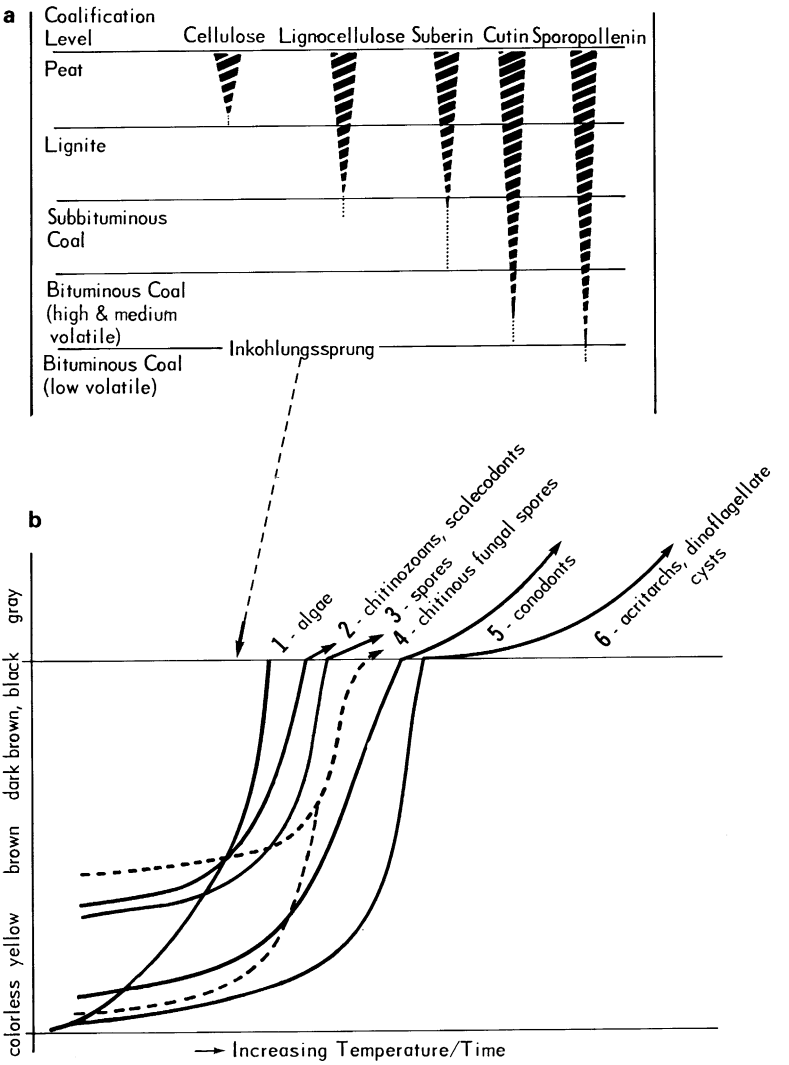

Figure 19.1 Alteration of sporopollenin and other organic substances with coalification by geothermal alteration (= "maturation": see Fig. 19.2.) Note that (a) reads *down* to more mature, (b) reads *up* to more mature. (**a**) Persistence of chemically distinct materials with coalification level. "Inkohlungssprung" is German for "coalification leap," referring to a quantum change in chemical structure between medium volatile and low volatile bituminous coal. Sporopollenin retains some of its distinctive properties (color, elasticity, refractive index) right up to that point. (**b**) Trends in alteration in color of various kinds of palynomorphs with geothermal maturation; "Inkohlungssprung" at top. (**1**) Algal remains start colorless, are relatively quickly altered in color. (**2**) Chitinozoans and scolecodonts, composed of pseudochitin and chitin respectively, start dark yellow and darken at first

250° C as metamorphism (R_o above 4). R is a measure of reflectance of organic matter in sediment, usually vitrinite. (see Glossary). R_o refers to reflectance in oil.

An interesting example of the principle of coalification of dispersed organic matter is the demonstration by Hatcher *et al.* (1982) that the organic matter in coal balls has the same rank as the enclosing coal. Such dispersed insoluble organic matter has often been called "kerogen" in the past (cf. Durand, 1980). Note, however, that in Chapter 18 I explain why in a palynodebris/palynofacies context, "kerogen"should be an avoided term. From a palynological point of view it is palynological matter = PM, consisting of palynomorphs (= PP) and palynodebris (= PD), and it should be classified as shown in Table 18.1. Spore/pollen exines in sub-bituminous coal behave more like exines prepared from living plants than the wood from the same coals resembles wood from a lumber yard, as to elasticity and staining properties. The principal observed change in spores/pollen exines along the carbonization-coalification route is change of color in transmitted light and of reflectance in reflected light. Fresh exines of modern plants are pale yellowish to almost colorless in transmitted light. If exines are heated, e.g., by deep burial or proximity of the enclosing sediment to a lava-flow, the color intensifies from yellow to orange to brown, dark brown, and ultimately black. Experiments by McIntire (1972) showed that temperature in excess of 200° C is the primary factor, along with length of time of exposure to the elevated temperature. Elevated pressure alone, not accompanied by heat, does not cause carbonization. Piérart (1980) found that heating in air at 150° C caused carbonization, whereas heating in a nitrogen environment required higher temperatures. Carbonized sporopollenin is more oxidation-resistant than raw sporopollenin. By reflected light on polished surfaces of the kerogen, the reflectance increases regularly in step with darkening of color in transmitted light.

Obviously, the darkest that exines can be and still be subject to study by transmitted light is dark brown. When enclosed in coal, exines reach this point at about the "Inkohlungssprung," the point in the natural carbonization process at

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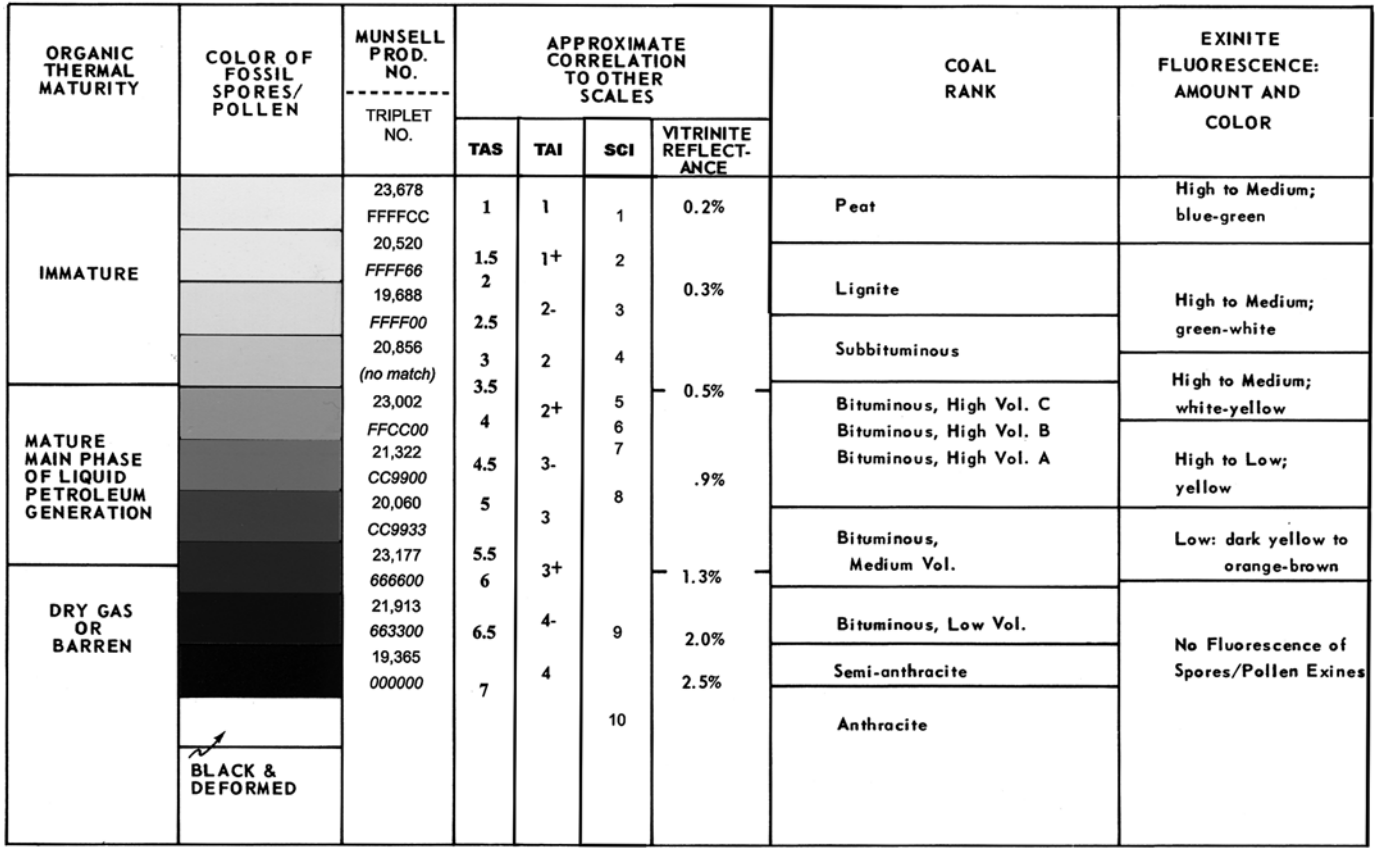
Figure 19.1 slowly, then rather rapidly to the "Inkohlungssprung." (**3**) Spores/pollen exines start yellow, alter to brown and black, at about the same rate as chitinozoans and scolecodonts. (**4**) Chitinous walled fungal spores start practically colorless to brownish yellow to light brown and, according to unpublished observations of W. C. Elsik, retain the original color longer than spores/pollen before darkening to black. As is true for (2),(3) (5) and (6), they presumably undergo a further, slower change in character beyond the "Inkohlungssprung." (**5**) Organic matter within conodonts, phosphatic animal microfossils, also undergo color change with geothermal maturation. (**6**) Dinoflagellate cysts and acritarchs require the greatest length of time to darken with geothermal maturation. In other words, samples with very dark spores/pollen may contain much lighter colored dinoflagellate cysts. (a) Redrawn from Potonié and Kremp (1955). (b) Redrawn from an unpublished poster accompanying Dorning (1984), to which the information about fungal spores has been added. Dorning (1986) gives additional explanations.


ORGANIC THERMAL MATURITY
COLOR OF FOSSIL SPORES/ POLLEN
MUNSELL PROD. NO.
TRIPLET NO.
APPROXIMATE CORRELATION TO OTHER SCALES
TAS
TAI
SCI
VITRINITE REFLECT-ANCE
COAL RANK
EXINITE FLUORESCENCE: AMOUNT AND COLOR
IMMATURE
MATURE MAIN PHASE OF LIQUID PETROLEUM GENERATION
DRY GAS OR BARREN
BLACK & DEFORMED
23,678
FFFFCC
20,520
FFFF66
19,688
FFFF00
20,856
(no match)
23,002
FFCC00
21,322
CC9900
20,060
CC9933
23,177
666600
21,913
663300
19,365
000000
1
1.5
2
2.5
3
3.5
4
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5.5
6
6.5
7
1
1+
2-
2
2+
3-
3
3+
4-
4
1
2
3
4
5
6
7
8
9
10
0.2%
0.3%
0.5%
.9%
1.3%
2.0%
2.5%
Peat
Lignite
Subbituminous
Bituminous, High Vol. C
Bituminous, High Vol. B
Bituminous, High Vol. A
Bituminous, Medium Vol.
Bituminous, Low Vol.
Semi-anthracite
Anthracite
High to Medium; blue-green
High to Medium; green-white
High to Medium; white-yellow
High to Low; yellow
Low: dark yellow to orange-brown
No Fluorescence of Spores/Pollen Exines

Figure 19.2

which a quantum jump in molecular organization of coal occurs (see Fig. 19.1b). It occurs in coal in the low volatile bituminous coal range at about 75% fixed carbon (= about 25% volatile matter).

As is shown in Fig. 19.1b palynomorphs consisting of organic compounds other than sporopollenin respond to geothermal maturation somewhat differently. Chitinous fungal spore walls, for example, start either lighter or somewhat darker (pale brown) than spores/pollen (usually pale yellow) but are a bit more resistant to change than even sporopollenin. Acritarchs and dinoflagellate cysts start almost colorless and require more temperature exposure to darken. In other words, when spores/pollen exines are already dark brown, acritarchs may be still relatively light in color. This means obviously that the substance of which such wall consists, though classed with sporopollenin and very similar to it, is a little different. (See Figures 19.2 and 19.3).

Inasmuch as exine enclosed in a shale is a "mini-coal" consisting of l00% exinite, study of the color of the exines by transmitted light, or of their reflectance by reflected light, can reveal the thermal history and state of the enclosing rock, a matter of considerable importance to hydrocarbon exploration. Early in the twentieth century, White (1915, 1935) showed that in the Appalachian coal field there is a direct relation between coal rank and occurrence of hydrocarbons: anthracite fields do not have any, low-volatile bituminous fields have gas but no liquid hydrocarbons, high- and medium-volatile bituminous fields may have liquid petroleum. The first proposals to use state of carbonization of dispersed organic material in rocks to predict hydrocarbon potential of the rocks came from

Figure 19.2 Spores/pollen exine coloration acquired with geothermal maturation (= coalification), along with related information about thermal alteration of organic matter in general. The left side of the chart is from Pearson (1984), as presented in the first edition of this book as color Plate 1, now with corrections, some of which were provided to me by Pearson in 1990. Fluorescence data are from Van Gijzel (1981). SCI numbers per Marshall (1999) are now added to those for TAI and vitrinite reflectance, with Batten's TAS scale (Batten, 1982), and further corrections and adjustments suggested by D. J. Batten (personal communication, 2006). In the first edition I gave an address for obtaining the Munsell color standards. For the second edition I advise going on Google, entering Munsell Color and be amazed at the selection of options for more information. However, I know from correspondents that getting the exact Prod. No. chips can be challenging. Therefore, I am also providing the numbers that for me were the closest match shown in the Triplet Color Chart (RGB Hexadecimal Color Chart) obtainable at http://www.hypersolutions.org/pages/rgbhex.html All such color comparisons made by human eye are of course only approximations. The color fourth from the top here, presumably what Marshall (1999) describes as "golden yellow" (TAI = 2), has no close match in the Triplet C. C.

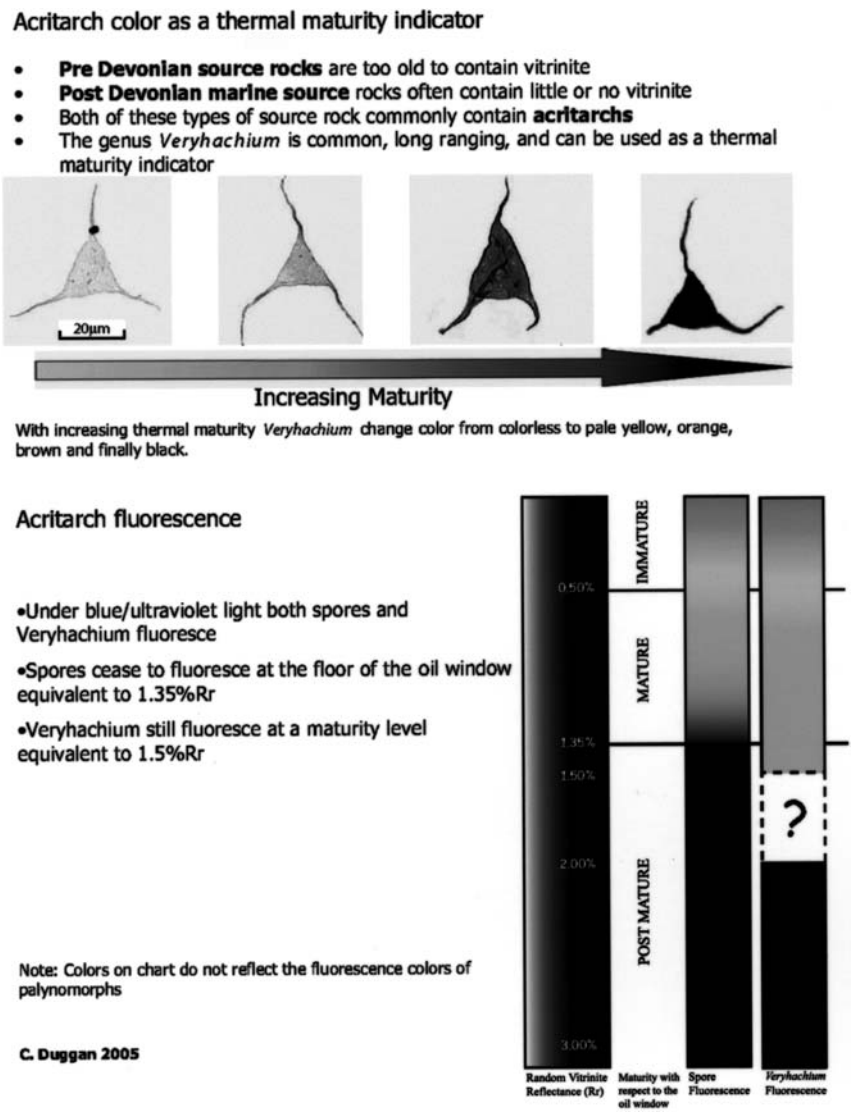

Figure 19.3 Paleozoic acritarchs display color changes with thermal maturity similar to those displayed by vitrinite and exinite in rocks containing such matter–mostly Devonian and more recent in age. The color in transmitted white light shown, and the color of fluorescence in UV, can be used directly to get an approximation of the maturity level of the rock from which the acritarchs are obtained, and hence of its petroleum source-rock prospects. This figure is a self-explanatory presentation of the idea by Catherine Duggan, per her presentation in Duggan and Clayton (2005).

palynologists who could do it by color (Gutjahr, 1966; he eventually used light transmission as measured by photometer).

This is still done, although the field of "thermal maturation" of dispersed organic matter is now mostly a separate endeavor of organic petrologists, who measure the reflectance of specially prepared dispersed organic matter, more often of vitrinite particles than of exinite. However, the color of palynomorphs in preparations is still useful as a measure of carbonization, and thus of the "maturity" of the hydrocarbons in the same rock sequences. Staplin (cf. 1969, 1977) was the pioneer in relating exine color change via the Thermal Alteration Index (TAI) to other measurements of thermal alteration of organic matter in sedimentary rock. The 10-point Spore Color Index (SCI) has somewhat finer tuning than the TAI. It was introduced by Fisher *et al.* (1980) and was presented in more detail by Collins (1990). Marshall (1991) described a method for measuring and mathematically expressing the color changes of sporomorphs during geothermal alteration, in an effort to make their description and use less subjective. However, for most practicing palynologists who like to express the level of maturation, the application of color measurement remains a matter of estimation from color charts. A very detailed summary of the whole subject of palynomorph color as it relates to organic maturation and source potential for hydrocarbons is to be found in Batten (1996a). A paper by Hartkopf-Fröder *et al.* (2001) is full of information about quantitative spore color studies, and also deals with the related matter of quantitative fluorescence microscopy. Among other things, this paper makes the interesting recommendation of making color estimates or measurements from the sacci of saccate pollen, if possible, because they are one-layered.

Batten (1980), early in the discussions of utilization of sporomorph color change for evaluating hydrocarbon potential of rocks, published a simple 7-point scale, which is reproduced here as Table 19.1. It still gets the basic idea across very well. Batten has more recently numericalized his scale as the TAS (Thermal Alteration Scale), and it is compared with TAI and SCI scales in Fig. 19.2 (cf. also Batten 1982 and 1996a).

Batten's TAS scale should be compared with Pearson's color chart, of which an expanded version is reproduced here as Fig. 19.2, in which the colors are also directly related to the numerical Thermal Alteration Index (TAI) and the Spore Color Index (SCI) and to other pertinent measurements, such as vitrinite reflectance. Batten (1981) has pointed out that normal oxidative methods used in laboratory procedures do not lighten the color of sporomorphs enough to invalidate the use of color of processed specimens as a general geothermal indicator. (There is a problem with measuring and controlling what constitutes "normal" oxidation.) Carefully recorded color observations by the working palynologist can usually be used for reconnaissance of the geothermal history of newly encountered rock sequences. Bujak *et al.* (1977) have pointed out, however, that various categories of organic matter in sedimentary rock do not all follow the

Table 19.1 Palynomorph colors/hydrocarbon maturity (Batten, 1980)

Observed color of palynomorgh	*Significance for hydrocarbons*
(1) colorless, pale yellow, yellowish green	chemical change negligible; organic matter immature, having no source potential for hydrocarbon
(2) yellow	some chemical change, but organic matter still immature
(3) light brownish yellow, yellowish orange	some chemical change, marginally mature but not likely to have potential as a commercial source
(4) light medium brown	mature, active volatilization, oil generation
(5) dark brown	mature, production of wet gas and condensate, transition to dry gas phase
(6) very dark brown-black	over-mature; source potential for dry gas
(7) black (opaque)	traces of dry gas only

same geothermal maturation course (see also Fig. 19.1). More about this matter, especially in connection with acritarchs, appears below.

In addition to the standard maceration slides necessary for palynomorph identification and counting, the various services that process palynological samples on an outsourcing basis will provide slides or residues from which slides can be made, containing non-oxidized material. These non-oxidized palynomorphs can be used for separate color estimates and fluorescence microscopy studies

The course of carbonization or thermal maturation can also be observed by use of fluorescence microscopy of both exinite (spores/pollen in coal) and vitrinite (wood and bark tissues in coal) (see Fig. 19.2). The particles in question are placed in an incident ultraviolet light beam, and the fluorescent light emitted is studied. Teichmüller and Ottenjahn (1977) have shown that fluorescence microscopy very sensitively shows diagenetic changes of spore walls and other organic substances in the context of oil formation.

Teichmüller and Durand (1983) demonstrate that fluorescence microscopy reveals changes in the macerals of coal, related to bitumen formation during coalification. Van Gijzel (1981) reports that the principal stage of petroleum generation ($R_{oil} = 0.50-0.85$) is characterized by double peaks in exinite fluorescence spectra, and the "oil death line" ($R_{oil} = 1.15-1.35$) is reached when fluorescence does not occur. For much more detailed information about the measurement

of vitrinite reflectance and its significance, see *Organic Petrology*, by Taylor *et al.* (1998). Coal petrologists refer to spore and pollen shells as exinite, and the geothermal effects on it and vitrinite, consisting of wood and bark, are very similar. An interesting publication that summarizes many aspects of the use of palynology in oil exploration is that of Mehrota *et al.* (2002). Among other things, fluorescence microscopy of palynomorphs and palynodebris is stressed.

The use of fluorescence properties of particulate organic matter in sediments, for assessment of thermal maturity is outlined by Pradier *et al.* (1991). They measured the fluorescence of a variety of organic particles, including palynomorphs, using incident UV light on polished surfaces of otherwise unprocessed rock fragments. This is much the same procedure as used by coal petrologists in measuring the reflectance of vitrinite and other coal macerals by incident white light. The results show a more complicated response to thermal maturity than is displayed by the relatively simple evaluation of palynomorph color or vitrinite reflectance in the course of thermal alteration. Obermajer *et al.* (1999) applied the fluorescence method (procedure similar to that of Pradier *et al.*) to the study of Paleozoic acritarchs in particular. They found that acritarch fluorescence has excellent potential in thermal maturity estimation. The fluorescence trends for the acritarchs were similar to those for the coal petrologic maceral, alginite. This is not surprising, given the near certainty that acritarchs are of algal origin. However, acritarchs are less sensitive to thermal alteration than is alginite, and the fluorescence measurements for acritarchs are therefore lower.

Waterhouse (1998) describes the use of palynomorph fluorescence measurement of palynomorphs in conventional palynological maceration residues, to detect oxidation from reworking, as well as thermal alteration. Waterhouse also summarizes the history of fluorescence studies of fossil palynomorphs. Talzina *et al.* (2000) describe study of Cambrian acritarchs by both microscopy with a special fluorescence microscope, as well as fluorescence flow cytometry. As has been noted by many, fluorescence characteristics of palynomorphs are manifold and complex, and interpretation of the observations may in the future be a potentially rich subject for exploration.

Duggan and Clayton (2005) reported studies of geothermally initiated color changes of early Paleozoic acritarchs (the initial studies were mostly made of *Veryhachium* spp.). The acritarchs have the same sort of color changes due to thermal alteration as do sporomorph exines. The acritarchs, presumably algal cysts, start out colorless and range through pale yellow to orange, brown and black (see Fig. 19.3). The change in color is more gradual than with spore exines. Collins (1990) in a pioneer contribution on the SCI scale had displayed a diagram of the acritarch color changes. Hartkopf-Fröder *et al.* (2004) state that acritarchs in Devonian rocks display paler colors compared to miospores in the same rocks, but that both groups of palynomorphs change in color in "parallel" fashion with increasing thermal alteration, as indicated by vitrinite reflectance, for example. As is shown in Fig. 19.3, spore exines cease to fluoresce at the floor of the oil

window, whereas *Veryhachium* still fluoresces at TAI levels higher than that. Duggan and Clayton (2005) stressed, as have those who have studied the fluorescence of Paleozoic acritarchs, that acritarchs are present in earliest Paleozoic rocks, whereas vitrinite is absent until Devonian, and sporomorphs, pre-Devonian, are rare, and pre-Silurian are very rare. Duggan's techniques (personal communication) are based on color estimates made from conventional palynological slides, using regular light microscopy, and fluorescence observations made with UV incident light and fluorescence objectives on a conventional microscope. The whole procedure is a "quick and dirty" way to get thermal alteration estimates for rocks too old to contain either spores or vitrinite.

Carbonization can be one of the banes of palynologists' existence. Because of the geothermal gradient alone, sedimentary rock buried more than about 5500 m does not yield palynofloras of recognizable spores/pollen. (The process of carbonization by geothermal gradient follows "Hilt's law"; see Dow, 1977). Carbonized spores/pollen are difficult to study even when they can be successfully separated from the enclosing rock. Furthermore, as the principles of maceration depend in part on the differential reaction of sporopollenin to oxidation compared to other organic matter present, highly carbonized spores when mixed with other organic matter are difficult or impossible to prepare for study. Spores/pollen cannot be macerated out of low-volatile bituminous to anthracite coals, even though presumably equivalent coal beds of medium to high volatile constitution yield abundant fossil palynomorphs. Furthermore, although other preservation problems can be partially overcome, carbonization due to deep burial or tectonic activity cannot. It was long felt that the Triassic-Jurassic rocks of the Hartford-Springfield Basin (Newark Supergroup) would not yield palynofloras, because the typical lithology is reddish sandstone and shale: too oxidized. However, productive grayish shales do exist in the basin, though the productive shales are not "typical" lithology for the area (Cornet and Traverse, 1975). On the other hand, samples of sediments buried by 10,000 m or more of rock, such as from deep wells now being drilled, are obviously thousands of meters too deep to be palynologically productive. Sediments from part of a mountain chain which has been subject to much tectonism are very unlikely to be productive. For example, Triassic sediments from the Alberta Rockies are in my experience in this category.

2 "Marginal Palynology"

Most of the photomicrographs of fossil palynomorphs in this book and in practically all palynological publications are of "super specimens" illustrating the critical morphological features of the taxa concerned. Most of the specimens encountered in practical palynology are not so well preserved. They may be variously torn, compressed, crumpled or folded (see Fig. 18.5a). They may be more or less corroded by oxidation or fungal-microbial attack. They

may be riddled by pyrite or other crystals, or rarely even by molds of coccoliths (Batten, 1985). Sometimes in extreme cases of corrosion, the palynomorphs are mere "ghosts." Worst of all, sometimes the palynomorphs may be far along the diagenesis-carbonization thermal alteration pathway and are just black silhouettes. Nevertheless, many of the sorts of miserable palynomorphs just mentioned can be recognized, at least to genus or group, e.g. "circumpolloid," and this sort of identification can be the basis of informative palynological study. I informally call this kind of work "marginal palynology" (Traverse, 1972). An example is the Danville-Dan River Basin (Newark Supergroup, Virginia and North Carolina), in the shales of which palynomorphs are scarce and highly carbonized, apparently because of higher than normal heat flow in the basin. It is probable that oxidizing conditions penecontemporaneous with deposition caused sparse and corroded palynomorphs even before depositional diagenesis. Pyrite precipitation occurred after deposition, further ruining preservation. Nevertheless Robbins (1982) showed that gross study of these spores/pollen "wrecks" was possible with ordinary light microscopy and permitted approximate dating of the sediments (see Fig. 19.4).

Sinha *et al.* (2004) published a marvelous example of marginal palynology, based on a study of heavily carbonized Permian sporomorphs from the Himalayan area of India. The authors do not comment on the marginal palynological aspect of their work, nor on the probable cause of the carbonization, but the geological description of the section studied notes that the samples came from shales interbedded with pillow lavas, which doubtless explains the situation. Montenari and Servais (2000) did a stratigraphically important study of Cambrian-Ordovician boundary acritarchs, based on very carbonized and fragmented specimens from metasedimentary rocks in Germany. Only 3 of 133 samples they studied produced acritarch-wrecks. They used SEMicroscopy to identify the specimens at the generic level, noting that was difficult and specific determination impossible. Others have used infrared microscopy for marginal palynology

3 Palynostratigraphy = the Use of Palynology for Stratigraphy

The principal application of the study of fossil palynomorphs is for stratigraphic purposes, in the simplest case to propose a geologic age for an unknown sample. Palynologists are frequently asked to perform this basic stratigraphic service, especially in sequences of sedimentary rock such as the Catskill Formation (Upper Devonian) of Pennsylvania-New York, which is often described as almost "unfossiliferous," meaning no megafossils of marine organisms with a limited stratigraphic range. During DSDP work in the Black Sea, my duty as on-board palynologist was to ascertain, based on what was known from surrounding areas, when the drilling reached Miocene, as a working decision had been made to drill

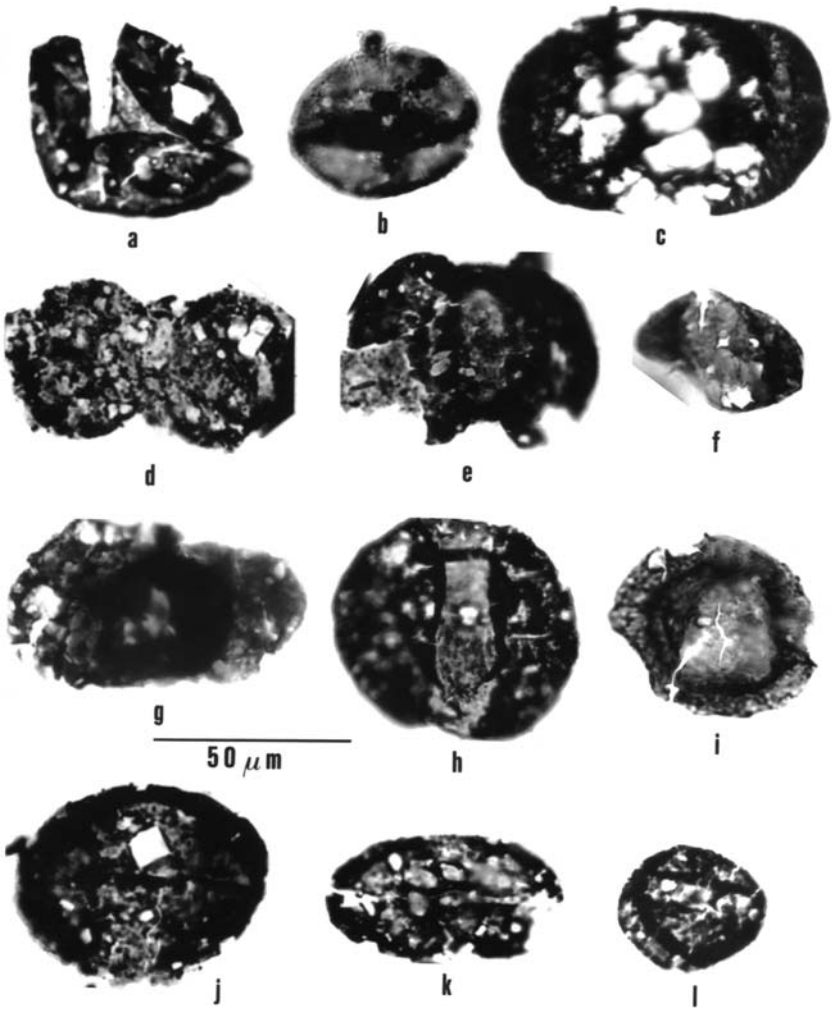

Figure 19.4 "Marginal palynology." The palynomorphs illustrated in publications are usually well-preserved, well-oriented specimens. However, even in good preparations many specimens are folded, crushed, or corroded and nevertheless often are identifiable by a palynologist who is familiar with well-preserved specimens of the same taxon. Furthermore, the palynologist is often called on to work with poorly or very poorly preserved specimens where they are the only, or among the few, fossils present. Often, after a "foothold" is attained to suggest the approximate age level, even execrable, badly preserved, corroded, and carbonized "wreck" specimens such as those illustrated here can be identified. The assemblage shown is from the Triassic (Karnian) sediments of the Danville-Dan River Basin of Virginia-North Carolina. The blackness (carbonization) is best explained by post-depositional heat flow in the basin, and the mineral (mostly pyrite)

that deep, if possible, and no further. The method usually employed for fixing a date is to plot from the literature and/or previous investigations the ranges of the forms found. The most probable date is the date showing the best control by upper limits ("tops") and lower limits ("bottoms"), making allowances for geographic position; for example, in the Black Sea drilling, none of the forms encountered is truly extinct, but pollen of palms is not usually found in the general area above (= not younger than) top Miocene. Beginning students in my courses, using this method, were almost always able to fix the age of this "unknown sample" to the nearest stage of a period. My good friend, W. G. Chaloner, has suggested putting this basic idea into a dichotomous key, and Fig. 19.5 represents his latest version of it. It provides a "seat of the pants" stratigraphic key to fossil sporomorphs. If used carefully by a student with a maceration residue containing a decent number of such fossils, this key will make it possible for her to get a rather good first approximation of the age of the sample in 10–15 minutes of study of a slide. The final examination in my palynology courses always included several such slides that the students "dated" without notes, and their performance over the years on this exercise was impressive. It should be noted that the students had to have an eye out for at least the presence of acritarchs, chitinozoans, and dinoflagellates, not just for the kinds of spores and pollen on the slides.

In oil company-oriented palynostratigraphy the operational task is to correlate sequences from one well with those from others. The purpose of this is simply orientation. If an oil pay zone is anticipated from other information just above

Figure 19.4 casts by reducing environment in the Danville-Dan River lake at the time of deposition. The specimens are brittle, and very gentle processing must be used. Magnification indicated by bar under (g). (**a**) *Duplicisporites granulatus* Leschik, proximal view. Note mineral casts, and torn, squashed nature of specimen. (**b**) *Aratrisporites saturni* (Thiergart) Mädler, proximal view of monolete, zonate microspore. (**c**) *Alisporites grandis* (Cookson) Dettmann, distal view of large bisaccate. Open spaces are due to mineral casts and corrosion. (**d**) *Platysaccus* sp. Despite carbonization, multiple mineral casts, and corrosion, the small corpus and large sacci make generic identification certain. (**e**) Probably *Lunatisporites* sp., distal view. Obviously a bisaccate, and the generic determination is suggested by apparent taeniae. (**f**) *Klausisporites schaubergeri* (Potonié & Klaus) Jansonius, distal view. Small sacci and relationship of sacci to corpus permit identification. (**g**) *Triadispora plicata* Klaus. Relationship of sacci and corpus, structure of corpus, and occasionally visible trilete mark allow identification. (**h**) *Sulcatisporites australis* (de Jersey) Dunay, distal view. Nature of sulcus and its relationship to sacci characteristic for taxon. (**i**) *Tulesporites briscoensis* Dunay & Fisher. Monosaccate. Despite tears and cracks, overall morphology recognizable. (**j**) *Ovalipollis* sp., distal view. Straight sulcus and shape suggests this taxon, despite mineral casts, carbonization and corrosion. (**k**) *Cycadopites* sp., distal view. Monosulcate. (**l**) *Paracirculina maljawkinae* Klaus, polar view, recognizable by angular folds associated with rimula. Photos courtesy of E. I. Robbins, from Robbins (1982).

zone "d," one can make money for his employer by recommending further drilling to reach it, or to stop drilling if correlations show that it has already been passed without luck. Correlation may show that zones have so thickened in comparison to a standard that the goal is too deep in a new well to make reaching the pay area feasible. An important publication on correlation in relation to hydrocarbon exploration is Collinson (1989), a volume containing several significant palynostratigraphic contributions, e.g., Hochuli and Colin, van der Zwan, and Riley *et al.*

A STRATIGRAPHIC KEY TO PALYNOLOGICAL ASSEMBLAGES OF LAND-PLANT SPORES AND POLLEN. (WGC, 2005)

This dichotomous key attempts to offer a means for a student with a general acquaintance with spore and pollen structure to offer an age assignment for a palynological assemblage. It aims only to give an assignment at the level of a geological period, but if that can be achieved, then it greatly facilitates reaching into the relevant palynological literature to get a finer stratigraphic resolution.

Bisaccate pollen[1,2] present.....2

No bisaccates present 8

2. Angiosperm pollen (with multiple pores, colpi or both[3,4], or monocolpate with a tectate wall[5]) also present 3

Angiosperm pollen absent.....5

3. Members of the *Normapolles*[6] group OR *Aquilapollenites*[7] group present (even if only as rare elements) ....**Late Cretaceous through Eocene.**

Normapolles and Aquilapollenites absent (**Oligocene or younger**).....4

4. [Further resolution offered only for high or middle-latitude, N. hemisphere:-]

Bisaccate pollen plus *Tsugaepollenites*[8] collectively less than 10% of the assemblage; *Spinizonocolpites*[9], *(Nypapollenites), Cicatricosisporites*[10] present .....**Eocene or Oligocene**

Bisaccate pollen more abundant, *Nypapollenites, Cicatricosisporites* absent.....**Miocene or younger**

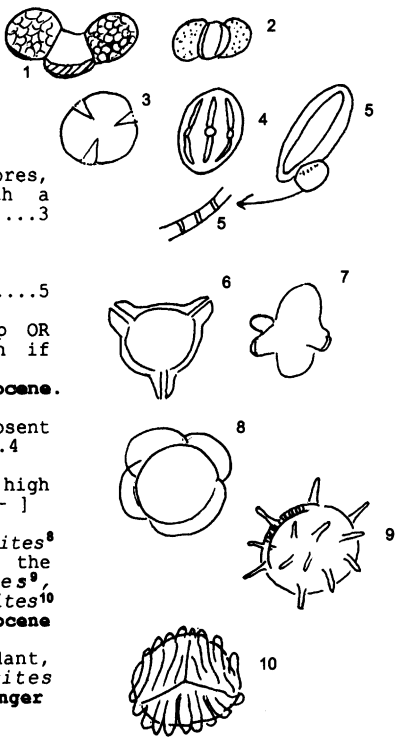

Figure 19.5

5.At least some of the bisaccates striate, (e.g. *Lueckisporites*[11], *Striatites*[12], *Taeniaesporites*[13]) .....(**Permian or Triassic**).....6.

None of the bisaccates striate, and with other conifer pollen (*Classopollis*[14], *Tsugaepollenites, Cerebropollenites*[15]) present...

.....(**Jurassic/Lower Cretaceous**) 7

6. Trilete spores typically less than 20% of the assemblage; *Vittatina*[16], *Nuskoisporites*[17], present in addition to forms cited in the lead from 5.....**Permian**.

Trilete spores typically more than 20% of the assemblage, diverse; bisaccate striates less than 20% of the assemblage ...

.....**Triassic**.

7. *Cicatricosisporites* and *Pilosisporites*[18] absent ...**Jurassic**

Cicatricosisporites or Pilosisporites present.... **Cretaceous**

8. Angiosperm pollen present in abundance.....**Eocene or Oligocene**.

No angiosperm pollen present; a diverse range of smooth or ornamented trilete spores dominate the assemblage

.....(**Pre-Permian**) ....9.

9. Trilete spores dominate, with no *Laevigatosporites*[19], *Florinites*[20], *Lycospora*[21], *Raistrickia*[22], *Tripartites*[23], *Waltzispora*[24] *or Reinschospora*[25]: - spores with grapnel spines[26] may be present .....**(Pre-Carboniferous)**... 10

Laevigatosporites, Florinites, Lycospora, Raistrickia or spores with pronounced radial extensions collectively forming at least 10% of the assemblage.....**(Carboniferous)**..... 11

10. A wide range of ornamented trilete spores , some with equatorial features (Zona/cingulum) or cavate exines

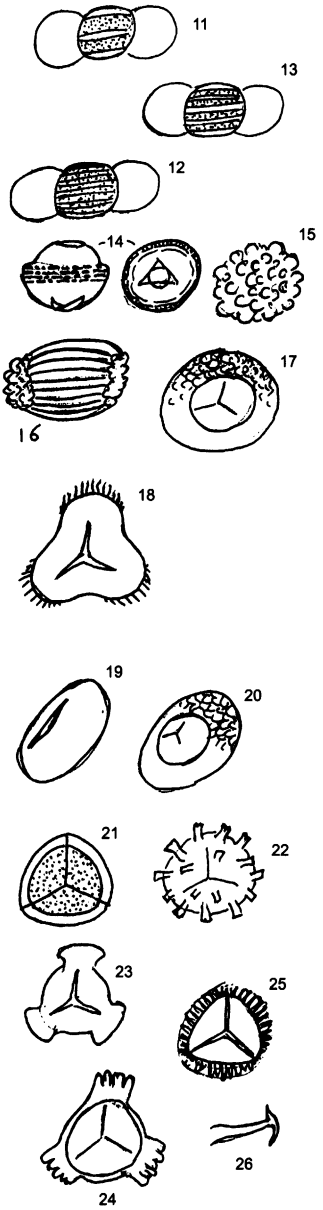

Figure 19.5 *(See caption on page 596)*

Calyptosporites[27]), radial ribs (*Emphanisporites*[28]) or grapnel spines (*Ancyrospora*[29]).....**Devonian**

Trilete spores without ornament (*Leiotriletes*[30]) or with minimal sculptural elements; or in adhering tetrads[31]..... **Silurian**

11. Assemblage with abundant *Lycospora, Laevigatosporites, Florinites, Densosporites*[32] but lacking spores with strongly developed radial features ....**Upper Carboniferous (Pennsylvanian).**

Assemblage with a range of trilete spores showing various equatorial features (*Densosporites, Cirratriradites*[33]) and forms with prominent radial structures (*Walzispora, Tripartites)* ... .**Lower Carboniferous (Mississippian)**

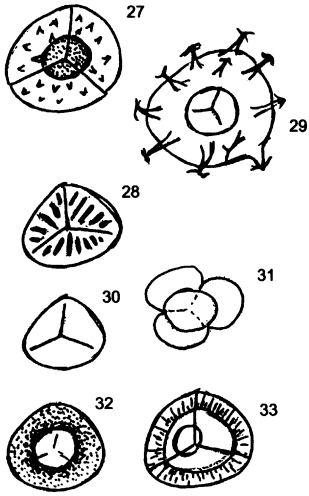

Figure 19.5 William G. Chaloner's "quick and dirty" dichotomous key for getting a first order approximation of the age of a productive palynological maceration of a rock sample. Students in thirty years of Traverse's palynology courses at Penn State had such a key in their minds when they successfully dated to period in the final examination several unlabelled slides of a variety of ages. Except for very minor cosmetic improvements (erasure of smudges caused by the author folding the key to fit an envelope on mailing it, and the like), this key is exactly as Professor Chaloner penned and typed it's final revision in 2005.

Paleopalynology has advantages and disadvantages for doing stratigraphy. One problem is that paleopalynological assemblages are very likely to be facies-controlled. As discussed earlier, palynofloras often are a reflection of the sediment type, and thus of energy levels in the water during sedimentation, and position with respect to cycles of flooding and lowstands of water. The apparent correlation of two Pennsylvanian coal beds by palynology, for example, can be not a true correlation at all, but merely a reflection of the similarity of coal-bed palynofloras over a considerable time span, given similar ecological conditions. See the discussion of palynofacies in Chapter 18. Correlation by palynofacies may even be practical within a small area, but such correlations cannot be extended far laterally.

Kuyl *et al.* (1955), long ago pointed out that palynomorphs have some advantages for biostratigraphy over marine fossils, such as foraminifera. This advantage is that palynomorphs of various kinds occur in all sedimentary environments: spores and pollen of land plants come into sedimentary basins primarily with the sediment-load of streams. Palynomorphs are found in all non-marine sediments of the requisite particle size and geochemical history. They also occur in practically all shaley marine sediments, although the same limitations as for non-marine shales apply. Acritarchs and dinoflagellate cysts mostly originate in

marine environments, and many marine sediments contain both pollen and spores from terrestrial environments and dinoflagellates, acritarchs, and other marine palynomorphs. Thus, palynostratigraphy is uniquely applicable in correlation of levels in marine sediments with those of non-marine sediments.

As is discussed in Chapter 18, palynology, especially palynofacies studies, can make a significant contribution to the recognition of the systems tracts that are the basis of sequence stratigraphy. Cycles of sequences of transgression and regression, high stands and low stands are often important factors in establishing stratigraphic correlation, even when stratigraphy based on ranges of palynomorphs and other fossils works poorly. Even before the dramatic increase in palynological coordination with sequence stratigraphy, Riley *et al.* (1989) pointed out that coupling of palynofacies information with taxa-based stratigraphic zonations can be very productive in establishing a sequence of sedimentary events in an oilfield area.

Obviously, correlation by palynofloras should ideally depend on real "tops" and "bottoms" (last occurrences of and first occurrences of taxa, respectively) based not on facies (migration) but on extinction of some forms and evolution of other new forms. In the time represented by some parts of the geologic column, plants were evolving rapidly, and spores/pollen are very effective for stratigraphy, e.g., during the Middle and Upper Devonian. At other times, dinoflagellates were more rapidly evolving than land plants, and dinocysts are very effective for practical stratigraphy if marine sediments are available, e.g., during much of the Jurassic. Palynostratigraphic zones for correlation are based on various combinations of first and last occurrences (see section 4, this chapter). A matter of critical importance, to which palynology makes significant contributions is that of establishing boundaries, for example those between rock systems (eras in time) and series (epochs in time). Such boundaries depend largely on extinctions of organisms, and some such organisms are represented by palynomorphs. An important book on this subject is that of Beaudoin and Head (2004). In that book the chapter by Macleod on extinctions and that by the editors on boundaries are especially significant for palynostratigraphy.

Another problem for spores/pollen-based palynostratigraphy is provincialism. Almost since their origin, land plant taxa have not been cosmopolitan, and therefore the lateral extension of correlation by spores/pollen is risky, the more so the greater the area involved. Precise transcontinental correlation is difficult, intercontinental correlation (except in very broad terms) usually impossible.

Reworking of fossil palynomorphs is discussed earlier. This problem can obviously lead to great difficulties with correlations in general, and with the determination of "tops" in particular, because reworking of palynomorphs from older sediments can appear to extend the range of taxa upwards. An example, extending beyond the confines of practical well correlation, is that of plant extinction at the end of the Cretaceous. One must consider whether Maastrichtian forms found in Danian rocks are reworked or represent persistence of the taxa. Megafossil plant compressions are not often recycled, but spores/pollen very often are. Thus, to

determine whether various *Aquilapollenites* species terminate at the end of the Maastrichtian (top of the Cretaceous) or march on into the Danian (bottom of the Paleocene) requires certainty that *Aquilapollenites* occurrences in the Danian are not examples of reworked pollen. As a general rule, one should be suspicious that spores/pollen/dinocysts occurrences may be reworked when they are relatively rare specimens, occurring stratigraphically well above rather abundant counts of the same form. Careful inspection of such specimens may yield preservational hints that they are not last-ditch stragglers but reworked. Because of the durability of palynomorphs generally, "bottoms" have a theoretical tendency to be sharper than "tops," but when drilling cuttings are used, the bottoms are usually blurred by caving of upper cuttings into lower levels.

Dinoflagellate cysts are both marine and non-marine, but marine forms are vastly more common. In the pre-Devonian, palynostratigraphy is only practicable with marine palynomorphs: chitinozoans, scolecodonts and acritarchs. The possibility of correlating non-marine with marine rocks is what put palynology in business as a practical oil-company tool (Kuyl *et al.*, 1955). In the Lake Maracaibo Basin (Venezuela), Shell palynologists demonstrated that they could do what foraminifera specialists could not do: correlate the extensive non-marine sections with one another, and with the associated marine sections.

4 Data Management in Palynostratigraphy

Correlation techniques based on palynofossils are basically the same as those used for other sorts of fossils, subject to the limitations already mentioned. Because the number of specimens obtained is normally large, palynostratigraphy is ideally suited to statistically-based, computer-managed methods. As pointed out by Wrenn (1990) not long after publication of the first edition of this book, computer-based manipulation of data, including photographic images of palyno-fossils, offers possibilities for relatively rapid worldwide integration of information that was unthinkable, pre-computer. The impact of digital photomicrography and massive use of scanner technology promise to affect even such matters as systematics of the forms.

Despite the fact that computer programs now play a big role in manipulation of the data, in practice the palynostratigrapher still depends on concurrent range zones, Oppel zones, or assemblage zones (where barren intervals intervene; see Fig.19.6). Oppel zones are based on upper and lower limits of several taxa each. Concurrent range zones are similar, but are determined by presence of ranging-through forms as well as first and last appearances. They are subject to the limitations mentioned: reworking which extends a top into a pseudo-top, facies-controlled distributions which show an apparent top based only on environmental factors. Assemblage zones (= cenozones) are characterized by 3 or more designated taxa, all of which must ordinarily occur together for the

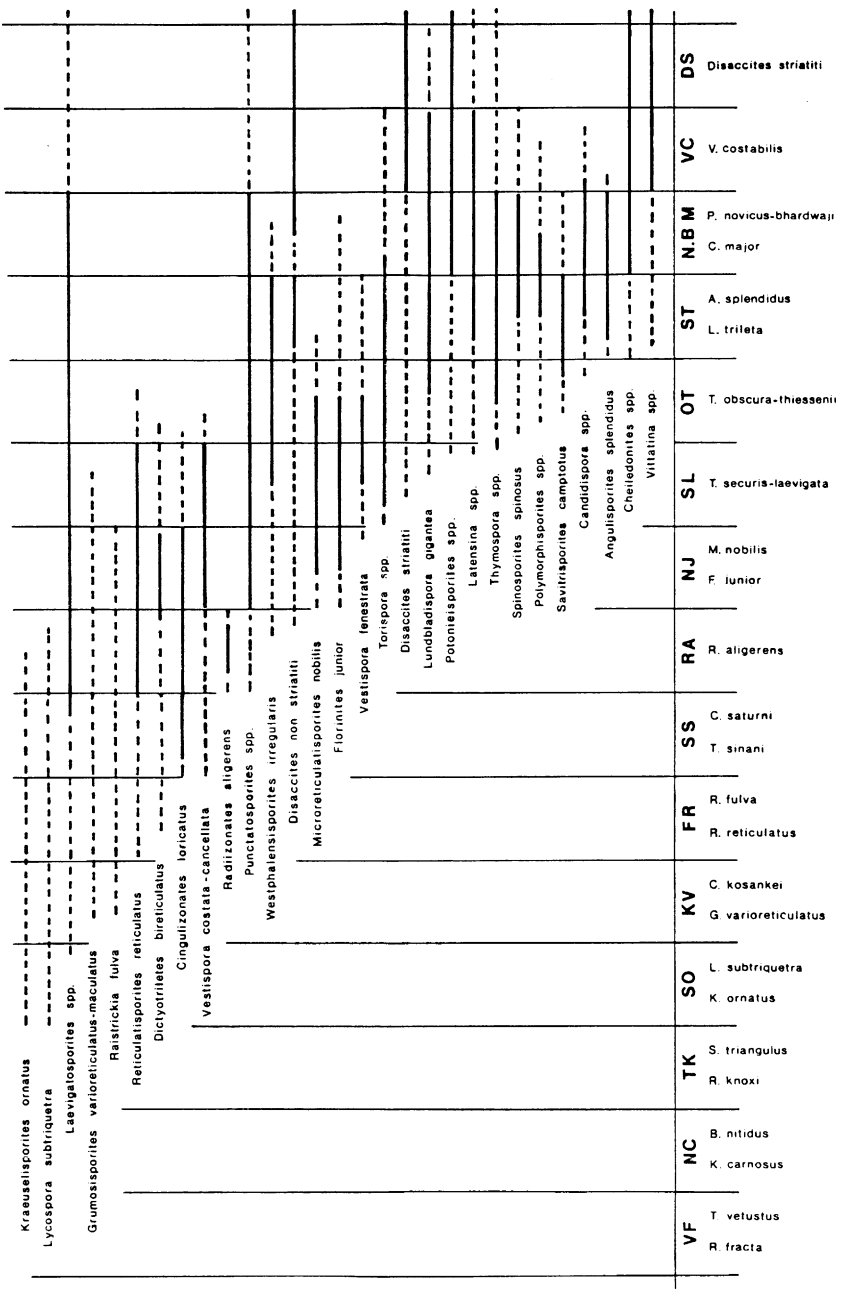

Figure 19.6 *(See Caption on page 600)*

zone to be present, although subsidiary taxa that commonly occur along with the key taxa are frequently mentioned (cf. Saxena, 2000).

Streel *et al.* (2000a), in explanation of their important work in relating miospore floras of western Europe to conodont-based international Devonian stratigraphy, base their work on assemblage zones based not only on co-occurrence of specified miospore taxa. but also on appearance of selected miospore characters, as well as on first occurrences ("bottoms") of selected taxa, two of which provide the name for the zone. Some such zones are also acme zones (= abundance zones), in which one or more taxa display maxima of relative abundance over a wide area. See also the *International Stratigraphic Guide* (Hedberg, 1976) for definitions of kinds of zones.

For some parts of the geologic column, palynostratigraphy has been practiced and results published over a long enough period of time that well accepted, named zones exist. The Devonian-Carboniferous of parts of the world is such an example. Some palynostratigraphers in some situations use "phases" instead of zones (see Fig. 19.7), emphasizing the progressive nature of alteration of palynofloras over time, instead of the disjunct nature of zones, each distinct. Many palynostratigraphic correlations and proposed zones exist only in files and computer storage of oil companies and related enterprises. Enough of this has been published from time to time that the literature provides sufficient information for most routine palynostratigraphic work.

I have found Agterberg (1990) to be a useful book for reference to various modern, computer-based approaches to stratigraphy. *Applied Stratigraphy*, edited by Koutsoukas (2005), is also an important book, with chapters on many, diverse aspects of stratigraphy, including six that deal directly with palynostratigraphy, and others with obvious connections to that subject. Sequence stratigraphy has been dealt with in Chapter 18 of the present book. In connection with the application of sequence stratigraphy to practical stratigraphic correlation, Olson and Thompson (2005) have presented a clear and readable explanation with understandable examples.

It should be emphasized that stratigraphic correlation based on sporomorphs, in contrast to marine-source palynomorphs, most needs to be tied in with stratigraphic schemes based on marine fossils, such as conodonts in the Paleozoic

Figure 19.6 Part of a range chart of palynomorph species in the Carboniferous of western Europe (zone SO is Namurian) to lowest Permian; (VC and DS are Autunian). Broken lines represent reduced or discontinuous presence. The palynological zones are concurrent range zones. Assemblage zones are similar but emphasize the biological integrity of the group of taxa. Oppel zones are also similar but are always determined by first and last appearances of several taxa. The zones are given a name and symbol based on the names of characteristic taxa included; thus, DS (*Disaccites striatiti*) for the uppermost zone. Simplified from Clayton *et al.*, 1977.

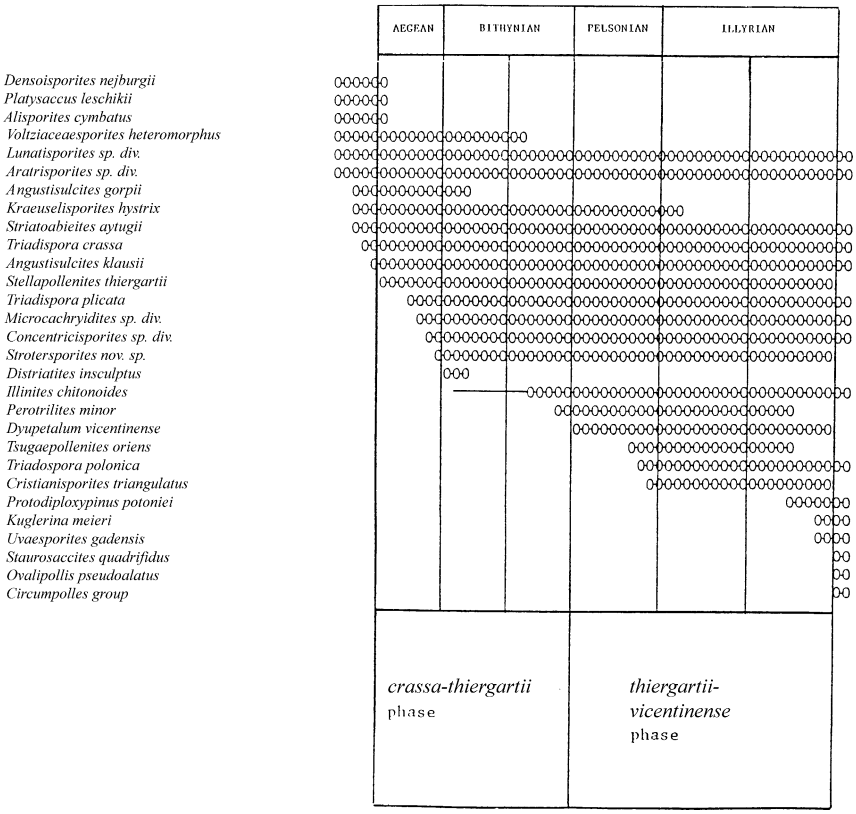

Figure 19.7 Use of "phases" instead of zones in the middle Triassic. Aegean, etc., are substages of the Anisian stage. The use of phases is subtly different from that of assemblage and other zones (compare Fig. 18.3). The emphasis is on gradual development over time of successive assemblages, rather than on the complete distinctiveness of each assemblage. To underscore this, the designation of successive phases typically includes a taxon name from the previous phase. Thus, in the two phases shown here, *crassa* is *Triadispora crassa*, *thiergartii* is *Stellapollenites thiergartii* and *vicentinense* is *Dyupetalum vicentinense*. In practice, one uses the phases very similarly to zones. From Brugman, 1983.

and early Mesozoic. The work of Streel and Loboziak (1996), for instance, has been particularly important in linking the miospore stratigraphy of western Europe to conodont stratigraphic schemes for the same area, by finding miospores and conodonts in the same rocks. Dinocysts in rocks of Jurassic to Holocene provide a natural source of coordination of marine palynomorphs with the non-marine sporomorphs, since they are often found in the same marginal marine rocks.

Pleistocene/Holocene palynostratigraphy has been assisted in some places by links to tephrostratigraphy, in which an external check on both absolute and

relative age is provided by dating of volcanic rock layers in a stratigraphic sequence. Lowe and Hunt (2001) even coined "tephropalynology" to cover the linkage of palynostratigraphic sequences to such external sources of chronological placement. The fuzziness of some sporomorph boundaries is probably explicable in part by the tenacity of plants in time–they are particularly susceptible to the "Lazarus effect", because minimum population sizes for survival of plant species are very small, and it is comparatively easy for plant species to rebound from near-extinction. *Metasequoia*, for example, was from any practical point of view extinct in the 1940s, down to a few specimens in a small area of China, when the intervention of an animal species (humans) brought about its expansion all over the world. (cf. Traverse, 1988a, 1990a). Another probable contributor to sporomorph stratigraphic fuzziness is the fact that spores and pollen morphospecies, based on studies of modern plants, very seldom represent a single species of plants.

Quantitative biostratigraphers of pre-Quaternary sections have generally concentrated on probabilistic or graphical methods (see Edwards, 1991, and Gradstein *et al.*, 2004, for summaries). These are sometimes modified with multivariate approaches (e. g., Christopher, 1978). Probabilistic and graphical methods use speciation and extinction events (the limits to a taxon's stratigraphic range) and ignore abundances. Because Quaternary palynologists generally do not deal with range-ending events, and historically mostly collected abundance data, they have concentrated on multivariate analysis of abundance changes for their stratigraphic research.

4.1 Probabilistic Methods

Probabilistic methods attempt to determine the most probable order of events (earliest and latest occurrences) based on their occurrence in multiple sections. This generates the average range for taxa. To do this effectively requires that events be present in most sections, which is not always true for palynostratigraphic datasets. The most common probabilistic method used today is Ranking and Scaling (RASC: see Gradstein *et al.*, 2004).

4.2 Multivariate Techniques

Most of the multivariate techniques used in stratigraphy belong to the group of statistical methods used for exploratory data analysis. The main point of these techniques is to summarize the variance in a multivariate dataset in a manner that supposedly makes the data easier to interpret. Variance in a dataset can be derived from multiple causes, some of which are not stratigraphic (changing environment, for example), so this approach requires care to ensure that the results are stratigraphic in origin. Two techniques that have been applied to biostratigraphy are

principal components analysis and cluster analysis. Principal components analysis (PCA) creates new variables that are mathematical combinations of the original variables (e.g., taxa). These new variables (the principal components) are calculated so that a high proportion of the variance in the samples is concentrated on the first few (typically five or fewer) new variables. Thus they explain the data more economically than all of the original variables. Examination of the specific mathematical combinations then allows interpretation of which original variables have the greatest effect on each principal component Cluster analysis (CA) uses calculated similarities to create (usually) hierarchial groups of related samples. These groups or assemblages, determined in a single section, can then be recognized in other sections. A good reference to get an understanding of how PCA, CA and some other multivariate techniques work is Kovach and Batten (1994).

Lenz *et al.* (2005) applied cluster analysis to a series of samples through the Messel Formation, Eocene of western Germany. They found groupings of taxa by this means that were based on thermophilic tendencies. This information enabled them to us principal component analysis to suggest a warming trend in time during the deposition of the Messel oil shale.

Pielou (1984) provides a helpful introduction to the mathematics of these techniques, and Birks (2005), in his section "Numerical methods and data synthesis" gives a very useful summary of how these approaches are applied in Quaternary palynology.

4.3 Graphic Methods

The basic idea of Shaw (1964) for graphic correlation has been applied to stratigraphy by various palynologists, as described by Edwards (1984, 1989, 1991). In contrast to probabilistic methods, graphic correlation is a deterministic method that generates maximum (= total) ranges for taxa. Graphic correlation treats pairs of sections in turn, building a synthetic composite or master "section" that incorporates relevant information from all sections. This method allows the inclusion in the analysis of general stratigraphic markers (for example, event beds), as well as biostratigraphic events. Mann and Lane (1995) summarize a variety of approaches used in this technique. An interesting example of application of graphic correlation is the work of Jaramillo and Dilcher (2001) in a stratigraphically challenging area of Paleogene rocks in Colombia.

4.4 Relational methods

Range charts are used to generate zonation by relational matrix. The zones are based on mutual presence (never absence) of two or more taxa. The zones devised are similar to assemblage zones.

Please note that Edwards and Guex have updated and expanded much of the above information in a series of contributions published in Jansonius and McGregor (1996), vol. 3: Edwards (1996, 1996a), and Guex and Edwards (1996).

5 Computer-based Programs for Palynostratigraphy and Other Paleopalynological Projects

The use of the computer, and things adjunct to it such as the internet with its search engines and retinues of dozens of pertinent websites providing an almost infinite source of useful information, have had a great impact in palynology. Most palynologists now use the computer routinely for handling of masses of palynological data by various kinds of multivariate statistical analyses and other mathematical and graphical manipulation, not only for stratigraphy but also for paleoecological and even for morphological studies. I recommend that readers turn to Lentin *et al.* (1996) for a helpful presentation of the application of computer programs to various aspects of palynology, including palynostratigraphy. Lentin *et al.* include an appendix with details about various programs. This aspect of paleopalynology changes so rapidly, however, that it is best to consult the appropriate personnel, e.g., in the palynological laboratories of national geological surveys, for information about the latest status of software for palynological data management.

The availability of dozens of specialty programs not only for preparation of distribution maps and graphs (e.g., of cluster analysis etc.; see Huntley and Birks, 1983; Boulter and Hubbard, 1982), but also for data storage and management in all aspects of palynology, was already important at the time of publication of the first edition of this book. Boulter and Hubbard, for example, employed cluster analysis and principal components analysis in an effort to reconstruct from their palynological data the vegetational patterns of Paleogene sediments in southern Britain.

It is worth emphasizing that unwary palynologists using the dendrograms generated by cluster analysis, or the information from principal-components analysis, etc., without really understanding the limitations of the various methods, may find "relationships" that are not real, or overlook relationships that are obscured by the misuse of these powerful mathematical tools. For the average student, study of range charts from the literature, showing zones, and correlation of them with informal zones generated from the sections studied, is the most useful approach in stratigraphy, until one needs help from statistical-mathematical consultants. Most educational institutions and research laboratories have people technically able to advise palynologists on statistical tests to use for a variety of purposes. For example, *t* tests can be used to determine if morphological features of palynomorphs are different enough to merit recognition; chi-square tests may be used to express variance between samples, and therefore to test

whether significant boundaries exist or whether the pollen counts of two analysts differ significantly.

Consultation in palynology is now done almost exclusively electronically, with the disadvantage that archiving of matters important to the development of science has dramatically declined. Communication techniques such as e-mail and the internet are by nature existential. It would be helpful if one or more of the palynologically oriented people who are also "fluent" in statistics and various statistical programs available for use would prepare a book or extended monograph outlining the methods and their applications and significance. In the absence of such a book or books I can only urge perusual of the literature for pertinent publications, plus seeking the assistance of statistically oriented colleagues. As of the writing of this second edition, it is axiomatic that using Google.com, Yahoo.com and other such search vehicles is of critical importance during research work in all aspects of palynology. Through the search engines, I am continually discovering websites that are palynologically useful.

As the second edition of this book was nearing completion, a paper by Jaramillo *et al.* (2006) was published that is an excellent illustration of points made in the above paragraphs, as to the modern interplay of graphic correlation methods for stratigraphy, multivariate statistics for the recognition of palynofloral types from large numbers of samples, oxygen isotope studies for recognition of climatic boundaries, and studies of pollen morphospecies diversity as a measure of floral response to changing climates–in this case, of northern South America. The principal graph of this study is displayed here as Fig.19.8.

6 Paleopalynological Systematics: Nomenclature

This section's heading almost ended with the words "formal nomenclature," but, of course, paleopalynology has only formal nomenclature for its fossils. Plant and animal systematists dealing with extant organisms must always take note of so-called "common names," most of which (especially for plants) are not really very common. Even some fossil organisms have "common" names: "saber-toothed tiger," "mammoth," "scale tree," "dawn redwood." For our palynomorphs there are only the scientific names. I suppose it is also doubtful that there will be much interest in the sale of palynomorph scientific names, although in recent years there has been a brisk trade, at astonishing prices, in the names of new taxa of animals (cf. Trivedi, 2005). Inasmuch as one can also pay to have a star formally named and catalogued for oneself or for a favored relative or friend, it is not inconceivable that an enterprising specialist in chitinozoans or acritarchs will offer some names for sale. Unlike stars, however, authentic new species of palynomorphs remaining to be named are now quite finite in number.

Other nomenclatural tomfoolery from which we should be grateful to be more or less sealed off are efforts by well-meaning but misguided folks to overturn the

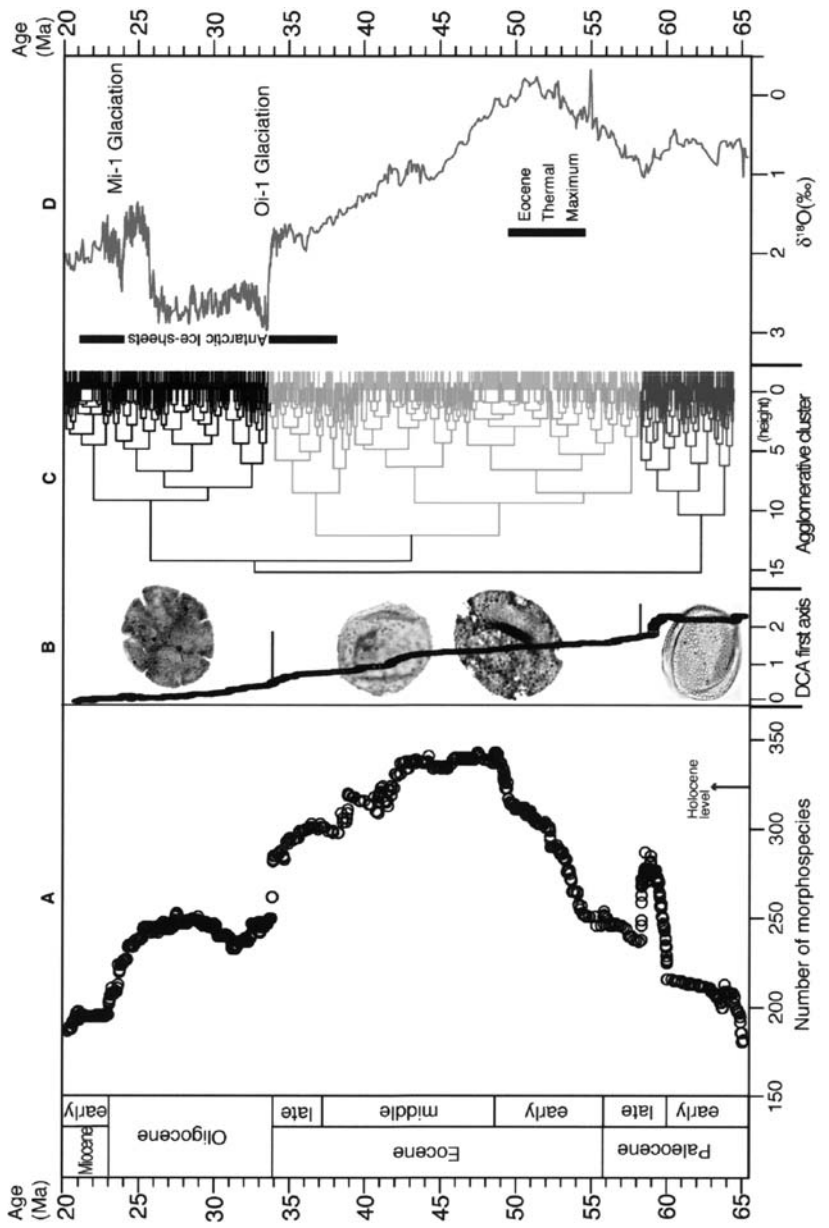

Figure 19.8 *(See Caption on page 607)*

existing system for naming organisms formally. That system stems from Linnaeus in the 18th century. Linnaeus convinced the scientific establishment of his time that binary nomenclature made sense and worked. Basically, the system divides all organisms rather arbitrarily into genera, and these into species. Both genera and species can be further subdivided formally, and they can be assembled into larger groups such as families, but the binomial set, genus and species, provides a convenient way of handling the necessary naming and cataloging of organisms, and of their fossils. It doesn't matter to this procedure that "genus" in the mosses almost certainly means something different in biological and biochemical content from "genus" in the animal group called rodents. Each genus is given a Latin generic name and a Latin specific name. This works astonishingly well as a practical method for recording, filing, and retrieving data about the things so named. Formal nomenclature has nothing directly to do with classification (= taxonomy, the other part of systematics). Indeed, binomial nomenclature could be used satisfactorily as a means of naming the units of a collection of buttons, and Linnaeus himself applied it blissfully to the mineral kingdom, as well as to (what he considered) the other kingdoms, of animals and plants. However, in 21st century biology there are movements gathering steam to overthrow the now huge system of hundreds of thousands of names of organisms and supplant it with this or that system based on the latest biological information. Today, that is personified by DNA data. See Moore (1998) for a glance at one group's concept of "phylogenetic nomenclature," as an example of what it would do to stability of nomenclature. The International Code of Botanical Nomenclature, in its Preamble (Greuter *et al.*, 2000), contains, as it has for a very long time, the statement that says it all: "The purpose of giving a name . . . is not to indicate . . . characters or history, but to supply a means of referring to it . . . ." One could add adjectives before "means," such as "unambiguous," "stable," etc. The notion that the names themselves should be more than just names but also indicate characters or (phylogenetic) history is, however, a very hardy perennial. In paleopalynology

Figure 19.8 Changes in palynofloral diversity and composition during the early to middle Cenozoic, based largely on studies of hundreds of samples from Venezuela. **A**. Pollen and spore standing diversity, with Holocene diversity level shown at the base line. **B**. First axis of detrended correspondence analysis explaining 45.9% of the total variance. Characteristic species are shown: *Proxapertites cursus* for the Paleocene, *Nothofagidites huertasi* and *Echitriporites trianguliformis* var. *orbicularis* for the Eocene, and *Jandufouria seamrogiformis* for the Oligocene to early Miocene. **C**. Agglomerative cluster analysis, showing three distinct palynofloras: Paleocene, Eocene, and Oligocene to early Miocene. D. Global oxygen isotope curve for the whole Cenozoic, showing correspondence between the general trend of the diversity curve and a proxy for average global temperature. Illustration from Jaramillo *et al.*, 2006, reproduced here with permission of the authors and of AAAS, publishers of *Science*.

it has taken various forms, one of the more egregious being an effort to rename all published morphogenera, the names of which ended with *-sporites* to names ending in *-pollenites*, if research had shown the genus consisted of pollen rather than of spores–and vice versa, of course. Fortunately, in palynology there has been only one serious effort to replace the existing system of binary nomenclature with a new one. The proposal was based on allegedly more rational linkage of information about the palynological entities being named to the nomenclature employed. The proponent, Norman F. Hughes (cf. Hughes, 1975; 1989), was a very talented and productive scientist and a good friend of this author. However, his nomenclatural proposals, if they had been widely adopted, would have taken our science many decades of confusion and hard work to digest, with no obvious benefit. Among other things, Hughes would have supplanted the whole basic generic/specific structure of our systematics with different concepts. (See also discussion in Chapter 14 of aspects of "non-traditional" nomenclature in paleopalynology.)

In addition to some advantages paleopalynological nomenclature has because of the relative isolation of our systematics from outside influences (nobody out there cares!), we have some disadvantages. For one thing, our fossils do not all come from one kingdom, or even from one domain. Only the palynological fossils that are considered nomenclaturally to be botanical are covered by the *International Code of Botanical Nomenclature* (= ICBN) (cf. Greuter *et al.*, 2000). Those are: spores, cryptospores, acritarchs (somewhat paradoxically, because acritarchs have not been proven–by definition– to be botanical or anything else), pollen, dinoflagellate cysts, fungal spores and other fungal spore "bodies," prasinophyte phycomata, various algal coenobia, zygnemataceous zygospores, and a few other "varia." At once the reader will notice that many of these items are not now considered plants, but they do fall into the category "vegetable," as opposed to animal" or "mineral," categories that go all the way back to Linnaeus. We now know that fungi are actually more closely related to animals than to plants, but they were traditionally regarded as "vegetable," and are hence governed by the ICBN. The dinoflagellates are members of an ancient group that is now known from chemical and DNA evidence to be neither animal or plant, but they were until fairly recently regarded as algal and hence plants. The ICBN has some special provisions for algae, and these are applied to the dinoflagellates, even though they are now known not to be algae. However, the framers of the Code try very hard to make sure that no special burdens are placed on dinocyst nomenclature, by always making "fossil algae" exceptions to rules that otherwise apply to algae. Algae are all governed by ICBN, even in groups such as the prasinophytes that may well have a separate history from the main lines of algal evolution. I was for some decades Secretary of the Committee for Fossil Plants of the organization that has effective charge of the ICBN (International Association for Plant Taxonomy = IAPT), and I remain a member of the committee. I think it is somewhat unfortunate that there is not a separate committee for the

nomenclature of plant microfossils, because the megafossil paleobotanists have rather different concerns. To take a very small example: the starting point for "fossil plants" (under the aegis of which paleopalynological names are governed) is 31 December, 1820, based on the publication by Sternberg of "*Flora der Vorwelt* . . . .," a publication on fossil stems, fructifications and leaves (cf. Greuter, 2000, Art. 13). A conference of paleopalynologists would almost certainly decide on a more relevant starting point for microfossils governed by the botanical rules, quite possibly more than a century later.

However, a quite different problem is the fact that many of our palynomorphs are not botanical, even by the acquisitive standards of the ICBN. They are animal fossils. Chitinozoans and scolecodonts make up well over 90% of these, but there are others, such as tintinnids, foraminiferal test-linings, and arthropod skeletal parts, although formal naming of these is uncommon. Chitinozoan nomenclature is governed by the International Code of Zoological Nomenclature (ICZN, cf. Ride *et al.*, 1999). and its provisions are in some respects quite different from those of the ICBN. (I am not an expert on the ICZN.) For example, in zoological nomenclature, the various parts of the mouth structure of the scolecodont-producing worm, when they are found apart, all may have their own Latin names. Well and good, that is not different from botanical practice. However, under the zoological rules, such names cannot be decreed to be synonymous unless they are found joined, at least once. When that happens, they will technically be obligatory synonyms, and the name with priority becomes the correct name for the two parts. Ultimately, one name could be the correct name for all the many kinds of mouth parts from one species of worm. For plant fossils governed by the ICBN, actual attachment is not required for synonymy. That is left to judgment of the scientists studying the fossils. Constant close association is often considered enough proof. Furthermore, the rules for botany categorically decree that even after various parts of one structure, such as a branch with cones, have been found attached, the names of the individual structures, such as wood, leaves, pollen, etc., can continue to be used when the fossils are found dispersed. In this connection it should be stressed that names of morphotaxa of dispersed fossil sporomorphs should only be used to refer to dispersed spores and pollen. When they are found *in situ* in anthers, male cones, and the like of megafossil plants, it is all right, in fact very desirable, to mention the fact that if this pollen grain were found dispersed it would belong to such and such a genus or species of *Sporae dispersae*. But as a part of the megafossil, the pollen should be considered pollen of the megafossil species and so named. No new morphotaxon of *Sporae dispersae* should ever be based on a spore or pollen grain found *in situ* in a megafossil. However, as has been well illustrated in a paper by Richardson *et al.* (1993), the feedback phenomenon between observations of *in situ* sporomorphs and obviously related *Sporae dispersae* can provide valuable information about the evolution of the producing plants (usually not very aptly called the parent plants), and about the relationship between related dispersed morphospecies. Richardson *et al.* stress

that dispersed spore morphospecies and infraspecific variants of them sometimes comprise a morphon (sometimes called a complex) of varying forms that can be very hard to untangle, and the comparisons with *in situ* forms can help in understanding the situation. Nevertheless, the nomenclature of dispersed forms, though influenced by information from *in situ* sporomorphs, should be kept separate from the nomenclature of the megafossil plants.

Indeed, the whole concept of morphotaxon in the ICBN, which has a long and checkered history, is intended to underline the concept that, for fossil plants, including microfossils such as pollen grains, a name applies only to the category of fossil organ or plant part originally described and typified for that name. *Classopollis torosus* is a morphospecies of fossil pollen, not a species of plants, though we know that the pollen in question comes from some members of an extinct group of Coniferales. The situation for dinoflagellate cysts is somewhat different, in that the fossils represent the cyst-shell of a whole organism, and in most cases are fully definitive of that taxon. The dinoflagellates are treated in the Code as algae, although it is now well known that dinoflagellates have a history separate from algae, and are not closely related to either one-celled algae such as diatoms or to one-celled animals such as protozoans. Because the Code states that names based on extant types take priority over names based on fossil material, dinoflagellate names based on fossil cysts do not have priority over names for a dinoflagellate organism based on living material. However, the Code also provides that morphotaxon names can continue to be used for fossils when the fossils themselves are studied and described. When speaking of the modern organism known to be represented by the fossils, however, the name of that organism, based on the living material, should be used. This can be somewhat confusing but is a fact in terms of the present Botanical Code. It could be that a future code for all of biology would have advantageous new provisions for such situations.

In citing the name of a morphospecies of fossil sporomorphs that has been transferred from one genus to another, the citation must include the name of the original author of the species in parentheses, as well as the author of the transfer, thus: *Classopollis meyerianus* (Klaus) de Jersey (cf. Chapter 11). ICBN doesn't actually say that the author names are a part of the species name, but the provisions of the Code definitely treat the subject, as if they were, stating that the author names should be cited, designating how to do it, and saying that authors' names, including those of transferring authors, must be cited.. In zoological practice the name above would be cited as *Classopollis meyerianus* (Klaus), without citing the transferring author at all. Indeed, the zoological Code states definitely that "The name of the author does not form part of the name of a taxon and its citation is optional . . . ."

Another, and really huge difference between botanical and zoological nomenclatural practice is that the ICZN provides for an International Commission on Zoological Nomenclature, which has sweeping powers regarding the

interpretation of the Code, and regarding the status of disputed names. In fact, the ICZN is itself a product of the Commission, whereas the ICBN is dependent on authorization by the latest International Botanical Congress. Between Congresses the various committees of IAPT are occasionally called on to decide what to do about proposals to amend the Code at the next Congress, but neither the IAPT nor the committees have much nomenclatural clout.

To take an example that may make the differences clear, consider the long-standing dispute in paleopalynology about the competing generic names *Classopollis* and *Corollina*. You can read all about the matter in Chapter 11 of this book. Had these been names governed by ICZN, a ruling could have been sought from the Zoological Commission, and I presume would have been sought decades ago. I am pretty certain that they would have ruled in favor of *Classopollis*, but no matter how they decided, that would have ended the matter and the confusion caused by it, and spared the printing of dozens of pages of dispute about the issue. Under the ICBN the only way to resolve the dispute was to publish in *Taxon* a proposal for the conservation of *Classopollis* against *Corollina*, get approval of the proposal by the Committee for Fossil Plants, get a positive vote at the nomenclatural session at the next International Botanical Congress, after which it can be assumed to be adopted, as required, at the closing plenary session of the Congress itself. It is then published in the Code itself, as part of an appendix containing such names, which as of the 2000 Code contains just short of 300 pages in a 474 page book. The time is near at hand when the "appendix" will have to be published as a separate volume. Because of the existence of the Commission for zoological names, the ICZN itself is seldom revised: the present edition, effective in 2000 (Ride *et al.*, 1999) is only the 4th in history. The Botanical Code, in contrast, is extensively edited at every International Botanical Congress, including many more pages of conserved or rejected names. The 2000 ICBN was the 10th since 1950, and an 11th, based on the 2005 Congress in Vienna, at which *Classopollis* was conserved against *Corollina,* is in the course of preparation as I write in 2006. Almost all of the nomenclatural business conducted in connection with a botanical congress is matter that in zoological nomenclature would have been handled by the Commission. The entire ICZN is only half as long as the abovementioned appendix in the ICBN, even though ICZN is published in two languages and ICBN only in English (official translations of it into other languages are available). In general, the ICZN is more liberal than the ICZN. For example, ICZN directs that descriptions must be written in, or translated into, English, French, German, Italian, or Latin. In botanical nomenclature, description in Latin is still required across the board, to which fossil taxa are an exception. They could be described in any language at all (apparently even a rare or extinct language; see Traverse, 1990b) until 1 January, 1996, after which the description of fossil plants, including sporomorphs, must be in English or Latin.

In my opinion (cf. Traverse *et al.*, 2004), a major problem for paleopalynological systematics is that our fossils are microscopic, biochemically perishable, and are normally stored in mixtures of hundreds or thousands of specimens mounted on small pieces of thin glass (microscope slides). The slides get lost or broken, the specimens degrade or move in their mountant so as to be unfindable. Of the 30,000 or so palynomorphs that have been designated as holotype specimens over time, I doubt if more than 10% can be located and if found are still in satisfactory condition. In zoology, illustrations could be designated as lectotypes, or the photos of the holotype specimens could be used as if they were the types, though ICZN is careful to insist that when referring to such an illustration one is actually referring (in theory) to the specimen of which the illustration is a proxy: "The designation of an illustration . . . as a lectotype is to be *treated as designation of the specimen illustrated* . . . the fact that the specimen cannot be traced does not . . . invalidate the designation." (ICZN, Article 74c, italicization provided here for emphasis of the point.) In ICBN, microfossils are the only microscopic plant entities for which illustrations cannot be designated as types. I have not given up hope that we can yet resolve this frustrating situation, perhaps somehow along the lines of the ICZN provision. Well, at least chitinozoan experts–because their nomenclature is governed by ICZN–can use illustrations as if they were types, although they are then supposed to have in the back of their minds the concept that the illustrations are merely proxies for perhaps non-existent actual specimens.

There are several very important resources for work in fossil palynomorph systematics/nomenclature. For fossil sporomorphs, an indispensable resource of great helpfulness with nomenclature is the *Genera File of Fossil Spores*, by Jansonius *et al.* (1976 *et seq.*). For the history, remarks about the organization, and suggestions about methods for using of this marvelous compendium, see Traverse (2004). The *File* in early 2006 was in production of *Supplement 14. The Catalog of Fossil Spores and Pollen*, vols. 1–44, published from 1957–1984 at Pennsylvania State University, was a valuable catalog of species (cf. Kremp *et al.*). It is now defunct, and the volumes are mostly available only in libraries, but are still helpful. For dinoflagellate cysts, the *Lentin and Williams Index of Fossil Dinoflagellates* (Fensome and Williams, 2004) and the *Eisenack Catalog of Fossil Dinoflagellates*, new series, of which vols. 1–4 were published by Fensome *et al.* (1991–1996), are invaluable resources. The original *Eisenack Katalog der fossilen Dinoflagellaten, Hystrichosphären und verwandten Mikrofossilien*, in seven volumes (two volumes, plus a supplement volume on dinoflagellates, four volumes on acritarchs), published between 1957 and 1979 by Eisenack, *et al.* is also an important resource, now available mostly in libraries. For acritarchs and prasinophytes, the *Index* thereof by Fensome *et al.* (1990), is still available and useful. Fensome *et al.* (1991), provides an alphabetical list of acritarch and fossil prasinophyte species. For chitinozoans, I am not aware of a comprehensive catalog, but I would recommend use of Miller (1996) to get a good view of

the general range of taxa at the generic level. The same sort of statement could be made about scolecodonts; in addition to publications on them recommended earlier in this book, I would suggest reference to Szaniawski (1996) for a general treatment including many of the important taxa names.

More information about paleopalynological systematics and nomenclature in particular is to be found in Traverse (1996). The ideas expressed in that chapter of the first volume of the Jansonius and McGregor's (1996) *Palynology: Principles and Applications*, regarding the potential impact of an all-organism unified code of nomenclature on paleopalynology, turned out not to be of immediate concern. The discussed code of bionomenclature has not come to fruition, though the idea is not dead, and it may well be the wave of the future and a good thing. Certainly, the botanical and zoological Codes (ICBN and ICZN) should be studied carefully, and kept close at hand for reference by anybody planning to publish new names or alter existing names of palynological fossil morphotaxa.

Appendix

Palynological Laboratory Techniques

1 General Introduction

This appendix provides simple directions for processing various sorts of samples for palynomorph study, along with comments about some techniques used elsewhere, and some related matters. The emphasis is on techniques that can be adapted easily to basic laboratory facilities even of small institutions. Since publication of the first edition of this book, a number of elegant "system" techniques have been described, using various very sophisticated pieces of equipment such as special microwave heating devices to facilitate the precise processing of large numbers of samples or smaller suites of samples in a highly controlled environment. These systems do not address the purposes of most people who will use this book, and they are not essential for the production of very good preparations of fossil palynomorphs. They mostly were introduced because of situations in certain installations and localities requiring very precise control of the processing chemicals and by-products of the procedures.

Simes and Wrenn (1998), for example, describe a microwave digestion system, combined with gravity-separations and sieving techniques, designed for the stringent requirements of processing in a facility in Antarctica. Poulsen *et al.* (1990) describe a "maceration tank" procedure and apparatus involving the use of polypropylene tanks for HF processing, with the acid and water and other washing solutions transported by plastic pipes from tank to tank and to drainage sinks. It was inevitable that microwave heating would be applied to palynological processing, as it is a marvelously effective way of getting fast heating that penetrates to all part of the contents of a vessel being so heated. Jones (1994, 1998) describes an outfit for the purpose based on focused microwave digestion in a commercially available digestion system. Samples are processed quickly and relatively safely because of the sealed vessel basis of the digestion. A somewhat different microwave heating for HF digestion of palynological rock samples is described by Ellin and McLean (1994).

Turning to methods of more practical use for most readers of this book, I would recommend Doher's (1980) 30-page publication about palynomorph processing, which contains directions for various preparation techniques. Another valuable publication on techniques is Phipps & Playford (1984). Kummel and Raup's (1965) *Handbook of Paleontological Techniques* contains a number of chapters about palynology. The chapter by Gray summarizes the then current maceration methods, most of which are still in use. Well-described techniques in Evitt (1984), intended for preparation of dinoflagellate cysts, are also applicable to spores/pollen. Bryant and Wrenn (1998) present some processing techniques that students may find instructive for unusual situations. Jones and Rowe (1999) have many chapters on palynological techniques, with potential help for a variety of laboratory problems encountered.

It should also be stressed that all of the lab techniques described herein fall into the category of "kitchen chemistry," and hardly any two laboratories perform the

various operations in exactly the same way. I noticed over the decades that my graduate students all developed their own "wrinkles" to the procedures I taught them–at least some of these were improvements. Always use common sense. For example, do not use a bleaching technique merely for cosmetic purposes; if the study involves close examination of exine sculpture, it is not sensible to risk ruining it by bleaching procedures. For studies in which estimation of thermal alteration is to be made (cf. Fig. 19.2), bleaching may affect the validity of your observations. Readers will find it useful to consider the studies by Colbath (1985) about the negative effects our processing techniques can have on the makeup of the palynofloras we obtain. His results do not mean that we need to abandon any of the methods he studied, but rather that we should be careful about too much dependence on statistical measurements of the exact proportions of fossils in a palynoflora, remaining mindful of the possible influence of the lab procedures on the data.

In recent years a number of commercial laboratories have appeared that will process rock samples for palynomorph study, or do other sorts of palynological laboratory work on a per-sample fee basis. This outsourcing is practical for a person who is able to establish a microscopic laboratory facility but for whom the establishment of a wet lab would be financially or practically impossible. However, the outsourcing approach is clearly not as good for the palynologist's understanding of the samples at hand as is processing in her/his own lab, because close observation of the effects of the various processes can be very instructive; furthermore, procedures can be adjusted to advantage in response to such observation. Users of this book may get information on outsource labs from the author or from other paleopalynologists. Officers of the American Association of Stratigraphic Palynologists (http://www.palynology.org) would be a good place to start in inquiring about this matter. The information changes too often for it to make sense to give individual addresses here.

2 Extant Spores/ Pollen

2.1 Introduction

People who work with fossil spores/pollen should study extant forms, at least to get ideas on morphology and structure potentially important for identification. When studying post-Cretaceous materials, awareness of modern forms is obviously important for suggesting possible botanical relationships. By late Neogene time practically all of the forms encountered are from extant genera, and collections of modern spores/pollen provide the basic material for all identification efforts.

It is possible to study "raw" pollen, and indeed aerobiologists routinely do this: atmospheric pollen is trapped, often directly on a slide to which Vaseline (petrolatum), glycerin or some other translucent sticky mountant has been applied, and

the spores/pollen are studied without treatment. It is possible to recognize pollen so prepared, especially as the aerobiologist has to recognize only a relatively few taxa that occur over and over. However, to determine the exine features with any degree of satisfaction, this is not a good approach, as untreated exines contain oil droplets and other intercalary inclusions, or there are external coatings that cover significant features. Furthermore, the protoplast and the intine of the spores/pollen make microscopic study of the exine very difficult, because the transmitted light of a conventional, biological type microscope must go through those structures before hitting the upper layer of exine. The adherent oils and included lipids and the whole protoplasm and intine need to be removed if the exine is to be properly studied. Also, since the exine alone is what a paleopalynologist studies, the reference materials need to be, as it were, artificially fossilized. One way this can be done is to boil anthers, sporangia, or even small flowers in 10% KOH. The cellulose is hydrolyzed and protoplasts lyzed. The resulting exines are, however, practically colorless and must be stained for proper light microscopy (safranin-O, basic fuchsin or other red stains are good, because optical systems are usually corrected for green light). G. Erdtman (with help from his chemist-brother) long ago introduced the practice of acetolyzing sporulating/flowering material in a mixture of nine parts acetic anhydride, and one part concentrated sulfuric acid. The procedure has been retained by palynologists since, with little change (Traverse 1955). The reaction is as follows:

$$\underset{\text{cellulose}}{(C_6H_{10}O_5)} + 3\underset{\substack{\text{acetic}\\\text{anhydride}}}{(CH_3CO)_2O} \xrightarrow[\text{catalyst}]{H_2SO_4\text{as}} \underset{\substack{\text{cellulose}\\\text{triacetate}}}{(C_6H_7O_5)(CH_3CO)_3} + 3\underset{\substack{\text{acetic}\\\text{acid}}}{CH_3COOH}$$

(For structure of cellulose, see Chapter 3. Cellulose is really a long chain compound, with thousands of repeating units.) The sulfuric acid is a catalyst and also a desiccating agent. Sporopollenin of most pollen comes through relatively unscathed, at least at the level of magnification usually used, but the color is altered from almost colorless to a yellow, amber or orange color depending on length of treatment and thickness and structure of the exine. Some modern pollen grains, e.g., Malvaceae, are characteristically thick-walled. It is impossible to prolong acetolysis long enough to remove the cellulose of anthers and other flower parts of these plants without getting the exines very dark brown, sometimes almost black. These grains should therefore be bleached carefully with sodium hypochlorite (use laundry bleach) after acetolysis. Some grains are very pale even after acetolysis. These can be stained. In practice, staining and bleaching are seldom necessary. If acetolysis is done carefully, 95% of the forms processed will come out an acceptable yellow to orange color. Apparently, exines of at least some sorts of pollen are considerably modified in microstructure by acetolysis when it is combined with other treatments, as demonstrated by

Aubran (1977) for the use of acetolysis, plus potassium permanganate fixation (of cycadeaceous pollen), and by Hafsten (1959) for acetolysis combined with HF and bleaching (oxidation). In my experience, this is not a serious problem for practical palynology, where one seldom uses these combinations of methods. For very thin-walled or otherwise delicate pollen and spore exines, it is possible to use enzymes such as cellulase and pectinase for digestion of the non-sporopollenin parts of the grains (Schols *et al.*, 2004). For applied paleopalynology this has little significance because such easily destroyed exines are unlikely to occur as fossils, but the method could be important for basic research studies of pollen morphology. The Schols method also employs a critical-point dryer, such as a Balzers CPD, an elegant way to dry plant material without application of either strong chemicals or microwave heating, when, for whatever reason, complete dryness is demanded quickly.

It is very important to understand that reference spores/pollen should not ordinarily be prepared from flowers, anthers or pollen collected by palynologists from the field into envelopes or vials, although it is possible to do this, and there are sometimes adequate reasons.

2.2 Preparation of Spores/Pollen for Microscopic Study

2.2.1 Drying Techniques

This assumes pressed, dried plants. Fresh flowers, etc., must be first dried. Both glacial acetic acid and acetone are readily available, good drying agents for this purpose, because one can go directly from a thorough soak in tightly covered containers (overnight is best) to acetolysis mixture after centrifuging off the drying liquid. Heating the glacial acetic acid and sample will expedite the reaction. If acetone is used, do not heat, because acetone is too volatile and flammable. Care should be taken not to breathe the fumes of either liquid. Freeze drying is another possibility, and it is also possible to dry plant material very quickly by a very brief (2-3 min) treatment in a microwave oven (Hall, 1981; Bacci and Palandri, 1985). Investigations in our laboratory showed that microwave drying damages varying percentages of pollen because of explosive production of internal steam inside some of the grains, but leaves ample undamaged pollen for adequate study. Incidentally, microwave treatment used for insect control on previously dried herbarium specimens does not harm pollen exines at all, although undried, fresh pollen is more or less damaged by the steam generated (see Arens and Traverse, 1989).

By far the best procedure (see Traverse, 1965) is to take the trouble to make pressed, dried plant specimens using conventional botanical techniques. These specimens will match up with field notes and numbers, and they can be used to prepare standard herbarium sheets. These are then "voucher sheets," and the identity of the plants producing the spores/pollen can be checked, even decades

later, by a plant taxonomist. Study of the pollen morphology has shown me that specimens of *Nyssa sylvatica* were marked "*Maclura pomifera*" in several prominent herbaria in various parts of the USA. This dramatizes the point: if university herbarium curators make mistakes in identification of material, the average palynologist should not depend exclusively on her/his own field identifications.

2.2.2 Outside the "Wet Laboratory"

(a) Isolate sporiferous/polleniferous material as much as possible, dissecting off leaves, stems, peduncles, sepals, petals, etc. Ideally, just sporangia/anthers are best (easy with *Magnolia, Lilium*, and some ferns), but for plants with tiny flowers, such as Apiaceae, or ferns with well protected sporangia, whole flowers or pieces of a frond with many sori/sporangia must be used, although one should take care to remove as much extraneous tissue as possible. Work on a piece of white paper, using needles, scalpel, and fine scissors. A dissecting microscope (or at least a hand lens) is very useful. The best material is several florets that, when collected, were just on the point of opening but not yet open. Younger florets will often contain immature, atypical pollen, while older, open florets may have shed much or all of the pollen. Where large flowers such as *Camellia* are the subject, one collects just anthers, and should avoid opening a flower that was still closed when collected, and thus damaging the specimen too much, if it is part of a specimen of potential systematic significance, for example in an institutional herbarium. In such cases, and with fern sori and gymnosperm male cones, always carefully study the anthers, sporangia or pollen sacs with a dissecting microscope or hand lens, to be sure that abundant spores/pollen are present. Spore/pollen-bearing material removed from the specimen which is difficult to pick up can be easily poured from the sheet of white paper mentioned above into a collecting envelope. For cleaner slides, use as little material as possible to get a good preparation. If the material is from a working herbarium, the curator will welcome palynological predation more cheerfully if one is very conservative: anthers only where possible, as few florets as possible, etc.

(b) Record data immediately on the collecting envelope; one can get too little information but never too much. Get the original collector's name and field number, locality information, and the herbarium where the voucher sheet resides. If it is one's own specimen, or if the herbarium curator permits it, annotate the sheet from which material is taken. Remember that all of this preliminary work should be done outside the processing laboratory because contamination, though seldom a serious problem, can become so if spores/pollen are willy-nilly introduced to the dust load of the "wet" laboratory. A data file should be created for each maceration that preserves all information from the collecting envelope. If the preparation is productive, assign a serial spore/pollen collection number to it. File the completed slides by family, then by genus and species. File the data by serial number, with cross-references to genus + species and family.

2.2.3 Inside the "Wet Laboratory": Acetolysis

(c) Working in a fume hood, prepare the acetolysis mixture of nine parts acetic anhydride and one part concentrated sulfuric acid. Each preparation will take about 12 ml of mixture. It is best to calculate how much will be needed for the number of samples you intend to process, and to make approximately that much, discarding the excess in a hooded sink with plenty of running water, or into a "decant bottle" of water which is periodically dumped in an approved place and manner (check with safety officers of your institution). The mixing-reaction is exothermic. Therefore add the acid to the anhydride a little at a time (acetic anhydride is very hydrophilic, and fumes will go for the moisture in your mucous membranes with uncomfortable results if you do not work in a hood!). Do not stopper or tightly cover the mixture until it has "settled down." (Be sure to wear lab goggles if you don't wear regular eyeglasses, in case there is spattering. Indeed, in my lab nobody was allowed in the door without eye protection.) Be certain that all utensils used in preparing the mixture are absolutely dry, as even a little moisture inadvertently introduced will turn the mixture immediately dark brown and render it useless. The correct color for the completed mixture is pale yellow. Acetolysis mixture can be stored in a refrigerator in a stoppered bottle for later (but not too much later) use. It will change with time from the original pale yellow through orange and eventually to brown, decreasing in effectiveness as it darkens. It is better not to store the stuff beyond the time required for one session of pollen preparation, but on occasion I have left it in a refrigerator for a week and found it still yellowish and usable. On other occasions even one day was too long.

(d) For each envelope of sporiferous/polleniferous material to be processed, prepare a 15 ml high quality, high temperature resistant glass centrifuge tube, to which a laboratory number has been affixed (I prefer the special laboratory tape for this purpose). This number should be recorded in a working laboratory book, along with the species name and more information, if more than one preparation of a species is to be made. Stand the tube in a tube rack and put a small glass funnel in the tube. On the top of the funnel put a slightly cupped square of 40×40-mesh (0.420 mm) brass screening. Pour the contents of one of the collecting envelopes on the screen and rub the anthers, etc., through with a thumb or fingertip. Note that the screen and human digits must be thoroughly cleaned and dried from previous use, or the resulting preparation will have contaminants! I favor cleaning the screen by brushing with a toothbrush, followed by flaming in a gas flame (hold square of screen with a longish pair of channel-lock pliers). However, the resultant preparation will then be contaminated with abundant black flecks of charcoal, unless the screen is thoroughly rid of them by vigorously and repeatedly knocking the square against the edge of the bench or other surface while holding it with the pliers.

(e) Wash polleniferous material from the screen and sides of funnel into the test tube with an acetone wash bottle (do not work near a flame! acetone is flammable). Invert the funnel on a labeled paper towel. Centrifuge sample for 3 min (top speed in a table-top clinical centrifuge, or 2500 rpm in a floor-model, tachometer-controlled machine) and discard acetone into running water in a hooded sink. Replace funnel in tube and now working in hood, carefully and slowly add acetolysis mixture to tube. Fill tube to within about 2 cm of the top. Equip tube with narrow stirring rod (about 3 mm (heavier stirrers sometimes break tubes). Put tube with stirring rod in a small beaker of boiling water on a hot plate in hood. A piece of heavy-duty aluminum foil with a hole for each centrifuge tube can be applied to the top of the beaker–this minimizes the chance of water drops getting into the tube. If more than 1-2 tubes are to be processed, I favor using a rack with holes for the tubes that fits into a saucepan of boiling water. (See Traverse, 1965, for description of the virtues of aluminum heating blocks for this purpose: no problem with constantly refilling water baths, no spoiling of acetolysis mixture by water condensate, more readily controlled temperature, e.g., at higher elevations where water boils at too low a temperature. Water baths are more likely to be available and are all right if properly monitored.)

(f) Continuing to work in the fume hood, heat tubes in the water bath at 100° C for 10–12 min (usually 12 min; however, if working at higher elevations, the water bath will not be 100 °C and the time must be adjusted upwards). Stir (gently) every 3–4 min, leaving stirring rod in the tube. (Pure samples of pollen can be acetolyzed for shorter periods of time, but if much cellulose from floral tissues is present, longer acetolysis is needed.) Acetolysis mixture turns dark brown during the reaction if the procedure is working. Remove stirring rod, then centrifuge sample in the same manner as for acetone removal, except that this step must be accomplished in a hood. Decant into hooded sink with plenty of water flowing, or into a decant bottle in the hood, depending on your laboratory circumstances. Never decant into an open sink, as the acetolysis mixture fumes are very toxic to people! Centrifuge tubes with a well-packed residue in the bottom end should be decanted in a quick, smooth, inverting movement. Novices make problems for themselves by too deliberate decanting, as this causes the liquid to bite into the sediment at the bottom. However, I would advise anybody who is having a decanting problem and wants to avoid redoing a lot of work, to decant centrifuge tubes into a clean beaker first, and then empty the beaker if all went well. If the decanting hasn't gone well, the liquid and residue can be poured back into the centrifuge tube for re-centrifugation and another try at decanting.

(g) Add distilled water to the tube. The semi-distilled water in laboratory taps labeled "distilled" is fine. So is water from a dehumidifier or commercial bottled distilled water. It is usually unwise to use the local ordinary tap water, which can be a source of contaminants and sometimes of distressing amounts of calcium salts. Stir thoroughly; I prefer to stopper the tube and shake it, but prior loosening of the residue with a thin stirring rod may be necessary. Centrifuge again. Decant

into hooded sink. Repeat washings followed by centrifugation until no acetolysis mixture remains. Usually this is three washings, unless there was too much plant material. If one is in doubt, after the third washing it is safe (and the best test) to taste for trace acidity with the tip of the tongue. If there is still a lingering acidic taste, repeat the washing. After the first wash it is all right to work in an unhooded centrifuge and to decant in an open sink. After the last decantation keep the tube in the inverted position and place mouth down on a paper towel to drain for about 10 min.

(h) Affix temporary labels to a vial to receive the residue and to the desired number of slides which should be placed along with coverslips on a warming table set at a temperature of 38–40 °C. Add warm (about 50 °C) glycerin jelly (see section on mounting media below) to the drained residue, the amount depending on the amount of residue and the density of spores/pollen desired on the slides. Start with about five times as much mounting medium as you have residue, and adjust if necessary after inspecting the first slide. To add glycerin jelly, I use a 10 ml commercially available pipette from which I have cut off a section of the tip, as the original tips are too narrow, and soon clog with jelly. Stir mixture of jelly and sample in tube thoroughly with a narrow, warmed (hold under hot water tap for about ten seconds, and shake off water drops) stirring rod, but take care to avoid introducing air bubbles. Keep the tube warm by frequently holding the lower end of it under hot water tap. Make desired slides by inserting a short glass tube (2 mm. diameter) with the end stopped by a finger, about half way to the bottom of the well-mixed jelly-residue, then releasing the finger to admit a few drops of mix. Put a drop of mix on the slide and cover with a coverslip (working on a warming table). To minimize introduction of bubbles, position the coverslip over the drop, resting one side on the slide (hold the top and bottom edges gently with one hand); with the other hand, insert a bent dissecting needle between the open side of the coverslip and the slide, drawing it out slowly as the coverslip descends. I favor placing the drop in the center of the slide, as a centered preparation is more conveniently studied microscopically than is a preparation which is too close to one edge or the other. Leave slides on warming table at least 24 and not more than 72 hours to cure (= lose water, mostly). Then clean the slide carefully with a moist tissue and label them. Although many use peel-off labels, these invariably fall off in time. In my opinion, the best way to label slides is to clean the end to be labelled with 50% alcohol (rubbing alcohol is satisfactory) to remove all traces of finger oiliness and then write the label directly on the glass with an India ink pen or a pen with similarly permanent ink. In a minute or two the label can be painted over with colorless fingernail polish. (Some black ink pens that will write on the glass nevertheless are unsatisfactory because the ink is soluble in the polish solvent.) The coverslip can be carefully ringed with the polish at the same time. Use a “bead” that just gets up onto the coverslip. It is not possible to study specimens critically that lie under the ring. If an important specimen is later encountered, use a little acetone on a folded corner

of tissue to remove the acetate film in that area, and polish the area with another folded corner of tissue moistened with saliva (or water for the squeamish–saliva is better). After studying or photographing the specimen, renew the ring. The ringing greatly prolongs the life of the slide. Oxidation-destruction of specimens on the slide is hastened by oxygen from the atmosphere, including that in bubbles on the slide.

2.2.4 Additional Information and Discussion

2.2.4.1 Contamination Problems. Although some palynologists use elaborate precautions against atmospheric and other pollen contamination in their laboratories, including even frequent vacuum cleaning, my experience is that this is hardly ever a problem. The pollen prepared from dried plant material or from sediment samples should completely overwhelm isolated contaminants for one thing, or the slide should not be used. Atmospheric contaminant pollen will seldom exceed 1-2 per slide even when conditions are relatively bad, for example, with many people coming and going during a flowering season. I have proven this to my satisfaction by many studies of blank slides made with just mounting medium. The relatively few atmospheric spores/pollen falling into the mounting medium or otherwise introduced after processing contain protoplasm with various inclusions and thus are recognizable as foreign to the preparation. This is just not a serious problem, though I advocate a moderate degree of sensible caution, e.g., no extraneous flowering material in the wet laboratory. Vials, beakers, tubes, and other specimen containers should be kept covered when left overnight or longer. A much more serious source of contamination in my experience is insufficiently cleaned glassware, especially centrifuge tubes. Plastic tubes are more likely to offend than glass because of the presence of numerous scratches. Phipps and Playford (1984) advise against using mortar and pestle for crushing, as their surfaces may be pitted and cause contamination. This is true, but is insignificant if only glass, not ceramic, mortar and pestles are used, and if they are carefully cleaned after each use. As noted above, a stray contaminant grain now and again really does little harm, as it will be completely overwhelmed by the palynomorphs that belong in the sample. Results should never depend on very rare specimens for just the reason that contamination cannot be completely excluded. Nevertheless, the Phipps and Playford method of crushing rock samples between two aluminum pie plates which are then discarded, instead of crushing in a mortar, is certainly elegant.

2.2.4.2 Coverslip Thickness, Upside-down Slide Curing, and Coverslip Sandwiches Sometimes one has difficulty with spores/pollen lying too far below the coverslip to be studied with the very short working distance of high-power oil-immersion lenses. Undestroyed chunks of plant tissue or foreign matter exacerbate the problem by holding the coverslip up. In the first place, never use coverslips thicker than no. 1 (some people use the even thinner no. 0, but they are very

fragile). It is possible to cure slides upside down, using coins or wooden strips on the warming table, under the ends of the slides, or slides can be cured upside down in racks in a warming oven. The spores/pollen will mostly sink in the liquid glycerin jelly to come to rest against the coverslip and will stay there if the slides are also cooled upside down while the glycerin jelly jells. (Another way to keep specimens near the plane of the underside of the coverslip is described below under double mounting.) Where really critical microscopy is planned, however, the best idea is to make coverslip "sandwiches," with the residue between two no. 1 coverslips. These can be fastened to a slide with bits of sticky tape. A specimen can be studied and photographed from both sides in this manner. (I also have used this technique for SEM work: see below.)

2.2.4.3 Centrifuge Tube Breakage Glass centrifuge tubes, even the best ones, do break. Yet for acetolysis work, they are preferable to plastic: the centrifuging works better, and they are easier to clean than plastic, which accumulate scratches, in which contaminating palynomorphs can hide. (Both glass and plastic centrifuge tubes can be cleaned of possible organic-matter contaminants with strong oxidants such as sodium hypochlorite. Stand the tubes in a beaker of such solution overnight.) Usually a preparation from a centrifuge tube that breaks can be saved, though it is better to start over if there is plenty of material. First, the centrifuge shields in which the tubes are spun must have been clean beforehand: wash and brush them out frequently. If a tube breaks, dump the contents, rubber cushion, broken glass, and all, into a beaker. Use needles and forceps to remove the cushion and glass shards. If the sample was in acetolysis mixture or other strong chemical, dilute with enough water in the beaker to make this possible. If necessary, strain through a small plastic sieve to separate small glass shards. Centrifuge to recover the residue and proceed as if nothing had happened. Obviously, it is tempting to use plastic tubes all the time, taking care to keep them meticulously clean, including treatment with laundry bleach.

2.2.4.4 Non-centrifugation Occasionally, for reasons I do not understand, an acetolyzed residue will display mutual repulsion of particles and will refuse to "go down" when centrifuged. It may be necessary to basify the mixture with some 10% potassium hydroxide to make the residue pack down normally. The alkali can then be washed out by a couple of water changes and centrifugations before proceeding. Addition of ethyl alcohol to reduce the specific gravity of the hydrous liquid has been used to encourage centrifugation in such difficult cases. It is interesting in this connection that Clarke (1994) found that some pollen forms, such as *Tsuga*, characteristically resist centrifugation, causing under-representation in analyses.

2.2.4.5 About Mounting Media Spores/pollen are mounted on microscope slides in a wide variety of transparent media. Some have even advocated corn syrup or various self-prepared plant gums. Today there are only a few preferred

mountants. The most common is glycerin jelly. Canada balsam, a natural resin from coniferous trees, is popular. It is soluble in xylene. Its index of refraction is good for pollen study (see Table A.1). The ideal index of refraction should be a little different from that of sporopollenin but not too different. Glass has an index of refraction of 1.54. Water, at 1.34, is too different from sporopollenin ($RI = 1.48$); specimens in water show too much contrast and a very dark outline. Glycerin jelly, a little below, and Canada balsam, a little above sporopollenin's *RI* are both good. However, specimens must be run through alcohol and xylene changes before they can be mixed with balsam, which is considerable extra labor, and the liquid balsam remains liquid (especially in the center of a preparation) until the xylene gradually evaporates, sometimes after many months.

Specimens can and do change position and location during the solidification process. In time, the originally almost colorless balsam turns dark, but balsam preparations are good for many decades. Elvacite, now used by many palynologists, is also dissolved in solvents and thus has the disadvantages of Canada balsam, but it does not discolor with age. Its *RI* of 1.49 is very close to that of sporopollenin, suggesting that it would not give as good definition as either balsam or glycerin jelly.

Although I have tried to find a satisfactory synthetic substance, I keep coming back to glycerin jelly. Despite the fact that it is not really permanent (most of my 40-year-old slides are spoiled–to say nothing of those that are now 60 years old–apparently by autoxidation of the sporopollenin), it is fairly durable: a well-sealed preparation will stay in good condition at least 10 years. J. Jansonius writes me that perhaps insufficient water-washing at the end of my procedures accounts for degradation over time of my glycerin jelly preparations, and that keeping residues slightly acid with a few drops of dilute HCl at the end of processing guards against destructive reactions. In any case, he states that glycerin jelly slides from the former Esso labs in Calgary are still good after several decades. D. M. Jarzen writes me that his 40-year-old slides are still good and asserts that careful sealing of the coverslips with varnish is probably the reason, but I also seal all coverslips. As stated elsewhere, the fact that the pollen in my vials of the same preparation as the slides is apparently good for at least 60 years, tells me that it is the slide-coverslip housing that is the problem somehow. Glycerin jelly has additional virtues: for example, its refractive index is perfect for photomicrography. It is thermoplastic at a lowish temperature (about 45 °C, depending on how it is made), so that residues can simply be stored in it, melted when needed, and new slides made. It is water soluble, so that no extra steps are needed to go from final water washes of a residue, before combining with mountant. As an alternative storage method, residues can be stored in water containing a biostatic compound, and slides made by mixing glycerin jelly with drops of the stored residue. Because of thermoplasticity, the mountant in the vicinity of a specimen on a slide can be touched with a warm instrument to melt the mountant locally and permit

Table A.1 Refractive indices (RI) of some palynological mounting media

Substance	*RI*
air	1.00
water	1.34
silicone oil	1.4
glycerin jelly	1.43
AYAF (vinylite)	1.46
glycerol (glycerin)	1.47
sporopollenin, acetolyzed or fossil	1.48*
Elvacite	1.49
Canada balsam	1.53
quartz glass	1.54
Lakeside 70**	1.54
polyvinyl alcohol (PVA), as solid film	1.55

*$RI = 1.55 - 1.62$ for fresh sporopollenin, according to Christensen (1954) and Jones (1984).

** Used as adhesive for rock thin sectioning.

Note: As has been frequently explained (Berglund *et al.*, 1959), palynomorphs give poor definition in transmitted light if mounted in a medium with refractive index either too different from or too similar to sporopollenin. An *RI* moderately above or moderately below that of the specimens is best. For example, water mounting gives very harsh contrast and a black outline to palynomorphs. Further, refractive index too close to that of sporopollenin gives poor definition without sufficient contrast. The relatively good definition of sporomorphs in Canada balsam would be difficult to explain if the *RI* for acetolyzed or fossil sporopollenin were as high as Christensen (1954) and Jones (1984) have reported for fresh sporopollenin. Polyvinyl alcohol, the usual primary mountant in double-mounting techniques, also gives good resolution at $RT = 155$. That glycerin jelly, Canada balsam, and PVA all give very good resolution with palynomorphs tends to support the measurement of 1.48 for acetolyzed or fossil sporopollenin.

turning of a specimen with gentle pressure of a needle. Because glycerin jelly's constituents can be purchased almost anywhere, one is independent of scientific suppliers, though very good glycerin jelly can also be purchased from them. Residues stored for many decades may have the glycerin jelly become as tough as leather and no longer readily soluble in water. These residues can be recovered by heating them in 20% HCL for varying periods of time, depending on the state

of the mountant. The residue can then be centrifuged, washed and recombined with fresh mountant.

In our laboratory, we have generally made our own glycerin jelly, using the following recipe: 50 g. plain gelatin (ordinary Knox's gelatin from a grocery store works fine), 150 gm. glycerin, 7 gm. phenol, 175 cc. distilled water: dissolve phenol in warm glycerin; dissolve gelatin in warm water (add gelatin gradually to water while stirring, then allow time for dissolving); mix both liquids together and warm gently to 80 °C (do not allow to get hotter), bottle in wide mouth jars, and store at room temperature.

Many palynologists who study and count late Pleistocene and Holocene pollen and spores find it essential to be able to turn over their specimens during counting to verify morphological features. They therefore prefer to use silicone oil, as it remains liquid, does not evaporate, and has a satisfactory index of refraction. It is true, however, that specimens will wander, especially if the slides are not stored horizontally. Glycerin (= glycerol), a liquid constituent of glycerine jelly, can be used in a similar fashion, but the refractive index is less satisfactory. (Tacking down the coverslips with nail polish retards but does not prevent wandering of specimens.) Silicone oil can be purchased from: Accumetric, Ring Road, Elizabethtown, KY 42701, USA. It is manufactured by Dow Corning Corp. as: 200 Fluid Dimethylpolysiloxane (viscosity: 2000 centistokes). This information is from Dr. Cathy Whitlock, Department of Earth Sciences, Montana State University, who uses the following modification of Faegri and Iversen's (1989) method for mounting fossil pollen residues in silicone oil:

(1) Wash with water.
(2) Wash with a few drops of water and 95% ethanol.
(3) Wash with 99% ethanol; stain with safranin-O or fuchsin if desired.
(4) Wash with t-butyl alcohol.
(5) Add about 1 ml t-butyl alcohol, transfer to small vial, add silicone oil, leave for evaporation for about 24 h. The vials may be kept for future use.
(6) Add the amount of silicone oil needed for optimal concentration of the pollen.

In making the slides the smallest possible amount of silcone oil should be used. The droplet spreads under the coverslip very slowly. For fossil slides small coverslips (18 × 18 mm) are to be recommended. Reference slides of recent pollen may be sealed with nail polish. (Paraffin is preferred by some, as there is some deterioration over a period of several years caused by a reaction between nail polish and the silicone oil.)

As I have noted elsewhere, I am not convinced that the mobility of palynomorphs in oil is really necessary, as the microscopist who has seen thousands of specimens of, say *Fraxinus* pollen will have no difficulty recognizing

it any position it is likely to assume in solidified glycerin jelly. In critical cases where moving the grain is absolutely necessary, this can be done by local melting of glycerin jelly with a very warm to hot pointed metal object, without losing the many advantages of a solid mounting medium.

2.2.4.6 "Double-mounting" Many laboratories use a technique for slide preparation that results in specimens closely adhering to coverslips, using two mountants, one a thin film in which the palynomorphs are enclosed, and the second to fasten the coverslip containing the specimens to the slide. The following is an example of double-mounting which was used in the palynological laboratory of the Geological Institute, Swiss Federal Technical Institute ("ETH"), Zürich, when I was there, 1980–81. It was adapted from procedures followed in palynological laboratories of the Geological Survey of Canada.

Ingredients:

(1) Polyvinyl alcohol solution: 50 gm polyvinyl alcohol in 500 ml distilled water. Mix and heat until solution clears–*do not boil*. Stir constantly, otherwise solution will form crystals. After PVA has dissolved, filter through filter paper and add a few drops 37% formalin to prevent fungal growth. Store at room temperature. (It should be rather viscous, like syrup.)
(2) Epofix™ (tradename for an epoxy resin; check on-line for current suppliers): mix with Epofix hardener as outlined by manufacturer. Mix only small amount needed, as it hardens within 30 min.

Procedure:

(1) Drain excess liquid remaining on the surface of the centrifuged, finished residue, and on the inside of the centrifuge tube, by inverting tube for a few minutes on a paper towel.
(2) Add few drops distilled water and one drop phenol (5% solution) to residue in test tube.
(3) Prepare coverslips to receive residue by affixing tiny numbered bits of press-on label to one side of coverslip, and inverting, so that unlabeled side will receive residue.
(4) Using capillary pipette, put one drop PVA on coverslip (two drops if coverslip is larger than 22 mm square).
(5) Using another capillary pipette, mix residue thoroughly with its few drops distilled water and drop of phenol (see step 2). Put one drop of residue on coverslip–mix thoroughly with PVA, and spread evenly, using side of pipette, being sure to get to edge of slip, and to eliminate areas of thick residue. Hold slip by edges with fingers while doing this. Set aside on sheet of white paper overnight. (It is desirable to cover all prepared coverslips

with a box lid or similar item to exclude dust or other contamination.) Be certain all coverslips are labeled (see step 3).

(6) Proceed to next residue, using another pipette, of course. Discard pipettes after use. You can use the same pipette in PVA for all samples being mounted at one time, provided you do not touch any of the residues with this pipette, i.e., always mix on coverslip with residue pipette. The easiest way to manage the PVA is to pour amount you intend to use for the job (25–50 ml perhaps) into a very small (100 ml) beaker. As long as you are certain you have not contaminated the PVA, you may return unused portion to your primary container.

(7) When job is done for the day (and it is best to save up residues until you have eight or ten to do), put a large box lid or other protection over the coverslips you have just coated with residue, as mentioned in step (5).

(8) Next day, or when convenient, mount coverslips on slides as follows:

   (a) If an adhesive such as Epofix is used, mix just the amount you need, as explained above. If a resin type mountant dissolved in a solvent, such as Elvacite, is used, such precaution is not necessary.
   (b) Using a capillary pipette, disposable probe wooden stick or other disposable utensil, put two drops of Epofix on slide and then lower the coverslip, residue side down, onto slide, using the same method (with needle, lowering coverslip slowly) that is used when mounting coverslips with glycerin jelly.
   (c) Set aside to harden completely (several days) before removing the tiny labels and affixing permanent labels. It is not necessary or desirable to ring the coverslips with fingernail polish, as is usually done with glycerin jelly preparations.

(9) Storing of residue still remaining in test tubes should be done as part of the first day's procedure, when all coverslips have been coated with that day's samples. Leftover residue may be stored upright in small glass vials with screw tops (taped shut for additional protection). An extra drop of phenol may be added. Residue liquid may evaporate, and this should be checked frequently.

Further notes on double mounting: There are many variants on this theme:

(1) Some do not use a primary mountant at all, but evaporate a residue in water or an organic solvent onto the coverslip, which is then mounted directly on a microslide with a drop of mountant. When this is done, the *RI* of the single mountant used is what counts optically, not the *RI* of the primary mountant, such as PVA.

(2) The secondary (or only, if no primary mountant is used) mountant can be any clear liquid that can either be polymerized, as Epofix, or can be a solution of a resin, such as a number of methacrylate compounds in use, for example Elvacite 2044 (formerly Lucite 2044), dissolved in xylol, which solidifies as the solvent evaporates. These substances have advantages and disadvantages, as for Canada balsam. Elvacite and other such synthetic resins have the advantage over Canada balsam of not discoloring with age. Elvacite has the apparent disadvantage of *RI* too close to that of sporopollenin for optimal definition (See Table A.1).

2.2.4.7 Bleaching Some spores/pollen are thick-walled or otherwise end up too dark (e.g., some Malvaceae become almost black, as mentioned earlier) in an acetolysis long enough to disintegrate the cellulosic tissues. Sometimes preparations are accidentally over-acetolyzed, and the pollen is rendered too dark. In these cases the preparation can be bleached after acetolysis, as follows:

Add to the washed residue in a 15 ml centrifuge tube enough laundry bleach (sodium hypochlorite solution, such as Clorox®) to fill the tube about one-third full. Reaction time and concentration of solution determines degree of bleaching. About 2–3 min is usual. After this time, fill the tube with distilled water and centrifuge. If desired, the reaction can be stopped rapidly by adding 5% KOH to basify, as the hypochlorite solution has to be acidic to bleach. Water wash the residue until clean (no trace of bleach odor or taste in water–usually two or three water changes).

2.2.4.8 Staining People who prepare spores/pollen by potassium hydroxide cooking usually stain. KOH-treated specimens look as if they had been acetolyzed and then strongly bleached. Some sorts of pollen, e.g., sedges such as *Juncus*, are so sensitive to acetolysis that KOH boiling is preferred. For these specimens, also for the relatively few things that come through acetolysis very pale, or for grains that were overbleached, staining is very helpful.

To a few drops of residue in neutral water, add a drop of basic fuchsin stain (saturated water solution of the stain, using 0.5 ml ethyl alcohol per 100 ml water). Centrifuge and add mountant, etc. Also frequently used is safranin-O, but it is not as good a stain in combination with glycerin jelly. Proceed as for basic fuchsin, except that safranin-O is normally dissolved 1:100 in 50% ethyl alcohol. Allow residue to stand in the stain solution for 1–2 min after stirring thoroughly. Then centrifuge and follow with one water wash. Safranin-O is a more general stain than basic fuchsin and will make nearly all organic matter on the slide reddish. Red stains are preferred, because optical systems are said to be corrected for green light, and it is felt that definition is best with reddish-orange color. However, malachite green and Bismarck brown have also had some popularity as pollen stains. Addition of a little basic fuchsin to the glycerin jelly used will counteract the tendency of the jelly to destain specimens when basic fuchsin is used.

3 Fossil Palynomorphs

3.1 General Instruction

Collection of suitable rock samples for paleopalynology requires the collector to understand the basic natural history of palynomorphs, discussed at various places in this book. Spores/pollen exines, other sporopolleninous palynomorphs, and chitinous/pseudochitinous palynomorphs occur in sedimentary rocks as organic, silt-sized particles, subject to certain constraints. They are sensitive to high pH over long periods and are thus not usually common in limestones. They are sensitive to oxidation even for short times, and are thus not usually found in redbeds or deeply weathered rocks. They are sensitive to heat alteration (carbonization = coalification, darkening of color, ultimately becoming opaque and otherwise devoid of sporopolleninous-chitinous characters such as flexibility), thus not occurring in rock that is or has been deeply buried (about 5,000 m or more) or much metamorphosed (palynomophs cannot be macerated out of slates or anthracites, even though examination of polished surfaces demonstrates their presence), or subjected to heat from lava flows or intrusions. They are sensitive to re-crystallization processes, thus are very seldom found in dolomites, because dolomites are normally formed by re-crystallization as calcium magnesium carbonates from the calcium carbonate limestone. Palynomorphs are rarely found in heavily cemented, indurated rock. As to size, they are silt to very fine sand particles and thus are not found in well-sorted claystones and well-sorted coarse sandstones. It should be emphasized, however, that many claystones and sandstones are "dirty" (= not well sorted), contain some silt-sized particles, and may contain palynofloras. I find the chewing method of detecting silt by its feel between the teeth to be very helpful in selecting the most promising samples when one must be selective in order to limit the number of samples collected–see below under field methods.

The field collector should therefore look for "fudgy" siltstones. All in all, cores are the best sample source when available. Fresh, unweathered roadcuts are just about as good and offer more possibility to study the geological environment, collect megafossils, etc. Well cuttings are poor because they are often contaminated with drilling mud containing rock fragments from up-well, and usually additive pollen from the drilling mud. Also, the bagged sample of cuttings is not exactly referable to the listed depth. Sidewall cores made by shooting into the wall of the hole are excellent but seldom available. Pieces of rock from museums are sometimes very good, usually associated with good collection data, and frequently tie in with important research projects. However, they are subject to bias because they were almost never collected with palynology in mind. For example, a palynologist once reported the near absence of palynomorphs in rocks of a certain age in North America, based on study of museum fossil matrixes. The rocks were collected mostly for fossil vertebrates and vertebrate

footprints and were mostly redbed coarse shales and sandstones. Non-redbed siltstones from most of the same areas are productive. Sometimes great perseverance is required. Leopold and Wright (1985) report that they processed over 450(!) rock samples to obtain 35 which were productive, some apparently only marginally so.

The dispersed palynomorphs in a sedimentary rock are actually "nanno-range" pieces of coal, and the rock in question would constitute a fossil fuel if palynomorphs instead of mineral clasts overwhelmingly predominated. (Cannel coal is such a palynomorph rock.) The principle of palynological maceration is to separate out these "nanno-coals" from the mineral clasts, and then further treat them for microscopy, as necessary–and no more. The initial treatment of a prevailingly mineral sample will ordinarily be with hydrofluoric acid to break down siliceous minerals. Concentration of the palynomorphs may then be required, for partial elimination of other "nanno-coals," such as wood, leaf cuticles, and amorphous organic matter. The most commonly needed additional treatment is oxidation to break up massive organic matter in order to release included palynomorphs, or to lighten very dark palynomorphs. This oxidation procedure must be applied as little as possible and with great caution because sporopollenin/chitin are quite oxidation-sensitive themselves. The oxidation makes humic acids available, and these must then be removed by solution in bases such as KOH solution. Sometimes pH 8 is enough. In other cases acetone or even hot 10% potassium hydroxide must be used. If the sample itself is already carbonaceous–a peat, coal or very carbonaceous shale–the initial treatment will have the purpose of structural breakdown of the organic mass by oxidation, which is then followed by hydrofluoric acid to remove the mineral matter remaining. Fig. A.1 shows the normal sequence of treatments for a sedimentary rock other than such a coal. Fig. A.2 shows the sequence of treatments for oxidation of coaly material, whether from coal or from an acid-treatment residue of carbonaceous sedimentary material generally. The oxidation procedure produces artificially "regenerated humic acids," which are soluble in alkaline solutions such as KOH, NaOH, or NH_4OH. Naturally occurring humic acids or naturally (by weathering, etc.) regenerated humic acids are also alkali-soluble.

In my experience, almost every suite of samples presents some unique problems, and the following directions are only a general guide. Modifications will constantly be necessitated by observations "in the kitchen," and indeed a kitchen is a better analogy to a paleopalynological laboratory than is a geochemistry laboratory. Different samples will behave quite differently under the same treatment. Further, there are usually alternative methods that one can use, as required by circumstances. For example, because HF was not allowed in the laboratory on the Glomar Challenger, when I worked on that vessel for the Deep Sea Drilling Project in 1975, I used wet physical disaggregation of the shales in an electric blender, followed by alternate phases of cooking in 10% hydrochloric acid and a laundry detergent (Calgon®). This freed enough palynomorphs so that

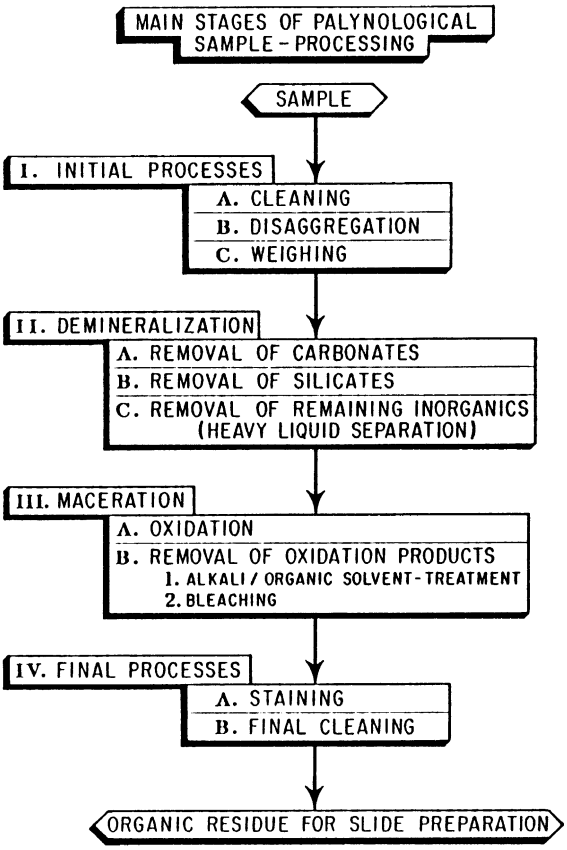

Figure A.1 Basic plan of palynological processing of an average sedimentary rock. Coals, and some other special sorts of rock, require different sequences of operations. From Ediger, 1986a.

they could then be floated off from the mineral clasts in a heavy liquid solution (zinc chloride, specific gravity 2.1).

There has been considerable interest in this sort of non-HF processing as a substitute for HF and other strong acid-based procedures because of stringent environmental requirements in some laboratories and in some special situations such as the one I faced on the Glomar Challenger. Riding and Kyffin-Hughes (2004) describe in detail a processing method based on use of physical disaggregation, plus treatment with the surfactant/dispersant substance sodium hexametaphosphate, plus sieving techniques. The substance is the active ingredient of the commercial product, Calgon®, which I used on the Glomar Challenger because

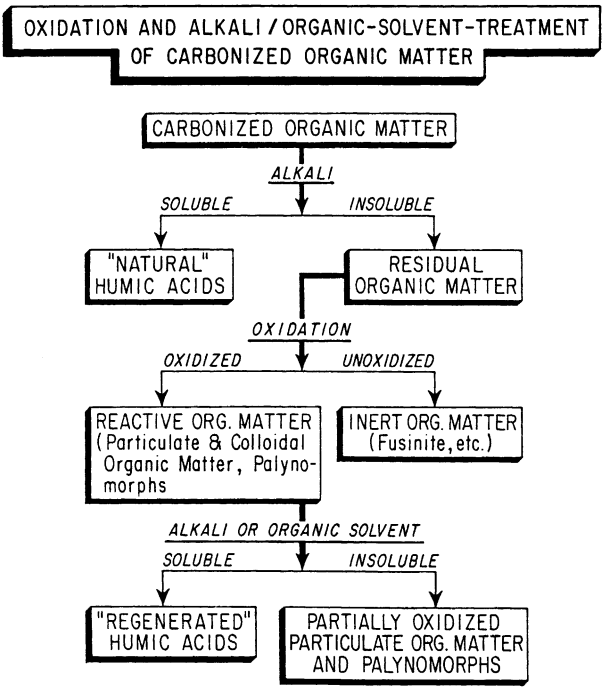

Figure A.2 Reaction scheme for oxidation (with Schulze's reagent or other oxidant) of carbonaceous matter, in order to release the sporomorphs, which are (slightly) more resistant to oxidation than other coal macerals. From Ediger, 1986a.

it was the surfactant that the ship's laundry had. Williams *et al.* (2002) reported on oil company use of well-site processing for palynology, using only physical disaggregation, plus heating in hydrogen peroxide, followed by gravity separation using only swirling and settling techniques in water, and surfactants for additional cleaning. Those interested in trying different approaches to acid-free process should certainly consult the manual on techniques in paleobiology by Green (2001: 124–5, 178–9, 290–1), in which some interesting ideas of breaking down rock structure after preliminary physical disaggregation by freezing, with and without addition of various salts, and accomplishing the same result by alternate kerosene and water (with and without surfactant) treatments, or by treatment with mineral spirits, followed by boiling water. I haven't tried these methods in the context of palynological processing, but combined with sieving and/or gravity methods, they are certainly worth experimentation.

Some samples will contain a great deal of very fine particulate matter, and the major preparation problem will be to disperse the fine particles after acid treatment with a dispersing agent (surfactant), sodium pyrophosphate, followed

by screening on very fine screen (or cloth mesh) that will pass the fine particles but not the palynomorphs (see Cwynar *et al.*, 1979 and section 3.2.4 in this Chapter).

Hardly anything is absolutely essential to palynological processing. Good results can be and have been achieved without most procedures we regard as routine. Few of the chemicals except for HF are particularly dangerous and *if diluted sufficiently* can go into any sewer. Instead of an electric centrifuge, a hand centrifuge can be used. If enough time is available, repeated decantation will work, using centrifugation only in the final, washing, steps of preparation. A student of mine even used this approach for simultaneous treatment of large numbers of samples, each in a labeled styrofoam cup. Batten and Morrison (1983) have shown that membrane dialysis can be used to rid a sample of acid without centrifuging or decanting. It is possible to use no centrifugation, and no agitation of the organic residue from acid-digestion of mineral matter at all, substituting great patience with the time required, for the efficiency of normal paleopalynological processing. When this is done, very delicate specimens that would be completely destroyed by conventional processing can then be carefully pipetted out of the residue in water (cf. methods section of Butterfield, 2005). Such specimens are not technically palynomorphs, and their study is not palynology, which by definition depends on preparation and manipulation of large numbers of robust specimens. That does not denigrate in any way the study of ultra-delicate organic specimens for sometimes important paleontological purposes. Indeed, reasonable steps to prevent destruction of somewhat weakly robust palynomorphs are occasionally required in our field.

I have used the chart displayed in Fig. A.3, and associated instructions, to teach new laboratory assistants and students how to process rock samples of unknown character. As has been emphasized, this is only a general guide and must be modified in one way or another for almost all sets of samples. For example, if concentration of palynomorphs is very low one may use massive samples (hundreds of grams) and physical disintegration in a large container, followed by large scale "swirling" to get off a silty fraction which will include the palynomorphs. This silty fraction can be drawn off, centrifuged to get rid of excess water, then processed conventionally. Some pollen-bearing samples seem more or less impossible. For example, chitinous insect parts make up most of the organic matter of bat guano. After demineralization, it is next to impossible to separate the matted mass of insect mouthparts, etc., from the spores/pollen. Many of the mouthparts are in the same size range as spores/pollen, preventing screening. Chemical techniques that destroy chitin (oxidation) also destroy sporopollenin.

There is plenty of pollen in Baltic and other amber, but no technique I have tried is really successful in dissolving the amber and leaving the pollen. (Marshall, 2005, described success with anisole as a solvent for terebinth resins for palynological purposes, and this breakthrough should be tried on ambers

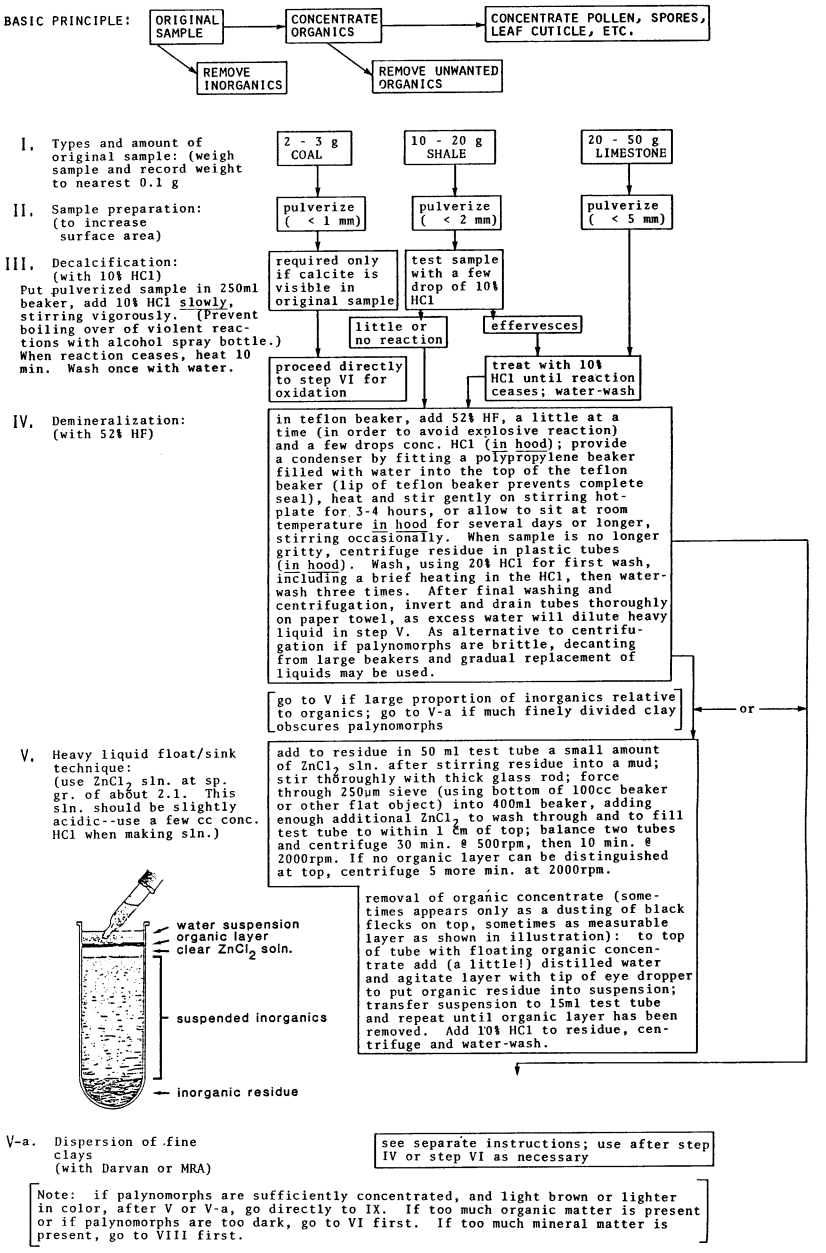

Figure A.3 *(See caption on page 638)*

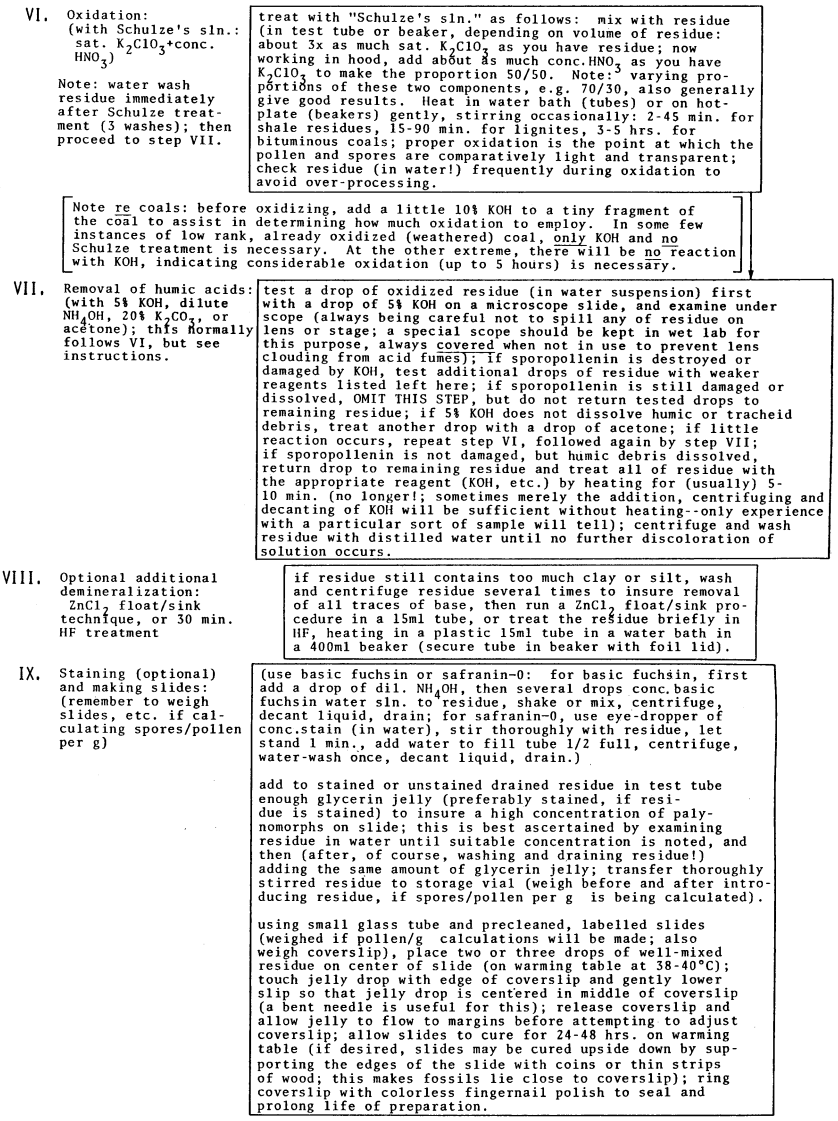

Figure A.3 Flowsheet for paleopalynological processing.

and other difficult resinous materials.). True oil shale, such as the Mahogany Ledge of the Green River Oil Shale, is also well nigh impossible. The "kerogen" matrix of the oil shale holds it together against all maceration processes I have tried.

3.2 Maceration and Slide Preparation

To supplement the schedule shown in Fig. A.3, consult the references mentioned at the beginning of this appendix. Use common sense and observe carefully what is going on.

3.2.1 Additional Cautions and Reminders

(1) Make complete notes of each process used, as to the amounts of chemicals, time, temperature, results, etc. Use a permanently bound notebook, not loose pieces of paper. Keep all notes about the sample together by allowing sufficient space in the notebook. Such note-keeping is of paramount importance.

(2) Many rocks will require different and/or additional procedures. Remember that the basic principle (Fig. A.1) is to separate first the total organic residue from the mineral matter present, then the pollen and spores from the other organic matter.
Coal and very highly organic shale are exceptions; removal of residual mineral matter in such cases is one of the final steps, not the initial one. Follow progress of a maceration by using a rough scope in the wet laboratory to look at a drop of the maceration in progress (never from HF or other strong acids without thorough water-washing first!). When palynomorphs are easily studiable, it is best to stop processing and begin studying. When in doubt about the wisdom of applying an additional procedure, it is best to divide the residue and experimentally further process only a part of it. Avoid "heroics" of processing. Too much processing often destroys the palynoflora, or selectively destroys it, so that it is no longer representative. (On the other hand, there are limits as to how "dirty" a preparation can be and still be studied effectively!)

(3) Never apply a float-sink procedure after HF digestion, if the residue is richly organic. All of the organics will float, and a grand mess will result.

(4) Never "store" a residue (overnight, over a weekend) in an oxidizing (e.g. nitric) acid, or in a strong alkali (e.g., potassium hydroxide mixture). However, it is all right to leave a partly processed residue at any stage in water, or even in a non-oxidizing acid (HCl, HF), for days or weeks.

(5) Do not use Schulze's mixture or other oxidizing technique on a residue that is already partly alkali soluble–test a bit of washed residue with 10%

KOH–a dark coffee color will be imparted to the solution if the residue is in part alkali-soluble.

(6) Label *everything*–especially beakers, slides and other things left unattended overnight.

(7) Always balance centrifuge heads carefully.

(8) Use distilled water for sample-washing to prevent contamination, and because tap water contains too much dissolved and suspended mineral matter, especially calcium salts.

(9) Hoods must have exhaust fans turned on all the time, not intermittently. HF is very bad for humans, as well as for equipment, even in tiny amounts. The hoods also should be checked on a regular basis for efficiency. A hood with poor suction is almost as bad as no hood.

(10) Do not put HF beakers on stirring warm plates until reaction has ceased at room temperature. Otherwise the reaction may become violent when the temperature is raised.

(11) If a reaction becomes too violent, cut it with *alcohol* (95% ethyl alcohol is good) from a spray bottle kept at the ready. This will knock down the reaction without significantly diluting the components.

(12) If it is not convenient to remain in the laboratory until a reaction is complete, the total treatment may be administered in increments–it never hurts palynomorphs to sit in HF, HCl or water, as mentioned above.

(13) Always decant spent acids, etc., into decant bottles with plenty of water in a fume hood. In our laboratory, we used decant bottles half-full of saturated calcium chloride solution for spent HF; the $CaCl_2$ converts the fluorides of HF used in rock digestion to relatively harmless CaF_2. Local authorities may have set up procedures for the regular collection of decant bottles of hazardous wastes such as spent acids. Always carefully check on the local regulations and follow them explicitly. If regulations permit, it is possible, using great care and a great excess of running water, to pour contents of decant bottles (the bottles should be no more than 3/4 full) down a hooded sink.

(14) Do not neglect to put a little concentrated HCl in the HF for stage IV in the Fig. A.3 flowsheet. This is very important to prevent accumulation of fluorosilicate gels, which once formed are difficult to eradicate, though heating in con. HCl may help.

(15) Clean all equipment after use. You may use it next!

3.2.2 *Calculation of Pollen/Spores Per Gram of Sample: Traverse Weighing Method*

This is simple if the vial is very well mixed before placing part of its contents on a slide. But you must remember to do some weighing as you go along and record the measurements.

(1) Weigh the original (*dry*) sample.
(2) Weigh the vial in which you store your residue, both before and after putting the residue in it.
(3) Weigh the slide and coverslip which will receive a drop of the residue both before and after putting the residue on the slide. A microanalytical balance is needed for this step.
(4) Use the equation $X = \dfrac{BD}{CA}$

outlined in the previous chapter to calculate the number of palynomorphs per gram of sample, where $X =$ number of microfossils per gram, $A =$ grams of sediment sample, $B =$ total grams of maceration residue plus glycerin jelly, $C =$ grams of residue plus glycerin jelly on slide, and $D =$ number of microfossils on slide. Obviously, this also requires that all the specimens on the slide be counted. One should therefore aim at a slide that has less than 1,000 specimens, as counting more than 1,000 is too time-consuming. If necessary, a line may be ruled in indelible ink, connecting opposite corners of the coverslip, and only half (or a quarter) of the slide counted, and the counts multiplied by 2 (or 4) before running the calculation per above equation. (See also Chapter 17 for a more extended explanation of this method and of the competing, more popular *Lycopodium* spore (or other microscopic "stick" or "spike") method.

3.2.3 *Additional Comments on Gravity-Separation Technique*

Gravity separation methods are commonly used in palynology to improve concentration of organics for spore/pollen analysis. Many methods or techniques are applicable. We have normally used the $ZnCl_2$ method in our laboratory, occasionally substituting $ZnBr_2$. Both are relatively safe: no dangerous fumes exist compared with bromoform-alcohol mixtures of the correct density, although the latter may be used with separatory funnels to get off the organic float very neatly. Bromoform, however, is expensive and very poisonous. Also, residues must be water-free before going into bromoform-alcohol.

Although $ZnBr_2$ costs more than $ZnCl_2$ per gram, it has a specific gravity of 4.2, as against 2.9 for $ZnCl_2$, meaning that it takes 1.4 times as much $ZnCl_2$ to make up a 2.1 specific gravity solution. (Some who use zinc bromide solution report using solutions of 2.4–2.5 specific gravity, which is easy to achieve with the heavier compound.) This makes $ZnBr_2$ almost as economical as the more

viscous and more difficult to manage $ZnCl_2$. Furthermore, recycling of used $ZnBr_2$ solution by dilution, centrifugation and re-concentration by evaporation is more practicable. In other words, if the relative price of $ZnBr_2$ permits, use $ZnBr_2$.

There is little or no chance of contamination by remnant palynomorphs if the solution is not reclaimed. This also saves time. Although $ZnCl_2$, like $ZnBr_2$ can be reclaimed (by dilution, centrifugation, evaporation to restore specific gravity of 2.1), reclamation works more easily with $ZnBr_2$. The relative cheapness of $ZnCl_2$ makes discarding that used solution practical. Stock solution does not deteriorate if properly stored, but one should always check the specific gravity before use!

The desired specific gravity of 2.0–2.2 is readily adjustable by addition of water or $ZnCl_2$. The basic principle of the method is that chitin-sporopolleninous palynomorphs have a specific gravity of about 1.4, whereas the lightest minerals have a specific gravity of about 2.5. The slow centrifugation that precedes the fast centrifugation is to permit minerals and palynomorphs to "work past each other in the traffic." An immediate fast centrifugation would cause the minerals to drag the palynomorphs down. "Slow centrifugation" can also be applied in water to separate palynomorphs by causing minerals to centrifuge out while palynomorphs are still suspended in the water. ("Short centrifugation" refers to using a short enough time for centrifugation to throw coarse minerals down, but not long enough to throw down palynomorphs, which can then be decanted off. On the other hand, the method can also be used to throw down spores but not suspended clay particles! See "Darvan" method below.) This may, however, result in differential loss of larger palynomorphs.

Processing can be maintained in a water base, whereas the bromoform-alcohol treatment requires alcohol washes both before and after the separation. The principal disadvantage is the high viscosity of $ZnCl_2$ solution. $ZnBr_2$ solution is much less viscous. However, the viscosity of $ZnCl_2$ solution does not seem to interfere with good organic retrieval.

The use of sodium polytungstate (SPT) solution at 2.2 s.g. as an alternative to the zinc salts for heavy liquid separation in palynology has been described by Simes and Wrenn (1998). This material is water soluble and relatively non-toxic and is thus ideal for situations where toxicity is carefully monitored, but there is a minor problem with insoluble precipitates that makes use of deionized water advisable. It is very easy to recycle the solution by filtration and evaporation, which is obviously an advantage in field localities where replenishment of supplies is a problem.

3.2.4 Dispersion of Fine Clays, Screening

As noted earlier, one often obtains a residue which is more or less unstudiable because of a profusion of very finely dispersed particles (usually clay minerals) in the 1 μm or smaller size range. These can be removed by a variety

of screening techniques, combined with use of dispersants (a better term for the cleaning compounds we use is surfactant = surface active agent) . The technique below is simple and inexpensive and usually works acceptably (see also Cwynar *et al.*, 1979).

3.2.4.1 Dispersing Agent/Surfactant Methods The use of Darvan, a deflocculant based on polyacrylic acid, the molecules of which attach to clay particles and cause them to repel each other, for dispersing excessive clay minerals, was described in the first edition of this book. Unfortunately, that admirable substance is no longer available. Sodium pyrophosphate can be used in the same general way (see Cwynar *et al.*, 1979). Another surfactant material is "Quaternary O," a high molecular weight quaternary ammonium surface active agent (see Hills and Sweet, 1972). This dispersing agent is favored by some for megaspore work. N. O. Frederiksen (personal communication, 1996) wrote me that his lab at the U. S. Geological Survey used the commercially available dish detergent, Sparkleen, as a surfactant for palynological processing: 60 cc of Sparkleen were dissolved 1.5 l water, then this mixture was filtered through a Whatman no. 3 filter to remove particulate matter, then more water was added to produce 4 l of the solution for dispersing/surfactant purposes; see Frederiksen (1996), in which this solution is referred to as "soapy water." I have found that various products commercially available as glassware cleaning compounds work equally well.

3.2.4.2 Procedure (Use after HCl-HF and/or gravity separation.) If you notice that your sample is full of finely divided clay which obscures the spores/pollen, you may disperse the clay at any stage in your maceration sequence.

(1) Start with washed, drained residue in 50 ml (or 15 ml, if residue very small) test tube. (If you have more than about 1 cm of residue in the bottom of a tube, divide into two tubes.) Add a little more than twice as much surfactant solution as you have residue. With stirring rod, stir up thoroughly from bottom of tube, so no residue is left sticking to sides and bottom.
(2) Agitate tube on tube mixer (such as Vortex Genie®) for 1 min to mix surfactant and residue.
(3) While still on mixer, fill tube with distilled water to within 2 cm of top.
(4) Centrifuge at 1,400 rpm (no more!) for 1 min (no longer!). Do not use brake to slow or stop centrifuge. Decant carefully into large beaker (check later for spores inadvertently poured off, although in our experience this practically never happens). This is called "short centrifugation" and will eliminate much clay because the fossils go down, but the clays are kept in suspension by the dispersing agent.
(5) Wash 3-4 times, or until decant is clear, stirring carefully, centrifuging as in step(4), and decanting into the large beaker. Most of the fine mineral fraction will be poured off in this way.

(6) Sieve to separate rest of fine fraction from residue. (If residue still contains large particles, sieve first through a 210 μm brass sieve, washing through thoroughly and saving what goes through for examination.) If no large particles, skip this and go directly to sieving through 7 μm nylon screen ("Nitex® bolting cloth"–go online and look for currently viable sources). Wash thoroughly with warm water. Palynomorphs will be held back on the screen, and unwanted fine particles will go through.
(7) Very carefully, using a funnel, wash residue from cloth into 15 ml test tube(s).
(8) Centrifuge, stain if desired, add mounting medium, make slides.

Discard screen after use for one sample. If you plan to macerate other fractions of the same sample, you may retain the original screen for this after washing it thoroughly. It may be kept between paper towels (labelled!) or in an envelope.

3.2.4.3 Other Filtering Techniques Several other filtering techniques involving more equipment are used with success in various laboratories. Neves and Dale (1963) described a filtering technique based on a sintered glass disk (porosity 2) in a Büchner funnel mounted on a pressure flask. An air pump reverses the flow of air periodically (50 s filtration flow, 5 s reversed air flow) to keep the sintered glass disk from clogging. Good results have been reported by various laboratories using variations of the method. In our lab, we used a "modified Reissinger apparatus" (M.R.A.), based on sintered glass (= fritted glass) filters attached to funnels; this procedure, can be employed at any stage in palynological processing (see Ediger, 1986a). M.R.A. is particularly useful after heavy-liquid separation and after oxidation. Raine and Tremain (1992) have published an interesting version of M.R.A.-type technique, including illustrations of the relatively simple equipment they use for generating the suction applied to the commercially available, cloth-based filter (7μm mesh) unit, and reverse flushing of it. As of the publication of this second edition, Raine is still able to provide the basic equipment to interested persons.

Caratini (1980) used an ultrasonic generator in combination with nickel filters. The technique has the advantage over sintered glass disk methods of not needing to be constantly unclogged, and over the nylon netting used in the "Darvan" method of being more or less permanent. However, the metal filter unit alone costs hundreds of dollars, and an ultrasonic generator must be added to this cost. Later, Caratini (personal communication, 1986) used the ultrasonic generator with Swiss bolting cloth filters (the Nitex® material mentioned above) on supporting perforated disks. Ultrasonic generators are much used in palynological laboratories, but they pose some problems, especially that they tend to break up brittle palynomorphs. If very carelessly used, they can also damage human retinas.

Batten and Morrison (1983) described the use of ultrasonics for cleaning samples in considerable detail, using vibration of 50 kHz.

3.2.5 "Swirling"

This technique takes advantage of the differential response to turbulence of palynomorphs of different sizes, conformation and specific gravity, and of the "junk" in palynological maceration residues, the same physical properties as form the basis for concentration of palynomorphs in sediments during deposition. "Swirling" involves agitation of palynomorph residues in water in a watch glass rather like panning for gold. The principle in "swirling," however, is probably based only partially on specific gravity. Sporopollenin is all pretty much the same in this respect, about specific gravity 1.4. However, different proportions of internal spaces can nevertheless give the different sorts of palynomorphs different effective specific gravities. Size, shape, and morphology of the microfossils also play roles. The technique is very helpful in separating palynomorphs from other organic "junk" in a particular residue, without resorting to screening and heavy-liquid gravity separation. As is true of slow (or "short") centrifugation, however, there is some danger of differential loss of certain palynomorph fractions. Clarke (1994) notes that swirling and sieving recover a larger percentage of large buoyant forms than centrifugation because such forms are routinely lost in decantation, having failed to centrifuge.

3.2.5.1 Procedure Although simple, it must be learned through experience, as different samples behave in different ways and are best treated by slightly different techniques. I have known a palynologist who could prepare a slide containing almost entirely one species of fossil pollen from a residue containing many species. For the neophyte it can be slow, messy, and frustrating, but with experience one is able to "clean up" a sample in a few moments. It is especially valuable in the separation of spores from large tissue fragments of similar density. Unless great care is used, certain size-groups of spores may be lost. Therefore, it is not generally recommended for quantitative work. The residue should be in a fluid, generally aqueous, carrier, of neutral pH to avoid equipment damage and flocculation.

(1) Place a small amount of residue (usually a few drops, although amount varies somewhat with spore content, degree of "cleaning" to be done, number and size of slides to be made, etc.) in a clean 3 inch watchglass and fill two-thirds full with water. Allow to settle a few seconds.
(2) Gently swirl the contents by moving the watchglass in a circular motion, so that the center of the watchglass circumscribes a small (1–5 mm) circle about a point on the work table. This causes a certain fraction of the residue to be suspended.

(3) Decant the suspended material, or pipet it to another watchglass and inspect both glasses with a dissecting microscope. If one fraction contains debris but no palynomorphs it may be discarded, and the process repeated with the palyniferous fraction to attain a desired concentration. By suitable adjustment of the swirling speed, particles of different size and general morphology from the palynomorphs can be separated from them. It is even possible sometimes to separate one kind of sporomorph from others by very critical "swirling," to make a super-clean preparation of that kind. This is seldom important, as capillary tube pipetting, working under the microscope to select specific fossils, does it more accurately. However, the most useful application of this technique is to rid a troublesome sample of unwanted minerals and large organic particles.

(4) Inspect separated fractions under the microscope. The scope must have at least a 1" working space. Magnification of 100× or 150× appears to be the best compromise between enlargement and field area. If a fraction is found to be barren (or essentially so in non-quantitative work) it is discarded.

(5) Repeat the process on the sporiferous fraction, using slightly varying swirling amplitude and vigor, until the particles heavier and lighter than the spores are removed. Material of the same density and size as the spores cannot be removed. Particles of different size from the sporomorphs can be separated owing to the difference in energy required for the micro-currents in the glass to "pick up" objects of different size. The very simplest form of swirling, letting the residue and water settle for a minute and then decanting the "discolored" water, is almost always beneficial in removing colloid-sized material. If the remaining residue is then somewhat violently swirled, the spore-bearing fraction may be decanted from the heavy and large "dregs" which escaped earlier processing (often mineral particles and heavy tissues).

Finest degree of separation is accomplished by gently jiggling the residue into the center of the watchglass and then very gently swirling it at a very small amplitude. This generates a column of "smoke" which is of slightly different density-size characteristic from the non-rising residue. In this way separation of different genera can sometimes be made. A very useful description of swirling techniques has been presented by Tripathi (1995), including some helpful illustrations of the method.

A number of techniques have been described which, like swirling, depend on exploiting differential physical properties of what remains after palynological basic maceration. Tschudy's (1960) "vibraflute" is a mechanically agitated tube with holes along it, permitting collection of fractions at intervals. The differences in size and other properties of various constituents of a residue cause the fractions to contain concentrated, "cleaned up" samples of various palynomorphs.

Forster and Flenley's (1993) technique of pollen purification, down to producing slides containing almost all one species from a mixed residue by equilibrium density gradient centrifugation clearly is based on the same factors that made the "vibraflute" work. Hansen and Gudmundsson (1979) describe a technique for utilizing the differential take-up of absolute ethyl alcohol by palynomorphs, permitting their separation by specific gravity difference, from organic debris that does not take up the alcohol.

3.2.6 Oxidation Notes

In addition to Schulze's mixture (see Fig. A.3), other oxidants, such as hydrogen peroxide or sodium hypochlorite (ordinary laundry bleach–NaOCl solution at a concentration of about 5–6%) may be used. Evitt (1984) suggests adding HCl to the NaOCl to intensify the reaction. The reaction can be stopped quickly by basifying the solution with 5% KOH.

Batten and Morrison (1983) point out that treatment with Schulze's mixture for the purpose of oxidation has the desirable side effect of eliminating pyrite (marcasite) crystals from the treated specimens. This is because of the solubility of FeS_2 in concentrated nitric acid (HNO_3).

3.2.7 Special Techniques for Megaspores, Chitinozoans, and Scolecodonts

Megaspores and many chitinozoans and scolecodonts have in common that they usually occur one or two orders of magnitude less abundantly than spores/pollen in sediments. Furthermore, they are usually much larger than most miospores and consequently are visible as dots to the naked eye. Therefore, different preparation techniques are required. First, because of low concentration, larger samples of rock should be used–several hundred grams instead of 20-40 g. Second, the preliminary fine grinding used on miospores must be avoided as this will destroy many specimens of macrospores and larger chitinozoans and scolecodonts. Breaking the rock sample into pieces about 1 cm across is as far as one should go. Secondly, strew slides are not acceptable because the concentration is too low. These large palynomorphs are best picked out of the maceration in water, using a brush or a capillary tube. The microfossils are mounted on SEM stubs, on microslides, or on special microfossil (foraminifera-type) slides. Thirdly, all of these microfossils tend to be opaque because of the size and the thick walls, and are best studied by reflected light and by SEM rather than with the LM. The following processing method, modified from Jenkins (1970), who developed it for chitinozoans, can be used also for scolecodonts and megaspores.

3.2.7.1 Preliminary Treatment Fragment about 250 g of sediment into pieces about 1 cm in size (smaller fragments yield broken specimens, larger ones require too long for maceration). Discard fines that are produced by the sample fragmentation.

3.2.7.2 Maceration

(1) Working in a fume hood, treat in largish Teflon beakers with 10% HCl until all reaction ceases. Wash and transfer to HF, as in conventional maceration procedure. From time to time, as other activities permit, use gradual decantation to go from one step to the next without centrifugation, as centrifuging damages large, ornate specimens. Thoroughly water wash after no further HF reaction is occurring. Do not move to the water wash without allowing plenty of time in HF.
(2) Sieve, using a brass sieve with openings appropriate to the category of fossil (ca. 125 μm for megaspores, 50 μm for chitinozoans, 100 um for scolecodonts). Hold the sieve containing the residue in water to within 1 cm of the top of the sieve. Gently move the sieve up and down in the water without allowing the water to flow over the top of the sieve. Fines pass through. Continue this procedure, frequently changing the water, until no material passes through the sieve, which can be checked by collecting small amounts of the wash water in a beaker.
(3) Bleach (if necessary) in commercial laundry bleach, checking the course of the procedure under the microscope: transfer approximately one-fifth of the residue to a white-bottomed petri dish (about 10 cm in diameter), or a clear petri dish on a white card or tile. Adjust water depth to 0.5 cm. Add a few drops of the bleach solution, mix thoroughly and observe under a low power microscope. Stop the bleaching by adding an excess of 5% KOH solution when the correct bleaching level is attained. The bleaching can be precisely controlled in this manner. Wash the residue by repeated addition of water and decanting until a drop of the residue in water leaves no trace of precipitate when evaporated on a microslide.
(4) "Picking" and mounting: spread the residue thinly over the bottom of a white-bottomed petri dish in about .5 cm of water. Search with a stereoscopic microscope. Pick up desired specimens with a capillary pipette. A pipette attached to a hypodermic-syringe plunger by a plastic tube can be used, or a simple pipette drawn out at one end to about 1 mm in diameter (larger for some megaspores), closing the other end with a finger until the specimen is near the orifice of the tube. Release of the finger allows specimen to rush into the tube with water. It can then be blown out onto the desired surface. These are the same techniques as described for spores/pollen under single-grain mounts, except that the orifice of the pipette must be larger.

Specimens may be transferred, as picked, to a little distilled water in a second petri dish, e.g. to group similar specimens before mounting. When ready to mount, transfer the specimens to a watchglass containing a 2% aqueous solution

of Cellosize. Take up specimens from the Cellosize solution with a pipette and put out as a small drop on a coverslip. (Up to 30 specimens can be grouped on one large coverslip.) Put the coverslip, face up, on a warming table at 50 °C for 1 h, or until dry. Invert the coverslip and carefully lower onto a drop of Canada balsam or other suitable permanent mountant on a slide. Alternatively, megaspores, chitinozoans and scolecodonts can be mounted in glycerin-jelly on slides, or they can be put (dry) on SEM stubs or on cross-hatched microfossil slides of the sort used for foraminifera studies. If it is desired to study and photograph the whole specimens by reflected light, or to study by SEM, this is necessary. In this case, a very small camel's hair brush is used for picking up the specimens, and, in the case of SEM studies, the cellosize must be washed off before mounting. Paris (1981) describes a useful method for mounting the specimens on a coverslip, which can be mounted on an SEM stub, and then later removed for LM microscopy.

Collinson *et al.* (1985) suggest that, after maceration, a panning ("swirling") process in water can be used to concentrate megaspores. Residues are stirred, allowed to settle for a few seconds, then the supernatant is decanted and passed through a 125 μm sieve. The process is repeated until no more plant material is brought up by stirring. If the original maceration was not done with HF, an HF treatment is applied now if necessary to remove adhering minerals.

Wilde and Hemsley (2000) describe a method for isolating megaspores from Cretaceous sediments consisting of virtually unconsolidated clays. These could be "macerated" by mere soaking in plain water, with occasional use of hydrogen peroxide. The disintegrated clay was then sieved, and the megaspores picked out of the wash water under a dissecting microscope and stored in glycerin for later study by SEM.

3.3 Field Methods

3.3.1 Sample Collecting

As stressed elsewhere, palynomorphs are sedimentary particles in the silt to very fine sand particle-size range with a characteristic set of chemical and physical properties. It is here necessary only to mention those aspects of collecting samples for paleopalynology which long experience has taught me are not always obvious to field geologists.

(1) Palynologists, or geologists well instructed by experienced palynologists, should whenever possible collect their own samples, whether in the field or from cores in a core storage area. This is the efficient approach because laboratory procedures in palynology are labor-intensive, and it is very important to avoid barren samples as much as possible.

(2) Cores or fresh outcrops are better than weathered outcrops. Palynomorphs are very sensitive to oxidation and much time is wasted macerating weathered rock. In hot, dry climates, weathering often extends so deeply into rock outcrops that blasting or bulldozing is necessary to get down to acceptable samples. Where this is not possible, look for places where the target layers are exposed along a stream cut or actually in the stream bed. Avoid collecting on exposed ridges.

(3) The best rock type is relatively unconsolidated "fudgy" siltstone in the gray to light grayish-brown color range. There are exceptions to the relatively unconsolidated dictum. I have had marvelously abundant and beautifully preserved palynofloras from local Devonian siltstones that were cemented so hard that they were difficult to break with a hammer on a lab splitting block. Plenty of samples with all the above desirable characteristics are nevertheless barren. Truly black shales are seldom good because the black color often comes from minerals, or the organic matter may be predominantly non-palynomorph, such as sapropelic material. Coals are often highly vitrinitic (vitrinite is derived from wood or bark and is of course barren of palynomorphs), hard to process, and usually contain an autochthonous flora typical of the original swamp and thus are less satisfactory for stratigraphy than shales. Sporonite-rich coals, however, may yield beautiful palynofloras! Red (and even dark brown) shales usually are oxidized and barren, very rare exceptions being shales reddish from included red minerals where the rock itself is not oxidized. Truly green shales are seldom productive. Because the siltstones we seek are soft, even a comparatively fresh outcrop, say a highway cut, will often yield the best rock for our purposes only in the soft layers that occur between consolidated, un-palyniferous shales or hard sandstones. Furthermore, because they are soft and often thin and hence easily eroded away, it is frequently necessary to get at these soft layers by excavating deeply into the rock face between the hard layers, deeper the longer the outcrop has been exposed to weathering. Avoid rock that shows evidence of post-depositional alteration as evidenced by slickensides, cleat and cleavage, or obvious secondary cementation, or proximity to a lava flow or volcanic intrusion such as a dike. Mottling of surfaces of otherwise promising siltstones is an indication of weathering and is usually a negative indicator.

(4) Test a very small piece of the rock between your incisor teeth for sediment size. If it is really smooth in texture, it is clay and not likely to be good. If it is really gritty, it is no good–sand. If it is on the smooth side, but slightly fine-granular, at least the particle size is acceptable–it contains at least a little silt. Remember that a "fudgy" silty rock is what you are looking for. If there is no problem with running as many samples as you like, by all means include clayey or sandy samples that seem

perhaps marginal – why not? Despite the odds, they sometimes contain floras. However, do not waste time on black shales or any reddish or mottled rocks.

(5) Limestones are seldom good, though marls and calcareous shales can be productive, and there are exceptional cases of beautiful preservation in limestone. Dolomites are nearly always barren, as previously noted. Look for stringers of siltstone associated with limestones/dolomites. These are sometimes productive.

(6) A moderately productive siltstone will yield a very good maceration from l0 g; a richly productive siltstone requires only 2-3 g. It is not necessary to collect large samples, although it is my custom where space or weight is not a problem to collect about 250 g (about half a cup) in labeled cloth bags, in case a future mass maceration might be desired. When visiting places where shipping rock samples is for various reasons a problem, it is possible to send perfectly good palynological samples home, folded flat into pieces of paper, in ordinary letter envelopes. (Because of newer automated sorting and canceling machinery put in service since the publication of the first edition of this book, I would now recommend padded envelopes for the samples.) I have found it useful when forced to have other geologists collect for me to mount a series of pieces of lithologically "super" silty gray shale on a small board for the collector to use in the field for comparison purposes.

(7) Patient searching of outcrops in a sedimentary basin will almost always yield at least stringers of suitable siltstone. An exception in my experience has been the Jurassic/Triassic rock of the Fundy Basin in Nova Scotia, where the prevailing rock type is red, oxidized shale and sandstone, the promisingly green horizons being apparently secondarily reduced, and the few grayish siltstones that occur almost always contain organic matter carbonized by proximity to the overlying North Mountain Basalt. However, even in Nova Scotia, after years of looking, a productive layer was eventually found–near Parrsboro, paradoxically only a meter under the basalt (see Fowell and Traverse, 1995).

3.3.2 Field Processing

It is possible to produce adequate slides for study from rock samples by processing in the field, and, of course, to study them there also, if a microscope is available. I have done this by using heavy duty stoppered large plastic jugs for HF digestion, working in a secluded spot in the open, well away from buildings and people, avoiding windy days and working upwind from the work table. Although this is doubtless against some local ordinances, the very small quantities of chemicals needed do no realistic harm. The acids can be decanted

into prepared, heavy-duty plastic jugs (containing $CaCl_2$ and alkali solution) that are taken later to a suitable place for disposal. Working in the open, a hand-operated centrifuge can be used after great dilution of acids by decanting. Final processing steps, slide making and microscopic study can be accomplished in a motel room, or even in a tent, provided that there is power for the microscope illuminator or that a microscope with a mirror for use of daylight is available. Kaars and Smit (1985) describe a method for field maceration based on use of dispersing agents, sieving and decanting, without use of strong acids, similar to that described above and to those outlined in great detail by Riding and Kyffin-Hughes (2004).

3.4 Manipulation of Spores/Pollen

3.4.1 Single Grain Manipulations and Mounts

A century ago, pre-TV, when microscopy was a popular hobby for the well-to-do, there were even folks who made beautiful *objets d'art* that could be viewed only with a microscope, by picking up and glueing down variously colored scales from lepidopteran wings and diatom frustules. Manipulating individual spores/pollen and dinoflagellate cysts under the microscope would not have surprised such folk. However, modern day students usually are appalled in elementary palynology when they discover that they will be expected to pick up and mount for study individual palynomorphs that they can't see without a microscope. There are several reasons for teaching these techniques.

(1) Nothing so dramatically teaches the meaning of the size range of palynomorphs as making single-grain mounts. Until then, when they are only untouched objects on microslides, the actual size of palynomorphs is not really grasped. Furthermore spores/pollen seem to "come alive" for students when they have actually handled them.
(2) For reference purposes single-grain mounts are very helpful, e.g., as a reference collection of the constituents of a palynoflora to have near at hand during the course of the study. They are ideal for type-specimens for new taxa although such specimens are very seldom designated. They are perfect for sending to another palynologist for discussion, because there is no question as to identity. (For this purpose I advocate mounting such specimens in a "coverslip sandwich," so that viewing from both sides is facilitated.)
(3) For SEM and TEM work it is often best to isolate single specimens. (For details, see section 3.4.1.3 later in this chapter.)

3.4.1.1 Glycerin Jelly-particle Technique (see Fig. A.4). This is the "quick and dirty" technique.

(1) Get some of the residue into glycerin and alcohol (50/50) or glycerin and water (25/75) in a tube or vial. The latter mixture is more viscous, but the former mixture evaporates rather quickly. Put a very small drop of this mixture on a slide and spread it out over the surface of the slide with a needle held parallel to the surface of the slide.
(2) Using the 10× objective of the scope, locate a specimen of the desired taxon. Verify the identification at higher power (20× or 24×) if necessary, but return to 10× and clear away mountant and other debris completely from the area of the subject grain with needles and other more or less

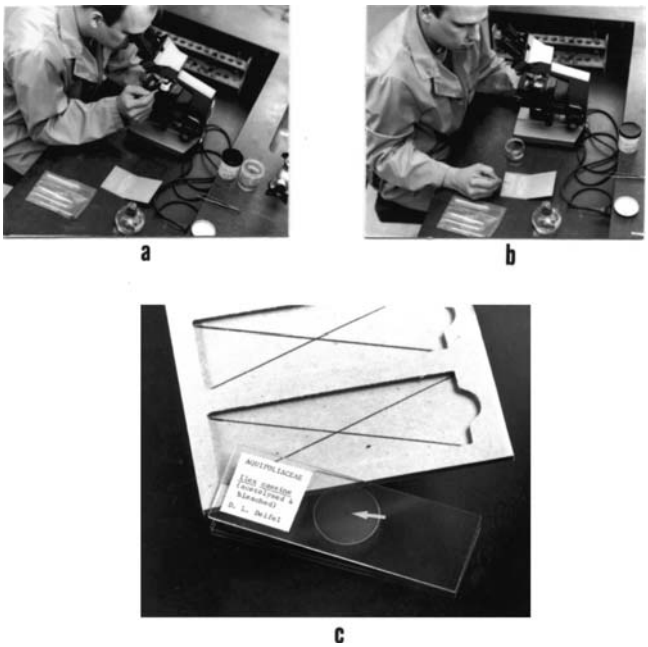

Figure A.4 Single-grain mounts by the glycerin-jelly-needle method. (**a**) under the microscope at low-power, needles are used to clean debris away from the vicinity of the desired palynomorph, which is in a glycerin/water smear on a slide; (**b**) the palynomorph is picked up with a tiny chunk of solid glycerin jelly on the point of a needle. The block of glycerin jelly is put on a microslide, using the center of an "x" on a slide-mailer as target. Pieces of paraffin wax are put around the glycerin jelly, and the wax and jelly are carefully melted over an alcohol lamp; (**c**) the wax hardens in about 30 seconds, leaving the glycerin jelly containing the palynomorph in the "window"(arrow).

pointed instruments (Fig. A.4a). I find certain dental explorer-type tools and scalpels with very small blades are especially handy.

(3) Have ready a slide, a circular coverslip, and a one-slide map-holder on which a "target" is ruled, in which the slide is placed. Also have ready a jar of paraffin cut up into tiny fragments, a jar with solid glycerin jelly, and an alcohol lamp.

(4) Take a needle-holder equipped with a fine needle and use the point to cut out a very tiny piece of glycerin jelly (about 200 μm across) and get this firmly onto the very tip of the needle. While watching the process under the 10× objective, bring the needle with the tiny piece of jelly into the field and delicately and lightly touch it to the specimen and remove the needle from the field (check to be sure the grain is gone). Put the tiny piece of glycerin jelly on the slide in the target area (Fig. A.4b).

(5) With a knife point arrange a small quantity of paraffin fragments (melting point about 50°) around the glycerin jelly blob. Heat slide very gently over an alcohol flame until jelly and paraffin melt. They will appear to have run together. Hold slide level. Put slide on table and carefully lower coverslip. When paraffin cools and solidifies, the glycerin jelly with enclosed specimen will appear as a clear window in the "ropey", whitish paraffin. If the slide is properly made, the specimen will be almost precisely in the target area (so that all single grains are easily found using the microscope), and the paraffin will flow only to the edge of the coverslip (Fig. A.4c). (If it flows beyond it is easy to clean up with a single-edged razor blade followed by a little xylene on a tissue.) The "window" should be tiny, but if it is too small, there is a tendency for the specimen to be enmeshed in the fibrous paraffin and therefore hard to see. Before discarding such a slide, it is useful to remelt the paraffin and gelatin; when it sets up again, the palynomorph may be visible. The size of the window is governed by the size of the glycerin jelly fragment that was affixed to the picking needle.

3.4.1.2 Capillary Tube Methods Many palynologists favor a capillary tube technique for single-grain mounts. The simple version Knut Faegri taught me, which I still use to good advantage, is as follows:

(1) Draw out a supply of capillary tubes for the purpose. I use 3 mm tubing in pieces about 15-20 cm long. If one starts with a piece of tubing about 20 cm long and heats the center to melting and pulls carefully, one almost always gets two useful tubes that may be broken apart carefully with a triangular file.

(2) Spread out residue in 50/50 glycerin-water (or water alone, if water is added occasionally; or glycerin alone, but it is quite viscous).

With needles, and other tools as described under the previous method, clear away debris and unwanted palynomorphs from around the specimen desired.

(3) Use 10× objective (about 100× magnification with a stereo dissecting microscope is also good) to observe the capillary as it is brought to the vicinity of the desired specimen. Carefully touch the tip of the capillary tube to the liquid around the specimen. The specimen and some liquid will rush up into the tube, which must be quickly lifted to prevent too much liquid from entering.

(4) Blow the droplet of material from the capillary tube onto a small piece of glycerin jelly which can be arranged on a target area, per the previous method.. Paraffin as a sealant can be arranged as in the other technique. If mobility of the specimen is desired, blow the droplet onto a drop of glycerin on a slide or onto a coverslip and cover with another coverslip. Such preparations are not permanent.

3.4.1.3 Variants on Capillary Tube Technique

(1) Pressure tube technique: Instead of using capillary tubes alone, it is more elegant to use capillary tubes attached to a rubber or rubbery plastic (such as Tygon) tube. If the other end of the tube is attached to a hypodermic type syringe, some glycerin may be sucked into the capillary and a negative pressure carefully controlled in the opening of the capillary, so that only a small amount of specimen plus liquid rushes into the tube when it is touched to the area of the specimen. The specimens may be ejected by depressing the syringe plunger. Also this control of the pressure makes it possible to put the capillary tube point into the specimen-liquid without drawing up the liquid until desired. Another advantage of this method for some purposes is that it is easy to pick up multiple (say 10) specimens, one after another, before emptying onto onto a slide, in order to make a mount displaying specimens in different orientations. Evitt (1984) has described this procedure and the "suction" device in detail.

(2) Coverglass-sandwich technique for LM, SEM, and TEM of one specimen: If the specimen is put onto a coverglass in glycerin, and covered with another coverglass, the "sandwich" can be temporarily fastened to a slide with small pieces of transparent tape and the specimen can be studied and photographed from both sides. The sandwich can then be removed from the slide, carefully pulled apart (inserting a razor blade is the best way) and the coverslips placed face up on a microslide. Find the specimen. Discard the empty coverslip. While watching the procedure under the scope, carefully flush the specimen with water, or better with t-butyl alcohol, several times wiping the flush liquid away from the specimen with the corner of a facial tissue. This removes the glycerin, to allow proper

gold-coating. The coverglass with the specimen may now be mounted on an SEM stub with appropriate adhesives, gold-coated and studied by SEM The specimen may be turned over by squirting alcohol on it from a small hypodermic needle and maneuvering the grain with a small hair on a stick (see Artüz and Traverse, l980). In this manner SEM pictures can also be made of both sides of the specimen, to match the light pictures (see Fig. A.5). (It is also possible to recover the specimen after SEM, remove the gold with aqua regia and make thin sections for TEM (see Walker and Walker, 1982).

Leffingwell and Hodgkin (1971) have published thorough descriptions of various other techniques for manipulation of palynomorphs in preparation for SEM. Leffingwell's laboratory used a micromanipulator attached to a microscope objective, for "picking" the fossils. Leffingwell also advocates polyurethane adhesive to stick the palynomorph to the SEM mount surface. In the Penn State laboratory we mostly used no adhesives at all and found that only very rarely did the fossils come off the coverslips mounted on SEM stubs. We stored the preparation (stub plus coverslip) in covered plastic boxes, to assure that air currents were not a problem. See Ambwani (1975 for useful, clear instructions for SEM studies of pollen and other microfossils.

3.4.2 Single Specimen Processing and Study

Sometimes it is desirable to treat a single specimen chemically, in order to isolate the procedure from other influences and to observe the results carefully. Johnson (1985), for example, did this in a study in our laboratory of the effect of oxidation on Silurian palynomorphs. Evitt (1984) has described a method for acetolyzing a single specimen, involving manipulation of the specimen in a syringe-type capillary tube (see above) and treating the specimen in the depressions of a glass cavity-slide. The specimen is passed through two changes of glacial acetic acid, then heated in acetolysis mix, and finally washed, transferring the specimen with a capillary tube each time.

It should be noted that sophisticated micromanipulators can be obtained for attachment to the objectives of microscopes. Several kinds are adaptable to the problem of picking up palynomorphs for the purpose of preparing single grain slides, or single grain mounts for SEM. For the operator with average dexterity and eyesight, such devices are not necessary.

3.4.3 Storage of Bulk Palynomorph Residues

I have always stored my residues in glycerin jelly. As noted elsewhere, glycerin jelly slides have a maximum life of about 40 years, much less in many cases. Long after the slides have disintegrated, however, the original glycerin jelly residues can usually be remelted and new slides made. However, a better storage

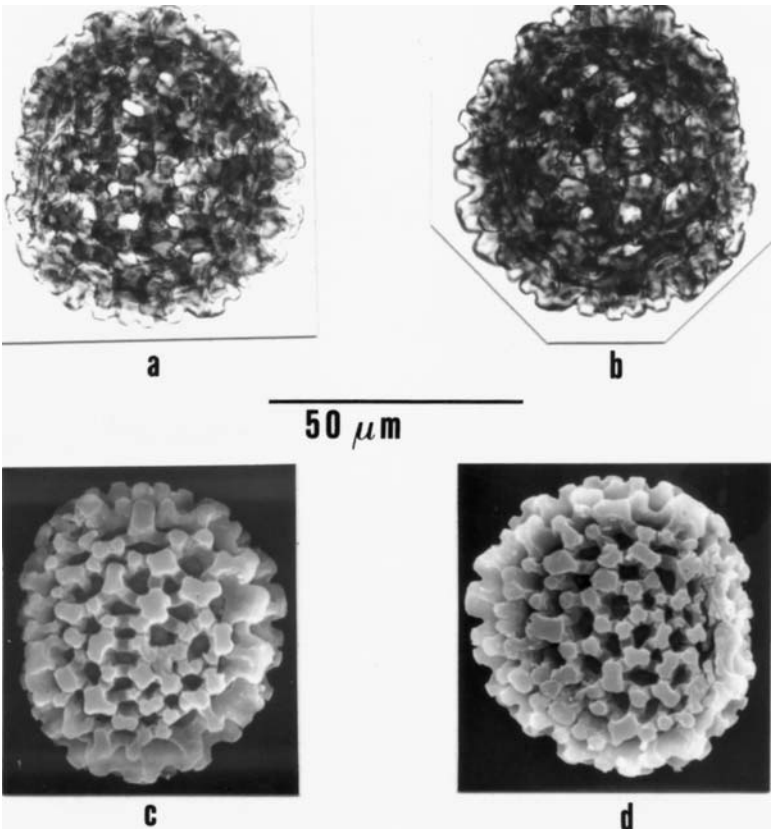

Figure A.5 SEMicrograph and light microscope photomicrographs of a single specimen of *Reticulatisporites karadenizensis* Artüz, Carboniferous, Turkey. The specimen was picked with a capillary tube from a glycerin/water preparation, mounted in a coverglass"sandwich" and photographed "front" (**a**) and "back" (**b**). The coverglasses were then separated, the water evaporated and glycerin removed by repeated washings with water and t-butyl alcohol. The coverglass with specimen was then mounted on an SEM stub and gold-coated. SEMicrographs were made from both sides of the specimen. Ethyl alcohol applied by hypodermic needle was used to tip the spore over after the first SEMicrograph, and gold-coating was repeated. Note that the light pictures are upside-down mirror images of the SEM pictures. Therefore individual sculptural elements are reversed as to up and down from (a) to (c) and from (b) to (d). The negatives of one set could be printed upside-down to achieve exact correspondence.

method should clearly be sought. Chapman (1985) recommends glycerin with phenol (to prevent fungal and bacterial growth), whereas Phipps and Playford (1984) recommend a 50/50 mixture of glycerin and 3% Cu_2SO_4 and a small amount of thimerosal ($C_9H_9HgNaO_2S$), a crystalline substance used in antiseptics

such as merthiolate. Slides are made from these glycerin residues by addition of glycerin jelly. Other laboratories use water plus phenol or alcohol for storage. With either glycerin or water storage, inspection of the storage vials at regular intervals for loss of liquid is essential, as evaporation occurs over time even with very tight vials. If final mounting is to be with a resin substance, residues should be stored in alcohol-water or in the resin's solvent, so that the storage liquid can either be evaporated on a slide or coverslip prior to adding the drop of mountant, or be mixed easily with the resin (see "double mounting"). Some laboratories (see Felix and Burbridge, 1985) have reported very satisfactory results from dry storage for years of macerated residues, after using the procedures outlined here for maceration of rocks. Felix and Burbridge advocated careful washing of the residue before dry storage, and re-wetting and re-dispersal of the fossils in the dried residue by treatment with KOH solution and washing before subsequent mounting.

3.5 Location of Palynomorphs, Photomicrography, and Related Matters

3.5.1 Location

The finding (refinding) of particular palynomorphs on a strew slide is a recurring problem. As long as one works with the same microscope, and nobody has changed the settings, the mechanical stage vernier-coordinated readings work fine. Also, if other microscopes of the same manufacture are used, in the same laboratory or elsewhere, conversions can readily be calculated by carrying with one a slide on which a reference point is marked. I use a diamond pencil, with which I make a small x on a slide, and use the center of the x as the reference point., for which mark the location readings are known on the original microscope. However, some brands of microscopes have mechanical stages on which the numbers run in directions opposite to those on other microscopes, making direct conversion difficult. In this case, it is possible to find a given palynomorph by marking the slide with a reference point such as an ink dot covered with a dot of clear fingernail polish, from which distances are given in millimeters and tenths of a millimeter upwards or downwards, to right or left. As mechanical stages all read in millimeters and tenths of a millimeter, palynomorphs can be located in this manner, but it can be difficult. Another approach is to use the England Finder (= EF, see Fig. A.6), a microslide on which a grid with reference numbers and letters appears. After a palynomorph is located (record mechanical stage location, in case the stage is accidentally moved), the slide is carefully removed, and the EF placed on the stage. A reading is taken from the EF and recorded. If the EF is then moved to another microscope, and the desired reference point found, the specimen slide can then be put on the microscope, and the fossil located. (In my experience, a small correction factor usually must be used with the EF if the second microscope's slide-holding device works differently from that of the first microscope, or if the specimen slide is of slightly different dimensions.) In

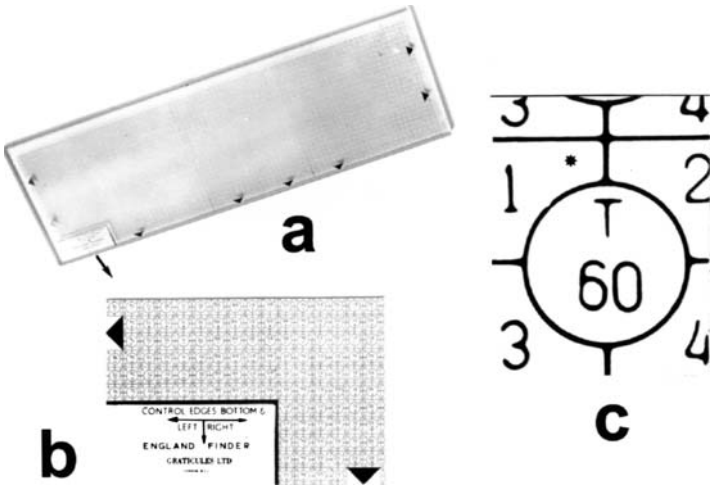

Figure A.6 England Finder, the most convenient method for stating locations of specimens on microslides. (**a**) the England Finder, a glass 3 × 1" slide on which a grid of letters and numbers is presented; the pattern (**b**) is upside-down and backwards, since most light, compound microscopes present their images that way. The EF images therefore appear in correct orientation under the scope, as shown in (**c**). A palynomorph is located and carefully centered, and the EF is put on the scope in the same position (if the stage moves easily, the mechanical stage coordinates must be used to control position). The reading of the center of the field is then recorded, e.g. "upper right of T-60-1" (see asterisk). Reversing the procedure locates the palynomorph on another microscope, providing that the specimen-slide is also 3 × 1." When slide-size differences or (very rarely) the design of the slide-holders on the two scopes is radically different, conversions can always be worked out. The corners of England Finders are easily damaged by the spring clips of slide-holders. If an EF is not available, a specimen can be located by giving its location with reference to a certain point such as a scratched '×' on the slide, e.g. "up 1.6 mm and to the left 2.9 mm," and this location can easily be found with any mechanical stage, as the stages are always calibrated in mm and tenths thereof.

our laboratory, when moving between Leitz microscopes in the research microscopy room to Olympus microscopes in the teaching laboratory, we found the England Finder to be an ideal locating device. Since the publication of the first edition of this book, however, I have heard from a colleague who reports that EF readings from colleagues don't work for him because his style of microscope inverts and reverses the image, and thus only EF readings from that sort of microscope are transferable. Other than such rather rare situations, the only disadvantage of the method is that to make use of the published EF readings, one must have an EF reference slide, and they of course can sometimes be hard to find just when needed, and there is a possibility that they will not be available for purchase some day.

Various techniques can be used to mark the surface of the coverglass with pen or brush, to help relocate palynomorphs on a slide. The coverslip can be marked with a circle of ink, and this ink protected with a little colorless fingernail polish. In our laboratory the favorite technique is to cut a tiny pointer from a gummed label, pick this up with a pair of iris forceps, moisten with the tongue and fasten down to the coverslip with the forceps points, while observing under low power of a microscope.. While still moist, the tiny pointer can be moved with a fine needle and finally labeled with a fine pen. However, as is true of all paper labels, the adhesive is not permanent, and the labels will one day fall off. Devices are available that can be screwed onto the nosepiece of the microscope in place of one objective, and which have an inking device to make a small "o" around a desired palynomorph. In my experience these devices are hard to keep in adjustment and properly inked, and may accidentally break a coverslip.

Much ink has been wasted in the paleopalynological literature by informing the reader what the mechanical stage coordinates are for illustrated or described specimens. Naturally, these readings are only good on the original microscope.

One would have to visit the subject laboratory to be able to use the readings, hoping that the original microscope would still be there and could be identified. Furthermore, it is a simple matter to reset the mechanical stage of any microscope with a screwdriver, so that none of the readings would agree with those previously recorded, and this is likely to happen, for example when the microscope is cleaned and adjusted or repaired. To summarize, the best methods for "permanent" location of important specimens are to mark the location of the specimens with ink, protected by varnish, on the coverslip, or to use measurements up or down, to right or left, from a reference point such as a scratched "x," in millimeters and tenths of a millimeter, somewhere on the slide. All other methods have at least one disadvantage.

3.5.2 Photomicrography

This is one part of paleopalynology that has changed dramatically since publication of the first edition of this book. A variety of digital cameras is now available for use with new and with older microscopes. The images thus produced can be fed into a computer, and manipulated in various ways, enlarged, reduced, arranged into plates, etc., using for example Adobe Photoshop. They can be sent as e-mail attachments to others for comments. They can be burned onto CDs or, better, onto electronic "memory sticks" for carrying to a conference or convention. Existing hard copy illustrations, whatever the technique used in preparing them, can also be made available for manipulation as if they were digital in the first place, with the use of a scanner (although if the original available is a half-tone dot matrix photo, the scanned copy is not very good). It seems to this observer that the quality of digital photomicrography illustration has not yet reached the brilliance of the very best film photography, but at the top level, it certainly is good enough.

However, the information in the first edition about film-based photomicrography is still pertinent. I continue to make photomicrographs with these techniques, although I can now scan the results into digital format, in order to combine such images with those digitally produced. Film-based photomicrography will remain useful for some time to people who still possess film photomicrographic equipment, which they will presumably use along with scanners and computers. As of the date of publication of the second edition of this book, even Polaroid film is still available.

For routine film-photomicrographic purposes, I favor 35 mm automatic cameras or simple attachment cameras. Automatic cameras make exposures and advance film automatically and are therefore much speedier in comparison with simple attachment cameras, but they present problems regarding cleanliness of almost inaccessible internal parts. Some authors using automatic photomicrographic cameras have even published photos that show the very same dust flecks on every picture! With automatic cameras it is difficult to cope with this, because there are prism surfaces inside the camera that are in the plane of focus and cannot readily be cleaned by the user. With simple attachment cameras all surfaces that are in focus are available for operator cleaning. A small piece of fine chamois attached to a small stick is good for cleaning the surface of an offending prism in the attachment camera.

For producing fine quality photomicrographic prints in connection with a study of slides for a small project, I still find Polaroid sheet film cameras very useful. Undoubtedly, the film will one day be no longer available, but in the meantime if you have an existing microscope such as a Leitz Ortholux with an Aristophot sheet film camera with a Polaroid adapter, keep using it! When I do, I am reminded that the best photomicrographs I have ever prepared were made at Harvard in the 1940s, using a Zeiss horizontal microscope and camera that filled most of a darkroom, and glass plates. That camera-microscope setup was obtained by Harvard from Germany about 1912. No camera film or digital camera has ever fully matched the perfect registration of a glass plate. (A useful book for explanation of particular techniques in photomicrography is Rost and Oldfield, 2000.)

3.5.2.1 Magnification Magnifications of 1,000, 750×, 500× or 250× should be standard for most published paleopalynological photomicrographs (100× or 150× for megaspores and other large palynomorphs). One reason for use of 1,000× is that a preponderance of palynomorphs are in the 30–50 μm range, and 1000× produces a picture 30–50 mm across, which is about right as a compromise between the largest possible picture and the usual space restrictions. Another great advantage of 1000× is that the size of the original fossil in micrometers can be read by measuring the photograph in millimeters. Within one paper an effort should be made to keep the number of different magnifications to a minimum. A bar should be placed on plates of photomicrographs showing the size of

specimens in micrometers, because enlargement or reduction in printing will not affect the magnifications represented by the bars, whereas "500×," etc., is effected by changes of size in printing.

It is easy to calculate the magnification from the measured size given in descriptions. The ratio between the photo in millimeters and the measurement in micrometers × 1,000 is the magnification. With a millimeter scale one can then read off the fossil' s size in micrometers (μm) if the magnification is known:

at 500×,	1 mm on photo	= 2.00 μm	on specimen
600×	"	1.67	"
750×	"	1.33	"
1,000×	"	1.00	"
1,200×	"	0.83	"

Unfortunately, application of this calculation to published figures frequently proves that the magnification is actually not as stated in the publication!

3.5.2.2 Microscopic Techniques. This is not the place for detailed instruction in the use of the microscope, though years of experience in teaching palynology convinced me that many students have problems in this area. First of all, the student needs to learn how to use the condenser. Close down the field diaphragm as far as possible and then close down the iris diaphragm too. The leaves of the field diaphragm should appear as a clear silhouette. If this circle is not clear, raise or lower the condenser until it is. Then center this circle, using the centering knobs. Then open the field diaphragm until the leaves exceed the edge of the field, and open the iris diaphragm to achieve an amount of light that produces neither too much contrast nor too little. If the microscope is an economy model on which the condenser cannot be centered, the student must still learn to use it at the right level for the various objectives, and to use the iris diaphragm efficiently. A blue filter is the most pleasing and restful for microscopy, but green filters produce the best black and white photomicrographs of most fossil palynomorphs. Color films usually require that no filter at all be used. However, sets of filters to insert in the light path in order to alter the color if necessary are available in camera shops. Do *not* leave the ordinary blue or green filter in place for color photomicrography. I have found that this dictum is easy to forget. All lenses should be kept absolutely as clean as possible. Immersion oil should be cleaned off of immersion objectives after use with lens paper, as it can damage the tiny exposed lens if allowed to accumulate

Most palynomorphs are more or less three-dimensional, though most are also more or less flattened. Therefore the student must learn to interpret the three-dimensional structure by focusing up and down. This is apparently very difficult for some people to accomplish. Especially difficult is the interpretation of sculpture. Many students have problems distinguishing between positive and negative sculpture. As pointed out by Erdtman, this is possible by focusing up

and down on the surface (LO analysis). Holes in the surface, for example, appear dark at high focus and lighter at lower focus. I have found it useful to instruct students to examine the outer edge of the grain in mid-focus (edge analysis) to check their observations by LO analysis. Spines or verrucae will stick out! Perforations will show as indentations. If there is time, making clay models of a form being studied is a very helpful exercise. I have found that beginning the instruction using a television camera in a demonstration microscope, with a small, portable monitor is very helpful.

3.5.2.3 Interference Contrast. Ordinary transmitted-light microscopy is bright field. Another of the many varieties of light microscopy is interference contrast or phase contrast. Special condensers and objectives make the examined specimen stand out against the darkened background with an appearance somewhat resembling an SEM image. The effect is especially helpful with specimens that are thin and/or colorless, such as some thin-walled pollen, very thin-walled dinoflagellate cysts, and acritarchs. No special preparation of the specimens is required. Interference contrast photomicrographs have the advantage that, while they show surface features in SEM-like contrast, internal features can also be shown, which is not the case with SEM. (Although broken fragments of exines seen in side view by SEM do reveal internal structure, it is necessary to use TEM to get a good concept of such structure with electron microscopy.)

3.5.2.4 Fluorescence Microscopy. This form of microscopy requires special light and filter equipment that can be used, however, with a regular light microscope. Specimens are illuminated with intense blue or ultraviolet light (either transmitted or incident) and fluoresce in different colors: that is, specimens on UV irradiation emit light of various intensities and wavelengths. For example, different states of carbonization-level yield different colors on fluorescing. The technique therefore has applications in study of coalification level (thermal alteration) and is discussed also in the section in this book on that subject. Some specimens reveal structure in fluorescence microscopy that isn't otherwise observable. Most palynomorphs fluoresce. Warning: UV and blue light can be dangerous to the eyes, and proper filters are required. One should check with a microscope distributor to be sure that one has the correct filters for the microscope to be used for this purpose.

3.5.2.5 SEM and TEM. Scanning electron microscopy (SEM) provides a three-dimensional appearing view of the surface of palynomorphs. Indeed, as the depth of focus is great, SEM pictures are ideal for stereo pairs, and these have been published for megaspores (Higgs and Scott, 1982: their Plate 1 and Figs. 4, 5) and other palynomorphs. Most people need a viewer to get the three-dimensional effect. Individual palynomorphs can be "picked" and mounted for SEM work, as described in the coverglass-sandwich technique above, or a strew preparation can be gold-coated and studied, even counted, by SEM. However, because SEM

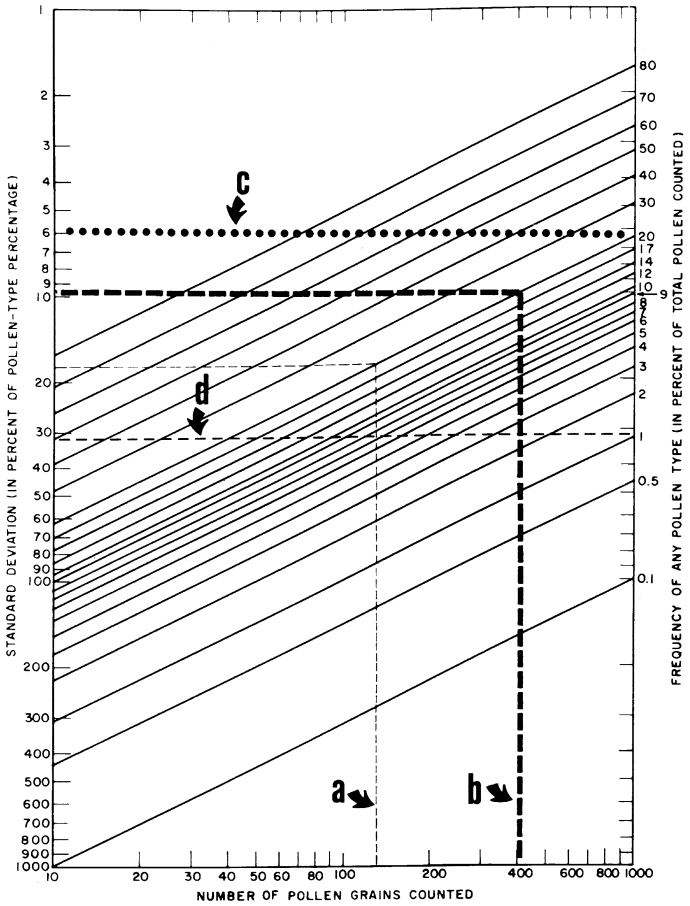

Figure A.7 Determination of standard deviation for pollen counts of various sizes. This graph provides a rough guide for estimating the size of count required for various levels of significance. We illustrate four examples. (**a**) If a certain pollen type represents roughly 20% of total pollen (based on preliminary counts), this percentage is shown by the sloping line labeled 20 on the right vertical axis. If 130 grains are counted, a vertical line from the base at 130 will intersect the sloping 20% line. Now project a horizontal line from the point of intersection to the left vertical axis to read the standard deviation of 17.4% (of 20%, i.e. 3.5%). This means that about two-thirds of all analyses may be expected to fall in the range of $20 \pm 3.5\%$. (**b**) If 400 grains of the same form are counted (about 3 times the number counted in (a)), using the same method of calculation shows a standard deviation of about 10%, meaning that two-thirds of all analyses would be expected to fall in the range of $20 \pm 2\%$. For most purposes, the extra labor is probably not justified. (**c**) Even with a count of 1,000, the standard deviation can only be reduced to 6%, demonstrating that for abundant forms large counts are not worth the extra work. (**d**) With a form present

equipment is expensive, and should be in the care of a skilled technician, light microscopes will continue to be the overwhelmingly more common instruments of choice for most aspects of palynology. Even more specialized is transmission electron microscopy (TEM). For a close look at internal structure of palynomorph walls, TEM is indispensable. Preparing palynomorphs for this purpose involves special embedding, usually in various plastics, sometimes special staining of the sections, which are made with an ultramicrotome. Naturally, this technique is practiced by only a few palynologists. Walker and Walker (1984) pioneered the elegant study of single palynomorphs by light microscopy, SEM and TEM. Such investigations are very important but are not likely to become routine. A technique suggested by Prössl (1996) seems potentially useful: a combination of SEM and incident (reflected) light microscopy for specimens that are opaque to white light.

3.5.2.6 Infrared Microscopy. It has been recognized for decades that objects appearing opaque in transmitted white light are sometimes translucent to infrared illumination. The use of infrared therefore has obvious application to study of opaque palynomorphs, which are frequently a big problem in sediments for which the thermal alteration level of the organics has reached TAI:4 or more (cf. Fig. 19.2). Marshall (1995) presents a technique for accomplishing infrared microscopy with minimal extra equipment beyond a good biological microscope.

3.6 Counting: How and How Many?

Nearly all paleopalynological projects sooner or later involve making a count of palynomorphs. As explained earlier, calculation of fossils per gram of sediment by my weighing technique requires counting all, or a fixed proportion (1/4 or 1/2) of all fossils on a slide. On the other hand, if a "stick"of *Lycopodium* spores is used, the incessant repetition of counting them tires the observer and affects accuracy of all the counts; I proved this long ago by experiments with a variety of individuals doing the counting. More commonly, percentages are used to provide an estimate of relative abundance. The percentage may be of all fossils or of a "pollen sum" that excludes some forms. A ratio between the number of one kind

◄

Figure A.7 only at the 1% level, a count of 1,000 yields a standard deviation of about 30%, whereas a count of 100 yields 100%: two-thirds of samples would then be expected to be between 0 and 2%. It is clear that forms present in amounts less than 1% will yield very large standard deviations, even with counts of 1,000. In other words, counts of such forms are intrinsically unreliable from a statistical point of view. The number of specimens that need to be counted for statistical significance depends on the abundance of the least abundant form of importance to the result. This graph was prepared by multiplying probable-error figures from Rittenhouse (1940) by 1/0.6745.

of fossil and others may be established, e.g., in calculating steppe/forest index, dinocyst/pollen and other such ratios. In any event, a strew slide is prepared, and the count is made by traversing the slide from side to side at a magnification sufficient to recognize the forms. The slide should not be too densely filled, or too many fossils will appear in each field for accurate counting. If only a percentage is sought, successive traverses should be counted far enough apart to prevent overlapping and double counting (especially of large) specimens. Where the whole slide is to be counted, double-counting can be minimized by counting specimens that are only partly in the field only at the top or at the bottom, but not at both. In any event, large forms are more likely to be counted at the edge of the field (see Faegri, 1951). A more serious problem really is that folding, squashing and so forth make many specimens unrecognizable, and this is more true for some forms than for others. For this reason, many palynologists, even though they may also make permanent preparations, as a rule prefer temporary, mobile preparations in glycerin or silicone oil for counting, because the grains can be manipulated for better inspection by tapping with a needle.

The question of how many specimens must be counted for statistical reliability of later calculations has been given far too little attention. Early in the history of Pleistocene/Holocene pollen analysis, it was held that, given the numbers of taxa involved and their relative abundance, counts of about 200 were satisfactory for reliable percentage calculations (see Barkley, 1934; Westenberg, 1947). The statement that "200 specimens per slide were counted" as a satisfactory requirement has ever since been a bit of the palynological folklore, echoed in hundreds of papers, and for most analyses it is based on a solid mathematical foundation. Gordon Rittenhouse of Shell Development Company, who had a few years before made calculations relative to mineralogical counting, showed me about 1957 how to calculate the number of specimens to count in order to get a reliable reading on the percentage of a certain species in a sample. He was convinced that many percentage-based palynological analyses being used for biostratigraphy were not statistically valid.

The Rittenhouse curve as applied to palynological counts is shown in Figure A.7. The gist of the chart is very simple: the number of specimens that must be counted to achieve a desired standard deviation depends on the abundance of the least abundant critical form. For example (not shown), in a total count of 200 (bottom axis), for a taxon that comprises about 60% of the total palynoflora (right hand side of chart), a standard deviation of 6% (of 60%, i.e. 3.6%) is achieved (project to the left the intersection of the vertical 200 count line with the sloping 60% line). This means that two-thirds of all analyses of such a sample would fall in the range of $60 \pm 3.6\%$, a quite acceptable reliability; that is, a calculation of, say, 58% for this form is a meaninngful datum. On the other hand, another taxon comprising about 2% of the palynoflora would have 50% standard deviation in a count of 200, meaning that two-thirds of the analyses of such a sample would be in the range 1–3%, so that many analyses would miss the form altogether

and others would pick up four palynomorphs. Even a count of 1,000 would give a standard deviation of 25%, or two-thirds of analyses would be in the range 1.5–2.5%. To achieve a 6% standard deviation, as for the form that comprises 50% of the palynoflora, would unrealistically require a count of several thousands (off the scale). The reliability in counts of 200 is satisfactory for abundant forms only, or if only a qualitative statement is required.

To put it another way, a decrease of a taxon from 2.4% to 1.6% looks big, especially if plotted logarithmically, but actually does not dependably mean anything at all, except presence/absence. Unfortunately, many published palynological data are in this category. Maher (1972) presents nomograms for calculation of the confidence limits of pollen analytical data, based on calculations by Mosimann (1965). The approach is considerably more sophisticated mathematically than that presented above, but the gist is the same, that large total counts are necessary to achieve meaningful data for uncommon forms. As a generalized endorsement of the principle, Dorning (oral statement recorded in my notes: 2005) observes that high diversity acritarchs require counts of a thousand, but the truth is that counts of forms that comprise less than 1% of the palynoflora would require counts even larger than 1000 for statistical reliability. Birks and Birks (1980) and Faegri and Iversen (1975) present discussions of this and related matters.

Glossary

The author wrote the spores/pollen palynological definitions for the 1972 first edition of the *AGI Glossary of Geology,* and I was again editor of the palynological definitions for the fifth edition of that compilation (Neuendorf *et al.*, 2005). The following definitions derive partly from those two projects. Other sources used in compiling definitions include: Beug (1961); preliminary versions of a glossary of fossil fungal spores morphology by Elsik *et al.*; Erdtman (1952); Evitt (1985); Evitt *et al.* (1977); Grebe (1971); the glossary of scolecodont terms from Jansonius and Craig (1971); for fungal spore terms, Kalgutkar and Jansonius (2000); Kremp (1965); the extensive, well illustrated general pollen and spore glossary of Punt *et al.* (1994); Smith and Butterworth (1967); Walker and Doyle (1975); for dinoflagellates, acritarchs and algal groups, Williams *et al*. (2000); and other references cited separately in the following glossary. This glossary aims to cover all terms used in this book. For others, please refer to the more recent of the abovementioned publications. It is also useful to check the index of this book, as that frequently will direct one to a desired description or definition.

aboral pole The end of a flask-shaped *chitinozoan* that includes the *chamber* of the *body* and the base. See *oral pole*, *apertural pole, antiapertural pole*.

absolute pollen frequency The estimate of the actual amount of *pollen* deposited per unit area in a given length of time, achieved by correcting the amount of *pollen* per gram of sediment by factors based on rate of sedimentation. Abbrev. *APF*. The expression has been mostly replaced by *pollen influx* (= *pollen accumulation rate*).

acalymmate Of the adhesion mode of members of a *polyad* or *tetrad*, characterized by lack of direct contact between *exines* of adjacent grains. Ant. *calymmate*.

acanthomorph acritarch An acritarch with clear differentiation of the *central body* and radially oriented processes.

accessory archeopyle suture An *archeopyle suture* that consists of a short cleft in the wall adjacent to the principal *suture*, or that may be more fully developed on the *operculum* of the *dinoflagellate cyst*, dividing that structure into two or more separate pieces.

accessory spore A *spore* present in a rock sample only in small quantities. Accessory spores include types with a very restricted range, and they have been used for correlation.

accumulation body (Also called "eyespot", and other terms.) Of *dinoflagellate cysts*, a small clump of resistant matter within the cyst, usually interpreted as waste metabolic matter.

acetolysis A chemical reaction in which acetic anhydride lyzes plant tissues, a sort of *maceration* in which peat or *palyniferous* material from extant plants (e.g., angiosperm flowers) is heated in a mixture of nine parts acetic anhydride and one part concentrated sulfuric acid. The reaction breaks down cellulose and other organic compounds and thus concentrates *sporopollenin*.

acme zone In *palynostratigraphy*, a zone which is of value for correlation based on dominance in percent of a *palynomorph* taxon or a related group of taxa, e.g., certain *Classopollis* spp. for the lowest Jurassic.

acolpate Of *pollen grains* without *furrows* (*colpi*) or other apertures. In practice, such pollen grains are sometimes difficult to distinguish from *alete* spores. Code POO. See *inaperturate*.

acritarch A unicellular, apparently unicellular, rarely multicellular, presumably algal, resistant-walled microscopic organic body of unknown or uncertain biologic relationship and characterized by varied *sculpture.* The substance of the wall is similar to sporopollenin. Acritarchs are assumed to be of algal affinity, but the group is artificial. They range from Precambrian to Holocene, but are especially abundant in late Precambrian and early Paleozoic. The term was proposed by Evitt (1963, pp. 300-1) as "an informal, utilitarian, 'catch-all' category without status as a class, order, or other suprageneric unit" consisting of "small microfossils of unknown and probably varied biological affinities consisting of a central cavity enclosed by a wall of single or multiple layers and of chiefly organic composition". See also *hystrichosphaerid*.

actuopalynology Study of extant *spores* and *pollen* and their distribution in atmosphere, hydrosphere and sediments, and related matters. See *paleopalynology, pollen analysis,* and *aerobiology*.

aerobiology Study of organisms and parts of organisms in the atmosphere. *Spores* and *pollen* are a major concern of aerobiologists, especially in their role as pollutants and causes of *pollinosis*. See *iatropalynology*.

air sac See *saccus*.

akinete Modified, thick-walled vegetative green algal cell, e.g., in *Zygnema*. Some *acritarchs* are probably akinetes.

ala An equatorial flange found in the *phycomata* of some modern *prasinophytes* and fossil *pteromorph acritarchs*.

alete Of a *spore* without a *laesura*. In practice, such spores are sometimes difficult to distinguish from *acolpate pollen*. Code SOO. See *inaperturate*.

allochthonous In *palynology*, *palynomorphs* that are produced at considerable distance from the site of their deposition. Ant. *autochthonous.*

alveolate Of pollen or spore structure characterized by sponge-like compartmentalization, as in *saccate* pollen.

amb The contour or outline of a *pollen grain* (less commonly of a *spore*) as viewed from directly above one of the *poles*. Also called *equatorial limb*. (It is possible but uncommon to describe also a *polar limb* or *profile*, the outline of a grain from a "side view", at right angles to the equatorial limb. However amb is used almost exclusively for the outline from the pole.) See also *profile*.

ambitus A less favored synonym of *amb*.

amerospore of Fungi, a single-celled, aseptate spore.

amoeba See *testate amoebae*

amphiesma Of *dinoflagellates*, the cell covering in general.

ana- A combining form used to indicate position on the *distal* surface of a *pollen grain* or spore, as anasulcate, having the *sulcus* on the *distal* surface. See *cata-*.

anamorph Of fungi, the asexual form of an ascomycete. Cf. *holomorph, teleomorph*.

anemophily Pollination by wind. Adj. anemophilous. See *entomophily* and *zoophily*.

annulus A ring bordering a *pore* of a *pollen grain*, in which the *ektexine* is modified (usually thickened). See *margo* and *endannulus*.

antapex Of *dinoflagellates*, the area at the posterior end of *theca* or *cyst*.

antapical series A series of antapical *plates* posterior to the *postcingular* series in *dinoflagellate theca* or *cyst*. See *apical series*.

antapertural pole Term introduced by Paris *et al.* (1999) to replace *aboral pole* for chitinozoans. See *oral pole, apertural pole.*

anteturma One of the two major groupings in which *turmae* are classified in the *turmal system* for fossil *sporomorphs*: Sporites (for *spores*) and Pollenites (for *pollen*).

AOM Term used in palynofacies studies: amorphous organic matter, a subset of *USTOM,* unstructured organic matter.

AOMA Term used in palynofacies studies: amorphous organic matter of aquatic origin, a subset of *AOM*.

AOMT Term used in palynofacies studies: amorphous organic matter of terrestrial origin, a subset of *AOM*.

AP arboreal pollen.

aperture Any of the various modifications in the *exine* of *spores* and *pollen* that can be a locus for exit of the contents; e.g., *laesura, colpus, pore*. See also *germinal aperture*. Also, the *oral* or *apertural* opening of chitinozoans.

apertural pole Term introduced by Paris *et al.*, 1999, to replace *oral pole*, for chitinozoans. See *antiapertural pole*, *aboral pole.*

APF absolute pollen frequency. See *pollen influx* and *pollen accumulation rate*.

apical archeopyle An *archeopyle* formed in a *dinoflagellate cyst* by the loss of the entire *apical series* of *plates*. See also *haplotabular archeopyle* and *tetratabular archeopyle*.

apical area Of an *embryophytic spore*, the *proximal* area associated with the *laesura*. See *contact area*.

apical papilla A dot-like thickening of an interradial area of a *spore*. When present, there is generally one *apical papilla* per interradial area, hence three per spore.

apical prominence In *megaspores*, mostly Paleozoic, variously constructed *proximal* projections formed by the intersection of the expanded contact areas.

apical series The series of *plates* forming an apical cluster in the *epitheca* or *epicyst* of a *dinoflagellate*. See *antapical series*.

apocolpium Area at *pole* of *pollen grain* delimited by a line joining the ends of the *colpi*. Syn. *polar area*.

apoporium Area including the *pole* of *porate pollen grain*, delimited by the poleward limit of a line connecting the poleward limit of the pores. Cf. *mesoporium*.

aporate Of *fungal spores* without *pores*.

appendage An elongated *sculptural element*; a *process*.

arboreal (*arborescent*) *pollen* The *pollen* of trees. Abbrev. *AP*. Syn. tree pollen. See *non-arboreal pollen*.

Archaea One of the three *domains* of organisms. Prokaryotic, mostly anaerobic, many found in extreme environments. Cf. *Bacteria, Eucarya*.

Archeophytic An informal division of geologic time, before the regular appearance of robust-walled *acritarchs* (about 1.0×10^9 years ago = beginning of *Proterophytic*).

archeopyle An opening in the wall of a *dinoflagellate cyst* by means of which the motile thecal stage emerges from the *cyst*. It is usually more or less polygonal in shape, and the *plate* (or plates) that drops out is the *operculum*. See also *apical archeopyle, cingular archeopyle, precingular archeopyle, combination archeopyle,* and *operculum*.

archeopyle suture A line of dehiscence on the *dinoflagellate cyst* that more or less completely separates a part of the *cyst* wall to form an *operculum*. See also *accessory archeopyle suture*.

arcus A band-like thickening in the *exine* of a *pollen grain* (as in *Alnus*), running from one *pore* apparatus to another.

armored Of *dinoflagellate* thecae (such as those of the order Peridiniales) possessing a cellulose envelope or cell wall that is subdivided into articulated *plates*. Ant. *unarmored*.

ascocarp Of fungi, any fruiting body containing *asci*.

ascospore A *fungal spore* produced sexually in an *ascus*.

ascus Of ascomycete fungi, an enlarged sac-like body containing a specific number of *ascospores* (usually eight, often four).

aseptate Of *fungal spores*, lacking a *septum.*

aspidate (Also spelled aspidote.) Having the *apertures* on dome-like protrusions (example *Betula*). Grains with aspidate external form are often *vestibulate* internally.

atectate Of an outer *exine* lacking *columellae* and hence also lacking a *tectum*. But compare *intectate*.

atrium A space between the external opening (*pore* or *ectopore*) and a much larger internal opening (*endopore* or *os*) in the *endexine* of a *pollen grain* with a complex *porate* structure. The internal opening is so large that the endexine is missing in the endopore area. Atrium is usually reserved for the space immediately around the endopore, and *vestibulum* for lateral space between pore and os. (Thomson and Pflug, 1953, define atrium and give *Myrica* as an example. *Betula*, by contrast, is *vestibulate*.) Pl. atria. See *pororate*.

attached operculum The *operculum* of a *dinoflagellate cyst*, not completely surrounded by *archeopyle* sutures and hence remaining joined to the main part of the **cyst** where the suture is not developed. Syn. *attached opercular piece*. See *free operculum*.

auricula One of the thickened "ears" of auriculate *spores*. Pl. auriculae. See *zone*.

auriculate Of *zonate spores* having *exine* thickenings in the *equatorial* region that project like "ears", generally from the area of the ends of the radii of the *laesura*. See *valvate*.

auto- In *dinoflagellate cysts*, single, such as *autophragm* (single wall).

autochthonous In *palynology, palynomorphs* that are more of less locally produced in or near the site of deposition. Ant. *allochthonous*.

autocyst Of *dinoflagellates*, *cysts* with a single wall (the *autophragm*).

autophragm See *autocyst*.

azonate Of *spores* without a *zone* or a similar (usually *equatorial*) extension.

bacteria One of the three *domains* of organisms. All of the non-*Archaea* prokaryotic microorganisms. Cf. *Eucarya.*

baculate Of *sculpture* of *pollen* and *spores* consisting of bacula (sing. *baculum*).

baculum One of the tiny rods (not thickened or thinned at either end), varying widely in size and either isolated or clustered, that make up the *ektexine sculpture* of certain *pollen* or *spores*. Also used for baculate-like, internal structures of Normapolles *germinals*. Pl. bacula.

basal plate In *scolecodonts*, a small to medium-sized right-hand *jaw* closely fitting into a posterior concavity of a simple jaw ("MId"). See *maxilla*.

basidiospore A *fungal spore* produced by the basidium of a basidiomycete. Fossil fungal spores are apparently rarely from basidiomycetes.

biform process A sculptural element with two different thicknesses. Term is usually restricted to elements with a broader base and abruptly constricted, spiny tip.

biome as used in palynology, a particular type of vegetation based on climatic requirements and dominant over a wide geographic area. Fossil biomes are best detected by pollen analysis.

bisaccate Of *pollen* with two *sacci*. Usually occurs in conifers but also found in other gymnosperms, such as Caytoniales and seed ferns. Code Pv2. Syn. *bivesiculate* and *disaccate*.

bivesiculate See *bisaccate*. Syn. *bisaccate* and *disaccate*.

bladder Syn. of *saccus, vesicle*, and *wing*.

body Of *saccate pollen*, the *corpus*; also loosely the *central body* of the saccate or saccate-like pollen of various *spores* and *pollen grains*. Of *chitinozoans*, the main, larger part of the unit (vesicle),, which lies below the *neck*.

BP Before present, "present" conventionally taken to be 1950.

Brevaxones A group of mid-Cretaceous and younger dicot angiosperm *pollen* in which the *polar* axis is shorter than the *equatorial* diameter, representing an apparent evolutionary advance over *Longaxones*, and including such forms as *Normapolles*.

brochate See *heterbrochate* and *homobrochate*.

callose A carbohydrate component of cell walls in certain plants; e.g., the amorphous cell wall substance that envelops the *pollen mother cell* during *pollen grain* development and acts as a barrier between *mother cells*, and subsequently between developing members of the *tetrad*, but that disappears as the *ektexine* structure is completed and impregnated with *sporopollenin*.

calymmate Adhesion mode of members of *tetrads* and *polyads*, in which the *ektexine* of the individual *monads* form a continuous envelope around the outside of the multicellular unit. Ant. *acalymmate*.

camerate As originally defined (Neves & Owens 1966), describes *spores* in which outer and inner *exine* are separated to various degrees by a chamber (= camera), but which lack infrareticulate *structure*. Includes *pseudosaccate*, which refers to spores with extensive separation of exine layers. In common usage, a syn. of *cavate*. Camerate (or cavate) is also used by some authors for spores with barely detectable or partial separation of wall layers. For acritarchs, the term is used in a similar sense. Camerate is also used for dinoflagellate cysts, in a quite different sense, to describe the condition in which a plate has five sides, with one side parallel to the cingulum and two sides away from the cingulum form a point resembling a roof or gable. Cf. *cavate.*

capillate A term for *sculpture* consisting of capilli. Favored terms are now *fimbriate* and *fimbriae*.

cappa The thick-walled *proximal* side of the *corpus* of a *saccate pollen grain*. See *cappula*.

cappula The *distal*, thin-walled region of the *corpus* of a *saccate pollen grain*. Unfortunately, the term is easy to confuse with *cappa*, the thick-walled *proximal* area.

cata- Combining form indicating position on the *proximal* surface of a *pollen grain* or *spore*, as catasulcate, having the *sulcus* on the proximal surface, as for example in some Annonaceae.

cavate (a) Descriptive of *pollen* (or, less precisely, of *spores*) whose *exine* layers are separated by a *cavea* or cavum (= cavity). The separation may be rather slight or more extensive, or eventually producing a bladder-like protuberance approaching the *pseudosaccate* or *saccate* condition. (In practice, these three terms are difficult to separate.) This term and *camerate* are also used of hollow *processes*. See *camerate*. (b) Of a *dinoflagellate cyst* with space or spaces of notable size between the *periphragm* and *endophragm* (as in *Deflandrea phosporitica*). See *chorate* and *proximate* cysts.

cavea a cavity or space between two layers of the exine, which extends to the colpus margin; very evident in polar views of some Asteraceae pollen, e.g. *Ambrosia.*

cella For *fungal* spores and hyphae, one chamber within the structure. Pl. cellae.

-cellate Of fungal spores, indicating the number or kind of *cellae*, as pluricellate. This term is used to avoid "cellular" because the cellae of a fungal spore are not necessarily biological cells.

Cenophytic An informal division of geologic time, based on the abundant occurrence of angiosperms in the fossil record, therefore equals approximately Aptian-Albian to present. The next older such division is the *Mesophytic*.

cenospheres More or less spherical pseudofossils, sometimes with a bubbly structure, rather commonly found in palynological macerations. Apparently most of them are produced by industrial activities, especially those that carbonize hydrocarbons at high temperatures. See Miller and Jansonius (1996). See *linotolypidae.*

central body The main part of a *pollen grain* or *spore*; e.g., the *corpus* of a *saccate pollen grain*, as distinct from the *sacci*; or the central part of a *zonate* or *camerate*

spore, exclusive of the *zona*, *pseudosaccus*, etc.; or the compact central part of a *dinoflagellate cyst* from which the projecting structures extend. Syn. *body*.

chagrenate Somewhat translucent and granular *sculpture* of *pollen* and *spores*. Also spelled *shagreen*, *shagrinate, chagranate.* This complex of terms is so confused in spelling and definition that it should be avoided. (The 2001 Random House Webster's Unabridged Dictionary likens the meaning to both that of the surface of untanned leather and that of rough sharkskin.)

chamber Of a *chitinozoan*, the central more or less enlarged cavity of the chitinozoan *vesicl*e.

cheilocardioid Of lipped, heart-shaped *spores*, as *Microbacilispora*. (The heart-shape results from lateral compression.)

cheno-ams Abbreviation for Chenopodiaceae-Amaranthaceae, the pollen of which families is prevailingly periporate and very hard to distinguish as to genus. In Neogene pollen analysis, it is conventional to lump such pollen under this term.

chevron Describing the *laesura* of a *dilete spore*.

chiropterophily A term for *pollination* by bats.

chitin A long-chain nitrogen-containing polysaccharide, structurally similar to cellulose, having, however, the carbon-2 -OH groups replaced by acetylamine groups (-NH-CO-CH_3). The compound is resistant to acid attack and biodegradation in a manner very similar to *sporopollenin*. The robust-walled *spores, fruit-bodies* and *hyphae* of some fungi consist of chitin, as do the walls of *microforaminifera*, *scolecodonts,* and insect exoskeletons, parts of which, such as lepidopteran scales, often occur as palynomorphs. Compare *pseudochitin*.

chitinozoan A marine microfossil of the extinct group Chitinozoa, having pseudochitinous walls, of uncertain affinity (generally assumed to represent animal remains), shaped in general like a flask, occurring individually or in chains. Stratigraphic range primarily from uppermost Cambrian to Devonian. Chitinozoans have thin, usually black, structureless, opaque walls, but they may be brown and translucent. Named by Eisenack (1931), who noted the resemblance of the walls to *chitin*.

chlamydospore A thick-walled, non-deciduous *spore*, such as a unicellular *resting spore* in certain fungi, usually borne terminally on a *hypha* and rich in stored reserves.

chorate cyst Encysted, unicellular alga with *processes*; especially a *dinoflagellate cyst* bearing little morphological resemblance to the motile *theca*. The ratio of the diameter of the main *body* to the total diameter of the *cyst* is 0.6 or less. Examples *marginate chorate cyst, membranate chorate cyst*, *pterate chorate cyst, trabeculate chorate cyst*. See also *proximochorate cyst* and *proximate cyst*.

cicatricose Marked with scars; especially said of *sculpture* of *pollen* and *spores* consisting of more or less parallel ridges, curving in the manner of a fingerprint.

cingular archeopyle An *archeopyle* formed in a *dinoflagellate cyst* by breakage along and within the *cingulum* (= *girdle*).

cingulate Having a *girdle*; especially said of a spore possessing a *cingulum*.

cingulizonate Of *spores* with a *cingulum* to which an outer, thinner *equatorial* extension is appended.

cingulum (a) An annular, more or less *equatorial* extension of a *spore* in which the wall is thicker than that of the main body of the *spore*. Pl. cingula. See *zone* and *crassitude*. (b) In a *dinoflagellate theca* or *cyst*, the girdle, a slightly depressed band of small *plates* separating *hypotract* from *epitract*.

Circumpolles A group of spherical gymnospermous pollen, commonly occurring as tetrads, characterized by a subequatorial *rimula*, a distal pseudopore and a proximal triangular area. Abundant occurrence indicates Late Triassic to Early Cretaceous age. Example: *Classopollis.*

clavate Of *sculpture* consisting of clavae, i.e., rods with enlarged, club-like ends. See *pilate*.

clavus Of *scolecodonts*, a lateral rudder-shaped *plate* or ledge projecting from and more or less perpendicular to the inner face, located at the dorsal part of the *jaw*, in some types of *MI*. See *maxilla*.

clitellate cocoons Mesh-like scleroproteinaceous mesofossils of Late Triassic to Cenozoic age, produced by certain leeches and other annelids. They are robust enough to occur occasionally in palynological macerations. See Manum (1996).

-coel Of *dinoflagellate cysts*, meaning cavity, as mesocoel, the middle cavity.

coenobium An algal colony with the number and distribution of cells fixed at its origin, as in *Pediastrum*.

collarette Of *chitinozoans*, the lip-like edge, surrounding the *mouth*, at the *oral pole.*

colony Of algae, a clonal assemblage of a few to many cells, not of fixed number, as is true of a *coenobiium.* Example: *Botryococcus.*

colpa A non-recommended synonym of *colpus*. Pl. colpae.

colpate Of *pollen grains* having more or less elongated, longitudinal *furrows* (*colpi*) in the *exine*.

colpi Pl. of *colpus*.

colpoid Erdtmanian term for a *colpus*-like *furrow* not situated or constructed as are *colpus, sulcus* or *sulculus*.

colporate Of *pollen grains* having *colpi* in which there is a *pore* or some other organized thinning of the *exine* (such as a *transverse furrow*), usually at the *equator*. See *colporoidate*.

colporoidate Of *pollen grains* having *colpi* in which there is no *pore* or other clearly recognizable thinning, but modifications of the *exine*, usually *equatorial*, are present: in other words, *colporate* but with a weakly developed pore.

colpus A longitudinal *furrow*- or groove-like modification in the *exine* of *pollen grains*, associated with germination (either enclosing a *germ pore* or serving directly as a place of emergence for the *pollen tube*) and often also important for *harmomegathic* swelling and shrinking. When the term is used strictly, a colpus must be meridional and will ordinarily cross the *equator*. In this sense the term is hence practically restricted to dicot angiosperms. In a looser sense, commonly used as synonymous with *sulcus* (*"monocolpate" pollen* are as a rule actually *monosulcate*).

colpus transversalis See *transverse furrow*.

columella One of the rodlets of *ektexine* that may branch and/or fuse distally to produce a *tectum* on *pollen grains* with complex *exine structure*. Pl. columellae.

columellate Possessing *columellae*; of *pollen grains* with a complex *ektexine structure* consisting of columellae.

combination archeopyle In *dinoflagellate cysts*, an *archeopyle* formed by the release of a part of the *cyst* wall that corresponds to *plates* of more than one *thecal plate series* (such as combining the plates of the *apical series* and of the *precingular series*).

commissure The groove more or less on the center line of a *laesura*, along which line an *embryophytic spore* usually germinates. It is essentially equivalent to *suture*.

compound operculum A *dinoflagellate cyst operculum* that is divided into two or more pieces that are separable from one another. See *simple operculum.*

conate Of *sculpture* of *pollen* and *spores* consisting of *coni*.

coni Pl. of *conus*.

conidiophore A structure that bears *conidia*; specifically a specialized, typically erect *hypha* that produces successive conidia in certain fungi.

conidiospore A *fungal spore*, synonym for *conidium*.

conidium An asexual *fungal spore* produced from the tip or side of a *conidiophore*; broadly, any asexual spore not borne within an enclosing structure, such as one not produced in a *sporangium*. Pl. conidia. Syn. *conidiospore*.

contact area One of the areas of the *proximal* side of a *spore* or *pollen grain* that contacted the other members of the *tetrad* before they separated. Contact areas are seldom visible in mature pollen grains but are frequently apparent in spores. *Trilete spores* have three contact areas; *monolete spores* have two contact areas.

conus One of the small pointed projections making up the (*echinate*) *sculpture* of certain *pollen* and *spores*, being more or less rounded at the base and less than twice as high as the basal diameter. Pl. *coni*.

copula Of *chitinozoans*, the stalk-like basal part of some species; it may terminate in a foot-like appendage. Both *copula* and *mucron* seemingly have to do with linkage of the chitinozoal units into chains.

corona A more or less *equatorial* extension of a *spore*, similar in disposition to a *zone* but divided in fringe-like fashion, such as in *Reinschospora*. Adj. *coronate*.

corpus That part of a *saccate pollen grain* or pseudosaccate *spore* exclusive of the *sacci* or *pseudosacci*. See *body*.

costa One of the rib-like thickenings in the *endexine* of *pollen*, associated with *colpi*. *Costae* are most often meridional and border *colpi* in pairs, but they may be transverse in association with *transverse furrows*. They are best seen in *equatorial* view. Example *Melia* (Fig. 5.7ak). Adj. costal.

crassinexinous Having thick *nexine*. The usual limit is nexine at least twice as thick as *sexine*.

crassitude A more or less local, usually *equatorial exine* thickening of a *spore*. See *cingulum* and *zone*.

crista One of the elevations making up the *sculpture* of certain *pollen* and *spores*, characterized by long, curved bases (sometimes irregularly fused) and variously bumpy apices. Pl. cristae.

cristate Crested, or having a crest; especially said of *sculpture* of *pollen* and *spores* consisting of *cristae*.

cryptarch According to proposal of Diver & Peat (1979), those of what others call *acritarchs*, which lack *spines*, *plates* or other features suggesting algal affinity. Cryptarchs thus would include sphaeromorph acritarchs, organic filaments, etc., whether or not sporopolleninous.

cryptopore Term used by some for *distal tenuitas* of *Classopollis* and similar *pollen grains* Some call the same structure a *pseudopore*.

cryptospore Early to mid-Paleozoic spore-like bodies, with no *haptotypic characters*. Cryptospores can be *monads, dyads, tetrads*.

curvatura A visible line of some (mostly mid-Paleozoic) *trilete spores*, connecting the extremities of the ends of the *laesura* and thus outlining the *contact areas*; a "curvatura perfecta" has three lines complete all around the spore's *proximal* face; a "curvatura imperfecta" has fork-like projections from the radial ends of the laesura, not joining with their neighbors (also called "reduced curvatura"). Pl. curvaturae.

cusp Of *scolecodonts*, the largest tooth in a series of denticles, especially in *basal plate*, MII, MIII, MIV.

cyst A microscopic resting body with a resistant wall, formed in algae by the breaking up of parts of filaments or by the enclosing of a cell or cell group and investment by a sheath or envelope. *Dinoflagellate cysts* form within *thecae*, as part of the normal life cycle. See *statospore* and *hystrichosphaerid.*

-cyst Of *dinoflagellate cysts*, combining form meaning *body*, as in *endocyst*, the inner body.

decussate Of *tetrads* of *pollen grains*, in which two pairs of elongated grains lie across one another, the pairs at right angles to each other.

demicolpate Having *apertures* resembling what would happen if ordinary *colpi* were interrupted in the *equatorial* area to make sets of two, in-line colpi, not crossing the *equator*. A 3-demicolpate form would therefore actually have six colpi-like apertures.

demicolporate Like *demicolpate*, but the demicolpi have *pores* or pore-like interruptions. A 3-demicolporate form can therefore have six pores (fossil example: *Sindorapollis*).

densospore A *trilete spore*, chiefly Paleozoic, with a pronounced *cingulum* which has a tendency to be "doubled", with a thicker part toward the center of the *spore*, and a thinner more external part; e.g., the genus *Densosporites* and other similar genera such as *Cristatisporites*.

dentary Of *scolecodonts*, a series of *denticles* along the inner dorsal margin.

denticles Of *scolecodonts*, the individual elements or teeth on the dorsal margin of the *jaw*.

desmid Single-celled green algae in which the cell consists of two semicells. The *zygospores* are sometimes resistant-walled (probably sporopolleninous) and occur rarely as *palynomorphs*.

diacromorph Of *acritarchs*, forms with sculptured polar area and equatorial areas free of sculpturing.

diad Alternate spelling for *dyad*.

diatom Usually single-celled algae of class Bacillariophyceae, the siliceous frustules of which occur in paleopalynological preparations if they have not been digested by HF or have been inadequately so digested.

dicolpate Of *pollen grains* having two *colpi*. Code Pb0.

dicolporate Of *pollen grains* having two *colpi*, with at least one colpus provided with a *pore* or *transverse furrow*. Dicolporate pollen are rare. Code Pb2.

dictyospore Of fungi, a *conidium* subdivided by longitudinal and transverse septa.

didymospore Of fungi, a monoseptate (dicellate) *conidium*.

dilete Of a *laesura* with only two *radii*. This morphological type is rare. See *chevron*.

dinocyst Contraction of *dinoflagellate cyst*, more or less synonymous for fossil *dinoflagellate*. The term is not popular with some dinoflagellate experts, who regard it as "slangy."

dinoflagellate A one-celled, microscopic, chiefly marine, usually solitary flagellated protist organism with resemblances to both animals (motility, ingestion of food) and plants (photosynthesis), characterized by one *transverse flagellum* encircling the *body* and usually lodged in the *cingulum* or *girdle*, and one posterior flagellum extending out from a similar median groove, the *sulcus*. Certain dinoflagellates have a *theca* (*test*; usually not resistant to decay), and that may be simple and smooth or variously sculptured and divided into characteristic *plates* and grooves. Some produce a resting stage or cyst with a resistant, sometimes complex organic wall (e.g., spiny) and may differ markedly from the theca of the same species. The compound composing the cyst walls is called *dinosporin*. *Dinoflagellate cysts* exist abundantly as fossils, and have a range primarily Triassic to present. Dinoflagellate cysts are known from the Paleozoic, but are important *palynomorphs* only from Jurassic to present. Dinoflagellates inhabit all water types and are capable of extensive diurnal vertical migrations in response to light. They constitute a significant element in marine plankton, including certain brilliantly luminescent forms and those that cause red tide. See also *hystrichosphaerid*.

dinosporin Substance of which the walls of dinoflagellates and acritarchs consist. Presumably chemically very similar to *sporopollenin.*

diploxylonoid Of *bisaccate pollen*, in which the outline of the *sacci* in *distal-proximal* view is discontinuous with the *body* outline so that the grain appears to consist of three

distinct, more or less oval figures. See *haploxylonoid*. (Terms come from *Diploxylon* and *Haploxylon*, sections of the genus *Pinus*.) The terms have unfortunately been used in different senses from this definition and are best avoided.

diporate Of *pollen grains* having two *pores*. Code P02.

disaccate See *bisaccate*.

distal The parts of *pollen grains* or *spores* away from the center of the original *tetrad*; e.g., of the side of a *monosulcate* pollen grain upon which the *sulcus* is borne, or of the side of a spore opposite the *laesura*. Ant. *proximal*.

distal pole The center of the *distal* surface of a *spore* or *pollen grain*, thus the very center of the *sulcus* of a *monosulcate grain*.

domain a level of classification of organisms above that of kingdom. There are three domains: *Archaea, Bacteria, Eucarya*.

dyad An uncommon grouping in which mature *pollen grains*, *spores* or *cysts* occur as fused pairs. Code Pdy. See *tetrad* and *polyad*.

echinate Of *sculpture* consisting of *spines* (echinae).

ectexine Variant of *ektexine*.

ecto- Of *dinoflagellate cysts*, more or less extreme outer location, as in *ectophragm*, extreme outer wall. Also used for pollen to indicate an outer structure, as in *ectoaperture.*

ectoaperture Of pollen, an outer aperture where there is a compound aperture, as many *triporate*, *stephanoporate* and *periporate* grains. Cf. *endoaperture.*

ectoexine Var. of *sexine*.

ectonexine Outer part of *nexine*.

ectophragm A thin, often discontinuous membrane lying between *distal* ends of *processes* on a *dinoflagellate cyst*. The term is also used in different senses. See *endophragm, periphragm, autophragm*.

ectopore An outer *pore*. Used for compound pore structures, in which there is also an *endopore* (= *os*).

ectosexine Outer part of *sexine*.

ektexine In Faegri and Iversen's scheme (see Faegri *et al.*, 1989), the outer layer of the two layers of the *exine* of *spores* and *pollen*, normally more densely or deeply staining than the *endexine*, and characterized by richly detailed external *sculpture* and often by complex internal *structure* of granules, *columellae*, and other elements. In contrast to Erdtman's "geographically" based *sexine*, the ektexine must be set off from the underneath (endexine) layer by demonstrable staining difference. See *ectexine, ectoexine* and *sexine*.

elater The ribbon-like, usually hygroscopic, filamentous appendage of certain *spores* (as of *Equisetum*), consisting of more or less coiled strips of *exine*, perhaps homologous with *perine*. It aids in spore dispersal.

embryophytic Of plants producing a 2N (diploid) embryo as part of a 1N-2N life cycle–usually restricted to bryophytes and tracheophytes (pteridophytes, gymnosperms, angiosperms). Noun embryophyte. Essentially equivalent to archegoniate.

endannulus An *annulus* formed by the *endexine* of a *pollen grain*. Thomson and Pflug (1953) illustrate it as characterizing some *Normapolles* pollen.

endexine The inner, usually homogeneous layer of the two layers of the *exine* of *spores* and *pollen* in the Faegri and Iversen scheme (see Faegri *et al.*, 1989), normally less deeply staining than the *ektexine*. See *intexine* and *nexine*.

endo- In *dinoflagellate cysts* means inner, as *endophragm*, inner wall.

endoaperture Of pollen with compound apertures, the inner aperture. Cf. *ectoaperture.*

endoblast Of two-walled *dinoflagellate cysts*, the *endophragm* and its contents.

endocoel The cavity formed by the *endophragm* in a *cavate dinoflagellate cyst*. See *pericoel*.

endocyst Of more or less *cavate dinoflagellate cysts*, the separate inner *body*, of which the *endophragm* comprises the wall.

endogerminal Especially used for *Normapolles*. Essentially equivalent to *os*.

endonexine Inner layer of *nexine*.

endophragm The wall of the inner *body* of a *cavate dinoflagellate cyst*. See *endoblast*.

endopore The internal opening in the *endexine* of a *pollen grain* with a complex *porate* (=*pororate*) structure. Syn. *os*. See *ectopore*.

endosexine Inner layer of the *sexine*.

endospore (a) Syn. of *intine*, for use in describing the *sporoderm* of *spores*, rather than that of *pollen*. Syn. *endosporium*. See *exospore*. (b) Some *palynologists* have also used *endospore* for the inner *exine* body of, e.g., *camerate spores*.

entomophily A term for *pollination* by insects. Adj. *entomophilous*. See *anemophily, chiropterophily, ornithophily, zoophily.*

epicyst The part of a *dinoflagellate cyst* anterior to the *cingulum* (*girdle*) region. See *hypocyst* and *epitheca*.

episome The anterior part of the cell *body* above the *cingulum* (*girdle*) of an *unarmored dinoflagellate*. See *hyposome*.

epitheca In a motile *dinoflagellate*, the portion of the *theca* anterior to the *cingulum*. See *epicyst*.

epitract Syn. of *epicyst*.

epityche An *excystment* (emergence) *aperture* in the *acritarch* genus *Veryhachium*. Originating as an arched slit between two *processes*, rupture allows the folding back of a relatively large flap.

equator An imaginary line connecting points midway between the *poles* of a *spore* or *pollen grain*.

equatorial extension Any equatorial extension of the *spore wall*, a less encumbered term for the general sense of *zone*.

equatorial limb A less satisfactory synonym for the term sometimes applied to the *amb* of a *pollen grain* or *spore*, as seen in *polar* view. See *limb* and *amb*.

equatorial view The lateral view of a *spore* or *pollen grain* from an aspect more or less midway between the *poles* and perpendicular to the *polar* axis.

Eucarya The eukaryote *domain* of organisms, typified by possession of a vesicular nucleus in the cells and complex protoplasmic organization.

eudicot Of dicot angiosperms, those that produce either tricolpate pollen, or a form derived from the tricolpate condition, such as Rosaceae, Asteraceae. Does not include *magnoliid*s and other basal angiosperms. See p. 28 of Soltis *et al.* (2005) for a concise chart.

eukaryote Cf. *Eucarya*.

eurypalynous Erdtmanian term for taxa with spores/pollen displaying much variety of morphology and/or exine structure. Antonym: *stenopalynous.*

eusaccate Saccate pollen grains lacking the extensive internal ektexinous webbing characteristic of the sort of fossil, extinct gymnosperm pollen that Scheuring (1974) called *protosaccate.* See *protosaccate*, *pseudosaccate, saccate.*

excystment Having to do with the emergence of the contents of a *cyst*. The excystment site of a *dinoflagellate cyst* is the *archeopyle*.

exine The outer, very resistant layer of the two major layers forming the wall (*sporoderm*) of *spores* and *pollen*, consisting principally of *sporopollenin*, and situated immediately outside the *intine*. It is divided into two layers either on the basis of staining characteristics (*ektexine* and *endexine*), or somewhat arbitrarily on the basis of being related

to *sculpture* (*sexine*) or not so related (*nexine*). Syn. *extine* and *exospore*. See also *perisporium*.

exinite Coal petrologic term. Essentially synonymous with *sporinite*, q. v.

exinous Consisting of *exine*.

exoexine A less satisfactory synonym of *ektexine*.

exogerminal Especially used for *Normapolles*. Essentially equivalent to *pore*.

exospore A synonym of *exine*, mostly applied to the non-perinous portion of the *sporoderm* of *spores*. Syn. *exosporium*.

extine Var. of *exine*. The term is not in good or current usage in *palynology*.

exuviation The removal of the *theca* of a *dinoflagellate*, either *plate* by plate, or as small groups of plates.

falx Of *scolecodonts*, a sickle-shaped extension of the anterior part of the *jaw*, often forming a hook.

fang Of *scolecodonts*, a poorly developed falcal hook.

fenestrate Of pollen exines, those with large open "windows" surrounded by exine wall, such as many genera of the Asteraceae (e.g., *Ambrosia*), or of *Passiflora*, in which case the windows are caused by the shedding of sections of the exine.

fimbriate Preferred synonym of *capillate*. Fimbriate sculpture consists of long, hair-like units (fimbriae).

Fischer's rule Of triaperturate, tetrad angiosperm pollen, in which the apertures form in pairs at six points on the tetrad, each pair involving two adjoining members of the tetrad. Example: *Vaccinium.* See Fig. 5.8. Cf. *Garside's Rule.*

flagellar pore One of the *pores* in a *dinoflagellate* for extrusion of flagella, usually located at the anterior or the posterior junction of *girdle* (*cingulum*) and *sulcus*.

Flandrian Western European term for what is variously called elsewhere "post-glacial", "recent", "Holocene", i.e., approximately the last 10,000 years, the present interglacial.

flange An *equatorial* extension of a *spore*; less precisely defined than *zone* or *cingulum*.

foot layer A lower part of *the ektexine*, partly surrounded by *endexine*. The foot layer can be distinguished from the endexine not only by staining difference, but also by electron density, which is different from that of the endexine.

foraminiferal test linings See *microforaminifera*.

forb A non-cultivated, dicotyledonous, herbaceous plant; an herb other than grass; a broad-leaved weed. The term appears in some palynologic literature dealing with Quaternary sediments.

forensic palynology The application of palynological methods to legal problems. Even paleopalynology has occasionally been used, for example, to pinpoint source of mud on a suspect's footwear. (See Bryant, *et al.*, 1996.)

"*fossiliferous"* This definitely includes all rocks that contain palynomorphs! However, I have found a number of examples in the literature that cite rocks containing plenty of palynomorphs as "non-fossiliferous," because they contained no *megafossils*.

fossulate Of *sculpture* of *pollen* and *spores* consisting of grooves that anastomose.

foveolate Means *pitted*; e.g., of *sculpture* of *pollen* and *spores* consisting of pits in the *ektexine* larger than 1 μm. See *scrobiculate, perforate.*

free operculum Part of a *dinoflagellate cyst* that is completely surrounded by *archeopyle* sutures, with no unsutured connection to the rest of the cyst. Syn. free opercular piece. See *attached operculum*.

fruit body Of fungi, a fructification, i.e. a spore-bearing organ. Chitinous fruit bodies occur as *palynomorphs*. Fossil fruit bodies characteristically lack *spores*. Microthyriaceous fruit bodies are more or less flattened and radially symmetrical. Syn. fruiting body.

fungal spore A *spore* of the usually multicellular, non-vascular, heterotrophic organisms belonging to kingdom Fungi. Such spores include a wide variety of types, from simple

unicellular to multicellular sclerotia; they have a range of Precambrian to Holocene. Those fungal spores preserved in sediments and surviving *maceration* are chitinous, and such fungal spores range primarily from late Jurassic to present. Examples: *basidiospore, chlamydospore, conidiospore*, *dictyospore, phragmospore, teleutospore* and *urediospore*.

Fungi Imperfecti Synonym for *Deuteromycetes* fungi, those presumably ascomycete fungi that have no known sexual stage, of which only asexual spores are produced.

furrow A *colpus* or *sulcus*.

galeate Of early Paleozoic acritarchs with a helmet-like detachable operculum usually missing from the large excystment structure.

gametophyte The sexual generation of a plant that produces gametes or an individual of this generation; e.g., the haploid generation of an embryophytic plant, produced by germination of the *spores*. In lower vascular plants and bryophytes, the gametophyte is a separate plant, but in seed plants, it is confined to the cells (several to many) of the *microgametophyte* in the *pollen grain* and multicellular *megagametophyte* in the ovule (the seed consists of the fertilized ovule and investing tissues). See *prothallus* and *sporophyte*.

Garside's rule Of angiosperm triaperturate, tetrad pollen, having the apertures formed in four groups of three, each group involving three of the tetrad 's grains. Example: some Proteaceae. Cf. *Fischer's rule.* See Fig. 5.8.

gemmate Of *sculpture* of *pollen* and *spores* consisting of more or less spherical projections (= gemma, pl. gemmae).

germinal Of *fungal spores*, a secondary opening in the *spore* wall at some point other than the primary or principal *pore* or *furrow*. The germinating plasm may emerge here rather than at primary pores. Often also used for porate pollen, especially for *Normapolles*, for both pore and *os* (*endopore*) and their associated structures.

germinal aperture An aperture (such as a *colpus, sulcus*, or *germ pore*) of a *pollen grain* through which the *pollen tube* emerges on germination of the grain. The term is sometimes used to include also the *laesura* of *spores* and *prepollen*.

germinal furrow A *colpus* or *sulcus*.

germ pore A membranous *pore* or thin area in the *exine* of a *pollen grain* through which the *pollen tube* emerges on germination. As ordinarily defined, a pore cannot have one dimension more than two times another dimension. Where one dimension is two times or more larger than another, the thin area is a *colpus* or *sulcus*.

girdle See *cingulum*.

gonal spine A spine situated only at *plate* corners on a *dinoflagellate cyst*.

grain Syn. of *pollen grain*.

granular Of tectate pollen in which the infratectal layer consists of very small granules rather than of columellae. Also used as a sculptural term essentially equivalent to *scabrate.*

gula A projecting, neck-like, rather ornate extension of the *trilete laesura* of certain fossil *megaspores*. Pl. gulae. See *trifolium*.

gulate Of *megaspores*, possessing a *gula*.

hamulate Of *sculpture* consisting of small, irregularly arranged hooks. The term is not widely used.

haplotabular archeopyle An apical *archeopyle* in a *dinoflagellate cyst*, consisting of a single *plate*.

haploxylonoid Of *bisaccate pollen*, in which the outline of the sacci in *distal-proximal* view is more or less continuous with the outline of the *body*, the *sacci* appearing more or less crescent-shaped in polar views, and the outline of the whole *grain* presenting a more or less smooth ellipsoidal form. See also *diploxylonoid*. (Both terms have been

used in other senses and are now best avoided. Pleistocene *palynologists,* for example, usually define haploxylonoid as having, and diploxylonoid as lacking, *verrucae* on the *distal* face or *cappula*.)

haptotypic character A feature of a *spore* or *pollen grain* that is a product of contact with other members of the *tetrad* in which it was formed; e.g., the *laesura* and *contact areas* of spores.

harmomegathus The membrane of a *pore, colpus, leptoma*, etc., (of a *pollen grain*) when it serves to accommodate, by expansion and contraction, changes in volume of the grain, which usually results from the taking up or loss of water. Pl. harmomegathi. Adj. harmomegathic. Noun, for the phenomenon of accommodation to moisture-content change, harmomegathy.

helicospore Of fungi, a coiled *conidium.*

herkomorph An acritarch with the surface divided by crests into polygonal fields.

heterobrochate A not much used term for *reticulate sculpture* in which the *lumina* (and their enclosing *muri*) are of different sizes. In some sculpture described as heterobrochate, there are small lumina or perforations in the surface of the muri that surround the first order lumina. See *homobrochate*.

heterocolpate Of *pollen grains* having *pores* in some *colpi*, not in others. This term is also used in other senses by some; e.g., for pollen with both colpi and (unassociated) pores.

heteropolar Of *pollen grains* and *spores* with marked difference between the two *poles*, as *monosulcate pollen* or *trilete spores*. See *isopolar*.

heterosporous Characterized by *heterospory*; specifically of plants that produce both *microspores* and *megaspores*. Also refers to dinoflagellate genera, the species of which produced several different cyst forms.

heterospory The condition in *embryophytic* plants in which *spores* are of two types: *microspores* and *megaspores*. See *homospory*.

high-spine Refers to pollen of Asteraceae (= Compositae), in which the spines of the echinate sculpture are over 3 μm long. Cf. *low-spine.*

hilate Of a *spore* or *pollen grain* possessing a *hilum*. Burgess and Richardson (1995) use the term only for *cryptospores*, but this is not a practical usage, because the term is in the literature in many other senses.

hilum An irregular *germinal aperture* of a *spore* or *pollen grain*, formed by the breakdown of the *exine* in the vicinity of one of the *poles*. The hilum in the spore *Vestispora* is associated with an *operculum* that may become separated from the spore.

holdfast Of fungi, a pad-like *process* from the hyphal body for attachment to substrate. When chitinous and dispersed, may mimic a *spore*.

holomorph Of ascomycete fungi, the entire organism in all its facets. Cf. anamorph, teleomorph, Fungi Imperfecti.

homobrochate A not much used term for *reticulate sculpture* in which the *lumina* (plus their enclosing *muri*) are of about the same size. See *heterobrochate*.

homospore One of the *spores* of an *embryophytic* plant which reproduces by *homospory*. Range is Silurian to Holocene. Syn. *isospore*. See *microspore*.

homosporous Characterized by *homospory*.

homospory The condition in *embryophytic* plants in which all *spores* produced are of the same kind; the production by various plants of *homospores*. Syn. *isospory*. See *heterospory*.

hypha Of fungi, an individual, septate or aseptate, filament that may be part of a *mycelium*.

hypnozygote Algal cell resulting from gamete fusion, often with a thick, *sculptured* wall. *Dinoflagellate cysts* and perhaps some *acritarchs* are probably *hypnozygotes*.

hypocyst The part of a *dinoflagellate cyst* posterior to the *cingulum*. See *epicyst*.

hyposome The posterior part of a *dinoflagellate*, below the *cingulum*. See *episome*.
hypotheca In a motile *dinoflagellate*, the portion of the *theca* posterior to the *cingulum*.
hypotract Syn. of *hypocyst*.
hystrichosphaerid A general term formerly used for a great variety of resistant-walled organic microfossils, ranging from Precambrian to Holocene, and characterized by spherical to ellipsoidal, usually more or less spinose remains found among fossil microplankton. These are now divided among the *acritarchs* and *dinoflagellate cysts*. The term has no formal taxonomic status. Syn. *hystrichosphere*.
hystrichosphere See *hystrichosphaerid*.
iatropalynology Study of *spores* and *pollen* as applied to human health problems, especially *pollinosis*. See *aerobiology*.
inaperturate Of *pollen* and *spores* having no *germinal, harmomegathic*, or other openings. See *acolpate* and *alete*.
infrasculpture The *structure* of *spores* and *pollen* consisting of organized internal modifications of *exine*. See *structure*.
infratectum Of pollen exines, the layer beneath the tectum, which may be variously alveolar, granular, amorphous, or columellate.
inner body In *dinoflagellates*, the *endoblast*. In *spores*, the preferred term for the separate, inner *exine* layer of, e.g., *camerate spores* See *endospore*.
in situ See *Sporae in situ.*
intectate Of an outer *exine* lacking a *tectum* but having *ektexinous* elements such as separated *bacula* that indicate *columellate structure*. Cf. *atectate*. (The difference between the two terms is not very useful.)
intercalary plate Of a *dinoflagellate*, a *plate* whose position lies between two major *plate series*.
intercolpium The area of a *colp(or)ate pollen exine* between the *colpi*, therefore delimited by the colpi and the *polar* areas. Syn. *mesocolpium*.
interloculum Laterally extensive space between the *sexine* and *nexine*. Term especially used for *Normapolles*. Interloculum connects with the *vestibulum*, if such is present.
interporium The area of a *porate pollen exine* delimited by lines tangential to the *pores*, and the pores themselves; thus a comparatively narrow band of *exine* as wide as the pores, extending from pore to pore. Syn. *mesoporium*.
interradial Pertaining to areas of the *proximal* face, or of the *amb* of *trilete spores*, lying between the arms of the *laesura*. Also sometimes applied to corresponding areas on the *distal* surface onto which the laesura can be conceptually projected. See *radial*.
intexine A less satisfactory syn. of *endexine*. Also spelled intextine.
intine The thin, inner layer of the two major layers forming the wall (*sporoderm*) of *spores* and *pollen*, composed of cellulose and pectates, and situated inside the *exine*, surrounding the living cytoplasm. The intine is not resistant to acetolysis and is therefore not present in pollen preparations made by that process. It is also not normally present in fossil *sporomorphs*. Syn. for spores *endospore*.
intratabular Of features of a *dinoflagellate cyst* that approximately correspond to the central parts of *thecal plates* rather than to the lines of separation between them. See *nontabular* and *peritabular*.
isopolar Of *pollen grains* with more or less radial symmetry and no marked difference between the two *poles*, as most *tricolpate pollen*. cf. *heteropolar.*
isopoll A line on a map connecting locations with samples having the same percentage or other measure of amount of *pollen* of a given kind. Syn. isopollen (not much used).
isospore A *spore* of plants such as bryophytes, producing only one kind of spore. Syn. *homospore*.
isospory The quality or state of having or producing *isospores*. Syn. *homospory*.

jaw Of *scolecodonts*, syn. for jaw piece, jaw plate, an individual major element of maxillary apparatus.

Kofoid tabulation system Of dinoflagellates, the most used method for description of the number and arrangement of the plates.

kyrtome A more or less arcuate fold or band in the *interradial* area outside the *laesura* of a *trilete spore*. Some *palynologists* prefer to use *torus* for separate interradial bands, and kyrtome for a connected figure. A wide variety of other terms are used for modifications of the borders of laesurae. See *torus*, *labrum*, and *margo*.

labrum Lip-like thickening of the edges of a *laesura*. Pl. labra. See *kyrtome*, *torus*, and *margo*.

lacuna A rarely used term for a depressed space, pit, or hole on the outer surface of a pollen grain.

laesura The trace or scar on the *proximal* face of an *embryophytic spore*, that marks the original contact with other members of the *tetrad*. It may be *trilete*, *monolete*, or rarely *dilete*. Pl. laesurae. (Note: Some palynologists speak of each ray of the trilete laesura as "a laesura". In this usage, a trilete spore has three laesurae. Despite the history of the term, which supports this usage, I find it confusing and think it should be avoided.) See *suture, tetrad scar*, and *Y-mark*.

laevigate Syn. of *psilate*. The term is more often applied to *spores* than to *pollen*.

lalongate Of pollen, refers to apertures that are laterally (transversely) elongated. cf. *lolongate*

lateral tooth Of *scolecodonts*, a slender element usually formed by a simple single large *denticle*, placed immediately in front of any or all of the regular *jaws* of an apparatus.

leiosphaerid A thin-walled, more or less spherical body of probable algal relationship, lacking processes, *septa*, etc., characterized by the genus *Leiosphaeridia*, and usually referred to the *acritarchs*. Mostly Ordovician to Silurian in age.

leiosphere Syn. of *leiosphaerid*.

leptoma A thin region of *exine* situated at the *distal pole* of a *pollen grain* and usually functioning as the point of emergence of the *pollen tube*. For bisaccate pollen, this is an alternate term for *cappula.* Example of use for non-bisaccate gymnosperm pollen: *Classopollis*, for which tenuitas is also used. See also *pseudopore, tenuitas*, and *cappula.*

limb Syn. of *amb* or *equatorial limb*.

limbus A crease at the edge of the *saccus* or *pseudosaccus* where outer and inner *exine* layers are more or less fused.

linotolypidae Thread like, sometimes webbed, pseudofossils of uncertain origin, sometimes occurring in palynological preparations. See also *cenospheres*.

lip The *labrum*.

liptinite Coal petrologic term for macerals derived from spores, pollen, leaf cuticles and related plant matter. cf. *vitrinite, sporinite.*

LO analysis From Latin *lux-obscurus* (= light-dark), a microscopic technique depending on projecting elements appearing bright in high focus, dark in low focus, whereas holes appear dark in high focus, etc.

lolongate Of pollen, referring to apertures that are longitudinally elongated, i.e. in the opposite direction of *lalongate* apertures, which are elongated parallel to the equator of the grain.

Longaxones A group of primitive, usually lightly *sculptured*, *tricolpate*, lower Cretaceous and younger angiosperm *pollen*, in which the *polar* axis is as long as, or longer than, the *equatorial* diameter. See *Brevaxones*.

longitudinal flagellum A thread-shaped flagellum in a *dinoflagellate*, trailing after the *body* and arising from the posterior *pore* in the *sulcus*. This flagellum propels the organism.

low-spine Refers to echinate pollen of the Asteraceae (= Compositae) in which the spines are less than 3 μm long.

lumina (singular form *lumen)* The depressions or open spaces between *muri* of *positive reticulate sculpture*, and similar depressions. See *muri*.

maceration The act or process of disintegrating sedimentary rocks by various chemical and physical techniques, in order to extract and concentrate acid-insoluble microfossils (including *palynomorphs*) from them. It includes mainly chemical treatment by halogen acids, oxidants, and alkalis and use of other separating techniques that will remove extraneous mineral and organic constituents.

macrospore Unsatisfactory syn. of *megaspore* in the botanical sense, antonym for *miospore* in the proposal of Guennel (1952), in which sense it is all pollen and spores larger than 200 μm.

magnoliid Certain basal angiosperms that do not produce tricolpate pollen, or any sort of pollen derived from that form. Cf. *eudicot.*

main body Of *dinoflagellates*, the *central body*.

mandible Of *scolecodont***s**, a single fixed pair of *jaw* pieces on the ventral side (not in the pharynx) of the animal, with long posterior shafts, often with an anterior calcareous cap. The mandibles are non-eversible (cannot be everted).

marginate chorate cyst A *dinoflagellate chorate cyst*, whose outgrowths are characteristically localized on the lateral margins, leaving the dorsal and more often the ventral surfaces free of outgrowths.

margo (a) Modified margin of the *colpus, sulcus* or *pore* of a *pollen grain*, consisting of a thickening or (less commonly) thinning of the *exine*. See **s** *annulus*. (b) A term sometimes used for marginal features associated with the *laesura* of *spores*. See *krytome* and *labrum*.

marine influence An expression for the proportion of a *palynoflora* composed of *palynomorphs* of marine origin. Abbrev. MI.

massula (a) A more or less irregular, coherent mass of many fused *pollen grains* shed from the anther as a unit. See *pollinium*. (b) A term sometimes applied to a structure associated with the *laesura* and the attached non-functional spores of certain *megaspores*. Pl. massulae.

maxilla Of *scolecodonts*, any major *jaw* piece of the mouth located in the pharynx. From posterior to anterior they are numbered MI, MII, etc.

MCT Of angiosperm pollen, those that are *monosulcate* with *columellate-tectate* exines. Term used by Hughes (1994) because of the prevalence of this sort of pollen in early angiosperms.

megafossil A fossil that can be studied for identification purposes at magnification of less than 10x. Cf. *mesofossil, microfossil.*

megagametophyte The female *gametophyte* or haploid generation that develops from the *megaspore* of a *heterosporous* embryophytic plant. In lower vascular plants, it is a small free-living plant bearing archegonia, but in seed plants it (e.g., embryo sac of angiosperms) is contained within the ovule, and the egg is produced in it. The embryo which develops from fertilization of the egg plus other gametophytic products and the enveloping tissues of the ovule comprise the seed. See *microgametophyte*.

megasporangium A *sporangium* that develops or bears *megaspores*.

megaspore One of the *spores* of a *heterosporous embryophytic* plant that germinates to produce a *megagametophyte* (multicellular female *gametophyte*). It is ordinarily larger than the *microspore*. Range mid-Devonian to Holocene. Free megaspores were common in the late Paleozoic but are produced only by a few genera of pteridophytes today. Unsatisfactory synonym, *macrospore*, which is antonym of *miospore*.

melitopalynology The study of *pollen* in honey and in connection with apiculture generally. Syn. *Melissopalynology.*

membranate chorate cyst A *dinoflagellate chorate cyst* with a prominent membrane; e.g., *Membranilarnacia*.

meridional Of pollen, features that that cross the equator along lines perpendicular to it.

meso- Of *dinoflagellate cysts*, the middle, as in mesophragm, middle wall.

mesocolpium, mesoporium (The "mesocolpus" and "mesoporus" of some authors.) Erdtmanian terms equivalent to *intercolpium* and *interporium.*

mesofossil A term sometimes applied only to paleobotanical material, for fossils larger than *miospores*, yet still requiring microscopy at more than 10x magnification, such as megaspores, small seeds, flowers, pieces of cuticle, etc. However, the term would be better applied to a size range of fossils than to their belonging to any particular systematic group. cf. *miospore, megafossil.*

Mesophytic An informal division of geologic time, extending from the coming to dominance of coniferophytes, ginkgophytes, cycadophytes, and other gymnosperms in mid-Permian time, to the *Cenophytic*.

MI Abbreviation for *marine influence*.

micro- A combining form used with *sculpture*, the elements of which are too small (less than 1 μm) for Faegri and Iversen's (1989) terms to apply: *micropitted*, etc.

microflora An unsatisfactory syn. of *palynoflora*. The term is properly applied to an assemblage of microscopic organisms, such as the bacteria of an animal gut.

microforaminifera The chitinous inner tests (test linings) of certain, almost always spiral foraminifers, frequently found in palynologic preparations of marine sediments, and generally much smaller than "normal" whole foraminifers, but displaying recognizable characteristics of "normal" species. The proposal of the formal group name "*Scytinascia"* for these linings should be ignored. The linings are parts of perfectly normal foraminifera, not a separate group of organisms. For more details, see Stancliffe (1996).

microfossil A fossil that must be studied at a magnification of more than 100x. (cf. Traverse *et al.*, 2004) cf. *mesofossil, megafossil.*

microgametophyte The male *gametophyte* or haploid generation that develops from the *microspore* of a *heterosporous* embryophytic plant. In lower vascular plants, a multicellular microgametophyte, as well as the sperm cells, develop within the microspore wall; in seed plants, the microgametophyte plus the surrounding microspore wall is the *pollen grain*, in which the microgametophyte is further reduced, being only 3-nucleate in the angiosperms. See *megagametophyte*.

micropitted sculpture with "holes" in the *exine* less than 1 μm. Synonymous with *foveolate.*

microplankton In *paleopalynology*, a term often used collectively for *acritarchs* and *dinoflagellate cysts*, to distinguish them from *spores* and *pollen*.

microreticulate Having *reticulate sculpture* in which the *muri* are so tiny that they can only be observed at high magnifications under oil.

microsporangium A *sporangium* that develops or bears *microspores*; e.g., the anther in an angiosperm or the *pollen sac* in all other seed plants. See *megasporangium.*

microspore One of the *spores* of a *heterosporous embryophytic* plant that germinates to produce a *microgametophyte* (male *gametophyte*). Ordinarily smaller than the *megaspore* of the same species. In seed plants, *pollen grains* consist of a *microspore* wall or *exine* with a *microgametophyte* contained inside. See also *miospore*. "Microspore" should never be used as a general term for "small spore!" Use of "microspore" means that an author is sure the producing plants were heterosporous, not *homosporous*. Most Mesozoic and Cenozoic ferns, for example, produced homospores, not microspores. When in doubt, say miospore!

miospore A term arbitrarily defined in *paleopalynology* (per Guennel, 1952) as a *spore* or *pollen grain* less than 200 μm in diameter, regardless of biological function. The word is unfortunately pronounced the same as meiospore, a cell stage in meiosis. If "miospore" is used, all spores or pollen grains greater than 200 μm in diameter are called *macrospores*, regardless of biological function. See *macrospore*, *megaspore*, *microspore*, and *small spore*.

monad Term used to describe single *sporopolleninous*- walled units, in contrast to *dyads, tetrads*, and *polyads*. Term is especially useful in studies of Silurian rocks, where all of the above-mentioned types occur, and it is desired to use the non-committal monad rather than *spore* or *acritarch*.

monocolpate Of *pollen grains* having a single, normally *distal colpus*. *Monosulcate* is preferred in most instances. Code Pa0.

monolete Of an *embryophytic spore* having a *laesura* consisting of a single unbranched line or mark. See *trilete*. Code Sa0.

monoporate Of *pollen grains* provided with a single *pore*, as in grasses.

monosaccate Of *pollen* with a single *saccus*, usually extending all around the *pollen grain* more or less at the *equator*. The monosaccate and *bisaccate* conditions are not sharply distinct. Many grains that appear bisaccate in one view can be shown to be actually monosaccate. Code Pv1.

monosulcate A term essentially equivalent to *monocolpate* in ordinary usage. Because the *germinal furrow* in such cases is practically always a *sulcus*, this is the preferred term. Code Pa0.

morphon As defined by Van der Zwan (1979), a group of palynological species (form-species) united by continuous variation of morphological characteristics. Others use the term "complex" in a very similar way. See also *palynodeme*.

morphotaxon (morphogenus, morphospecies) These terms refer to the concept that fossil plant taxa for isolated parts such as spores and pollen, are not taxa of whole plants, but are taxa referring only to the parts represented by the nomenclatural type. Thus, *Classopollis* is not a genus of gymnospermous plants, but a morphogenus of fossil pollen that we know to have been produced by a family of gymnospermous trees and/or shrubs. See discussion of nomenclature at the end of Chapter 19 in this book.

mother cell A cell from which new cells are formed; e.g., *spore mother cell* and *pollen mother cell*.

mouth Of *chitinozoans*, the opening at the *oral pole* (see Fig. 6.11).

mucron Of *chitinozoans*, the nipple-like extension at the center of the base of some species. Both mucron and *copula* apparently have to do with the linkage of chitinozoal units into chains.

multisaccate Of *pollen* with more than two *vesicles*. Code Pv3, etc.

murus, usually used in plural form, *muri.* The more or less vertical walls which form positive *reticulate sculpture* in *pollen* and *spores*. Also the ridges that separate the grooves of striate and rugulate sculpture. See *lumina*.

mycelium The tissue of the vegetative structure (*thallus*) of a fungus, consisting of *hyphae*.

nannofossil Very small (mostly 5 μm or less) calcareous fossils, by definition not *palynomorphs*. The term is usually restricted to platelets of the walls of Coccolithophoridae, marine single-celled green algae (platelets are called coccoliths and discoasters). The term is unfortunately used by a few writers for all tiny fossils, including, e.g., *acritarchs* and *cryptarchs*. Sometimes spelled *nanofossil*.

NAP Abbrev. for *non-arboreal pollen*. Synonym: *NTP*.

neck Of *chitinozoans*, the narrowed region between *collar* and main *body*.

negative sculpture A term for *sculpture* engraved into rather than standing upon the outer surface of the *exine*; e.g., negative *reticulum*.

netromorph Of acritarchs with an elongate to fusiform shape. May have processes at poles. Examples: *Dactylofusa, Leiofusa.*

nexine The inner layer of the *exine* of *pollen* in Erdtman's scheme. The nexine is purely "geographic" in definition: the lower unsculptured part of the exine. See *endexine*.

non-arboreal (*non-arborescent*) *pollen* The *pollen* of herbs and shrubs. Abbrev. *NAP*. Syn. *non-tree pollen*.

non-tabular Of projecting surface features of a *dinoflagellate cyst* that are neither sutural nor *intratabular* and that have a random arrangement, or show no apparent relation to a tabulate scheme. See *peritabular*.

non-tree pollen Syn. of *non-arboreal pollen*. Abbrev. *NTP*.

Normapolles A group of Cretaceous and lower Paleogene *porate* (usually *triporate*) *pollen* with a complex *pore* apparatus (e.g., *oculus*) and sometimes other peculiarities such as double *Y marks*. See *Postnormapolles*.

NTP Abbrev. for *non-tree pollen*. See *non-arboreal pollen*.

oblate Of *pollen*, flattened (foreshortened) along the *polar* axis; e.g., *pollen*, whose *equatorial* diameter is much longer than the dimension from *pole* to pole. Ant. *prolate*.

obligate Of *tetrads* or *polyads* of *spores* or *pollen*, meaning that such union is typical for the taxonomic unit. Usually this is interpreted to mean that more than 50% of the specimens of the taxon found are so united, not broken up. This condition is sometimes termed "permanent."

oculate A group designation (Oculata) for *Wodehouseia* and similar Cretaceous *pollen*.

oculus A much-enlarged part of the *pore* structure of (usually *triporate*) *pollen*, consisting of a bulging, very thick protrusion of *ektexine*. Pl.oculi.

operculate Having an *operculum*; e.g., of *dinoflagellates*, possessing an *archeopyle* associated with an operculum, or of a *pollen grain* having *pore* membranes with an *operculum*.

operculum (a) A lid consisting of the *plate* or plates that originally filled the *archeopyle* of a *dinoflagellate cyst* or the *pylome* of an *acritarch*. Also, the lid-like closure of the *mouth* of a *chitinozoan*. (b) A thicker central part of a *pore* membrane of a *pollen grain*, or a large section or cap of *exine* completely surrounded by a single *colpus*. For certain *hilate* spores and *pollen*, the operculum is a less well-defined lid of exine associated with the formation of the *hilum*.

ora Pl. of *os*.

oral pole That end of a flask-shaped *chitinozoan* that includes the *neck* and the *mouth*. See *aboral pole*. Cf. *apertural pole*, *antapertural pole.*

oral tube Of chitinozoans, the more of less constricted portion of the *vesicle*, toward the *oral* or *apertural pole*, including the *aperture* or *mouth*, the *collarette*, and the *neck*.

orate Of a *porate pollen grain* having an internal opening (*endopore* or *os*) in the *endexine*.

orbicle Alt. spelling for *orbicule*. See *ubisch bodies*.

orbicule See *ubisch bodies,* the term I prefer, mostly because I find it easier to recall. It also has the advantage that it is not likely ever be used in another sense.

ornament, ornamentation Less satisfactory syn. of *sculpture*. Modifications in the exines of pollen grains or in the outer walls of other palynomorphs do not have a decorative function, as far as we know.

ornithophily A term for *pollination* by birds (mostly hummingbirds).

os Syn. for *endopore*, an inner *aperture* of a complex structure. Pl. *ora*.

ostiole Of fungi, the opening in the *neck* of a flask-shaped *fruit body*, or a rounded opening in any fruit body, through which the *spores* are released.

paleopalynology A division of palynology concerned with the study of a wide range of fossil microscopic, usually organic bodies, in addition to spores and pollen: animal remains such as *chitinozoans*, as well as *fungal spores*, *dinoflagellates*, *acritarchs*, and

other organisms resistant to acids and found in sedimentary rocks of all ages (*nannofossils* and *diatoms* should therefore not be included). The usual criteria for inclusion are that the bodies be microscopic in size (from about 5 μm to about 500 μm) and composed of a resistant organic substance (usually *sporopollenin, chitin*, or *pseudochitin*), resulting in the bodies being preserved in sedimentary rocks and available for separation by *maceration* from such rocks. The subject includes a rich panoply of applications of the subject to various scientific subjects, including evolutionary studies, stratigraphy, climatology, paleoecology, and even forensics.

Paleophytic An informal division of geologic time, extending from the first appearance of land plant *spores* (Ordovician) to the beginning of the *Mesophytic*.

palyniferous Literally, bearing *pollen*. The term in *palynology* usually refers, however, to rocks or sediment samples that yield pollen, *spores*, or other *palynomorphs* on *maceration*.

palynodebris The *palynomorph*-size particles, other than palynomorphs, in a sediment, as wood fragments, leaf cuticles, etc. See *phytoclast, palynofacies.*

palynodeme An expression for a group of *palynomorph* species that intergrade and probably represent "... the palynological reflection of a known or hypothetical plant species" (Visscher, 1971). As originally used, the concept was phylogenetic and referred to characters changing in time. In practice, the term is used by many as if synonymous with *morphon* or the less formal term, "complex."

palynofacies (a) the assemblage of *palynomorph* taxa in a portion of a sediment, a *palynoflora* representing local environmental conditions and not typical of the regional palynoflora; or (b) the total assemblage of *palynodebris* and *palynomorphs* found in a certain kind of sediment, and characterizing that sediment and its environment of deposition.

palynoflora The whole suite of plant-derived *palynomorphs* from a given rock unit. The term *microflora* is sometimes used as a synonym, but should be avoided as it specifically applies to assemblages of extant microscopic algae, fungi, and bacteria. As palynomorphs do not really constitute a "flora,"–many non-plant items are included– a term such as "palynomorph assemblage" is better, when non-botanical forms are included. *Palynoflorule* refers to the plant-derived palynomorph assemblage from a single sample or level.

palynology Originally, the study of pollen and spores, extant and fossil, including stratigraphic and paleoecological applications. Now includes study of a wide range of other robust-walled, microscopic remains of various plants, animals, fungi and protists. Term suggested by Hyde and Williams (1944). Etymol.: Greek παλυνω, "to strew or sprinkle", suggestive of παλη, "fine meal" cognate with Latin pollen, "fine flour, dust". See also *paleopalynology* and *pollen analysis*.

palynomorph A microscopic, resistant-walled organic body found in palynologic *maceration* residues; a palynologic study-object. Palynomorphs include *pollen*, *spores* of many sorts, *acritarchs, dinoflagellate thecae* and *cysts*, certain colonial algae, *scolecodonts, chitinozoans* and other acid-insoluble microfossils. See *sporomorph*.

palynostratigraphy The stratigraphic application of palynologic methods.

panto- (or pan-) A prefix indicating distribution spread over the whole surface, a synonym preferred by many for the prefix *peri-* used in this book.

pantocolpate, pantoporate See *pericolpate* and *periporate*.

papillate Of sculpture, parallel sided exinous elements with rounded tips, less than 1 μm in length. *papillate* sculptural elements are a subset of *scabrate*, q. v.

PAR Abbrev. for *pollen accumulation rate*. See *pollen influx.*

para- In *dinoflagellate* studies, a prefix sometimes assigned to *thecal* terms when these are applied to *cysts*, e.g., paracingulum, paratabulation, paraplate, etc.

patina A thickening of the *exine* of *spores* that extends over approximately half of the surface, i.e., over the entire surface of one hemisphere. Adj. patinate.

PDR Abbrev. for *pollen deposition rate*. See *pollen influx*.

perforate Of pollen, sculpture consisting of holes less than 1 μm. See *foveolate*.

peri- Of *dinoflagellate cysts*, means outer, as *periphragm*, outer wall. However, if the outermost wall has supporting structures, that wall is an *ectophragm.* If there are no supporting structures, it is a *periphragm.*

pericoel The space between the *periphragm* and *endophragm* in a *cavate dinoflagellate cyst*. See *endocoel*.

pericolpate Of *pollen grains* having more than three *colpi*, not meridionally arranged (see *stephanocolpate*). In Erdtman's terms, this is called *polyrugate*. Code Px0. Syn. *pantocolpate*. (However, pantocolpate means the colpi are "evenly distributed", and pericolpate is not so restricted.)

pericolporate Of *pollen grains* having more than three *colpi*, not meridionally arranged, with at least part of the colpi provided with *pores* or *transverse furrows*. Code Pxx.

pericyst Of more or less *cavate dinoflagellate cysts*, the separate outer body, of which the *periphragm* comprises the wall.

perine Syn. for *perinium* and *perisporium.*

perinium A sometimes present, more or less sculptured outer coat of a *pollen grain*. Pl. perinia. Adj. perinate. See *perisporium*.

periphragm The outer layer of a *dinoflagellate cyst*, usually carrying extensions in the form of spines, and projecting to the position of former thecal wall. It may have served as a support during the period of cyst formation. See *ectophragm* and *endophragm*.

periporate Of *pollen grains* having many *pores* scattered over the surface. In Erdtman terminology, when there are more than 12 pores, the term is *polyforate*. Code P0x. Syn. *polyporate* and *pantoporate*. (Pantoporate means that the pores are "evenly distributed", whereas periporate is not so restricted. Polyporate is a less favored equivalent of periporate, both meaning more than three pores, not more or less on the *equator*, and either evenly or irregularly spaced.)

perispore Syn. for *perisporium*.

perisporium An additional wall layer external to the *exine* in certain *spores* and *pollen*. It is composed of thin and loosely attached *sporopollenin* and is therefore not usually encountered in dispersed fossil *sporomorphs*. Syn. *perine, perinium*, and *perispore*.

peritabular Of the surface features of a *dinoflagellate cyst* that originate immediately interior to the margins of reflected *plate* areas (as in *Areoligera* and *Eisenackia*). See *intratabular* and *non-tabular*.

peroblate Of the shape of a *spore* or *pollen grain*, having the *pole*-to-pole axis very much shortened, producing a discus-like shape. See *oblate* and *prolate*.

perprolate Of the shape of a *spore* or *pollen grain*, having the *pole*-to-pole axis very much elongated, producing a cigar-like shape. See *prolate* and *oblate*.

-phragm Of *dinoflagellate cysts*, wall, as *autophragm*, single wall. As a synonym for wall, it is written *phragma*.

phragmospore Of fungi, a *spore* having two or more transverse septa.

phycoma a cyst-like, sporopolleninous-walled body produced by marine prasinophytes. Unlike a cyst, a phycoma can grow during its existence and produces multiple flagellate cells. Pl. *phycomata.* Example: *Tasmanites.*

phytoclast Plant-derived, more or less resistant-walled particles in a sediment, including *palynomorphs*, cuticular and wood fragments, etc. See *palynodebris*.

PI Abbrev. for *pollen influx*. More or less the same as *PDR* and *PAR*.

pila Pl. of *pilum*.

pilate Of *spores* and *pollen* having *sculpture* that is similar to that of *clavate* forms but that consists of smaller hair-like *processes (pila)* with more or less spherical terminal knobs. Syn. *piliferous*.

piliferous Bearing or producing hairs; e.g., said of *pollen grains* bearing *pila*. The synonymous term *pilate* is preferred by some *palynologists*.

pilum One of the small, spine-like rods comprising *sculpture* of the *exine* of certain *pollen* and *spores*. The rodlets are characterized by rounded or swollen knob-like ends. Pl. *pila*. See *clavate*.

pitted Syn. of *foveolate*.

plate Of *dinoflagellates*, the individual elements of the thecal wall numbered in Kofoid or Taylor systems. The corresponding *plates* of the *cyst* are sometimes called paraplates. Of *scolecodonts*, an alternative term for *jaw*.

plate equivalent Of the part of the *dinoflagellate cyst wall* judged to occupy a position equivalent to that occupied by a certain *plate* of the corresponding *theca*. See *para-*.

plate formula In *dinoflagellate* studies, a numerical expression for the arrangement and number of *plates*. There are several schemes for such enumeration, of which the most popular is Kofoid's (1907).

plica One of the ridge-like folds comprising most of the surface *exine* of *Ephedra* and some other fossil *pollen*. Also thickened fold-like area in the exine of certain *pollen grains*; in *Normapolles*, usually Y-shaped, centered over the *pole*. Adj. plicate.

polar area The part of a *pollen grain* poleward from the ends of the *colpi* and their associated structures. Syn. *apocolpium*.

polar area index The ratio between the diameter of the *polar area* of a *pollen grain* and the diameter of the grain.

polar limb A seldom used term to express the outline of a *pollen grain* as observed laterally (equatorially). Syn. *profile*. See *amb*.

polar view The view of a *spore* or *pollen grain* from directly above one of the *poles*. See also *amb*.

pole Either termination of the axis of a *pollen grain* or *spore* running from the center of the original *tetrad* to the center of the *distal* side of the grain; hence, the center of both distal and *proximal* surfaces. The term is especially useful for angiosperm pollen grains such as *tricolpate*, in which it is not apparent which is the proximal and which the distal surface. Also of *chitinozoans*, the two ends of a chitinozoal unit. See *aboral pole* and *oral pole*.

pollen The several-celled *microgametophyte* of seed plants, enclosed in the *microspore* wall. Fossil pollen consists entirely of the microspore wall or *exine*, from which the microgametophyte and *intine* were removed during or before lithification. The term "pollen" is a collective plural noun, and it is incorrect to say "a pollen"; the correct singular form is "a pollen grain"; the correct plural is "pollen," not "pollens." Examples: Correct: The pollen of all sections of family Poaceae is monoporate. Incorrect: The pollens of euphorbiaceous plants are eurypalynous.

pollen accumulation rate Syn. for *pollen influx*, preferred by many.

pollen analysis (a) A branch of *palynology* dealing with the study of Quaternary (especially late Pleistocene and Holocene) sediments by employing *pollen diagrams, isopoll* maps, and other graphic displays to show the relative abundance of various *pollen* types in space and time; e.g., the identification and calculation of frequency of *pollen grains* of forest trees in peat bogs and lake beds as a means of reconstructing past plant communities and vegetation, thus of paleoclimates. It is used as a geochronologic and paleoecologic tool, sometimes in collaboration with archeology. The former application to dating is mostly superseded by radiocarbon and other absolute methods. Syn. pollen

statistics. (b) A term used prior to the acceptance of the expression *palynology*, in a manner very similar to the present use of that word.

pollen deposition rate Syn. for *pollen influx*.

pollen diagram Any diagram of *pollen* abundance showing the fluctuations in time of concentration of various pollen types, as revealed from studies of cores and other samples of sediment; strictly, the graphical presentation of abundances of various genera of pollen and *spores* at successive levels of cores of late Neogene sediment studied in *pollen analysis*. (The expression is rarely used for studies of older rock.) Syn. *pollen profile*.

pollen grain Singular form for *pollen*.

pollen influx A mathematical expression for the amount of *pollen* (and/or *spores*, or other *palynomorphs*, as specified) sedimented/accumulated/deposited per year, per square centimeter, of a surface of deposition. In effect, pollen concentration per weight or volume is corrected for the rate of sedimentation to produce pollen influx. Syn. *pollen accumulation rate* and *pollen deposition rate*.

pollen mother cell A *mother cell* in the *pollen sac* of a seed plant giving rise by meiosis to four cells, each of which develops into a *pollen grain*. See also *spore mother cell*.

pollen profile A vertical section of an organic deposit (such as a peat bog) showing the sequence of buried or fossil pollen (essentially synonymous with *pollen diagram*). *Profile* is also used for the outline of a *pollen grain* or *spore* as seen in *lateral* (= *equatorial*) view.

pollen rain The total deposit of *spores* and *pollen* in a given area and period of time, as estimated by study of sediment samples and by pollen-trapping devices.

pollen sac One of the pouch-like organs of a seed plant, containing the *pollen*; e.g., each of the pollen chambers in the anther of an angiosperm.

pollen spectrum A horizontal line in a *pollen diagram*, showing the relative abundances (percentages) of the various sorts of *pollen* and *spores* in a single sample from a single given level.

pollen statistics Syn. for *pollen analysis*.

pollen sum A portion of the total *pollen* count (in *pollen analysis*), from which certain sorts of pollen are excluded by definition, and which is used as the denominator for calculation of percentages. The most usual pollen sum excludes all *non-arborescent pollen* and sometimes *arborescent pollen* likely to be over-represented as well. Where pollen sums are used, pollen abundances are calculated as ratios of given sorts of pollen to the pollen sum, rather than as percentages of total count.

pollen symbol An arbitrary sign formerly much used in Quaternary *pollen diagrams*, representing a genus or other group of plants, and serving as an internationally understood identification for a line in the pollen diagram (see Erdtman, 1943).

pollen tube A more or less cylindric extension that emerges from the wall of a *pollen grain* and protrudes through one of its apertures when the grain germinates on contact with the stigmatic surface of flowering plants or the *megasporangium* of gymnosperms. The tube acts primarily as a haustorial (absorptive) organ to nourish the *microgametophyte* in lower seed plants (such as cycads), but in flowering plants it also conducts the male nuclei to the vicinity of the female *gametophyte* (embryo sac) to effect fertilization.

Pollenifera A term introduced by Hughes (1994) for the plants that produce pollen, starting with prepollen in the latest Devonian. The term is practically synonymous with Spermatophyta, plants that produce seeds, but puts the emphasis on the development of the microspore into pollen instead of on the development of the megaspore into a seed.

pollenkitt A viscous complex lipid derived from the *tapetum*, which when occurring on the surface of animal-pollinated angiosperm *pollen* helps the pollen adhere to an animal *pollination*-vector.

pollination In general, the fertilization of a seed plant; specifically the transfer of *pollen* from a stamen (anther) or *microsporangium* to an ovule or *megasporangium*.

pollinium A large, coherent mass of *pollen*, usually the contents of a whole locule of an anther, shed in the mature stage as a unit (as in *Asclepias*). Pl: pollinia. Code: Ppd (not distinguished from polyad). See *polyad* and *massula.*

pollinosis The allergenic disease caused in some persons by adverse reaction to *spores* and *pollen* in the air. Syn. "hay fever". Subject matter of *iatropalynology*. One of the practical applications of *aerobiology* has to do with investigation and alleviation of this disease.

polster A small cushion of plant material topped by layers of moss and/or lichen in which silt, sand and *palynomorphs* are frequently trapped.

polyad A group of more than four mature *pollen grains* shed from the anther as a unit (as in *Acacia*). The number of grains within the polyad is usually a multiple of 4. Code Ppd. See *pollinium, dyad*, and *tetrad*).

polyannulate Refers especially to *germinal* structures of *Normapolles*, in which the *sexine* of the outer *germinal* has multiple layers of thickenings.

polyforate See *periporate*.

polygonomorph Of acritarchs, having a polygonal outline and simple processes.

polymorphic (*dimorphic*, etc.) Having *pollen* regularly of more than one size and/or morphological type, presumably as an anti-self-pollination device. The Rubiaceae are especially characterized by this phenomenon.

polyplicate Of *pollen grains* (such as those of *Ephedra*) with multiple, longitudinal, linear thinnings in the *exine* that resemble, but are not, *colpi*. Code. Ppl. See *plica*, *taeniate*, and *striate*.

polyporate See *periporate*.

polyrugate See *pericolpate*.

porate Of *pollen grains* having a *pore* or pores in the *exine*.

pore (a) One of the external, more or less circular or slightly oval thinnings or openings in the *exine* of *pollen grains*, having dimensions in ratios of less than 2:1. Pores may occur by themselves or in association with *colpi*. See *colpus*. See also *germ pore*. (b) In fungi, a primary, structural rounded opening in the *spore* wall. Some "pores" in fungi occur at the point of attachment of the spore, or they may be terminal or otherwise disposed.

pore canal An elongated opening in *porate pollen* such as *Normapolles*, connecting the *pore* proper to the openings beneath, such as *atrium* and *vestibulum*.

pororate Of *pollen grains* with complex *pore* structures having both external (pore) and internal (*os*) openings.

positive sculpture A term for *sculpture* consisting of elements projecting from the surface, such as *scabrae, muri, spines*, etc. See *negative sculpture*.

postcingular series The series of *plates* immediately below the *cingulum* of *dinoflagellate thecae*, usually fewer in number and often larger in size than those of the *precingular series*.

Postnormapolles A group of Cretaceous-Cenozoic (usually *triporate*) *pollen* without the usual *pore* apparatus or other features of the *Normapolles* group, from which it presumably derived.

prasinophyte Primarily marine green algae, with motile cells having flagella with scales and a non-motile stage that produces highly resistant *phycomata*. See *phycoma*, *sphaeromorph.*, *pteromorph, ala.*

precingular archeopyle An *archeopyle* formed in a *dinoflagellate cyst* by loss of the middorsal *plate* of the *precingular series*.

precingular series The series of *plates* between the *apical series* and the *cingulum* in *dinoflagellate thecae*. See *postcingular series*.

prepollen Functional *pollen grains* that have haptotypic characters like those of *spores*, e.g., a *trilete mark*, and germinate *proximally* for release of fertilizing nuclei, presumably in anterozoids–thus zoidogamy. It seems probable that some fossil prepollen also had a *sulcus* from which a primitive pollen tube for haustorial purposes emerged. Prepollen is typical of certain extinct primitive gymnosperms (mostly Mississippian to Permian), but the extant modern gymnosperms, *Ginkgo* and cycads, also can be argued to have prepollen: germinating proximally for delivery of nuclear material, and distally to produce a haustorial pollen tube. Others would exclude these modern from the category because they lack proximal laesurae. See discussion in Visscher (1997).

prismatomorph Of acritarchs with prismatic to polygonal shape, with more or less sharp edges that may be extended into a flange, entire or serrate, with or without processes at the angles. Example: *Polyedryxium.*

process A longish element extending from the surface of a *spore, pollen grain, dinoflagellate cyst* or *acritarch*. They are much longer than ordinary sculptural elements such as *spines*. Some have suggested a fixed limit such as 5 μm for minimum length of *processes* (shorter elements would be sculptural), but this has not been widely adapted.

profile See also *pollen profile*. Sometimes used term for the outline of a *spore* or *pollen grain* as seen in *lateral* (= *equatorial*) view.

prolate Extended or elongated in the direction of a line joining the *poles*; e.g., "prolate pollen" whose *equatorial* diameters are much shorter than the dimensions from pole to pole. Ant. *oblate*.

prosome Of *chitinozoans*, an enigmatic, sometimes complex internal layer extending for some distance from the *neck* downward, either as a sort of plug or as an annulate tube.

Proterophytic An informal division of geologic time, from the first regular appearance of robust-walled *acritarchs* (about 1.0×10^9 years ago) to the first appearance of *spore*-like bodies (= cryptospores) (beginning of the *Paleophytic*, about 440×10^6 Ma. This definition from the first edition of *Paleopalynology* needs now to be revised downwards, at least to Mid-Ordovician, at about 480×10^6 Ma).

prothallus The *gametophyte* of a fern or other pteridophyte; usually a flattened, thallus-like structure living on the soil. Pl. prothalli. Syn. prothallium.

protosaccate Extinct form of *saccate* gymnosperm *pollen* in which the *sacci* have extensive ektexinous webbing in the *sacci*, in contrast to *eusaccate* pollen, such as modern *Pinus*, in which the sacci are nearly hollow. See discussion in Chapter 9. Cf. *eusaccate*, *pseudosaccate, saccate.*

proximal Of the parts of *pollen grains* or *spores* nearest or toward the center of the original *tetrad*; e.g., of the side of a *monosulcate pollen grain* opposite the *sulcus*, or of the side of a *trilete spore* provided with *contact areas*. Ant. *distal*.

proximal pole The center of the *proximal* surface of a *spore* or *pollen grain*, thus the midpoint of a *monolete laesura* or the point of a *trilete laesura* from which the *radii* originate.

proximate cyst A *dinoflagellate cyst* of nearly the same size as, and closely resembling, the motile *theca* of the same species. The ratio of the diameter of the main *body* to the total diameter of the *cyst* exceeds 0.8. The term refers to the supposed proximity of the main cyst wall to the theca at the time of encystment. See *chorate cyst* and *proximochorate cyst*.

proximochorate cyst A *dinoflagellate cyst* not as condensed (condensation of 60-80%) from the thecal cell as are *chorate cysts,* and which show some sutural outgrowth evidence of *tabulation*.

pseudochitin Resistant, C-H-O-N compound of uncertain structure, occurring in the walls of *chitinozoans* (see *chitin*). Behaves like chitin but does not give chitin test, e.g., on staining.

pseudocolpus A *colpus*-like modification of the *exine* of *pollen grains*, differing from a true colpus in that it is not a site of *pollen tube* emergence. A good example is the fossil genus *Eucommiidites*, which has one true colpus and two pseudocolpi. See *colpus*.

pseudopore An especially thin area in the *leptoma* of certain coniferous *pollen* (as in the families Cupressaceae and Taxaceae, and the fossil family Cheirolepidiaceae). See *cryptopore* and *tenuitas*.

pseudopylome A prominent thickening of the wall at the *antapical* end of the *vesicle* in some *acritarchs*, resembling the rim of a *pylome*.

pseudosaccus An *ektexinous saccus*-like outer part of a fossil *spore* or *pollen grain* (such as *Endosporites*), resembling the true saccus of some pollen grains but not showing internal *alveolate structure* characteristic of sacci. The distinction between a pseudosaccus on the one hand and a saccus or the *cavate* condition on the other hand is often rather slight. Some would limit use of term pseudosaccus to spores only (e.g., Richardson, 1965, in proposing the Subturma Pseudosaccititriletes).

psilate Of the relatively smooth walls of *pollen* and *spores* lacking prominent *sculpture*. The term is usually also applied to *exines* with *pits* or *reticular* openings, *mural* units, etc., less than 1 μm in diameter. Syn. *laevigate*.

pterate Of *chorate dinoflagellate cysts* which have *processes* linked distally in a mesh-like fashion.

pteromorph Of acritarchs, spheroidal, surrounded by an equatorial flange (*ala)*. Most are believed to be *prasinophyte* algae. See *phycoma, prasinophyte, ala.*

pycnidiospore Of fungi, a conidium (an asexual spore) borne in a pycnidium (an asexual fruiting body).

pylome Of *acritarchs*, a more or less circular opening, presumably for excystment but lacking clues of *plate* arrangement present in *dinoflagellate archeopyles*.

radial Pertaining to *trilete spore* features associated closely with the arms of the *laesura*. See *interradial*.

radius One arm of a *trilete laesura*. Also called *ray*.

ramus Of *scolecodonts*, any arm-like lateral extension of the face of a *jaw*, usually pointing posteriorly.

ray One arm of *trilete laesura*. Also called *radius*.

resting spore A *spore* that remains dormant for a period before germination; e.g. a *chlamydospore*, or a desmid *zygospore*, having thick cell walls and able to withstand adverse conditions such as heat, cold, or drying out; some are apparently *sporopolleninous* and can occur as *palynomorphs*. See *statospore* and *cyst*.

reticulate A term for *sculpture* of *pollen* and *spores* consisting of a more or less regular network of ridges (*muri*) enclosing open areas called *lumina*. Such sculpture is a *positive reticulum*. See *negative sculpture*, *muri, lumina.*

retipilate Of sculpture with a reticulum made up of *pila* instead of continuous muri.

retusoid Of *spores*, mostly Paleozoic, with prominent *contact* areas and *curvaturae*, such as in *Retusotriletes.*

ridge Of *scolecodonts*, the main criterion for recognizing the constituent elements of compound *jaws*. The ridges indicate the existence of the elements.

rimula Of circumpolloid *pollen* (*Classopollis, et al*.), the *furrow* of thinned *exine* encircling the *grain* "sub-equatorially." Some sources say that the rimula is really pre-equatorial,

that is, where its position can be accurately determined, the rimula is *distal* to the *equator*.

ring furrow A sometimes-used expression for the continuous encircling *sulculus* of *zonisulculate pollen*.

R_o Syn. of R_{oil} A measurement made microscopically under oil of the reflectance of organic matter, usually vitrinite. The numbers, e.g., 0.2 for certain peaty organic matter, are the percent reflectance of vertical incident light, in terms of the reflectance of glass standards. See Fig. 19.2.

ruga In Erdtmanian terms, regularly disposed but not meridional germinal *furrows*. Because of confusion with *rugulate*, it is better to use *colpus*, thus *pericolpate*, not *polyrugate*.

rugulate Of *sculpture*, consisting of wrinkle-like *ridges* that irregularly anastomose. Often approaches *reticulate*.

Saccardoan spore groups A classification for dispersed *conidia* and other asexual spores produced by extant *Fungi Imperfecti*, based on the number of cells, their disposition, and the organization of septa in the spore. See *Amerosporae, Didymosporae*, *Phragmosporae, Dictyosporae*, *Scolecosporae, Helicosporae,* and *Staurosporae.*

saccate Of *pollen*, possessing *sacci*. Code Pv1, Pv2, etc.

saccus A wing-like extension, or *vesicle* of the *exine* in gymnospermous, especially (but not exclusively) in coniferous *pollen*. The saccus is an expanded, bladdery projection of *ektexine* extending beyond the main *body* of a *pollen grain* and typically displaying more or less complex internal *structure*. Pl. sacci. See *air sac, bladder, vesicle, wing*, and *pseudosaccus*.

scabrate Of *sculpture*, consisting of more or less isodiametric projections (*scabrae*) less than 1 μm in diameter.

schizomorph Of acritarchs with a spherical, ellipsoidal, or discoidal shape, tending to divide into two symmetrical halves. Most are considered to be *zygospores* of *zygnemataceae* algae.

Schulze's reagent An oxidizing mixture very commonly used in palynologic *maceration*, consisting of a saturated aqueous solution of $KClO_3$ and varying amounts of concentrated HNO_3. Named after Franz F. Schulze (1815-73). The term "Schulze's solution" is very commonly used for this mixture, but in biological microtechnique this expression means $ZnCl_2$-KCl-I mixture used for staining.

sclerine A term for *exine* and *perine* collectively–useful term for *spore wall* when it is not certain whether a fossil *spore* has a *perine* or not. See *sculptine*.

sclerotium Of fungi, a more or less rounded mass of hyphae with thickened walls. If chitinous, may occur as a *palynomorph*.

scolecodont Any *jaw* piece of a polychaete annelid worm; originally intended only for dispersed, chitinous fossil elements. This glossary includes a few of the most important *scolecodont* terms. For more complete information, see Jansonius and Craig (1971) and Szaniawski (1996).

scolecospore Of fungi, an elongated "wormlike" spore.

scrobiculate Of *sculpture* having *scrobiculi* (sing. scrobiculus). Scrobiculi have *lumina* which are too small, and the *muri* too wide, for the sculpture to be regarded as *reticulate*. Grades into *foveolate* (Erdtman, 1952: "Very small foveolae are termed scrobiculi….").

sculptine A term for *sexine* and *perine* collectively. Sometimes used if doubt exists whether the outermost *sporoderm* layer may include perine. See *sclerine*.

sculptural element An individual unit of *sculpture*, such as a *spine*, a *clava*, a *baculum*, etc. Contrast *process*.

sculpture The external textural modifications (such as *spines, verrucae*, grana, *pila*, pits, grooves, reticulations, etc.) of the *exine* of *pollen grains* and *spores*. It is usually

a feature of the *ektexine* but may be a *perine* character. Syn. *ornamentation*. See *sculptine, sclerine*, and *structure*.

"*Scytinascia"* This proposed name for chitinous foraminiferal linings occuring as palynomorphs should be avoided. See *microforaminifera*.

secondary pollen As usually applied, e.g., Faegri and Iversen (1989), this means recycled or reworked *pollen*, e.g., pre-Pleistocene pollen from boulder clays in Holocene sediments. (Some authors, e.g., Bryant and Holloway, 1985, speak of secondary pollen counts, meaning counts from which certain over-represented forms are excluded.)

seed megaspore Refers to the very large (half a centimeter or more across) *megaspores* of some Paleozoic lycopsids, which although true free-sporing *megaspores* were in the size range of seeds and as disseminules presumably acted like seeds.

septal pore Of *fungal spores* with one or more *septa, pore*(s) found in the center of the septum or septa.

septate Of *fungal spores* having *septa*. See *septum*.

septum Of *fungal spores*, a cross-wall partitioning the inner space. Septa may be transverse or longitudinal.

sequence stratigraphy Study of sedimentary sequences, based primarily on sea-level changes, with the resulting flooding of surfaces during high-water stands and widespread exposure of land during low-water stands. The subject has many paleopalynological connections, as palynomorphs are sensitive indicators of paleoecology based on sea-level changes: for example, on land through spores and pollen, and in flooded areas through dinoflagellate cysts. See Chapter 18, this book.

sexine The more or less arbitrarily delimited outer division of the *exine* of *pollen*. See *nexine* and *ektexine*.

shadow band In *fungal spores*, incomplete *septa* showing as a shadowy line across the *spore*.

shaft Of *scolecodonts*, a posterior extension of a *jaw* of proportionately large dimensions.

shagreen, shagrenate, cf. *chagrenate*

shank Of *scolecodonts*, a backward extension (without teeth) of the posterior part of the inner face of a *jaw*.

shape class The general group (*peroblate* to *perprolate*) to which a *pollen grain* belongs in terms of the ratio between the *equatorial* diameter and the *pole*-to-pole dimension.

sicula Skeletal structure of a graptolite. Siculae are apparently chitinous or pseudochitinous, and can occur in early Paleozoic palynological preparations (cf. Plate 18.3e).

siphonogamous Of plants fertilized by means of pollen tubes (cf. *zoidogamous*), such as some gymnosperms and all angiosperms.

skolochorate Pertaining to *chorate dinoflagellate cysts* that have *processes* only, not processes and high *septa*. Low *ridges* and septa may be present.

small spore An outmoded term that was formerly used to contrast with "large spore" (= *megaspore*). However, the term has included *pollen* and *prepollen*, as well as isospores and microspores, making it essentially synonymous with the now more common *miospore*, but lacking miospore's precise size definition.

SOM Term used in palynofacies studies: sedimentary organic matter.

spectrum Syn. for *pollen spectrum*.

sphaeromorph A heterogeneous group of acritarchs with spherical to ellipsoidal vesicles lacking processes. Some of them are produced by *prasinophytes*.

spine One element in *echinate sculpture*.

spiraperturate Of *pollen* with one or several spiral (sinuous or winding) *apertures*, such as those of *Anemone, Coffea* or *Thunbergia* (see Furness, 1985).

Sporae dispersae The *spores* and *pollen* obtained by *maceration* of samples of whole rock, in contrast with those that have been found within the fossil *sporangia* that bore them (*Sporae in situ*).

Sporae in situ The *spores* or *pollen* obtained from fossil *sporangia* of *megafossil* plants.

sporal Being, pertaining to, or having the special characteristics of a *spore*. The term is not in good or current usage in *palynology*.

sporangium An organ within which *spores* are usually produced or borne; e.g., an organ in *embryophytic* plants in which spores are produced, such as a *pollen sac* of a gymnosperm or each chamber of the *anther* of an angiosperm. Pl. sporangia. See also *microsporangium* and *megasporangium*.

spore Any of a wide variety of minute, typically unicellular reproductive bodies or cells, often adapted to survive unfavorable environmental conditions. *Embryophytic spores* develop into *gametophytes*. Various fungal and algal *spores* develop into a number of different phases of the complex life cycles of these organisms. As usually used in *paleopalynology*, one of the haploid, dispersed reproductive bodies of *embryophytic* plants, having a very resistant outer wall (*exine*), and frequently occurring as fossils from Silurian to Holocene. See *sporomorph*.

spore case A *sporangium*. The term is not in good or current usage in *palynology*.

spore coat The *sporoderm*.

spore mother cell The *mother cell* in the *sporangium* of a spore-bearing plant, which, by reduction division, produces the *tetrad* of haploid *spores*. Syn. See also *pollen mother cell*.

spore wall The *sporoderm*.

sporinite Coal petrologic term for the kind of *liptinite* consisting of spore and/or pollen walls. Essentially synonymous with *exinite*.

sporocyte The *spore mother cell*.

sporoderm The entire wall of a *spore* or *pollen grain* collectively, consisting of an outer layer (*exine/exospore*) and an inner layer (*intine*), and, when present, an extra third layer (*perine*) outside of the exine. Syn. *spore coat* and *spore wall*.

sporogenous Producing or adapted to the production of *spores*, or reproducing by spores, e.g., "sporogenous tissue" in a *sporangium*, from which *spore mother cells* originate.

sporomorph A fossil dispersed *pollen grain* or *spore*. Some palynologists disapprove of the use of this term, but it is more specific than *palynomorphs* and often useful.

sporophyte The asexual generation of a plant (or an individual of that generation), producing *spores*: therefore, the diploid generation of an *embryophytic* plant, produced by fusion of egg and spermatozoid in lower vascular plants, or by fusion of egg nucleus and the sperm nucleus (produced by the *pollen*) of seed plants. See *gametophyte*.

sporopollenin The very resistant and refractory organic substance of which the *exine* and *perine* of *spores* and *pollen* are composed. The walls of *dinoflagellates* and *acritarchs* consist if a similar substance called *dinosporin*. It is this substance which gives the *sporomorph* its extreme durability during geologic time, being readily destroyed only by oxidation or prolonged high temperature. It is a high-molecular-weight polymer of C-H-O, perhaps a carotenoid-like substance, but the exact structural composition has not yet been established. Adj. sporopolleninous.

statospore A *resting spore*, e.g., the siliceous, thick-walled resistant *cyst* formed within the frustules of various chiefly marine centric diatoms. The term is also used for certain other 2-partite algal *cysts* in the division Chrysophyta.

staurospore Of fungi, a star-shaped *conidium*.

stenopalynous A typically erudite Erdtman term for taxa with spores or pollen that are relatively very much alike morphologically and or in exine structure, such as the Chenopodiaceae. Antonym: *eurypalynous*.

stephano- Of pollen having apertures arranged regularly on the equator, or crossing the equator meridionally in a symmetrical fashion. Syn. *zono-*, which I regard as less satisfactory because it is used in other senses.

stephanocolpate Of *pollen grains* having more than three *colpi*, meridionally arranged. Code Pn0.

stephanocolporate Of *pollen grains* having more than three *colpi*, meridionally arranged and provided with *pores*. Code Pnn.

stephanoporate Of *pollen grains* having more than three *pores*, disposed on the *equator*. Code P0n.

"*stick"* Term used for *Lycopodium* spores, *Eucalyptus* pollen or inorganic spherules added in known approximate numbers to palynological samples before processing, to permit calculation of palynomorphs per gram of sample.

STOM Term used in palynofacies studies: Structured organic matter.

striate "Streaked" *sculpture* characterized by multiple, more or less parallel grooves and ribs (the ribs are also called *muri)* in the *exine*; also used in a general sense to describe *polyplicate* or *taeniate* structure, as of the *Striatiti*. It would be better to use polyplicate or taeniate, as appropriate, for these morphological features, and to restrict striate to description of streaked sculpture.

Striatiti Abundant upper Paleozoic and lower Mesozoic *pollen* with very characteristic *taeniate* or *plicate structure* in the *exine* of the *body* of the *pollen grain*, the grooves and "ribs" (taeniae) usually (but not always) oriented perpendicular to the axes of the *sacci* (if these are present). They are presumably pollen of conifers, gnetaleans, glossopterids, and other gymnosperms.

stroma Of fungi, a mass of *hyphae* in which fructifications (*ascocarps*) are formed.

structure (a) The internal makeup of the *ektexine* of *pollen grains* and *spores*, usually consisting of rodlets (*columellae*) that may be branched and more or less fused laterally. (When the fusion creates a coherent outer surface layer, this is the *tectum.*) (b) A term that is sometimes, but less desirably, used to describe major morphologic characteristics of spores, especially those of the Paleozoic.

subsaccate Syn. of *pseudosaccate*.

sulcal plate One of the *plates* of the *ventral furrow* region in *dinoflagellate thecae*. The plates are subdivided as to left or right, and anterior or posterior position.

sulculus Of pollen, an elongate *aperture* (*furrow*), more or less parallel to *equator*, either at the equator or toward a *pole*, generally *distal* to the equator but not centered at the distal pole, as is a *sulcus*. Sulculi may join to form a ring. Adj. form: sulculate. See *zonisulculate*.

sulcus (a) An elongate *aperture (furrow)* in the *exine* of *pollen grains*. The term is usually restricted to a *distal furrow* of pollen grains with only one such *aperture*, when this furrow has the *distal pole* in its center. See *colpus*. (b) A longitudinal groove on the *ventral* surface of *dinoflagellate thecae*. One of the two *flagella* runs posteriorly in it and trails behind the organism. The sulcus, reflecting its thecal progenitor, is also a part of the visible morphology of many *dinoflagellate cysts*.

suture The line along which the *laesura* of an *embryophytic spore* opens on germination; loosely, the laesura. More precisely, the *commissure*.

syncolpate Of *pollen grains* in which the *colpi* join, normally near the *pole*. Code Pns. See *zonocolpate*.

tabulation Of *dinoflagellate thecae*, the pattern according to which the constituent *plates* are arranged. Reflected tabulation is the evidence in *dinoflagellate cysts* of the arrangement of the plates in the theca from which the cyst was derived.

*taenia*e Straplike, more or less elongated and parallel strips of *exine* characteristic of many upper Paleozoic and lower Mesozoic *pollen grains*. They occur on one or both sides

of the corpus of *saccate* grains (e.g., *Lunatisporites*) or much less commonly on non-saccate grains such as *Vittatina*. Singular: taenia. Adj. taeniate. See *striate, polyplicate* and *Striatiti*.

TAI Thermal Alteration Index, a scale based on color and vitrinite reflectance data, indicative of the thermal maturity of organic matter in rocks. Useful in hydrocarbon exploration. See discussion in Chapter 19, this book, for comparison of TAI with the related SCI and TAS scales.

tapetum Tissue of nutritive cells in the *sporangium* of terrestrial *embryophytic* plants, largely used up during development of the *spores*. In angiosperms, it is the inner wall of the anther locules and provides nutritive substances for the developing *pollen*. *Pollenkitt* is a sticky tapetal residue often found on and in *exines*. See *ubisch bodies*.

tasmanitid An informal term for members of the genus *Tasmanites* and related forms, large, spherical *palynomorphs* with thick perforate walls presumably representing the *phycomata* of certain green algae (Prasinophyceae). These fossils range from Ordovician to Cenozoic, and were formerly classed with the *acritarchs* before their assignment to the prasinophytes was established. Certain organic-rich shales (tasmanite) contain enormous numbers of tasmanitids.

TCT Acronym for Taxodiaceae, Cupressaceae, and Taxaceae, a term used for the pollen of these families, especially in Neogene paleopalynology, because in routine microscopy the inaperturate pollen of the families are difficult to distinguish from each other (cf. Martin and Gray, 1962). The Taxodiaceae are now regarded by most systematists to be a subfamily of the Cupressaceae, so the expression should perhaps be altered to CT.

tectate Of a *pollen grain* whose *ektexine* has an outer surface supported by more or less complicated inner *structure* usually consisting of *columellae* supporting the *tectum*.

tectum (a) The surface of *tectate pollen grains*. (b) A term which should now be avoided, formerly used to designate thickened, upward projecting *exospore* associated with the *laesura*, usually of *megaspores*.

tegillum Erdtman distinguished between the *columellae*-supported outer surface of angiosperm *pollen* with less than 80% coverage as a tegillum and those with more than 80% coverage as a *tectum*. Most palynologists now call both tectum.

teleomorph Of fungi, characterized by presence of only sexual propagules, such as *asci* (in Ascomycetes) or *basidia* (in Basiomycetes).

teleutospore A *fungal spore* developed in the final stage of the life cycle of rust fungi. When the thick walls are composed of chitin they may occur as microfossils in *palynologic* preparations. See *urediospore*.

teliospore Syn. of *teleutospore*.

tentaculite Of *zoomorphs,* probably chitinous, forms resembling a stocking, possibly referable to mollusks/pteropods. For example, see Fig. 1.1ao, this book.

tenuitas A thin area in the *exine* of a *pollen grain* or *spore*, as the *distal germinal* area of *Classopollis* pollen grains. More regular in form than an *ulcus*, less regular than a *colpus*. Syn. *leptoma*.

teratoid pollen/spores Deformed pollen and produced are produced by plants under some genetic, nutritional and environmental circumstances. These are teratoid sporomorphs.

test Syn. for *dinoflagellate cyst*. See *tract*.

testate amoebae Some amoebae produce a proteinaceous tough test that can marginally be considered a palynomorph, because it survives fairly well in sediments and even under fairly gentle laboratory maceration techniques.

tetrad A usually symmetric grouping of four *embryophytic spores* (or *pollen grains*) that result from meiotic division of one *mother cell*. Such tetrads may be *tetrahedral* (most common) or *tetragonal*, rarely of other types. A number of pollen types regularly

remain in united tetrads as mature pollen when shed by the *pollen sacs* (as in some fossil circumpolloid forms). If the grains are always in such tetrads (as in Ericaceae) the tetrads are "obligate tetrads"). See *dyad* and *polyad*.

tetrad scar Syn. for *laesura*.

tetragonal tetrad A *tetrad* of *spores* or *pollen grains* in which the centers of the individual grains lie more or less in one plane.

tetrahedral tetrad A *tetrad* of *spores* or *pollen grains* in which each grain rests atop three others, so that the centers of the grains define a tetrahedron.

tetratabular archeopyle An *apical archeopyle* formed in a *dinoflagellate* cyst by the loss of four *plates*.

thallus Of non-vascular plants in general, the vegetative tissues as a whole; of fungi, the entire assimilative organism.

thanatocoenosis Fossils that occur together as a result of post-depositional sedimentation, not as a result of association as living organisms. The contrast is to *Biocoenosis,* which refers to either fossils that occur where the producing organisms lived or to the living association itself. Palynofloras are almost all more or less thanatocoenoses, but the degree to which this is true is often significant.

theca The outer covering or "shell" of a motile *dinoflagellate*. See *amphiesma.*

thermal alteration The chemical and physical alteration of organic matter in sedimentary rocks, as a result of pressure and temperature applied over time. Depth of burial is the most important factor. The darkening of color in transmitted light of sporopollenin, dinosporin, and chitin in this process from pale yellow via orange and brown to black, and the concomitant increase in reflectance on surfaces of vitrinite can all be measured, and there is a close relationship to the amount and kind of associated hydrocarbons. See *TAI* and discussion at the beginning of Chapter 19, this book.

tintinnid A ciliate protozoan, range Jurassic to present, the probably chitinous test of which can be present in some palynological preparations. Cf. van Waveren (1992, 1993).

torus An arcuate invagination or protuberance of *exine* outside of and more or less paralleling the *laesura* of a *spore* in the *interradial* area. Some palynologists use *torus* for separate arcs, and *kyrtome* for a completely connected figure. Pl. tori. See *kyrtome* and *labrum*.

TP Abbrev. for *tree pollen*. See *arboreal pollen*.

trabeculate Of dinoflagellate cysts, having connections between the *processes*.

tract Syn. for *test*, as in epitract, etc.

transverse flagellum A flagellum, often more or less ribbon-like, encircling a motile *dinoflagellate*, usually in a deep encircling groove or *cingulum*, arising from a *pore* in the *sulcus*.

transverse furrow A *colpus*-like thinning in the *exine* of a dicotyledonous *pollen grain*, usually occurring at the *equator* in association with and running perpendicular to a colpus. Syn. *colpus transversalis*.

tree pollen Syn. of *arboreal (arborescent) pollen*. Abbrev. *TP*.

trichotomocolpate Syn. of *trichotomosulcate*.

trichotomosulcate Of *monosulcate pollen grains* in which the *sulcus* is more or less triangular, often simulating a *trilete laesura*. Code Pac.

tricolpate Of *pollen grains* having three meridionally arranged (120° apart) *colpi* which are not provided with *pores, transverse furrows* or other such modifications. Tricolpate pollen are produced by dicotyledonous plants, and they first appear in the fossil record in rocks of early Cretaceous age. Code Pc0. See *tricolporate*.

tricolporate Of *pollen grains* having three *colpi* which are provided with *pores* or other, usually *equatorial*, modifications. Code Pc3.

tricolporoidate An intermediate state between Pc0 and Pc3, in which some modification of the *colpus* is present equatorially, but not a *pore*, transverse colpus, or other organized thinning. Code Pc0.

trifolium Of *megaspores*, a *proximal* figure similar to a *gula* but less massive, with three blade-like divisions and no broad base.

trilete Of *embryophytic spores* and some *pollen grains* having a *laesura* consisting of a three-pronged mark somewhat resembling an upper-case "Y". The usage of this term as a noun ("a trilete") is improper. Code Sc0. See *monolete* and *Y mark*.

triplan Refers to *trilete spores* with the *radii* of the *laesura* on deeply indented radial lobes. When seen laterally, such spores have a characteristic flapped appearance.

triporate Of *pollen grains* having three *pores*, usually disposed at 120° from each other, on the *equator*. Some palynologists distinguish from this term *tripororate*, for grains with compound pores, an *ectopore* and an *endopore* (*os*).

triprojectate A group designation (triprojectacites) for *Aquilapollenites* and similar, presumably related forms of late Cretaceous-early Cenozoic angiosperm *pollen*, in which the three *colpi* are borne on the projecting ends of colpal arms, so that typically the three colpal arms (hence, "triprojectate") and two *polar* projections give the pollen a five-pronged appearance.

triradiate crest or *ridge* Of *trilete spores*, the three-rayed figure on the *proximal* surface caused by intersection of the *contact areas*.

tula Of gymnospermous pollen, a relatively small saccus-like inflation at the ends of the distal sulcus or tenuitas. Example: *Ovalipollis.*

turma An artificial suprageneric grouping of form genera of fossil *spores* and *pollen* (mostly in use for pre-Cenozoic forms), based on morphology. *Turmae* are grouped under two large headings, *Anteturmae* Sporites and Pollenites. Pollen and spores are functional in meaning, not morphological, which therefore creates some problems for classification. Turmae are subdivided into groups such as "Subturmae" and "Infraturmae". The system is not governed by the International Code of Botanical Nomenclature. See *anteturma*.

ubisch bodies Small (about 2-5 μm) pieces of *sporopollenin* formed from the *tapetum* after the rest of the sporopollenin available has been built into *spore* or *pollen sporoderm*. Ubisch bodies are sometimes rather abundant in palynological preparations. Also called *orbicules*. The name stems from description in 1927 of the particles by Ubisch (see Rowley, 1963). However, others apparently described them earlier, which is one reason the term orbicules is favored by many. See cover illustration, this book.

ulcerate Of pollen with ulci. Code Pul.

ulcus A thin place in the *exine*, more or less *pore*-like, but irregular in outline, and often broken up into patches, as in some Restionaceae. Pl. ulci. Cf. *leptoma, tenuitas*.

unarmored See *armored*.

urediospore A *fungal spore* of brief vitality, whose thin walls may be composed of *chitin*. Such spores may occur as *microfossils* in palynologic preparations. See *teleutospore*.

USTOM Term used in palynofacies studies: unstructured organic matter.

valva One of the *radial* thickenings of a *valvate spore*.

valvate Of *trilete, zonate spores* with the *equatorial* thickenings more pronounced at the "corners", that is in the areas beyond the ends of the *laesural radii. Auriculate* can thus be regarded as an extreme valvate condition.

velum Used to describe the "frilly" (convoluted) sort of sculpture/structure of *Tsuga* pollen exine, also seen in many fossil gymnosperm pollen grains.

ventral Of *dinoflagellates*, the side on which the *sulcus* and the ends of the *cingulum* occur.

vermiculate A *sculptural* pattern formed by elongate, irregularly placed depressions.

verrucate Warty, or covered with wart-like knobs or elevations; of *spores* and *pollen* having *sculpture* consisting of wart-like projections. Syn. verrucose.

vesicle Syn. of *saccus*. Also, per Paris *et al.* (1999) the basic flasklike unit of chitinozoans.

vesiculate Syn. of *saccate*.

vestibulate Of *porate pollen* having a *vestibulum*.

vestibulum The space between the external opening (*exopore* or *pore*) in the *ektexine* and the internal opening (*endopore* or *os*) in the *endexine* of a *pollen grain* with a complex *porate structure*. The openings in ektexine and endexine are of similar or dissimilar size.

viscin threads Despite the name, non-viscous, *sporopolleninous* threads originating in the polar *ektexine* of a relatively limited number of angiosperms (Onagraceae, some legumes), functioning as attachment-organs for dispersal by animal pollinators. One end is attached to the polar ektexine, the other end is free. Threads on *spores*, e.g., the *megaspore Balmeisporites*, not serving for attachment in *pollination*, and non-sporopolleninous threads (such as in some orchids), or threads not arising from the polar ektexine, or with both ends attached should not be called viscin threads (Patel *et al.*, 1985). Viscin threads have been encountered in fossil onagraceous pollen.

vitrinite Coal petrological term for organic matter derived from wood or bark. cf. *liptinite*, *sporinite*

wing Syn. of *saccus*

Y-mark A *trilete laesura* on *embryophytic spores, prepollen*, and some *pollen*, consisting of a three-pronged mark somewhat resembling an upper-case "Y". It commonly also marks a *commissure* or *suture* along which the spore germinates. The term is also applied to similar marks, which are not laesurae, on some pollen grains.

zoidogamous (or zooidogamous) Of plants fertilized by means of ciliated, free-swimming antherozoids (or spermatozoids), for example bryophytes and pteridophytes. See *siphonogamous.*

zonasulculate Best regarded as a syn. for *zonisulculate*.

zonate Of *spores* or *pollen grains*, possessing a *zone* or other similar *equatorial* extension. Note that some authors would restrict "zonate" to spores with a zone, whereas others use it as here defined, to include other equatorial features as well. (Some specialists in angiosperm pollen use zonate to denote pollen grains with a ring furrow).

zone A more or less *equatorial* extension of a *spore* or *pollen grain*, having varying equatorial width and being as thick as or thinner than the spore wall. It is much thinner than a *cingulum.* The term is also used, however, in a general sense for any equatorial extension of the spore wall. Because zone is used in a specific sense, simply "equatorial extension" would be better for the general term. Syn. zona. (Zone is also used stratigraphically, as in biozones, acme zones, etc. (see Hedberg, 1976.) See *flange, corona, equatorial extension, auricula* and *crassiude*.

zonisulculate Here advocated as a general term for *pollen* having a *sulculus* that encircles the *grain* forming a ring (*ring furrow*). (Some palynologists use *zonasulculate* specifically for pollen with ring furrows parallel to or on the equator.) Zonisulculate can be used even for instances such as *Nypa* (Palmae = Arecaceae), in which the ring furrow runs around the grain through both *poles*.

zono- Of pollen, apertures occurring at, or crossing, the equator. Cf. *stephano-*, which I prefer because *zono-* is used in other connections.

zonotrilete Of a *trilete spore* characterized by an *equatorial* zone or other thickening.

zooanthella An algal cell living symbiotically in the cells of certain invertebrate animals and protists, e.g., in the endoderm of some coral polyps. Most zooanthellae are *dinoflagellates*.

zooclast a particle of animal origin, in the palynomorph size range, found in sediments, such as pieces of insect exoskeleton, particles of graptolites. Contrast *zoomorph.*

zoomorph a palynomorph of animal origin, usually representing an entire organism, as a *foraminiferal lining*, a *chitinozoan*, a *tentaculite*, a *testate amoeba*.

zoophily A term for *pollination* by animals. See *entomophily* and *anemophily*.

zygnematacean algae Green algae of freshwater streams and lakes. They produce thick-walled, resistant *zygospores* with an equatorial line of rupture into two more or less equal parts. Example: *Mougeotia* (see Fig. 1.0, this book). Cf. *schizomorph.*

zygospore A resting *spore* of various non-vascular plants (such as desmids and Zygnemataceae), produced by sexual fusion of two protoplasts. The wall is often thick, apparently *sporopolleninous*, resistant, and can therefore occur as a *palynomorph*.

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