Paleogene Fossil Birds

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Preface

Since birds are predominantly diurnal and often quite vociferous animals, their behavior and ecological requirements are probably better studied than those of any other vertebrate group. Detailed knowledge of their evolutionary history is, however, still limited to a small circle of specialists, and there is a widespread belief that the avian fossil record is poor. This is certainly true if the abundance of bird bones is compared with that of mammalian teeth, which are robust enough to survive even rough depositional environments and collection techniques. In many fossil localities complete skeletons and postcranial elements of birds are, however, not much rarer than those of other small land vertebrates. Numerous avian fossils in collections worldwide have remained further unstudied for decades, so the significant underrepresentation of birds in vertebrate paleontology seems to be due to a low number of specialists rather than a low number of fossils.

Concerning certain geological periods and geographic areas, our knowledge of the early evolutionary history of birds is anything but poor. In fact, so many new fossils were described during the past two decades that it becomes increasingly difficult for a single person to cover the whole field of paleornithology.

This book gives an account of the evolution of modern birds in the first half of the Cenozoic, aiming not only at specialists in the field of paleornithology, but also at ornithologists and paleontologists in need of detailed information, either for the calibration of molecular data or to set Paleogene faunas into a full context. Given the current pace of new discoveries, I am not cherishing the illusion that this survey will remain up to date for a long time. I do hope, however, that the overall framework outlined for the early diversity and evolution of modern birds will form a stable basis for future studies, and that the readers will find the book a useful source for their own research.

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Gerald Mayr

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Contents

Chapter 1
Introduction

With around 9,000 extant species, birds are the most species-rich group of land vertebrates. As seed dispersers, flower pollinators, predators, prey, and through numerous other interactions they play an important ecological role in today's world. Although a picture of past ecosystems is thus likely to be quite incomplete without consideration of their avifaunas, Cenozoic fossil birds are still significantly underrepresented in even the most recent treatises of vertebrate paleontology. This is particularly true for Paleogene taxa, whose diversity has just begun to be appreciated.

The Paleogene covers the first half of the Cenozoic, from the mass-extinction events at the end of the Mesozoic era, 65 million years ago (Ma), to the beginning of the Miocene, 24 Ma. It has long been recognized that this geological period was pivotal for the early diversification of modern mammals and birds. Whereas, however, the mammalian Paleogene fossil record is intensely studied and set into a paleobiogeographic and paleoecological context (Rose 2006), no comprehensive surveys exist for that of birds.

Until a few decades ago, our knowledge of the early evolution of modern birds was indeed very patchy and mainly based on fragmentary bones of often uncertain phylogenetic affinities. As will be evident from the present work, this situation has dramatically changed. At least in the Northern Hemisphere, the Paleogene fossil record of birds is no longer much short of the mammalian one concerning the number of well-represented higher-level taxa. In some renowned fossil localities, such as the London Clay in England and the Green River Formation in North America, remains of birds are even much more abundant than mammalian remains.

Numerous Paleogene avian taxa were described after the publication of Olson's (1985) comprehensive and often-cited survey of the fossil record of birds, and most of these are also not covered in the more recent book of Feduccia (1999). These fossils not only afford information on major morphological transformations which occurred in the evolutionary lineages of the extant avian taxa, but also provide otherwise unknown data on the historical biogeography of the latter. Many further belong to remarkable extinct groups without modern counterparts, and allow intriguing insights into the past diversity of long-vanished avifaunas.

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In the present book the Paleogene fossil record of birds is detailed for the first time on a worldwide scale. I have developed the idea for such a project for several years, and think that it is an appropriate moment to present a summary of our current knowledge of the early evolution of modern birds. Meanwhile not only is there a confusing diversity of fossil taxa, but also significant progress has been made concerning an understanding of the higher-level phylogeny of extant birds. Hypotheses which were not considered even a decade ago are now well supported by independent analyses of different data. In several cases these group together morphologically very different avian groups and allow a better understanding of the mosaic character distribution found in Paleogene fossil birds. The book aims at bringing some of this information together, and many of the following data are based on first-hand examination of fossil specimens.

In the first chapter, the most important fossil localities for Paleogene birds are introduced. I then outline current hypotheses on the higher-level phylogeny of birds and summarize the Mesozoic fossil record of Neornithes. Discussion of the Paleogene fossil record forms the main body of the book and is distributed over 12 chapters, in which the reader finds data on basic morphological features of the various taxa and their temporal and geographic distribution. As far as this is possible, the fossils are placed into a phylogenetic context in the light of current hypotheses on the interrelationships of extant birds. General aspects of their paleobiogeographic and paleoecological significance are summarized in a concluding chapter.

Although I tried to be exhaustive, I did not intend to write a catalogue and some fragmentary remains of uncertain affinities are not accounted for (for comprehensive lists, see Lambrecht 1933; Brodkorb 1963, 1964, 1967, 1971, 1978; Bocheński 1997; Mlíkovský 1996a, 2002). Fossil remains other than bones (e.g., trackways, feathers, and eggs) are also only occasionally mentioned, as these often cannot be assigned to particular taxa with confidence. I further largely ignored the poorly founded synonymizations made by Mlíkovský (2002) (see Mourer-Chauviré 2004 for a critical review).

Throughout the text, English equivalents of the Latin standard nomenclature of avian anatomical features (Baumel and Witmer 1993) are used. Author names are only given for fossil species at first mention, unless the describer of a taxon is not obvious from the context. Extinct taxa are indicated by a dagger in the headings of the sections. The terms “crown group” and “stem group” specify the position of fossil taxa with respect to their extant relatives. As used in the following, the crown group of a certain taxon is the clade including the stem species of the extant representatives of this taxon and all its extant and extinct descendants. Stem group representatives are all taxa outside the crown group. Whereas stem group representatives are always extinct, not all crown group representatives need to be extant taxa. Unspecified clade names refer to the total group, i.e., the clade including stem and crown group representatives, which in some instances is denoted with the prefix “Pan-.” The term “Neornithes” is used for crown group Aves.

A while ago, the stratigraphy of the Eocene–Oligocene boundary in North America was substantially revised, owing to refined temporal correlations and calibrations (Prothero 1994). Accordingly, taxa which were originally described as “early Oligocene” (Chadronian land mammal age) are now considered to be from the late Eocene, and those from “middle” or “late” Oligocene deposits (Orellan and Whitneyan land mammal ages) are of early Oligocene age. Whereas the mammalian fossil record has already been adjusted to these new calibrations, the incorrect earlier stratigraphic ages continue to be used in most recent paleornithological accounts (e.g., Feduccia 1999; Caley 2007; and several of my own publications). Because these changes are incorporated in the present book, the ages of some North American taxa depart from those in earlier publications. The same applies to the stratigraphy of the Oligocene of South America, where the Deseadan land mammal age is now regarded to be from the late Oligocene, not the early Oligocene as assumed by earlier authors (see also Sect. 2.4).

Chapter 2
Stratigraphy and Major Fossil Localities

In this chapter some of the major sites which yielded Paleogene fossil birds are briefly introduced to avoid redundancies in the taxonomic sections. Dyke et al. (2007, p. 341) stated that "aquatic environments of preservation dominate the early Paleogene avian fossil record, because these were the habitats in which more modern birds lived at the time of the transition." Actually, however, the majority of Paleocene fossil birds are from terrestrial deposits, and a predominance of fossil lagerstätten of aquatic origin can only be recognized for the early and middle Eocene record of the Northern Hemisphere. Large areas of this part of the globe were covered with paratropical rainforests in the early Paleogene, which offered unfavorable conditions for the preservation of animal carcasses on land. The predominance of fossil birds in early/middle Eocene sediments of aquatic origin thus clearly reflects a preservational bias.

2.1 Europe

Undoubtedly, Europe has the most extensive and best studied Paleogene fossil record of birds. Recent reviews were conducted by Mlíkovský (1996a, 2002) and Mayr (2005a), and in the following only major localities which yielded significant numbers of avian remains are listed. Comprehensive data on most European fossil sites where Cenozoic bird remains have been discovered can be found in Mlíkovský (1996a).

The European Paleogene is subdivided into biostratigraphic units of the Mammalian Paleogene (MP), whose definitions are based on local mammalian faunas (Legendre and Lévêque 1997). According to this stratigraphy, the Paleocene covers the units MP 1–6 (ca. 65–55 Ma). The Eocene comprises the units MP 7–20, of which the early Eocene (Ypresian) includes MP 7–10 (ca. 55–50 Ma). The middle Eocene is split into the Lutetian (MP 11–13; ca. 50–42 Ma) and Bartonian (MP 14–16; ca. 42–38 Ma), and the late Eocene (Priabonian) covers MP 17–20 (ca. 38–33 Ma). The Oligocene contains the units MP 21–30, with the early Oligocene (Rupelian) being from MP 21 to 24 (ca. 33–29 Ma), and the late Oligocene (Chattian) from MP 25 to30 (ca. 29–23.5 Ma).

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Very little is still known on Paleocene avifaunas of Europe. Although hundreds of Paleocene bird bones were found in the Walbeck fissure filling in northern Germany, these remained unstudied for almost 70 years (Weigelt 1939; Mayr 2007a). The Walbeck avifauna is comparatively species-poor and its exact age is uncertain, but is probably late middle Paleocene (?MP 5; BiochroM'97 1997).

In the mid-nineteenth century, late Paleocene (MP 6) birds were further described from the deposits of the Reims area, i.e., Cernay-lès-Reims and Mont Berru, in France (Hébert 1855; Lemoine 1878, 1881). The fossils from these localities also consist of isolated bones and the avifauna is dominated by very large forms.

By contrast, the early and middle Eocene European fossil record of birds is extensive, and numerous new taxa were described in the last two decades. Study of one of the earliest localities, the early Eocene (MP 7; 55–54 Ma) sediments of the Fur Formation ("Mo-Clay") of northwestern Jutland in Denmark, has only recently begun. Although the sediments from these deposits consist of marine diatomites, most avian taxa belong to land birds. Several of the fossils are represented by virtually three-dimensional, hardly crushed skeletons (Kristoffersen 2002a; Lindow and Dyke 2006).

Most avian specimens from the slightly younger London Clay in southern England come from two localities, the Isle of Sheppey (MP 8–9; Mlíkovský 2002) and Walton-on-the-Naze (MP 8; Mlíkovský 2002). Many of those from the latter locality are in the private collection of Michael Daniels (Daniels 1988, 1989, 1990, 1993, 1994; see Table 4.1 in Feduccia 1999). Fossil birds from the London Clay were collected in the nineteenth century, and actually the first two fossil avian species named scientifically, *Halcyornis toliapicus* Koenig, 1825 and *Lithornis vulturinus* Owen, 1840, are from the Isle of Sheppey. Although the London Clay Formation is of marine origin, it yielded a great number of terrestrial and arboreal birds, which lived in the forests near the shoreline. Most fossil specimens consist of three-dimensionally preserved bones, and often even partial skeletons are found. The taxonomy of these fossils is, however, much complicated by the fact that numerous very fragmentary and noncomparable bones were named by earlier authors (see Steadman 1981 for a critical review).

Several hundred bird skeletons were found in the middle Eocene fossil site Messel near Darmstadt in Hesse, Germany. The Messel "oilshale" was deposited during the lower middle Eocene (MP 11; 47 Ma) in a small lake, which was surrounded by a paratropical rainforest (Schaal and Ziegler 1988). Birds are among the most abundant land vertebrates and more than 50 species have been distinguished so far, many of which are known from multiple specimens (Mayr 2000a; Morlo et al. 2004; Peters 1988a, 2006). The fossil avifauna of Messel is biased toward small to medium-sized birds and only few remains of large species were found. Some specimens exhibit well-preserved soft tissue remains, including feathers (Wuttke 1983; Davis and Briggs 1995), foot scales (Peters 1988a), and even uropygial glands waxes (Mayr 2006a, 2008a)

Middle Eocene fossil birds were further recovered in the now abandoned opencast brown coal mines of the Geisel Valley (Geiseltal) near Halle in eastern Germany (Mayr 2002a). The fossiliferous deposits of these localities pertain to different stratigraphic horizons (MP 11–13; 44–46 Ma) and originated in peat bogs and small lakes (Krumbiegel et al. 1983). Some fossils from the Geisel Valley also show exceptional soft-part preservation, including even epithelial cells with nuclei and red blood corpuscles (Voigt 1988).

The “Phosphorites du Quercy” in France have yielded a large number of middle Eocene to late Oligocene (MP 10/11–28) bird bones, which accumulated in karstic fissure fillings (Mourer-Chauviré 2006). Many fossils were found during phosphate mining activities in the nineteenth century and lack accurate locality and horizon information, but numerous bones from later excavations in the second half of the twentieth century could be ranked stratigraphically. The deposits of the Quercy fissure fillings originated in different paleoenvironments. Most avian taxa were either terrestrial or arboreal, whereas aquatic birds are very rare. The more than 70 named species were listed by Mourer-Chauviré (1995a, 2006). The Quercy deposits are of particular importance not only because the avian remains are very well studied, but also because of the great number of three-dimensionally preserved bones, and the wide stratigraphic range they cover. Virtually all specimens consist, however, of isolated bones, and an unambiguous assignment of different postcranial elements to the same taxon is sometimes difficult.

Late Eocene (MP 19; Mlíkovský 2002) birds were described from the Paris Gypsum in France (*gypses de Montmartre*). Most of these are represented by articulated skeletons but are so poorly preserved that only very limited osteological comparisons are possible (Brunet 1970; Harrison 1979a). A late Eocene (MP 17; Mlíkovský 1996b) avifauna is also known from the Hampshire Basin in southern England, and a number of early Oligocene (MP 21–23; Mlíkovský 1996b) birds was discovered in the Hamstead Beds of the Isle of Wight (Harrison and Walker 1976a, 1979a).

Avian remains from early Oligocene (Rupelian) deposits in Belgium, which were published in the nineteenth century, are based on a few isolated bones and the remains mainly represent marine taxa. More recently, earliest Oligocene (MP 21) avifaunas were reported from the fluviolacustrine Belgian Boutersem Member (Mayr and Smith 2001, 2002a). Well-preserved skeletons of early Oligocene birds were further found in the locality Wiesloch–Frauenweiler in southern Germany. This former clay pit is well known for its Rupelian (32 Ma; Micklich and Hildebrandt 2005) marine fish fauna, but because the sediments stem from a near-shore environment it has also yielded a diverse array of small arboreal birds (Mayr and Knopf 2007a, b). Other important localities for early Oligocene birds are situated in the Lubéron in southern France. Most fossils from this area stem from the Calcaires de Vachères in the region around the villages Vachères and Céreste. They are represented by skeletons in fine-grained limestone, which originated in brackish coastal lagoons (Mayr 1999a; Roux 2002; Louchart et al. 2008).

2.2 Asia

There is an outstanding Cretaceous fossil record of nonneornithine birds from China and Mongolia (Chiappe 2007), but very little is still known about Paleogene Neornithes from Asia. The Cenozoic avian fossil record, or parts thereof, was summarized by Kurochkin (1976), Rich et al. (1986; China, Japan, and Southeast Asia), Nessov (1992; area of the former Soviet Union), and Hou (2003; China). Most of the published pre-Oligocene taxa stem from late Eocene and Oligocene sites of Mongolia, Kazakhstan, and China. Avian remains were also described from the Vastan Lignite Mine, a promising early Eocene (about 52 Ma) locality in India (Mayr et al. 2007).

2.3 North America

North America has a comprehensive Paleogene fossil record of birds, of which however no up-to-date reviews exist. In chronological order, the North American Paleogene is divided into the following land mammal ages (after Prothero 1994 and Rose 2006; age estimates after Alroy 2000): The Paleocene comprises the Puercan (65–63.3 Ma), Torrejonian (63.3–60.2 Ma), Tiffanian (60.2–56.8 Ma), and Clarkforkian (56.8–55.4 Ma). The Eocene is subdivided into the early Eocene Wasatchian (55.4–50.3 Ma), the early/middle Eocene Bridgerian (50.3–46.2 Ma), the middle Eocene Uintan (46.2–42.0 Ma) and Duchesnean (42.0–38.0 Ma), and the late Eocene Chadronian (38.0–33.9 Ma) land mammal ages. The Oligocene is composed of the early Oligocene Orellan (33.9–33.3 Ma) and Whitneyan (33.3–30.8 Ma), and the late Oligocene Arikareean, which begins at 30.8 Ma and extends into the Neogene.

The Cretaceous–Paleogene transition is covered by the marine sediments of the Navesink and Hornerstown Formations of New Jersey. Whereas the Navesink Formation is of late Cretaceous (Maastrichtian) age, the upper parts of the Hornerstown Formation were deposited in the Paleocene (Parris and Hope 2002). Unfortunately, most avian specimens come from the basal part of the Hornerstown Formation, whose age is more controversial and is either latest Cretaceous or earliest Paleocene (Olson 1994; Parris and Hope 2002). Bird bones were also reported from the late Paleocene (Tiffanian) marine Aquia Formation of Maryland and Virginia (Olson 1994), and from early Tiffanian fluviolacustrine beds of the Wannagan Creek Quarry of North Dakota (Benson 1999).

After refinement of the collection techniques (Houde 1988), the early Eocene (latest Wasatchian to early Bridgerian) sediments of the Willwood Formation of the Bighorn Basin in Wyoming yielded a great number of fossil birds, many of which are still undescribed (see Table 4.2 in Feduccia 1999). Isolated avian bones were also described from the early Eocene (ca. 53 Ma) Nanjemoy Formation of Virginia in eastern North America (Olson 1999a). These deposits are of marine origin, but similar to those of the London Clay also include remains of land birds.

Certainly the most renowned North American locality for early Eocene bird skeletons, however, is the Green River Formation of Wyoming, Colorado, and Utah (Grande 1980; see Table 4.2 in Feduccia 1999; Weidig 2003). Its deposits represent the sediments of three lakes, Lake Gosiute, Lake Uinta, and Fossil Lake, which existed, at least in parts, from the late Paleocene to the middle Eocene. Most nonpresbyornithid fossil birds come from Fossil Lake, which was smaller and much deeper than the other two lakes, and whose existence was confined to the early Eocene (late Wasatchian; Grande 1980).

The sediments of the middle Eocene (Bridgerian) Bridger Formation of the Green River Basin in southwestern Wyoming originated in different depositional environments, including river channels, floodplains, and lakes, and most birds are represented by isolated bones.

Important North American localities for middle Eocene to late Oligocene bird fossils are situated in the extensively eroded badlands of South Dakota, Colorado, Wyoming, Nebraska, and Utah. According to the revised biostratigraphy (Prothero 1994), the White River Group of the badlands is formed by the middle Eocene (Uintan) Uinta Formation, the late Eocene (Chadronian) Chadron Formation, and the Oligocene Brule Formation, which is divided into the Orellan Scenic Member and the Whitneyan Poleslide Member (Prothero and Emry 1996; Terry et al. 1998; Stoffer 2003). The paleoenvironment of these localities is characterized by an increasing aridity toward the Oligocene. Whereas there were dense forests in the late Eocene, wooded grassland occurred in the early Oligocene, and rather dry open grasslands dominated in the late Oligocene (see p. 153 in Prothero 1994).

A few avian fossils were also found in the latest Eocene (34 Ma) fluviolacustrine deposits of the Florissant Fossil Beds National Monument in Colorado, and are of particular interest as they consist of articulated skeletons (Chandler 1999; Ksepka and Clarke 2009).

2.4 Central and South America

Apart from a humerus fragment of a pelagornithid bird from the middle Eocene of Mexico (González-Barba et al. 2002), there are no published bird fossils from the Paleogene of Central America. The Cenozoic avian fossil record of South America was summarized by Tonni (1980), but many Paleogene fossils were described after this study. The earliest specimens stem from late Paleocene (Itaboraian) marl fillings of the Bacia Calcária of Itaboraí in Brazil. The described fossils from this site belong to a palaeognathous bird (*Diogenornis*), a representative of the Phorusrhacidae (*Paleopsilopterus*), and a small, long-legged taxon (*Eutreptodactylus*).

Some bird fossils were described from the Casamayor Formation of the Chubut Province in the Argentinian part of Patagonia. This formation was considered to be of early Eocene age by earlier authors, but the exact age of the Casamayoran land mammal age is now regarded uncertain, possibly spanning most of the early and middle Eocene (see p. 17 in Rose 2006).

Avian remains are more abundant in the late Oligocene (Deseadan land mammal age) of the Santa Cruz Province of Patagonia (the Deseadan was assumed to be of early Oligocene age by earlier authors; see Berggren and Prothero 1992; Rose 2006). The paleoenvironment of these temperate latitude localities during the Oligocene was dominated by an open woodland savanna with river banks and floodplains (Webb 1978). Several avian taxa were also reported from the late Oligocene or early Miocene of the Tremembé Formation of the Taubaté Basin of São Paulo State in Brazil. These lacustrine deposits consist of bituminous shales in which articulated skeletons are found, and layers of montmorillonitic clay that yielded isolated bones; the sediments were deposited in a shallow, alkaline lake (Alvarenga 1999). The first avian remain, a fossilized feather, was already mentioned by Shufeldt (1916).

2.5 Africa

Paleogene bird remains from Africa are scarce. A substantial but rather taxon-poor avifauna was reported from the late Paleocene and early Eocene phosphatic beds of the Ouled Abdoun Basin in Morocco, whose fossiliferous deposits originated in an epicontinental sea (Bourdon 2005, 2006; Bourdon et al. 2005). All avian species described so far represent marine taxa, and remains of the Pelagornithidae and Prophaethontidae predominate.

A few bird fossils were also found in the middle Eocene of Nigeria (Andrews 1916) and Togo (Bourdon 2006), but the only other Paleogene African avifauna of significance comes from the late Eocene–early Oligocene deposits of the Jebel Qatrani Formation of the Fayum in Egypt (Rasmussen et al. 1987, 2001). This formation is of fluvial origin and stretches over the Eocene–Oligocene boundary. Although the age of the lower sequences has been debated, it is now considered to be late Eocene (Rasmussen et al. 2001). The avian specimens from the Jebel Qatrani Formation consist of isolated and often fragmentary bones.

2.6 Australia, New Zealand, and Antarctica

Likewise, very little is known about the Paleogene avifaunas of Australia, and most fossil birds from this period were described after the reviews by Vickers-Rich (1991) and Boles (1991). The continent has no Paleocene fossil record of birds, and the only Eocene avian specimens stem from the deposits of the early Eocene Tingamarra Local Fauna near Murgon (Queensland), whose sediments are of fluviolacustrine origin and have a minimum age of 54.6 million years (Boles 1999). The Oligocene fossil record is more comprehensive, and a fair number of late Oligocene bird fossils come from the Riversleigh Formation in Queensland. The more than 200 named sites of this locality were deposited in large lakes, shallow pools, and caves, and cover a wide stratigraphic range, from the late Oligocene into the Neogene (Boles 1997a, 2001a, 2005a). The described fossil birds include both aquatic and terrestrial taxa. Late Oligocene (24–26 Ma) birds were also found in the Lake Eyre Basin from the Namba and Etadunna Formations in South Australia, whose sediments were deposited in a primarily lacustrine environment and yielded remains of the Casuariidae, Anatidae, Accipitridae, Rallidae, Burhinidae, Palaelodidae, Phoenicopteridae, and Columbidae (Boles 2001b; Worthy 2009).

Unlike in the abundant Quaternary fossil record and except for penguins, Paleogene birds are also rare in New Zealand (Worthy and Holdaway 2002). The Eocene and Oligocene localities where penguins have been found were summarized by Simpson (1971). More recently, well-preserved remains of fossil stem group representatives of the Sphenisciformes were found in the Paleocene (ca. 58–61 Ma) Waipara Greensand (Slack et al. 2006).

The Paleogene record of neornithine birds from Antarctica was reviewed by Tambussi and Acosta Hospitaleche (2007). Most specimens come from Seymour Island. Except for one Paleocene record from the Cross Valley Formation (Tambussi et al. 2005), these were found in the early and late Eocene of the La Meseta Formation, which was deposited in a nearshore deltaic environment (Tambussi and Acosta Hospitaleche 2007).

Chapter 3
Higher-Level Phylogeny of Extant Birds

Despite their paramount importance for stimulation of new research in avian systematics, the often-cited DNA–DNA hybridization studies of Sibley and Ahlquist (1990) have proven to be an unreliable basis for phylogenetic inferences (Harshman 2007). The higher-level phylogeny of neornithine birds remains incompletely understood, but some consensus has been reached in recent phylogenetic analyses, and provides a framework for an interpretation of fossil taxa (Cracraft et al. 2004; Ericson et al. 2006; Mayr 2008b; Hackett et al. 2008).

Results of molecular analyses are particularly convincing, if clades are congruently obtained by analyses of independent data, such as nuclear and mitochondrial DNA, or gene sequences on different chromosomes. However, although molecular analyses are an important tool for the reconstruction of the higher-level phylogeny of birds, only a phylogeny which is based on morphological characters allows the assignment of fossil taxa.

There have been some attempts to analyze the higher-level phylogeny of extant birds with large morphological data sets (e.g., Mayr and Clarke 2003; Livezey and Zusi 2007). Concerning several major clades, the results of these analyses are, however, not in concordance with well-supported clades obtained in studies of molecular data. As detailed elsewhere (Mayr 2008b), such large-scale analyses of equally weighted morphological characters run the risk that many simple homoplastic characters overrate fewer ones of greater phylogenetic significance. Analyses of smaller sets of well-defined characters may thus be a more appropriate approach in the case of morphological data. As a basis for the phylogenetic assignment of fossil taxa, identification of morphological apomorphies is further needed for many clades.

Figure 3.1 shows the cladogram which serves as a phylogenetic framework for the present study. This tree summarizes clades which were congruently obtained by two molecular analyses of different gene sequences, i.e., combined sequences of the c-*myc* exon 3, RAG-1 exon, myoglobin intron 2, and ornithine decarboxylase introns 6 and 7 with the intercepting exon 7, as well as the β-fibrinogen intron 7 (see Figs. ESM-4, ESM-6 in Ericson et al. 2006; Mayr 2008b). All of these clades were also recovered in a recent analysis of Hackett et al. (2008), and several can be supported with derived morphological characters. In the following some of the major clades are briefly discussed.

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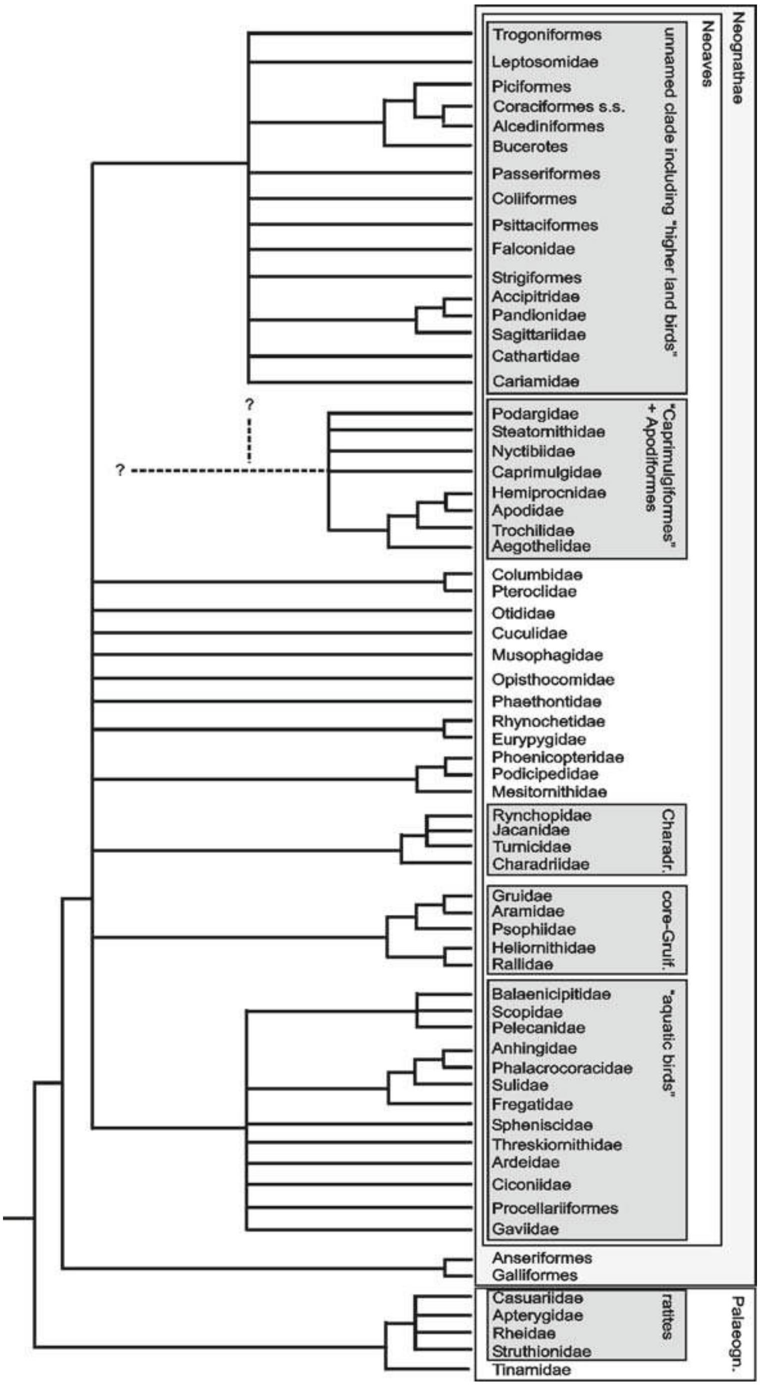

Fig. 3.1 Hypothesis on the phylogeny of the extant representatives of Neornithes. Concerning the interrelationships of neognathous birds, clades are depicted that were congruently obtained in analyses of two independent molecular data sets (see Figs. ESM-4, ESM-6 in Ericson et al. 2006; Mayr 2008b)

There is consensus among most systematists that neornithine birds can be divided into the sister taxa Palaeognathae and Neognathae (Cracraft et al. 2004; Harshman 2007; Livezey and Zusi 2007). Presumably apomorphic features of palaeognathous birds are, among others, the lack of fusion between the maxillar process of the nasal bone and the maxillary bone, as well as the presence of a pair of furrows on the ventral surface of the mandibular symphysis, whose dorsal surface further is flat. Neognathous birds exhibit an intrapterygoidal joint, which develops in early ontogeny and allows a greater mobility of the palate; in addition, there is a conjoint auditory tube (tuba auditiva communis) and the ilioischiadic foramina of the pelvis are caudally closed.

Within Neognathae, Galloanseres, i.e., a clade formed by Galliformes (landfowl) and Anseriformes (waterfowl), is the sister group of the remaining taxa, the Neoaves. The latter share a derived reduction of the phallus and associated structures, which independently occurred in some Tinamidae and Galliformes (Livezey and Zusi 2007; Montgomerie and Briskie 2007; Mayr 2008b; Brennan et al. 2008).

The phylogeny within Neoaves is only poorly resolved, and many of the traditional (e.g., sensu Wetmore 1960) higher-level taxa have been shown to be nonmonophyletic. Prime examples therefore are the “Pelecaniformes” (pelicans and allies), “Ciconiiformes” (storks and allies), “Gruiformes” (cranes and allies), “Caprimulgiformes” (nightjars and allies), and “Coraciiformes” (rollers and allies).

The “Pelecaniformes” were long considered to be well established, because the representatives share a number of derived features that are not found in other birds, such as totipalmate feet and a gular pouch. In current analyses, however, only a clade including the Fregatidae (frigatebirds) and Suloidea [Sulidae (gannets and boobies), Phalacrocoracidae (cormorants), and Anhingidae (anhingas)] is congruently obtained. The Pelecanidae (pelicans) belong to a clade that also includes the Balaenicipitidae (shoebill) and Scopidae (hamerkop), i.e., taxa that were traditionally assigned to the “Ciconiiformes.” The position of the Phaethontidae (tropicbirds), which were assigned to the “Pelecaniformes” by earlier authors, is uncertain (Cracraft et al. 2004; Fain and Houde 2004; Ericson et al. 2006; Harshman 2007; Mayr 2008b; Hackett et al. 2008).

The traditional “Gruiformes” encompass various groups of superficially rail- or crane-like birds. Monophyly of a taxon including these birds has never been well established and current analyses only support monophyly of the “core-Gruiformes,” i.e., a clade including the Rallidae (rails), Heliornithidae (finfoots), Psophiidae (trumpeters), Aramidae (limpkin), and Gruidae (cranes). The affinities of most other gruiform taxa are still subject to debate, although there is consensus that the Eurypygidae (sunbittern) are the sister taxon of the Rhynochetidae (kagu) (Cracraft et al. 2004; Ericson et al. 2006; Fain et al. 2007; Harshman 2007; Mayr 2008b; Hackett et al. 2008). As shown by various molecular analyses of both mitochondrial and nuclear gene sequences, the Turnicidae (buttonquails), quail-like birds of open habitats of the Old World, which were traditionally also classified into the “Gruiformes,” are aberrant representatives of the Charadriiformes (shorebirds and allies; Paton et al. 2003; Paton and Baker 2006; Fain and Houde 2007).

The “Caprimulgiformes” include five extant taxa of crepuscular or nocturnal birds: the Steatornithidae (oilbird), Podargidae (frogmouths), Caprimulgidae (nightjars), Nyctibiidae (potoos), and Aegothelidae (owlet-nightjars). There is now congruent support for a clade including these birds and the Apodiformes (swifts and hummingbirds). The “Caprimulgiformes” are, however, paraphyletic, and the Aegothelidae are the sister taxon of the Apodiformes (Mayr 2002b, 2008b; Mayr et al. 2003; Ericson et al. 2006; Hackett et al. 2008).

The phylogenetic affinities of the Leptosomidae (courol) are unresolved, but the taxon clearly does not belong to the “Coraciiformes” (Mayr 2008b, c). Analyses of nuclear gene sequences also congruently support paraphyly of the remaining “Coraciiformes” with respect to the Piciformes (woodpeckers and allies; Mayr et al. 2003; Fain and Houde 2004; see Fig. 27.4 in Cracraft et al. 2004; Ericson et al. 2006; Hackett et al. 2008).

Concerning the “Falconiformes” (diurnal birds of prey), there is congruent molecular evidence for a clade including the Sagittariidae (secretary bird), Pandionidae (osprey), and Accipitridae (hawks and allies), which also share a derived syrinx morphology. The affinities of the Cathartidae (New World vultures) are less certain, but some molecular analyses indicate sister group relationship to the clade (Sagittariidae + (Pandionidae + Accipitridae)). The position of the Falconidae (falcons) is unresolved (Griffiths 1994; Cracraft et al. 2004; Ericson et al. 2006; Mayr 2008b; Brown et al. 2008; Hackett et al. 2008).

There are few strongly supported clades within Neoaves, but one of these is certainly that including the Podicipediformes (grebes) and Phoenicopteriformes (flamingos), which is obtained in virtually all molecular analyses including these two taxa (van Tuinen et al. 2001; Cracraft et al. 2004; Ericson et al. 2006; Harshman 2007; Brown et al. 2008; Hackett et al. 2008). Although grebes and flamingos are quite different in external morphology, they share a number of derived morphological characters, including the presence of 11 primaries (except for the Ciconiidae all other avian taxa have ten or fewer primaries), nail-like ungual phalanges, and a chalky layer of amorphous calcium phosphate on the eggshell (Mayr 2004a; Manegold 2006). Phoenicopteriformes and Podicipediformes are further parasitized by an exclusively shared taxon of cestodes (Amabiliidae), and their phthirapteran feather lice are closely related (Mayr 2004a; Johnson et al. 2006). The closest extant relatives of the flamingo/grebe clade are unknown. Whereas nuclear gene sequences indicate a possible sister group relationship to the Madagascan Mesitornithidae (mesites; Mayr 2008b), a study based upon mitochondrial sequences suggests a sister group relationship to the Charadriiformes (Morgan-Richards et al. 2008; Mesitornithidae were not included in that analysis).

Fain and Houde (2004) suggested an early dichotomy within Neoaves into two lineages called “Metaves” and “Coronaves,” with “Metaves” including the Columbiformes (doves and sandgrouse), Phoenicopteriformes, Podicipediformes, Mesitornithidae, Rhynochetidae, Eurypygidae, Opisthocomidae (hoatzin), Phaethontidae, Apodiformes, and the nonmonophyletic “Caprimulgiformes.” However, a “metavian” clade has so far only been obtained in analyses including β-fibrinogen sequences (see also Morgan-Richards et al. 2008; Hackett et al. 2008).

Whereas individual "metavian" taxa share derived characters with representatives of the "Coronaves," there exist no morphological apomorphies, which support a clade including such exceedingly different groups as hummingbirds, flamingos, and the hoatzin. Fain and Houde's (2004) assumption that the presence of a notarium is such a character was erroneous, as apodiform birds, Phaethontidae, and most "Caprimulgiformes" lack this feature, which instead occurs in some "Coronaves," e.g., the Gruidae, Threskiornithidae (ibises), and Falconidae.

Molecular analyses support a clade including various aquatic or semiaquatic taxa, i.e., Gaviiformes (loons), Procellariiformes (tubenoses), Sphenisciformes (penguins), the nonmonophyletic "Pelecaniformes" except Phaethontidae, as well as the taxa of the nonmonophyletic "Ciconiiformes." This clade resulted from analyses of combined sequences of four nuclear genes (see Fig. ESM-6 in Ericson et al. 2006), a further large-scale study of nuclear DNA (Hackett et al. 2008), and is also supported by analyses of whole mitochondrial genome sequences (Gibb et al. 2007; Morgan-Richards et al. 2008; Slack et al. 2006). A "waterbird clade," albeit with a somewhat different composition, was assumed by earlier authors (e.g., Olson 1985). A similar clade was obtained in an analysis of morphological characters by Livezey and Zusi (2007), but also included the Phoenicopteriformes and Podicipediformes in the analysis of these authors.

Most authors regarded penguins as closely related to either the Procellariiformes or the Gaviiformes. The morphological evidence for either hypothesis is, however, weak and penguins share several derived characters with representatives of the clade (Fregatidae + Suloidea) which are absent in the Gaviiformes and Procellariiformes (Mayr 2005b). Most notable among these are greatly reduced external narial openings, opisthocoelous thoracic vertebrae, a very large patella which bears a marked furrow/canal for the tendon of the ambiens muscle (absent in the Fregatidae), a single-lobed nasal gland with only a single efferent duct, a very short tarsometatarsus, and a layer of amorphous calcium carbonate which covers the eggshell. The young of penguins, Fregatidae, and Suloidea are further fed down the gullet of the adults. Although penguins lack a totipalmate foot, this feature appears to have evolved several times independently. In addition to the Fregatidae and Suloidea, it is also present in the Pelecanidae and Phaethontidae. Moreover, because the hallux of extant Sphenisciformes is greatly reduced, the possibility cannot be excluded that their stem lineage representatives had totipalmate feet.

Molecular analyses do not show congruent results concerning the affinities of penguins (Sibley and Ahlquist 1990; van Tuinen et al. 2001; Cracraft et al. 2004; Watanabe et al. 2006). Sister group relationship to the clade (Fregatidae + Suloidea) resulted from an analysis of nuclear gene sequences by Fain and Houde (2004). Mitochondrial sequences support a clade including the Fregatidae, Suloidea, Spheniscidae, and Phaethontidae (Brown et al. 2008), whereas Hackett et al.'s (2008) analysis of nuclear gene sequences resulted in a sister group relationship between the Sphenisciformes and the Procellariiformes.

Earlier authors assumed that various extant birds whose hindlimbs lack the ambiens muscle are closely related, and a group including these birds was informally termed "higher land birds" by Olson (1985). In its usual composition, this assemblage includes the Strigiformes (owls), Coliiformes (mousebirds), Trogoniformes (trogons), Piciformes, Passeriformes (passerines), Apodiformes, "Caprimulgiformes," and "Coraciiformes" (Olson 1985; Mayr et al. 2003). Molecular analyses do not support a clade including these taxa, but the two analyses that form the basis of the cladogram in Fig. 3.1 congruently obtained a clade including the "higher land birds," as well as the "Falconiformes," Psittaciformes (parrots), and, certainly most unexpectedly, the Cariamidae (seriemas), which were traditionally assigned to the "Gruiformes." At present, this clade, which also resulted from the analysis of Hackett et al. (2008), cannot be characterized with morphological apomorphies.

Chapter 4
Mesozoic Neornithes

To set the following sections on Paleogene birds into a full context, the Mesozoic fossil record of Neornithes is briefly outlined in this chapter. In-depth information on Mesozoic nonneornithine birds can be found in Chiappe and Witmer (2002) and Chiappe (2007).

Hope (2002) reviewed the Mesozoic fossil record of putative Neornithes and listed the described taxa; a similar table was published in Dyke (2001a). All of the specimens that were considered correctly identified by Hope (2002) are from late Cretaceous deposits, mainly from the Maastrichtian of the North American Lance Formation. They were assigned to stem group Galliformes (*Palintropus*), the anseriform Presbyornithidae, ?Charadriiformes (*Graculavus*, *Cimolopteryx*, *Volgavis*), Gaviiformes (*Neogaeornis*, *Polarornis*), ?Procellariiformes (*Lonchodytes*), Pelecaniformes (*Torotix* and unnamed species, which were identified as representatives of the Phalacrocoracidae), Psittaciformes, and Neornithes incertae sedis [*Ceramornis*, *Elopteryx*, *Iaceornis* ("*Apatornis*")].

Most of these taxa are based on very fragmentary remains, and none can be unambiguously identified. The taxon *Palintropus*, for example, is only known from a scapula and omal extremities of the coracoid, and was tentatively assigned to the galliform Quercymegapodiidae (see Sect. 6.1.4) by Hope (2002). However, *Palintropus* can at best be the sister taxon of all other Galliformes, because the coracoid exhibits a foramen for the supracoracoideus nerve (see Fig. 15.3 in Hope 2002), a plesiomorphic feature, which is invariably absent in Cenozoic and extant galliform birds including the Quercymegapodiidae (see p. 353 in Hope 2002). Longrich (2009) described further material of *Palintropus* from the late Cretaceous (Campanian) of Canada, and questioned its neornithine affinities.

Dyke and Mayr (1999) detailed that assignment of a fragmentary mandible from the late Cretaceous of the Lance Formation to the Psittaciformes (Stidham 1998) is far from convincing, and even neornithine affinities of the specimen cannot be reliably established. Hope (2002) retained this fossil in the Psittaciformes, noting that the presence of a fused mandibular symphysis supports its assignment to Neornithes. However, this feature also occurs in the edentulous oviraptorosaurs (Elzanowski 1999), and it is well possible that the Lance Formation mandible comes from a representative of the Caenagnathidae, a North American taxon of the Oviraptorosauria.

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Hope's (2002) discussion of the phylogenetic affinities of *Apatornis celer* Marsh, 1873 was based on skeletal remains, which because of a lack of overlap of skeletal elements with the *A. celer* holotype were assigned to the new species *Iaceornis marshi* by Clarke (2004). Hope (2002) classified these specimens as Neornithes incertae sedis, but discussed a possible sister group relationship to the Anseriformes. By contrast, an analysis by Clarke (2004) supported the position of *I. marshi* outside crown group Neornithes, although the character evidence for either placement is still weak (see p. 149 in Clarke 2004).

The fossil material of the putative gaviiform *Polarornis gregorii* Chatterjee, 2002 from the late Cretaceous López de Bertodano Formation of Seymour Island (Antarctica) consists of a partial skeleton, including the proximal part of the bill and the rostral portion of the cranium, parts of the otic region, a few vertebrae, a small sternum fragment, femora, and a proximal tibiotarsus. Despite this very fragmentary representation, detailed reconstructions of the entire skull and skeleton were published in the original description (Chatterjee 2002; see also Mayr 2004b). This presumably led Hope (2002) to erroneously state that *P. gregorii* is based on a "relatively complete skeleton"; Dyke and van Tuinen (2004, p. 160) likewise mistakenly assumed that the skull of this species is largely complete. The other putative late Cretaceous gaviiform, *Neogaeornis wetzeli* Lambrecht, 1929, is known from a tarsometatarsus from the Quiriquina Formation of Chile (Olson 1992a). *N. wetzeli* is a smaller species than *P. gregorii*, but because the tarsometatarsus of the latter is unknown, the affinities between these species cannot be established with confidence. Identification of neither *Polarornis* nor *Neogaeornis* can be considered unambiguous. However, the presence of well-developed, proximally protruding cnemial crests on the tibiotarsus of *Polarornis* indicates that this taxon had a foot-propelled aquatic locomotion, and was thus certainly not a stem group representative of the Spheniscidae (contra Feduccia 1999, p. 403). Chatterjee et al. (2006) briefly commented on a second, smaller and more gracile species of *Polarornis* from the late Cretaceous of Vega Island in Antarctica that awaits formal description.

Not included in Hope's (2002) survey were the birds from the late Cretaceous or early Paleocene Hornerstown Formation of New Jersey (Olson and Parris 1987; Parris and Hope 2002). Most of these were assigned to the "form-family" Graculavidae by Olson and Parris (1987), which was regarded a "convenient catch-all, intended as such" by Olson (1999a, p. 125). The species from the New Jersey deposits originally included in the "Graculavidae" by Olson and Parris (1987) are *Graculavus velox* Marsh, 1872, *Palaeotringa littoralis* Marsh, 1870, *P. vagans* Marsh, 1872, *Telmatornis priscus* Marsh, 1870 (which also occurs in the unambiguously late Cretaceous Navesink Formation), *Anatalavis* ("*Telmatornis*") *rex* (Shufeld, 1915), and *Laornis edvardsianus* Marsh, 1870.

Although Olson and Parris (1987) already considered it likely that the "Graculavidae" constitute a polyphyletic assemblage, "graculavids" found their way into the literature as "transitional shorebirds" (Feduccia 1999). However, *A. rex* was meanwhile referred to the Anseriformes by Olson (1999; Sect. 6.4.2), and Olson (1985) and Olson and Parris (1987) showed that the other New Jersey taxa of the "Graculavidae" are very similar to the Presbyornithidae, which are now also regarded as anseriform birds (Sect. 6.4.3). The resemblances to presbyornithids are especially strong in the case of *Graculavus velox*, which is known from a proximal humerus (see Fig. 4 in Olson and Parris 1987). Another species of *Graculavus*, *G. augustus*, was described by Hope (1999) from the late Cretaceous Lance Formation, and is also only represented by the proximal end of a humerus. This species is larger than *G. velox*, but otherwise is morphologically very similar.

Likewise, the holotype and only known specimen of the large *Laornis edvardsianus*, a distal tibiotarsus, was likened to the Presbyornithidae by Olson and Parris (1987). Because of its large size and similar overall morphology, it also needs to be compared in detail with the Pelagornithidae (Sect. 6.5).

Novacaesareala hungerfordi Parris and Hope, 2002 from the Hornerstown Formation is based on the distal end of a humerus and associated wing fragments. The phylogenetic affinities of this species were considered uncertain by Parris and Hope (2002), who noted, however, that it resembles extant “Pelecaniformes” in the very short flexor process of the humerus. Compared with other Cretaceous taxa, and as detailed by Parris and Hope (2002), *N. hungerfordi* most closely resembles *Torotix clemensi* Brodkorb, 1963 from the Lance Formation, which is known from a distal humerus and was classified into the “Pelecaniformes” by Hope (2002).

Other taxa from the Hornerstown Formation were tentatively assigned to the palaeognathous Lithornithidae (Parris and Hope 2002; unnamed species; see Sect. 5.1) and to the Procellariiformes (Olson and Parris 1987; *Tytthostonyx glauconiticus* Olson and Parris 1987; see Sect. 7.5).

Also omitted from Hope’s (2002) survey was *Gargantuavis philoinos* Buffetaut and Le Loeuff, 1998 from the late Cretaceous of France that was described as “a bird with an advanced synsacrum, possibly as large as a modern cassowary or ostrich” (see p. 110 in Buffetaut et al. 1995). The published material assigned to this species consists of a synsacrum and a referred femur (Buffetaut and Le Loeuff 1998), the morphology of both being very different from that of neornithine birds. The locality also yielded remains of very large azhdarchid pterosaurs, whose femur and pelvis are still unknown (Buffetaut 2001). Trevor Worthy (personal communication) considers a possible pterosaurian identity of *Gargantuavis*, which would be in line with the cranially positioned acetabular foramen. In any case, the wide pelvis of *Gargantuavis* is very unlike the narrow one typically found in large groundbirds (ratites, Gastornithidae, Phorusrhacidae).

Since Hope’s (2002) account, a few additional Mesozoic birds with a neornithine morphology have been reported. The fragmentary wing bones of *Limenavis patagonica* Clarke and Chiappe, 2001 from the late Cretaceous of Patagonia (Argentina) are of essentially modern appearance, but the species was assumed to be outside crown group Neornithes by Clarke and Chiappe (2001). Owing to the very fragmentary nature of the material, the affinities of this bird are best regarded uncertain.

Clarke (2004) hypothesized that the incomplete distal tarsometatarsus that formed the holotype of “*Ichthyornis*” *lentus* Marsh, 1877 is from a galliform bird, and assigned it to the new taxon *Austinornis*. Possible affinities to the galliform-like *Palintropus* (see above) thus need to be taken into consideration.

A fragmentary skeleton from the late Cretaceous López de Bertodano Formation of Vega Island (Antarctica) which was assigned to the Presbyornithidae by Noriega and Tambussi (1995) was described as *Vegavis iaai* by Clarke et al. (2005b). The analysis of these authors supported a position of *V. iaai* within a clade including the Presbyornithidae and Anatidae. Although Clarke et al. (2005b) noted differences to *Presbyornis* in limb proportions, close comparisons with the above-mentioned New Jersey fossils still have to be undertaken. Also from the late Cretaceous of Vega Island, Case et al. (2006) reported a femur of a large and putatively cursorial bird.

Agnolin et al. (2006) described an incomplete, odd-looking coracoid from the late Cretaceous of Patagonia, which they considered to be from a neornithine bird. This specimen comes from a quail-sized species and its position within Neornithes has not yet been convincingly established.

In summary, the late Cretaceous fossil record of neornithine birds is still poor and includes many fragmentary specimens of uncertain phylogenetic affinities. If *Vegavis*, *Austinornis*, and *Palintropus* indeed belong to the Galloanseres, they imply the existence of at least stem lineage representatives of palaeognathous birds and Neoaves by the late Cretaceous (Clarke et al. 2005b). The earliest unambiguous records of virtually all neoavian taxa stem from Paleogene deposits, so much the more so as the age of the Hornerstown Formation, where the putative procellariiform *Tytthostonyx* comes from, is uncertain. Given the fact that the Paleocene fossil record already includes such morphologically disparate taxa as Sphenisciformes (penguins) and Strigiformes (owls), there can, however, be little doubt that stem lineage representatives of some taxa of crown group Neoaves were already in existence in the late Cretaceous. Such an assumption has received further support from the recent discovery of as yet undescribed sphenisciform-like fossils from the latest Cretaceous (about 65 Ma) of Chatham Island (Hansford 2008).

Molecular clock data also consistently support a diversification of neoavian higher-level taxa in the late or even middle Cretaceous (Cooper and Penny 1997; Paton et al. 2002; van Tuinen and Dyke 2004; Pereira and Baker 2006a, b; Crowe et al. 2006; Baker et al. 2007; Brown et al. 2008). Much more controversial is the exact degree of the Mesozoic radiation of crown group Neornithes, i.e., whether there already was a late Cretaceous diversification of crown group representatives of extant "orders" or even "families," as suggested by many molecular analyses (van Tuinen et al. 2006; Baker et al. 2007; Brown et al. 2008). The literature on this subject is quite extensive, and it is beyond the scope of the present work to give a full account of it. However, molecular studies not only face problems with the lack or inadequacy of calibration errors and with heterogeneous nucleotide substitution rates (Graur and Martin 2004; van Tuinen et al. 2006; see also Heads 2005), but also with the correct identification of fossil taxa used for calibration of the molecular clocks. This is true, for example, for several molecular studies which yielded a Cretaceous divergence age of crown group Galliformes, with calibration points based on misidentified fossil taxa (van Tuinen and Dyke 2004; Pereira and Baker 2006a, b; Crowe et al. 2006; for a critique see Mayr and Weidig 2004; Mayr 2008d).

It has been assumed that this discrepancy between molecular and fossil data may in part be due to the fact that early stem group representatives of extant taxa are difficult to recognize as such in the fossil record (van Tuinen et al. 2006; Brown et al. 2008). This concern is at best appropriate to a certain phylogenetic level. If early stem group representatives of major neoavian clades had a plesiomorphic "Galloanseres-like" morphology in the late Cretaceous, their correct identification would be hardly possible on the basis of fragmentary material. A diversification of, for example, crown group Passeriformes (Ericson et al. 2003; Pereira and Baker 2006b) or Psittaciformes (Miyaki et al. 1998) in the late Cretaceous, however, implies the presence of modern-type passerines or parrots by that time. These would certainly be recognizable by their osteological features. On the basis of our current knowledge of the fossil record, a Cretaceous diversification of, for example, crown group Galliformes, Psittaciformes, and Passeriformes is a highly unlikely assumption, so much the more so as crown group representatives of these taxa do not even occur in the fairly well known early Paleogene fossil record (see also Rose 2006 concerning a similar controversy surrounding the mammalian fossil record).

Finally it should be noted that although it is generally assumed that all nonneornithine birds became extinct at the Cretaceous–Paleogene boundary (Feduccia 1995, 2003; van Tuinen et al. 2006), the factual evidence for this hypothesis is rather weak, given the poor early Paleocene fossil record of birds. At least *Qinornis paleocenica* Xue, 1995 from the early Paleocene of China may represent a nonneornithine avian lineage, which survived the Cretaceous–Paleogene extinction events (Mayr 2007a). This species is known from a partial foot, and the incomplete fusion of the metatarsals is more reminiscent of the condition in Mesozoic taxa outside Neornithes than in juvenile neornithine birds (contra Xue 1995).

Chapter 5
Palaeognathous Birds

Extant Palaeognathae include the South American and Central American tinamous (Tinamidae) and the flightless ratites, i.e., the New Zealand Apterygidae (kiwis), the South American Rheidae (rheas), the African Struthionidae (ostrich), and the Casuariidae of the Australian region (cassowaries and emus). Recently extinct ratite taxa are the Aepyornithidae (elephant birds) of Madagascar and the Dinornithidae (moas) of New Zealand.

Whereas monophyly of palaeognathous birds is supported by virtually all recent analyses, the relationships within the group are still controversial. Most authors (e.g., Sibley and Ahlquist 1990; Livezey and Zusi 2007) assumed sister group relationship between the Tinamidae and ratites, but analyses of nuclear DNA by Hackett et al. (2008) and Harshman et al. (2008) strongly supported a clade including tinamous, Casuariidae, and Apterygidae (see also Fig. 27.4 in Cracraft et al. 2004). If paraphyly of ratites is confirmed by future studies, flightlessness evolved independently within several palaeognathous lineages, as already assumed by some earlier authors (e.g., Olson 1985; Houde 1988; Feduccia 1999; contra Hackett et al. 2008, who considered an origin of the volant tinamous from a flightless ancestor).

Studies of morphological data resulted in a sister group relationship between the Apterygidae and all other living ratites (see Fig. 7.2 in Lee et al. 1997; Livezey and Zusi 2007), but molecular analyses of both nuclear and mitochondrial sequences congruently supported a sister group relationship between the Apterygidae and Casuariidae (see Fig. 7.3 in Lee et al. 1997; van Tuinen et al. 1998; Haddrath and Baker 2001; Paton et al. 2002; Hackett et al. 2008). Apterygidae and Casuariidae share very short wings and reduced feather vanes, but kiwis (and moas) differ from other ratites in several presumably plesiomorphic features, such as the absence of supraorbital processes and the presence of a hallux. In contrast to that of other ratites, the distal tibiotarsus of the Apterygidae and Dinornithidae exhibits a supratendinal bridge.

The distribution of extant palaeognathous birds is restricted to the Southern Hemisphere, but several fossil taxa were reported from the Paleogene of Europe and North America. Of the modern groups, however, only the Rheidae and Casuariidae have a Paleogene fossil record. The earliest unambiguous stem group representative of the Struthionidae is *Struthio coppensi* Mourer-Chauviré et al., 1996 from the early Miocene of Namibia. According to Mourer-Chauviré et al. (1996),

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the fossils of this species suggest that didactyl ostriches originated in Africa before the Miocene, from where they dispersed into Eurasia in the Neogene. The earliest fossil Tinamidae are from the Miocene of Argentina (Bertelli and Chiappe 2005). Eggshell fragments of putative Dinornithidae were reported from the early/middle Miocene of New Zealand (Worthy et al. 2007). Fossil Aepyornithidae and Apterygidae are so far only known from Quaternary deposits.

5.1 †Lithornithidae

Unambiguous representatives of these superficially tinamou-like birds (Fig. 5.1) were reported from the late Paleocene to middle Eocene of North America and the early and middle Eocene of Europe. Although some remains from the London Clay

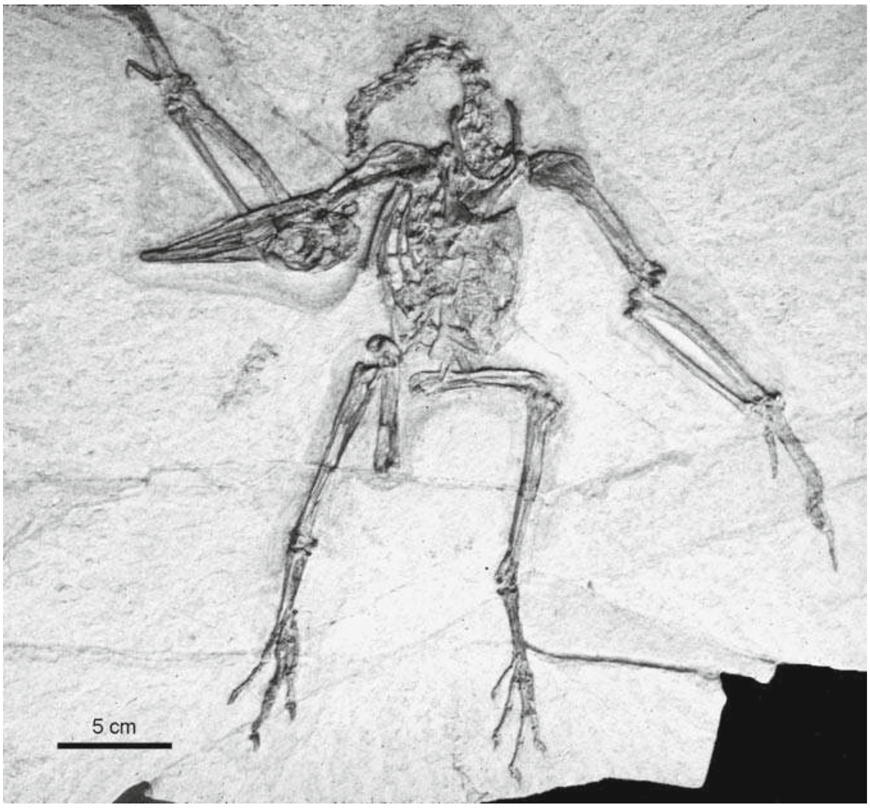

Fig. 5.1 Skeleton of the lithornithid *Pseudocrypturus cercanaxius* Houde, 1988 from the early Eocene Green River Formation (private collection in Switzerland, cast in Forschungsinstitut Senckenberg, Frankfurt am Main, Germany). (Photo courtesy of Peter Houde)

are among the earliest fossil birds to have been described scientifically, lithornithids were first recognized as a distinctive palaeognathous taxon by Houde and Olson (1981) and Houde (1986, 1988).

According to Houde (1988), lithornithids include the following eight species: *Lithornis vulturinus* Owen, 1840 (early Eocene of the London Clay and the Fur Formation), *L. plebius* Houde, 1988 (early Eocene of the Willwood Formation and possibly the London Clay), *L. promiscuus* Houde, 1988 (early Eocene Willwood Formation), *L. celetius* Houde, 1988 [late Paleocene (Tiffanian) of Montana and Wyoming], *L. nasi* (Harrison, 1984) (early Eocene of the London Clay), ?*L. hookeri* (Harrison, 1984) (early Eocene of the London Clay), *Pseudocrypturus cercanaxius* Houde, 1988 (early Eocene of the Green River Formation and the London Clay), and *Paracathartes howardae* (Harrison, 1979) (early Eocene of the Willwood Formation).

Parris and Hope (2002) tentatively assigned a scapula from the latest Cretaceous/earliest Paleocene of New Jersey to the Lithornithidae, but noted that the similarities shared with lithornithids may be plesiomorphic. The same could be true for an omal extremity of a coracoid from the Paleocene of Walbeck in Germany, which was described as *Fissuravis weigelti* Mayr, 2007, and tentatively referred to the Lithornithidae (Mayr 2007a). A very well preserved partial skeleton of *L. vulturinus* from the Danish Fur Formation was described by Leonard et al. (2005; see also Kristoffersen 1999 for further lithornithid remains from this locality). The latest fossil evidence of the group is a postcranial skeleton of an unidentified species from the middle Eocene of Messel (Mayr 2008e).

Lithornithid species significantly vary in size, with the turkey-sized *P. howardae* being about twice as large as *P. cercanaxius*. In palatal morphology they most closely resemble the Apterygidae. As in other palaeognathous birds, the upper beak bears a pair of distinct furrows rostral to the narial openings, and the ilioschiadic foramina of the pelvis are caudally open, which represents the plesiomorphic condition for Neornithes. Lithornithids had tinamou-like overall limb proportions, a long rhynchokinetic skull, and a well-developed sternal keel. As in extant Tinamidae, the frontoparietal suture remained open in adult birds. Other diagnostic features of the lithornithid skeleton include a long and pointed acromion of the scapula, and the absence of incisions in the caudal margin of the sternum. In contrast to that of tinamous, the distal end of the tibiotarsus lacks a supratendinal bridge, and in contrast to that of all extant palaeognathous birds, the hallux of at least the smaller species was well developed. On the basis of the morphology of the caudal vertebrae, Houde (1988, p. 113) assumed that the tail of lithornithids was short as in extant Tinamidae.

Several lithornithid fossils were found in association with eggshells, whose structure resembles that of the Tinamidae both microscopically and macroscopically (Houde 1988; Grellet-Tinner and Dyke 2005). According to Houde (1988), the large accumulations of eggshells in some sites indicate large clutches.

Lithornithids may have used their long and narrow beak for probing along shorelines or other bodies of water (Houde 1988). In contrast to extant Tinamidae, they were probably strong flyers capable of sustained flight; the long hallux and curved ungual phalanges indicate perching capabilities (Houde 1988).

The interrelationships between the lithornithid taxa and the phylogenetic affinities between lithornithids and other palaeognathous birds are poorly understood and in need of revision. Houde (1988) considered it possible that the taxon Lithornithidae actually is not monophyletic. As noted by him, the large *Paracathartes* differs from the smaller lithornithids in bone ultrastructure, in which it agrees with extant ratites. *Pseudocrypturus* is distinguished from all other lithornithid taxa by the absence of a large pterygoid fossa, which the other species share with extant Apterygidae.

In discussing the phylogenetic affinities of lithornithids, Houde (1988) assumed a sister group relationship between the Tinamidae and neognathous birds, which is not supported by current analyses (Cracraft et al. 2004; Hackett et al. 2008). The cladogram he regarded as best supported by the morphological data (see Fig. 39 in Houde 1988) shows lithornithids as a nonmonophyletic group, with *Pseudocrypturus*, *Lithornis*, and *Paracathartes* being successive sister taxa of ratites.

Lithornithids were considered to be the sister taxon of the Tinamidae by Leonard et al. (2005), who did, however, not detail the character evidence for this hypothesis. Although lithornithids share with extant Tinamidae the presence of an open frontoparietal suture, this feature also occurs in Mesozoic stem group representatives of the Neornithes (Elzanowski and Galton 1991) and seems to be plesiomorphic. An analysis by Dyke (2003a) resulted in a sister group relationship between *Lithornis* and ratites, but featured several incorrect character codings (e.g., scapula and coracoid of lithornithids are not fused to a scapulocoracoid, and the hallux and supratendinal bridge of the tibiotarsus are not lost in the Apterygidae and Dinornithidae). The analysis of Livezey and Zusi (2007) supported a sister group relationship between lithornithids and all other neornithine birds; the character evidence for this placement was not listed.

5.2 †Palaeotididae, †Remiornithidae, and †Eleutherornithidae

These three taxa are discussed together in this section because they are ratite-like birds and come from European fossil deposits. Whereas the Palaeotididae and Remiornithidae may form a clade, the Eleutherornithidae are too poorly known to be even certain that they were palaeognathous.

5.2.1 †Palaeotididae

This distinctive group of early Paleogene palaeognathous birds was reported from the middle Eocene of the Geisel Valley and Messel in Germany (Houde and Haubold 1987; Peters 1988b). The single species included in the taxon *Palaeotis weigelti* Lambrecht, 1928 was originally described as a bustard (Otididae) by Lambrecht (1928). Houde (1986) recognized its ratite affinities, which were further substantiated by Houde and Haubold (1987). *P. weigelti* is known from articulated skeletons and had a standing height of slightly less than 1 m. Its palaeognathous affinities can be unambiguously established by the morphology of the palate (Houde and Haubold 1987). *P. weigelti* was a long-legged, flightless bird, which certainly had cursorial habits, although it lived in a forested paleoenvironment. The species is distinguished from the Lithornithidae and shares with the Struthionidae, Rheidae, and Casuariidae caudally projecting supraorbital processes on the skull, the loss of a sternal keel, a scapulocoracoid, a bilaterally compressed pelvis, and the lack of a hallux. It has a narrower beak than all extant ratites except cassowaries (Casuariinae). As in extant Struthionidae and Rheidae, the humerus and ulna are fairly long, whereas the wing skeleton is much more reduced in the Casuariidae, Apterygidae, and Dinornithidae (Peters 1988b). In contrast to that of all extant ratites, the tarsometatarsus of *Palaeotis* further exhibits deep furrows along the midlines of its dorsal and ventral surfaces, which give the bone an almost H-shaped cross section (Fig. 5.2; Mayr 2002a). The proximal phalanx of the second pedal digit bears a proximally directing process, which led Lambrecht (1928) to assume a ground-scratching habit for *Palaeotis*.

The relationships between *Palaeotis* and other palaeognathous birds are not well understood. The presence of well-developed supraorbital processes and a scapulocoracoid, as well as the reduction of the sternal carina and loss of the hallux support a position within a clade including the Struthionidae, Rheidae, and Casuariidae. As noted above, such a clade is, however, not obtained in molecular analyses, which casts some doubt on the phylogenetic significance of these shared morphological characteristics. Whereas Houde (1986) and Houde and Haubold (1987) considered a sister group relationship between the Palaeotididae and Struthionidae, Peters (1988b) assumed a sister group relationship to the Rheidae. Mainly owing to the limited osteological information available from the specimens, the evidence for either hypothesis is ambiguous. An analysis by Dyke (2003a) resulted in a sister group relationship between *Palaeotis* and a clade including the Struthionidae, Rheidae, and Casuariidae.

5.2.2 †Remiornithidae

The Remiornithidae are a further group of Paleogene Northern Hemisphere palaeognathous birds. The single species included in the taxon *Remiornis heberti* Lemoine, 1881 is represented by leg bones (tibiotarsus and tarsometatarsus) and a few associated remains from the late Paleocene of France (Martin 1992). The tarsometatarsus is about the length of that of *Palaeotis weigelti* but is much stouter, indicating a significantly larger overall size of *Remiornis heberti*. The tibiotarsus lacks an ossified supratendinal bridge. As in *Palaeotis* the tarsometatarsus exhibits a marked furrow along its dorsal surface. Except for the more deflected trochlea for the second toe, the bone also resembles the tarsometatarsus of *Palaeotis* in the configuration of the distal trochleae (compare Fig. 8 in Martin 1992 and Fig. 1 in Mayr 2002). I thus consider it not unlikely that future specimens will support a clade including *Remiornis* and *Palaeotis*, for which the name Palaeotididae would have taxonomic priority.

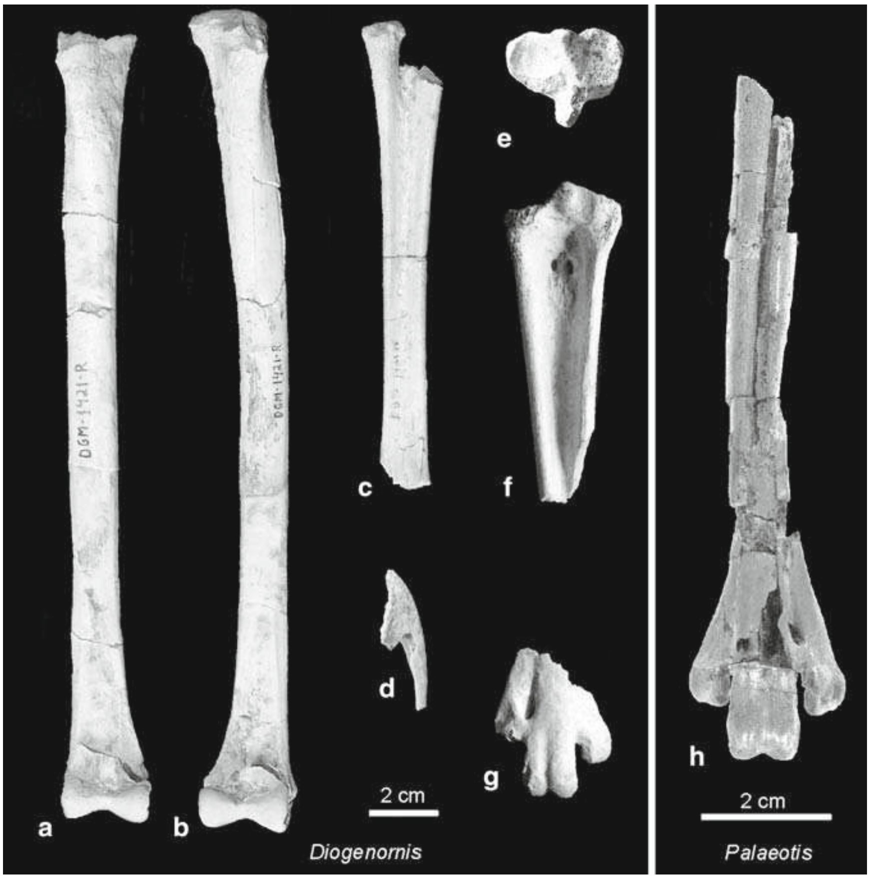

Fig. 5.2 **a**–**g** *Diogenornis fragilis* Alvarenga, 1983 (Rheidae) from the late Paleocene of Itaboraí in Brazil; **h** *Palaeotis weigelti* Lambrecht, 1928 (Palaeotididae) from the middle Eocene of the Geisel Valley in Germany (holotype, Geiseltalmuseum, Halle/Saale, Germany, GMH 3605). **a** Right tibiotarsus (holotype, Coleção da Seção de Paleontologia do Departamento Nacional da Produção Mineral, Rio de Janeiro, Brazil, DGM-1421-R, juvenile individual); **b** left tibiotarsus (holotype, DGM-1421-R, juvenile individual); **c** incomplete right tarsometatarsus (holotype, DGM-1421-R, juvenile individual); **d** upper beak (DGM-1428-R); **e**, **f** proximal right tarsometatarsus (DGM-1422-R); **g** distal right tarsometatarsus (DGM-1422-R); **h** incomplete left tarsometatarsus. Same scale for **a**–**g**. (Photos of *D. fragilis* courtesy of Herculano Alvarenga; photo of *P. weigelti* by Sven Tränkner)

5.2.3 †Eleutherornithidae

A cranial portion of a large pelvis from the middle Eocene of Switzerland was described as *Eleutherornis helveticus* by Schaub (1940), who assumed that it is from a ratite bird. *E. helveticus* was about the size of a Lesser Rhea (*Pterocnemia* *pennata*). The pelvis fragment has not yet been compared in detail with that of the neognathous Gastornithidae (Sect. 6.2), and there is no compelling evidence that it is from a ratite. Schaub (1940) noted several features in which it differs from extant ratites but agrees with neognathous birds. Pedal phalanges from the same locality, which were reported some years earlier by Schaub (1929), were considered to be too large to belong to the same species (Schaub 1940).

The size of *E. helveticus* corresponds to that of the contemporaneous "?*Diatryma*" *cotei* Gaillard, 1937, which is based on a distal tarsometatarsus and pedal phalanges from the middle Eocene (MP 14; Mourer-Chauviré 1996) of France (Gaillard 1937). According to Andors (1992), this species is not a representative of the Gastornithidae; without discussion of any supporting evidence it was assigned to the Phorusrhacidae (Sect. 13.1) by Mlíkovský (2002). The ungual phalanges of "?*D.*" *cotei* are more curved than those of typical gastornithids, but resemble the ungual phalanges described by Schaub (1929) from the type locality of *E. helveticus*. Although "?*D.*" *cotei* and *E. helveticus* may well belong to the same clade, this cannot be conclusively shown with the material at hand.

Proceriavis martini Harrison and Walker, 1979 from the early Oligocene of England is based on a fragmentary cervical vertebra and a referred pedal phalanx, and was tentatively referred to the Eleutherornithidae by Harrison and Walker (1979a). Houde and Haubold (1987) confirmed the similarity between these specimens and the corresponding bones of extant Casuariidae. Nonetheless, the fragmentary remains cannot be considered convincing evidence for the presence of ratites in the early Oligocene of Europe. Harrison and Walker (1979a) also described a distal portion of a radius of a very large volant bird, which they regarded as a representative of the Pelagornithidae (Sect. 6.5). As long as the vertebrae of pelagornithids are not described, there remains a possibility that the holotypic vertebra of *E. helveticus* likewise is from a bony-toothed bird.

5.3 †Eremopezidae

The Eremopezidae occur in the late Eocene of the Jebel Qatrani Formation (Fayum) in Egypt. The original description of the rhea-sized *Eremopezus eocaenus* Andrews, 1904 was based on the distal end of a tibiotarsus (Andrews 1904). Subsequently, Lambrecht (1929a) reported a fragmentary tarsometatarsus from the same locality, which formed the holotype of *Stromeria fajumensis*. Lambrecht (1929a) erroneously (Rasmussen et al. 2001) considered the specimen to be of early Oligocene age, and assumed a close relationship to the Madagascan Aepyornithidae. Rasmussen et al. (1987) already supposed that these two fossils belong to a single species, but synonymy of *E. eocaenus* and *S. fajumensis* could not be proven until Rasmussen et al. (2001) identified new and better preserved specimens from the Fayum. Still, however, *E. eocaenus* is only known from hindlimb elements. The distal end of the tibiotarsus lacks an ossified supratendinal bridge, which seems to have been the main reason why the species was associated with palaeognathous birds.

The tarsometatarsus is distinguished from that of all palaeognathous birds in that the distal end is unusually flattened and the trochleae are splayed. The trochlea for the second toe is considerably shorter than that for the fourth toe (see Figs. 1, 4 in Rasmussen et al. 2001). Judging from the presence of a well-developed tarsometatarsal articulation facet, *Eremopezus* had a hallux, which is absent in all ratites except the Apterygidae and Dinornithidae.

As noted by Rasmussen et al. (2001, p. 334):

> Madagascar split from Africa at a very early date (Jurassic) and the presence of a giant flightless bird on Africa during the early Tertiary therefore makes it a less likely ancestor for aepyornithids than would be a volant species. If the aepyornithid ancestor flew to Madagascar, it was no close kin of *Eremopezus*.

Rasmussen et al. (2001) even questioned palaeognathous affinities of *Eremopezus*, and the phylogenetic affinities of this remarkable bird probably cannot be conclusively resolved without further material. At least the distal tibiotarsus, however, is indeed quite similar to that of ratites.

Just because of its geographic distribution and possible ratite affinities, it is tempting to assume that *Eremopezus* is a stem group representative of the Struthionidae. But even though the tarsometatarsus of *Eremopezus* has a somewhat reduced trochlea for the second toe, which is completely lost in extant Struthionidae, its morphology is otherwise very different.

5.4 Rheidae (Rheas)

Putative stem group representatives of the Rheidae were reported from the Paleocene of South America, with the earliest fossils being pedal phalanges from the middle Paleocene of the Río Chico Formation in Argentina (Tambussi 1995).

More comprehensive is the fossil record of *Diogenornis fragilis* Alvarenga, 1983 from the late Paleocene of Itaboraí in Brazil, a flightless species which reached about two thirds the size of the extant Greater Rhea, *Rhea americana*. Various limb bones, vertebrae, and the tip of the premaxilla were discovered and represent a minimum of four to five individuals (Fig. 5.2; Alvarenga 1983). In the original description, *Diogenornis* was assigned to the Opisthodactylidae, a taxon which was first erected for a species from the early Miocene of Argentina. Because the similarities between these early forms are, however, likely to be plesiomorphic, they are best assigned to stem group Rheidae. *D. fragilis* has a narrower beak and somewhat less reduced humerus than extant Rheidae, but otherwise is quite similar in the morphology of the known bones. The distal tibiotarsus lacks a supratendinal bridge. Compared with other Paleogene palaeognathous birds, the osteological features of *D. fragilis* are most similar to those of the Palaeotididae and Remiornithidae (Fig. 5.2). As in the latter two taxa, there is a marked fossa (sulcus extensorius) along the dorsal surface of the tarsometatarsus.

5.5 Casuariidae (Emus and Cassowaries)

The Casuariidae include two extant taxa, the Casuariinae (cassowaries) and Dromaiinae (emus). Whereas cassowaries live in forested environments of northern Australia and New Guinea, the single extant species of emus is widely distributed across open areas of Australia. The earliest Casuariidae stem from the late Oligocene Riversleigh and Etadunna Formations of Australia and belong to the taxon *Emuarius* (Boles 1992, 2001b). Two species can be distinguished, *Emuarius* ("*Dromaius*") *gidju* (Patterson and Rich, 1987) and *E. guljaruba* Boles, 2001. The former is known from a number of skeletal elements including a partial beak, whereas for *E. guljaruba* only a tarsometatarsus was described. *Emuarius* was considered to be a stem group representative of the Dromaiinae (Boles 1992, 2001b), and mainly differs from extant emus in the more slender femur, whose proportions are similar to the femur of cassowaries. The tip of the premaxilla is rounded as in extant emus, whereas it is narrower and more pointed in cassowaries. If it is correctly assigned to the Dromaiinae, *Emuarius* indicates that the lineages leading to cassowaries and emus separated in the Paleogene. The weight of *E. gidju* has been estimated at 19–21 kg (Boles 1997b), and the species was probably less cursorial than extant emus but more so than the graviportal cassowaries (Boles 1997b).

5.6 Putative Ratite from the Eocene of Antarctica

Tambussi et al. (1994) reported a fragmentary distal tarsometatarsus of a reputed ratite bird from the late Eocene of the La Meseta Formation of Seymour Island in Antarctica (see also Tambussi and Acosta Hospitaleche 2007). Just because of its large size, this specimen certainly comes from a flightless bird, whose weight has been estimated at 60 kg (Tambussi and Acosta Hospitaleche 2007). The fossil differs, however, from the tarsometatarsus of all unambiguous ratites in the unusually large trochlea for the second toe. As there were other large groundbirds in the early Paleogene (see Sect. 6.3), its identification needs to be verified with additional material.

Chapter 6
Galloanseres

Monophyly of the Galloanseres is supported by virtually all molecular analyses of different kinds of data, including DNA–DNA hybridization as well as mitochondrial and nuclear gene sequences, and also resulted from analyses of morphological characters (Sibley and Ahlquist 1990; Mayr and Clarke 2003; Cracraft et al. 2004; Fain and Houde 2004; Ericson et al. 2006; Livezey and Zusi 2007). Morphological apomorphies of this clade mainly concern skull features such as the presence of sessile, i.e., stalkless, basipterygoid processes, long, blade-like retroarticular processes on the mandible, and a derived morphology of the quadrate (Mickoleit 2004). The postcranial skeleton of extant Galliformes and Anseriformes is quite different, but the plesiomorphic morphology of some Paleogene stem group representatives of the Galliformes bridges the morphological gap between the extant taxa (see later).

Various Paleogene taxa have been assigned to the Galloanseres, which greatly differ in morphology and presumed ecological preferences. If assignment of all of them is confirmed by future studies, the morphological and ecological diversity within Paleogene Galloanseres was extraordinarily high, including giant flightless groundbirds with greatly reduced wings, long-legged filter-feeders, and pelagic taxa with a wingspan of 4–5 m. Figure 6.1 depicts a hypothesis on the interrelationships of these birds.

6.1 Galliformes (Landfowl)

Crown group Galliformes include the Australasian Megapodiidae (megapodes), which are the sister taxon of a clade including the New World Cracidae (guans, chachalacas, and curassows) and the globally distributed Phasianidae (grouse, quails, pheasants, and allies) (Cracraft et al. 2004; Ericson et al. 2006). Although stem group Galliformes may have already existed in the late Cretaceous (see Chap. 4), identification of the fragmentary remains needs to be corroborated with additional specimens. The Paleogene record of galliform birds, however, is quite extensive and provides some insights into the evolutionary history of the group. Most notably, no Paleogene galliform birds have as yet been recorded from Africa, and the fossils indicate a Northern Hemisphere diversification of the taxon (see also Sect. 17.2.1).

G. Mayr, *Paleogene Fossil Birds*, DOI: 10.1007/978-3-540-89628-9_6,

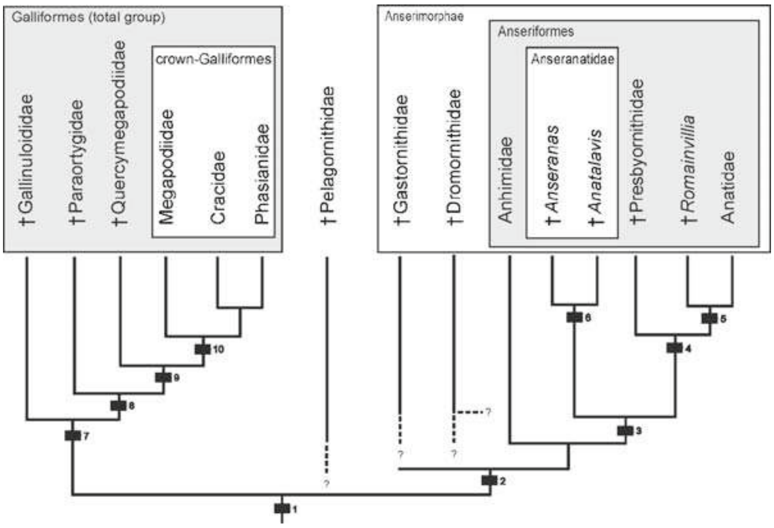

Fig. 6.1 Hypothesis on the phylogenetic relationships between Paleogene and extant representatives of the Galloanseres. Selected apomorphies of the nodes: *1* basipterygoid processes ovate and sessile, quadrate with only two mandibular condyles, mandible with long, blade-like retroarticular processes (unknown for Pelagornithidae); *2* palate desmognathous, postorbital process long, with truncate tip, and projecting in rostroventral direction (not comparable in Gastornithidae), zygomatic process reduced; *3* beak duck- or goose-like, with broadly rounded tip; *4* three anterior toes connected with a web; *5* lack of fossa for first metatarsal, distal vascular foramen with plantar opening recessed and situated distal to dorsal opening; *6* sternal extremity of coracoid with large pneumatic opening, sternal extremity of furcula greatly widened; *7* humerus with markedly elongated dorsal tubercle, plantar side of articular surface of tarsometatarsal trochlea for third toe asymmetric, with lateral ridge protruding farther proximally than medial ridge; *8* deltopectoral crest of humerus reduced; *9* capital groove of humerus with transverse ridge; *10* scapular articulation facet of coracoid flat. (After Andors 1992; Mourer-Chauviré 1992a; Murray and Vickers-Rich 2004; Bourdon 2005; Mayr 2006b)

6.1.1 †Gallinuloididae

The earliest substantial and unambiguously identified fossils of galliform birds belong to the early Eocene Gallinuloididae. Originally, this taxon was established for *Gallinuloides wyomingensis* Eastman, 1900, which is known from three skeletons from the Green River Formation (Fig. 6.2), and which is the first avian species described from this locality (Eastman 1900; Lucas 1900; see Figs. III.16, III.22 in Grande 1980; Mayr and Weidig 2004). Representatives of the Gallinuloididae were also reported from the early Eocene of Europe and include *Paraortygoides messelensis* Mayr, 2000 from Messel (Fig. 6.3) and *P. radagasti* Dyke and Gulas, 2002 from the London Clay (Mayr 2000b, 2006b; Dyke and

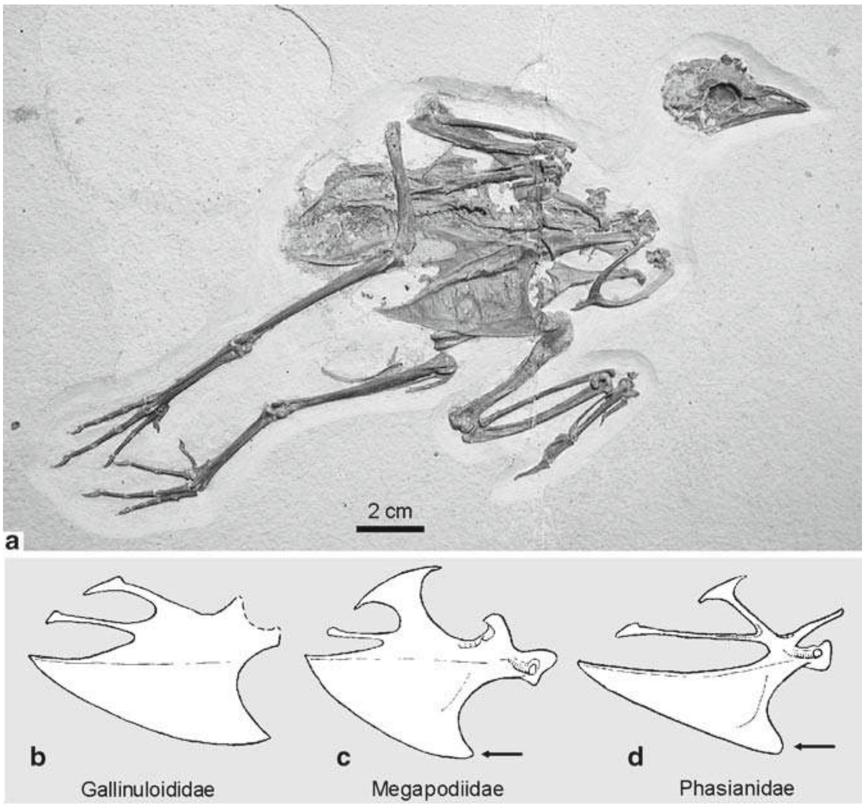

Fig. 6.2 **a** Skeleton of *Gallinuloides wyomingensis* Eastman, 1900 (Gallinuloididae) from the early Eocene Green River Formation (Wyoming Dinosaur Center, Thermopolis, USA, WDC CGR-012). **b–d** Comparison of sterna: **b** *G. wyomingensis*, **c** *Alectura lathami* (Megapodiidae), **d** *Rollulus rouloul* (Phasianidae); not to scale. The *arrows* point to the caudally displaced tip of the sternal carina of extant Galliformes. (After Mayr 2006b, modified. Photo courtesy of Ilka Weidig)

Gulas 2002). The latter may be a junior synonym of either *Argillipes paralectoris* Harrison and Walker, 1977 or *A. aurorum* Harrison and Walker, 1977 from the same locality (Fig. 6.4; Mayr 2005a).

Mayr and Weidig (2004) remarked that *Taoperdix pessieti* (Gervais, 1862) from the late Oligocene (MP 25) of France is not a member of the Gallinuloididae (contra Brodkorb 1964). The geographic and temporal distribution, as well as the morphology (carpometacarpus with bowed minor metacarpal but without intermetacarpal process), suggest that this species belongs to the Paraortygidae (Sect. 6.1.2), with which it has not yet been compared. In size, the two skeletons assigned to *T. pessieti* (Milne-Edwards 1867–1871; Eastman 1905) correspond to *Paraortyx brancoi*. The affinities of a distal tarsometatarsus from the late Eocene of the

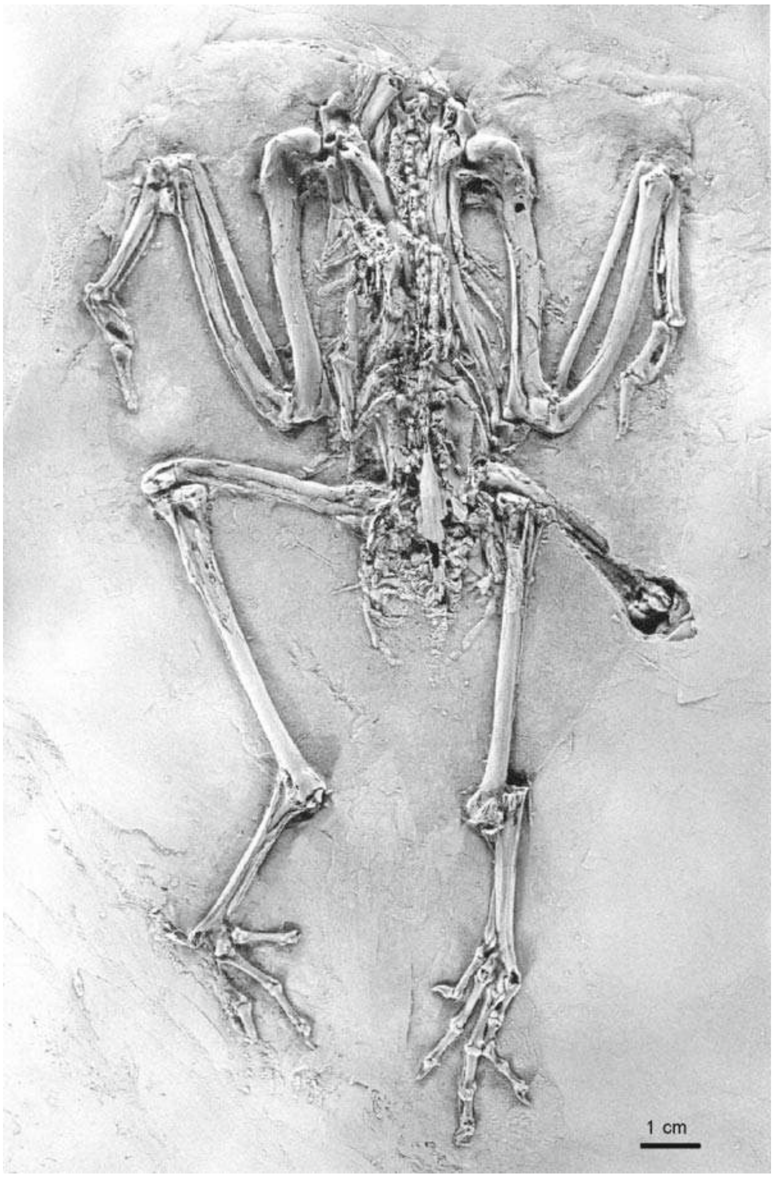

Fig. 6.3 Postcranial skeleton of *Paraortygoides messelensis* Mayr, 2000 (Gallinuloididae) from the middle Eocene of Messel (holotype, Forschungsinstitut Senckenberg, Frankfurt am Main, Germany, SMF-ME 1303a). Coated with ammonium chloride. (Photo by Sven Tränkner)

Quercy fissure fillings, which was identified as *Taoperdix* sp. by Mourer-Chauviré (1988a, 1992a), also need to be restudied. Another species which was incorrectly assigned to the Gallinuloididae is *Archaealectrornis sibleyi* from the early

Oligocene of Nebraska (Mayr and Weidig 2004; see Sect. 6.1.3). Legs of a putative galliform bird were described by Lindow and Dyke (2007) from the Danish Fur Formation; whether these can be assigned to the Gallinuloididae, as assumed by Kristoffersen (2002a), needs to be shown by more complete material.

Gallinuloidids are the only stem group representatives of the Galliformes which are known from well-preserved skeletons. Although the skull of *G. wyomingensis* resembles that of extant Galliformes in overall morphology, the postorbital processes are less developed and there are no ossified zygomatic aponeuroses, which are a derived characteristic of many extant Galliformes (Mayr and Weidig 2004). As in the Paraortygidae (Sect. 6.1.2) and some extant galliform taxa, the humerus exhibits a well-developed second pneumotricipital fossa. Otherwise, however, the pectoral girdle and wing skeleton of gallinuloidids display a plesiomorphic morphology, which is quite different from that of their extant relatives. The humerus is less robust than that of crown group Galliformes, and especially the proximal end is more similar to that of to ducks (Anatidae) in its proportions. The shorter and more protruding deltopectoral crest in particular shows that gallinuloidids are the sister taxon of all other galliform birds (Mayr 2006b). As in the Anseriformes and other stem group Galliformes (see below), the coracoid of gallinuloidids exhibits a plesiomorphic, cup-like scapular articulation facet. The very long scapula and the long and slender carpometacarpus are also more similar to the corresponding bones of anseriform birds than to those of crown group Galliformes (Mayr 2000b; Mayr and Weidig 2004). The shafts of the furcula are much wider than in crown group Galliformes, and the tip of the sternal carina reaches farther cranially (Mayr 2006b). The bodies of the thoracic vertebrae bear marked lateral depressions (Fig. 6.4; Dyke and Gulas 2002), which also occur in Mesozoic stem group representatives of Neornithes (e.g., *Ichthyornis*; Clarke 2004) and the anseriform Presbyornithidae (Sect. 6.4.3), but are absent in extant Galliformes.

Most earlier authors (e.g., Tordoff and Macdonald 1957; Brodkorb 1964; Ballmann 1969a; Dyke 2003b) considered *G. wyomingensis* to be a representative of either the Cracidae or the Phasianidae, i.e., assumed a position within crown group Galliformes. Because of the poor preservation of the holotype specimen, this misclassification is comprehensible. I find it more difficult to understand, however, why a position within crown group Galliformes was still advocated for gallinuloidids by Crowe et al. (2006), and Dyke and Crowe (2008), especially in light of the fact that Dyke and Gulas (2002) agreed upon a position outside crown group Galliformes for the very similar *Paraortygoides*.

The very robust furcula and cranially protruding tip of the sternal carina (Fig. 6.2) indicate that gallinuloidids had a less voluminous crop than their extant relatives (Mayr 2006b). Their vegetable food component thus probably consisted of fruits and other easily digestible plant matter, rather than coarse material such as seeds. This assumption is in concordance with the fact that in none of the known specimens of the Gallinuloididae gastroliths are preserved, whereas extant Galliformes regularly ingest grit and small pebbles to mechanically break down plant matter in the gizzard.

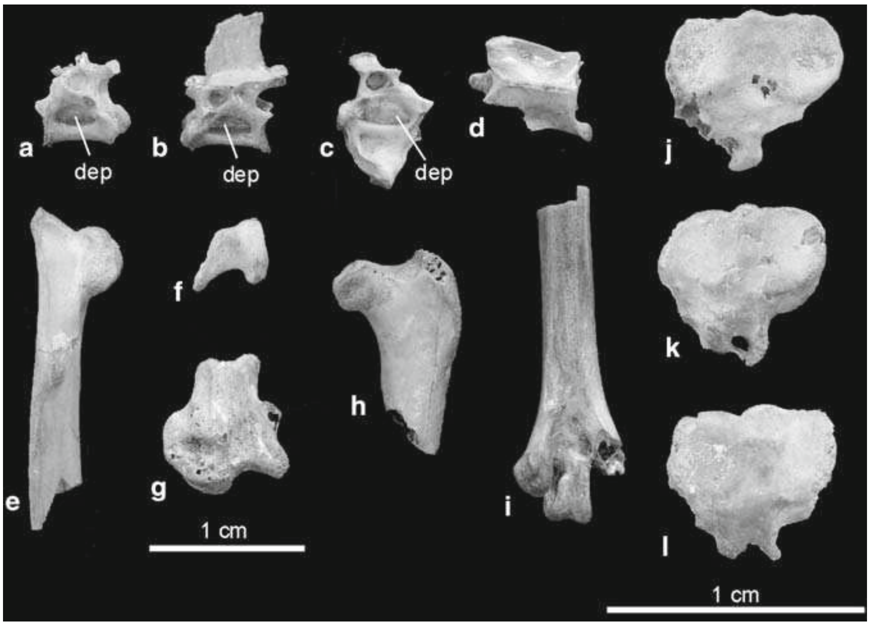

Fig. 6.4 Galliform birds from the early Eocene London Clay. **a–j** Selected elements of the holotype of *Paraortygoides radagasti* Dyke and Gulas, 2002 (Natural History Museum, London, UK, BMNH A 6217); **k** holotype of *Argillipes aurorum* Harrison and Walker, 1977 (BMNH A 3130); **l** holotype of *Argillipes paralectoris* Harrison and Walker, 1977 (BMNH A 3604). **a–c** Thoracic vertebrae; **d** third cervical vertebra; **e** cranial extremity of right scapula; **f** ulnar carpal bone; **g** proximal right carpometacarpus; **h** proximal left femur; **i** distal right tarsometatarsus; **j–l** proximal tarsometatarsi (**k**, **l** reversed to facilitate comparisons). *dep* depression on body of thoracic vertebrae. Same scales for **a–i** and **j–l**. (Photos by Sven Tränkner)

6.1.2 †Paraortygidae

A further taxon of Paleogene stem group Galliformes are the Paraortygidae. These birds are known from well-preserved postcranial bones from middle Eocene to late Oligocene deposits of the Quercy fissure fillings and from the early Oligocene of Germany (Mourer-Chauviré 1992a; Fischer 1990, 2003). Three species are currently recognized (Mourer-Chauviré 1992a), the late Eocene and early Oligocene *Paraortyx brancoi* Gaillard, 1908 and *P. lorteti* Gaillard, 1908, as well as *Pirortyx major* (Gaillard, 1939), which was reported from early and late Oligocene fossil sites. As already noted in the preceding section, *Taoperdix pessieti* from the late Oligocene of France may be a further representative of this group.

Like that of gallinuloidids but in contrast to that of the Quercymegapodiidae (Sect. 6.1.4), the humerus of *Paraortyx* exhibits a marked second pneumotricipital fossa. In the larger taxon *Pirortyx* this fossa is less developed. Paraortygids differ from gallinuloidids and quercymegapodiids in the less elongated and less slender carpometacarpus, which more closely resembles the corresponding bone of extant Galliformes in its proportions. In contrast to that of the Quercymegapodiidae and extant Galliformes, the capital incision (incisura capitis) of the humerus lacks a transverse ridge.

6.1.3 †*Procrax*, †*Archaealectrornis*, and †*Palaeonossax*

These three taxa from the late Eocene and early Oligocene of North America may be closely related and are thus discussed together in this section.

Procrax brevipes Tordoff and Macdonald, 1957 is based on a dissociated postcranial skeleton from the late Eocene (Chadron Formation) of South Dakota. The species was initially placed into the Gallinuloididae, which were considered to be most closely related to the Cracidae by Tordoff and Macdonald (1957). In contrast to the humerus of the Gallinuloididae, however, the robust humerus of *Procrax* lacks a marked second pneumotricipital fossa, and there are also numerous other differences in the postcranial skeleton features. As far as comparisons are possible, the bones of *Procrax* resemble those of the Paraortygidae. *P. brevipes* was somewhat larger than the males of the extant Chaco Chachalaca, *Ortalis canicollis*, and differed from all extant Cracidae except *Pipile* in the proportionally shorter legs and ungual phalanges (Tordoff and Macdonald 1957). In contrast to that of the Gallinuloididae and Quercymegapodiidae, the minor metacarpal of the carpometacarpus is markedly bowed, and unlike in Paleogene Phasianidae, this bone lacks an intermetacarpal process.

From the published illustrations, I conclude that *P. brevipes* is closely related to, if not conspecific with, the equally sized *A. sibleyi* Crowe and Short, 1992. The latter species is known from a humerus from the early Oligocene Brule Formation of Nebraska, and was not differentiated from *P. brevipes* in the original description (Crowe and Short 1992). On the basis of morphometric comparisons, *A. sibleyi* was considered to be most closely related to the Phasianidae by Crowe and Short (1992); however, the absence of a transverse ridge in the capital incision clearly shows that the species is outside crown group Galliformes. Apart from being somewhat stouter, the humeri of *Procrax* and *Archaealectrornis* match well with that of the paraortygid *Pirortyx major*.

Palaeonossax senectus Wetmore, 1956 from the early Oligocene Brule Formation of South Dakota was described as a member of the Cracidae by Wetmore (1956). This species is represented by a distal humerus and also needs to be compared with *Procrax* and *Archaealectrornis* to which it appears to be quite similar, judging from the published drawings. The Cracidae thus have no unambiguously identified Paleogene record.

6.1.4 †*Quercymegapodiidae*

The taxon Quercymegapodiidae was first erected for two species from the late Eocene (MP 16–19) of the Quercy fissure fillings, i.e., *Quercymegapodius depereti* (Gaillard, 1908) and *Q. brodkorbi* Mourer-Chauviré, 1992. *Ludiortyx hoffmanni*

(Gervais, 1852) from the late Eocene of the Paris Gypsum is probably also a quercymegapodiid (Mayr 2005a). Possibly because of its slender carpometacarpus, a plesiomorphic feature shared with gallinuloidids, the species was classified into the Rallidae (rails) by Brunet (1970) and Cracraft (1973a). The same happened to *Taubacrex granivora* Alvarenga, 1988 from the late Oligocene/early Miocene of the Taubaté Basin in Brazil, which was also assigned to the Rallidae in the original description (Alvarenga 1988), but was identified as a representative of the Quercymegapodiidae by Mourer-Chauviré (2000). Also from the Oligo-Miocene of the Taubaté Basin, Alvarenga (1995) described *Ameripodius silvasantosi* as a species of the Quercymegapodiidae. Mourer-Chauviré (2000) noted that *T. granivora* and *A. silvasantosi* differ in the shape of the coracoid, but this bone is slightly crushed in the holotype of *T. granivora*, and direct comparisons of the actual specimens are needed to exclude the possibility that these two species are conspecific. *Taubacrex* provides the earliest fossil record of gastroliths in galliform birds.

The coracoid of quercymegapodiids still exhibits a cup-like articulation facet for the scapula. Among other features (Mourer-Chauviré 1992; Mayr 2000b), quercymegapodiids differ from gallinuloidids in the more robust humerus which lacks a second pneumotricipital fossa. They agree with crown group Galliformes in the derived presence of a ridge in the capital groove (incisura capitis) of the humerus, which is absent in the Gallinuloididae and Paraortygidae.

Despite their name and initial comparisons with megapodes (Mourer-Chauviré 1982), quercymegapodiids are stem group representatives of the Galliformes, and the similarities to extant Megapodiidae are plesiomorphic (Mourer-Chauviré 1992a). Nevertheless, these birds were incorrectly used for the calibration of molecular divergence times in some recent studies (van Tuinen and Dyke 2004; Crowe et al. 2006; see Mayr and Weidig 2004; Mayr 2008d).

6.1.5 Megapodiidae (Megapodes)

The only Paleogene fossil record of the Megapodiidae is *Ngawupodius minya* Boles and Ivison, 1999 from the late Oligocene of Central Australia (Namba Formation). This species is known from a tarsometatarsus which measures only two thirds of that of the smallest extant megapodes, to which it is otherwise quite similar in its morphology. Apart from its larger size, this bone also resembles the megapode-like tarsometatarsus of the Quercymegapodiidae, but from a biogeographic point of view an assignment to the stem group of the Megapodiidae is certainly justified. Boles and Ivison (1999) assumed that *N. minya* lived in wet riparian forests and that its extinction was due to environmental changes.

6.1.6 Phasianidae (Grouse, Quails, Pheasants, and Allies)

The Phasianidae are the most species-rich and most widely distributed group of extant Galliformes and occur in a great variety of habitats, from semideserts to tropical forests and subantarctic tundra. Molecular studies indicate that the Numidinae (guinea fowl) and Odontophorinae (New World quail) are successive sister taxa of the remaining Phasianidae (Kriegs et al. 2007). Osteologically, all nonnumidine phasianids are characterized by the presence of an intermetacarpal process on the carpometacarpus.

Amitabha urbsinterdictensis Gulas-Wroblewski and Wroblewski, 2003 from the middle Eocene Bridger Formation of Wyoming has been considered to be the sister taxon of the Phasianidae (Gulas-Wroblewski and Wroblewski 2003). This species is based on several fragmentary bones (including an incomplete humerus, scapula, sternum, and pelvis), which show little resemblance to galliform birds, let alone Phasianidae. The results of the phylogenetic analysis of Gulas-Wroblewski and Wroblewski, (2003) are unpersuasive, because only galliform birds (mainly extant Phasianidae) were included. Until the holotype is restudied and compared with other taxa from the early Eocene of North America, its phylogenetic affinities are best regarded unresolved. Although *A. urbsinterdictensis* was used for the calibration of molecular clocks by van Tuinen and Dyke (2004), it undoubtedly is not within crown group Galliformes (for a critique see Mayr and Weidig 2004; Mayr 2008d).

Telecrex grangeri Wetmore, 1934 is represented by an incomplete femur from the late Eocene of Mongolia and was originally classified into the Rallidae, within the monotypic taxon Telecrecinae. The species was assigned to the Numidinae by Olson (1974), but because guinea fowl are the sister taxon of all other extant phasianid Galliformes (see above), the similarities between *Telecrex* and extant guinea fowl may well be plesiomorphic for the Phasianidae. Although *Telecrex* has already been used to calibrate molecular clocks (Cooper and Penny 1997), its assignment to the Numidinae cannot be considered well supported without further skeletal elements (see also p. 69 in Mourer-Chauviré 1992a). A record of *Telecrex* from the late Eocene of France (Mlíkovský 1989) was based on a femur of *Elaphrocnemus phasianus*, a stem group representative of the Cariamidae (Mourer-Chauviré 1992a).

Putative Odontophorinae from late Eocene (Chadronian) deposits of Canada were described as *Nanortyx inexpectatus* by Weigel (1963). Assignment of these remains, a fragmentary coracoid and a distal tarsometatarsus, to the Odontophorinae seems to have been based on the fact that the specimens are from very small galliform birds and were found in the New World. However, because these bones are not particularly distinctive in the Odontophorinae, identification of *N. inexpectatus* as a New World quail also needs to be substantiated with additional specimens. The same applies to a distal tarsometatarsus from the early Oligocene (Orellan) of Colorado, which was assigned to the Odontophorinae by Tordoff (1951).

Unambiguous representatives of the Phasianidae were reported from Oligocene deposits of the Quercy fissure fillings and Allier in France, and belong to the taxon *Palaeortyx* (Mourer-Chauviré 1992a; Mourer-Chauviré et al. 2004). According to Mourer-Chauviré (2006), the Quercy species can be assigned to *P. brevipes* Milne-Edwards, 1869, *P. gallica* Milne-Edwards, 1869, *P. prisca* (Milne-Edwards, 1869), and *P. phasianoides* Milne-Edwards, 1869. A nearly complete articulated skeleton of *Palaeortyx* cf. *gallica* was found in the late Oligocene (MP 28) maar lake deposits of Enspel in Germany (Mayr et al. 2006). In this specimen gastroliths are preserved.

Assignment of *Palaeortyx* to the Phasianidae is supported by the presence of a well-developed intermetacarpal process on the carpometacarpus. The humerus exhibits a double pneumotricipital fossa, which also occurs in the Gallinuloididae and Paraortygidae, extant Odontophorinae, as well as in *Arborophila* and *Ammoperdix* (both Phasianinae). If not plesiomorphic for galliform birds in general, this feature is likely to be plesiomorphic for nonnumidine Phasianidae. The tarsometatarsus of *Palaeortyx* lacks a spur, a feature present in the males of several extant Phasianidae. Ballmann (1969a) assumed a closer relationship between *Palaeortyx* and hill partridges of the taxon *Arborophila*, which live in the tropical and subtropical regions of Asia. This hypothesis was based on overall similarity, and the plesiomorphic leg proportions (femur subequal to humerus in length as in Paleogene stem group Galliformes) rather support a position of *Palaeortyx* outside crown group Phasianinae (Mayr et al. 2006).

Schaubortyx keltica (Eastman, 1905) from the late Oligocene (MP 25) of France had the size of a Northern Bobwhite (*Colinus virginianus*) and is known from a dissociated skeleton on two slabs (Eastman 1905; Schaub 1945). This species differs from *Palaeortyx* in its intermembral proportions, with the femur being longer than the humerus (Mourer-Chauviré 1992a; contra Mlíkovský 2002 who synonymized *Schaubortyx* and *Palaeortyx*). *S. keltica* is a representative of the Phasianidae, but its affinities within the group are unresolved.

The Meleagridinae (turkeys) and Tetraoninae (grouse), which according to recent molecular studies are sister taxa and nested within the Phasianinae (Kriegs et al. 2007), have no Paleogene fossil record and may not have diversified before the Neogene.

6.2 †Gastornithidae

The Gastornithidae are large, flightless, and graviportal birds, which occurred in the Paleocene to middle Eocene of Europe and the early Eocene of North America and Asia. The first fossils were reported from the late Paleocene of France by Hébert (1855) and were classified in the taxon *Gastornis*. Owing to the fragmentary nature of the then known specimens, early reconstructions of these European gastornithids were patently false (Martin 1992). This prevented recognition of their close similarity to the much better represented North American species, which were described as *Diatryma*, within the taxon Diatrymidae (Cope 1876; Matthew and Granger 1917). The Eocene European gastornithids were also assigned to *Diatryma* by earlier authors. Although Martin (1992) noted morphological differences between the latter taxon and *Gastornis*, synonymization of *Gastornis* and *Diatryma* was suggested by Buffetaut (1997) and formalized by Mlíkovský (2002). Buffetaut (2008) concurred that the slight morphological differences do not justify taxonomic separation of *Diatryma* and *Gastornis*. I also consider it advisable to unite the North American and European species in the taxon *Gastornis*, which has taxonomic priority. If *Gastornis* and *Diatryma* are kept separate, the former is likely to be paraphyletic (see below).

The earliest record of the Gastornithidae is a coracoid from the Paleocene of Walbeck in Germany (Fig. 6.5; Mayr 2007a); Weigelt (1939) mentioned other gastornithid remains from this locality, which however seem to have been lost. The Walbeck coracoid is from a comparatively small species and may belong to *Gastornis russelli* Martin, 1992, which is the smallest named species. *G. russelli* was originally based on a tarsometatarsus and beak fragment from the late Paleocene of the Reims area in France, and has a more slender tarsometatarsus than other gastornithids; it is probably conspecific with *Gastornis minor* Lemoine, 1878 from the same locality, which was considered a nomen dubium by Martin (1992).

G. russelli measured less than half of the ostrich-sized and much better known late Paleocene to early Eocene *G. parisiensis* Hébert, 1855. According to Martin (1992), the latter species is synonymous with "*G. edwardsi*" Lemoine, 1878 from

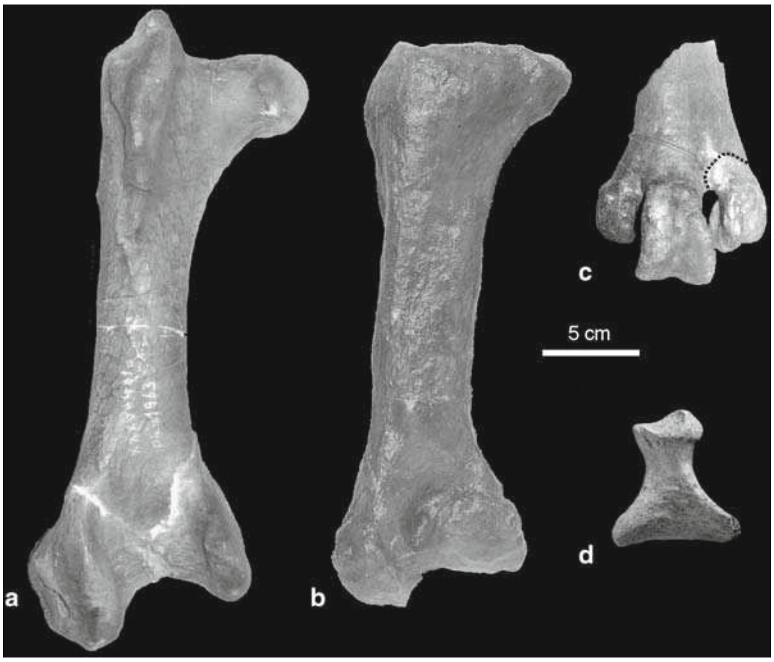

Fig. 6.5 Bones of the Gastornithidae. **a** Right femur of *Gastornis* ("*Diatryma*") *geiselensis* (Fischer, 1978) from the middle Eocene of the Geisel Valley in Germany (Geiseltalmuseum, Halle/Saale, Germany, GMH 1968/Dia 18); **b** left femur of *G.* cf. *geiselensis* from the middle Eocene of Messel (cast of hollow mold in matrix; Hessisches Landesmuseum Darmstadt, Germany, HLMD-Me 6116); **c** distal left tarsometatarsus of *G. sarasini* (Schaub, 1929) from the early Eocene of Monthelon near Epernay, France (holotype, Naturhistorisches Museum Basel, Switzerland, NMB T.S.94), trochlea for fourth toe reconstructed as indicated by the *dotted line*; **d** right coracoid of *Gastornis* sp. from the late Paleocene of Walbeck, Germany (Institut für Geologische Wissenschaften of Martin-Luther-Universität Halle-Wittenberg, Halle/Saale, Germany, IGWuG WAL347.2007). All images to scale. (**b** By Wolfgang Fuhrmannek; **d** by Sven Tränkner; others by the author)

the Paleocene of France and "*G. klaasseni*" Newton, 1886 from the early Eocene of England. Mlíkovský (2002) regarded *G.* ("*Diatryma*") *geiselensis* (Fischer, 1978) from the middle Eocene of Messel and the Geisel Valley (Fig. 6.5; Fischer 1962, 1978; Peters 1988a, 1991) as a junior synonym of *G. sarasini* (Schaub, 1929) from the early Eocene (MP 10; Mlíkovský 2002) of France (Fig. 6.5; Schaub 1929). Still, however, a thorough revision of these species is needed, in which the type specimens are directly compared with each other.

The North American Gastornithidae were revised by Andors (1992), who recognized two species, *G.* ("*Diatryma*") *gigantea* (Cope, 1876) and *G.* ("*D.*") *regens* (Marsh, 1894), which differ in toe proportions. Both occur in the Rocky Mountain region of western North America and are restricted to the early Eocene (mainly Wasatch and Willwood Formations).

Zhongyuanus xichuanensis Hou, 1980 from the early Eocene of China is based on the distal end of a tibiotarsus (Hou 1980, 2003). According to Andors (1992), this species is morphologically distinct from the European and North American Gastornithidae. The degree and significance of this difference is, however, still in need of critical revision.

Buffetaut (2004) commented on footprints of giant, tridactyl groundbirds from the late Eocene of France, which were assigned to *Gastornis*, but whose identification conflicts with the fact that the latter has no late Eocene skeletal record. Patterson and Lockley (2004) described a track of a large tridactyl bird from the middle Eocene (45 Ma) of Washington as *Ornithoformipes controversus* and assigned it to a *Gastornis*-like bird. Again these footprints are about five million years younger than the known North American skeletal remains of the Gastornithidae, and some controversy surrounds their authenticity (Patterson and Lockley 2004). If they indeed stem from a species of *Gastornis*, they would establish the presence of hoof-like ungual phalanges in this taxon.

The discovery of gastornithid remains in the early Eocene of southern France supports earlier hypotheses (Dughi and Sirugue 1959; Fabre-Taxy and Touraine 1960) that large eggs from contemporaneous deposits of Provence belong to the Gastornithidae (Buffetaut 2008). According to Fabre-Taxy and Touraine (1960) some of these eggs measure 24 cm × 15 cm and would thus be of a size to be expected for gastornithids; Dughi and Sirugue (1959) even estimated the size of the largest eggs at 40 cm × 20 cm (see Buffetaut 2008).

Putative feathers of *Gastornis* ("*Diatryma*") were described by Cockerell (1923) from the early Eocene of Colorado, but identification of these hair-like filaments was disputed by Wetmore (1930).

Gastornithids are characterized by a huge, bilaterally compressed beak, which has a convex culmen and lacks a hooked tip. The cranium exhibits upper temporal fenestrae. The wings are greatly reduced and the sternum has no keel. At least in the larger species scapula and coracoid are fused to form a scapulocoracoid; such fusion is absent in the Walbeck coracoid (Fig. 6.5), which in contrast to that of other gastornithids also lacks a foramen for the supracoracoideus nerve. The palate is of neognathous structure, and, in contrast to those of palaeognathous birds, the ilioischiadic foramina of the pelvis are closed. The ribs lack ossified uncinate processes. The legs are very robust, with a short tarsometatarsus and a short hallux. The largest species were nearly 2 m tall and had an estimated weight of about 175 kg (Andors 1992).

Andors (1992) revised the phylogenetic affinities of gastornithids and concluded that they are the sister group of the Anseriformes. Derived characteristics shared with other Galloanseres include the presence of retroarticular processes on the caudal ends of the mandible, sessile basipterygoid processes, and features of the quadrate. The evolutionary origins of the Gastornithidae are, however, unknown. Because of its smaller size and more slender tarsometatarsus, *G. russelli* may be the sister taxon of the other gastornithids. If true, this would argue for a European origin of the group, which is also in concordance with the temporal occurrence of the known species (Andors 1992; Buffetaut 1997). Current evidence suggests that gastornithids dispersed into North America in the early Eocene (Andors 1992).

Gastornithids lived in a forested environment and most earlier authors assumed that they were carnivorous. However, Andors (1992, p. 117) elaborated the hypothesis that these birds actually were folivores, and noted that

> Against the received view of diatrymids [=gastornithids] as cursorial predators…, it can be argued that the weakly developed rostral hook, reduced flexor tubercles on the ungual phalanges of the toes, and shortened tarsus seriously impeded this mode of feeding and may have precluded it altogether. The folivore hypothesis…best fits the known morphology of the diatrymid jaw apparatus, and it agrees also with the large size, flightlessness, neck and pelvic limb proportions, vegetated palaeoenvironment, and presumed anseriform affinities of these singular birds.

Witmer and Rose (1991, p. 95) countered that

> Suggestions that *Diatryma* [=*Gastornis*] was an herbivore seem improbable in that they require the postulation of excessively high safety factors in the construction of the skull. The traditional hypothesis of *Diatryma* as a carnivorous bird accords as well or better with the data at hand. Carnivory raises the probability of "accidental" encounter with bones, thus explaining the high safety factors.

A folivorous diet may, however, also include very hard food items, such as seeds and twigs, and I consider the evidence presented by Andors to be the more compelling. Folivory in gastornithids is further supported by the fact that a herbivorous diet has been conclusively shown for the Dromornithidae, which are discussed in the next section, and some of whose representatives closely resemble gastornithids in bill shape.

6.3 †Dromornithidae

These flightless birds are a characteristic element of the Cenozoic avifauna of Australia. Our state of knowledge about them was summarized by Murray and Vickers-Rich (2004), on whose book the following notes are based. Dromornithids have a comparatively abundant Neogene fossil record, but few remains were described from Paleogene deposits. The earliest named species is the Southern Cassowary (*Casuarius casuarius*) sized *Barawertornis tedfordi* Rich, 1979 from the late Oligocene/early Miocene of the Riversleigh Formation, which is also the smallest known dromornithid. A tentative record consisting of impressions of pedal phalanges comes from the early Eocene of Queensland, and putative dromornithid trackways were also reported from the late Oligocene of Tasmania (Vickers-Rich 1991). Dromornithids were graviportal birds and in some osteological features are superficially similar to gastornithids. As in the latter, there are well-developed Galloanseres-like articulation facets for basipterygoid processes, and the mandible bears long retroarticular processes. In several other features, however, dromornithids are clearly distinguished from gastornithids, including the presence of a marked ventral crest on the palatine bone, the absence of a hallux, and the fact that the fourth toe consists of only four phalanges.

As detailed by Murray and Vickers-Rich (2004), there exists convincing evidence for a herbivorous diet of dromornithids. Not only are some specimens preserved with gastroliths, but analyses of stable isotopes from the eggshells of a Pleistocene species also point at plant matter as food components.

Although anseriform affinities of dromornithids are well based, their position within waterfowl and their affinities to the Gastornithidae have not yet been conclusively resolved. Murray and Vickers-Rich (2004) considered them to be the sister taxon of the Anhimidae, i.e., to be within crown group Anseriformes, whereas they assumed that gastornithids are outside crown group Anseriformes. However, the two characters listed by the authors as supporting evidence for a sister group relationship between the Dromornithidae and Anhimidae, i.e., absence of uncinate processes and presence of a tubercle on the deltopectoral crest of the humerus (see p. 156 in Murray and Vickers-Rich 2004), are also present in the Gastornithidae.

6.4 Anseriformes (Waterfowl)

Crown group Anseriformes include the South American Anhimidae (screamers), the Anseranatidae (magpie goose) of Australia and New Guinea, and the globally distributed Anatidae (swans, geese, and ducks). Morphological and molecular evidence supports a sister group relationship between the Anhimidae and the clade (Anseranatidae + Anatidae) (Livezey 1997; see Fig. 27.7 in Cracraft et al. 2004; Hackett et al. 2008). Despite the fact that the fossil record of anseriform birds may go back into the late Cretaceous (Chap. 4), their early evolution is still rather poorly understood.

6.4.1 Anhimidae (Screamers)

The three extant species of the Anhimidae are endemic to South America and most conspicuously differ from other anseriform birds in bill morphology, the absence of webbed feet, and the highly pneumatized skeleton.

The only published Paleogene remains of this group of birds were described by Alvarenga (1999) from the late Oligocene/early Miocene of the Taubaté Basin in Brazil. The description of *Chaunoides antiquus* Alvarenga, 1999 was based on several isolated postcranial bones. *C. antiquus* was smaller than the smallest extant species of screamers, the Northern Screamer *Chauna chavaria*, and had a less pneumatized skeleton. According to Alvarenga (1999), *Loxornis clivus* Ameghino, 1895 from the late Oligocene (Deseadan) of Argentina, which is based on a distal tibiotarsus, may also be a representative of the Anhimidae.

Ericson (1997), Olson (1999b), and Feduccia (1999) mentioned unpublished remains of early Eocene anhimid-like birds from the Willwood Formation (Wyoming) which are under study by Peter Houde. A similar species also occurred in the early Eocene London Clay of Walton-on-the-Naze (see Table 4.1 in Feduccia 1999; own observation).

6.4.2 Anseranatidae (Magpie Geese)

The Australian/New Guinean Magpie Goose (*Anseranas semipalmata*) is the sole extant member of the Anseranatidae. Putative stem group representatives of this taxon were reported from fossil sites in North America and Europe. The first species hypothesized to be such belong to the taxon *Anatalavis*, which was originally erected for *A. rex* from the late Cretaceous/early Paleocene Hornerstown Formation of New Jersey (Olson and Parris 1987). The holotype and only known specimen of this species is a distal humerus. However, a second species, *A. oxfordi* Olson, 1999 from the London Clay of Walton-on-the-Naze, is represented by a three-dimensionally preserved partial skeleton, which includes elements of the wing and pectoral girdle, as well as the skull and portions of the sternum and pelvis (Fig. 6.6; Olson 1999b). Although it is rather unlikely that the goose-sized *A. oxfordi* belongs to the same "genus" as a North American species which lived some ten million years earlier, the fossil material does not allow an unambiguous separation. Mlíkovský's (2002) erection of a new taxon, *Nettapterornis*, for *A. oxfordi* is not well founded (Mourer-Chauviré 2004; Mayr 2005a).

The presence of a large pneumatic foramen on the sternal end of the coracoid and the very wide sternal extremity of the furcula (Olson 1999b) are derived similarities of *Anatalavis* and *Anseranas* (Fig. 6.6), but the two taxa otherwise have a quite different skeletal morphology. The humerus of *A. oxfordi* is proportionally shorter and more robust than that of crown group Anseriformes, and Olson (1999b) hypothesized that the taxon was capable of powerful and rapid flight.

The plesiomorphic presence of a foramen for the supracoracoideus nerve on the coracoid shows *Anatalavis* to be outside crown group Anatidae. Nevertheless, the beak is very duck-like and *A. oxfordi* was probably a filter-feeder, whereas extant Anseranatidae have a goose-like beak and are macrofeeders (Olson 1999b). In contrast to those of all extant Anseriformes, the temporal fossae are well developed. The shape of the pterygoid also differs from that of crown group Anseriformes,

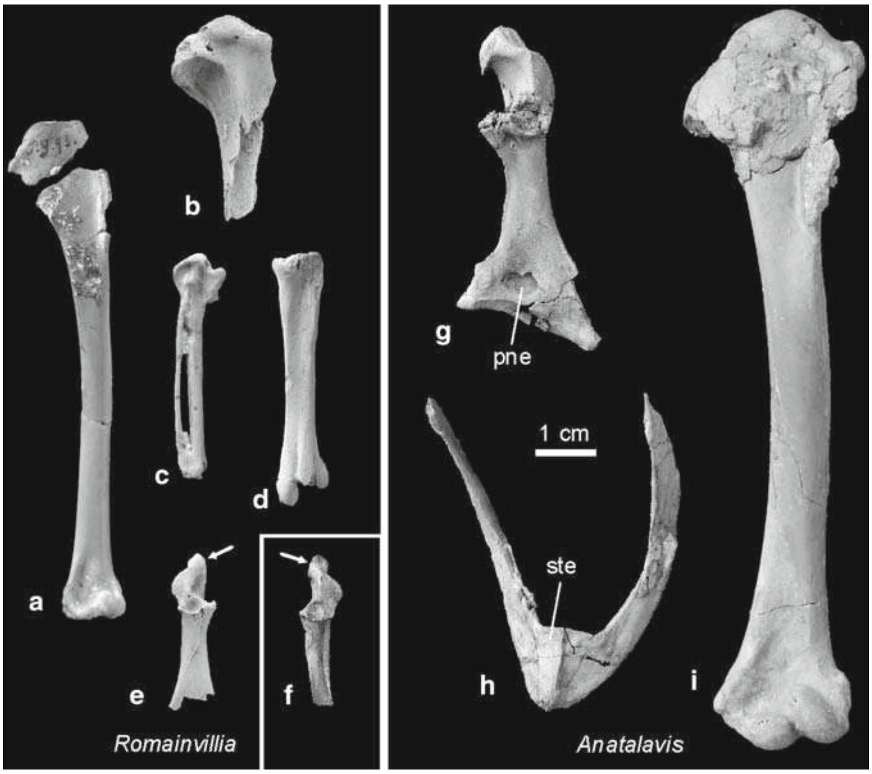

Fig. 6.6 **a–e** *Romainvillia stehlini* Lebedinsky, 1927 (Romainvilliinae) from the late Eocene of Romainville in France; **f** holotype of *Paracygnopterus scotti* Harrison and Walker, 1979 (Romainvilliinae) from the early Oligocene of the Isle of Wight in England (Natural History Museum, London, UK, BMNH A 4404); **g–i** holotype of *Anatalavis oxfordi* Olson, 1999 (?Anseranatidae) from the early Eocene London Clay of Walton-on-the-Naze (BMNH A 5922). **a** Left humerus (Naturhistorisches Museum Basel, Switzerland, NMB P.G.77 and NMB P.G.93); **b** proximal right humerus (NMB P.G.53.c); **c** left carpometacarpus (NMB P.G.53); **d** right tarsometatarsus (NMB P.G.25.l); **e** left coracoid (lectotype, NMB P.G.38.a); **f**, **g** right coracoid; **h** furcula; **i** left humerus. The specimens in **b**, **d**, and **e** were coated with ammonium chloride. The *arrows* point to the furcular articulation facet of the coracoid. *pne* pneumatic opening, *ste* sternal extremity of furcula. All images to scale. (Photos by Sven Tränkner)

which led Olson (1999b) to assume that the skull of *Anatalavis* departed from that of extant waterfowl in aspects of its functional morphology. *A. rex* is further distinguished from all crown group Anseriformes in the short and blunt postorbital process (skull) and the short and broad praeacetabular portion of the pelvis (Olson 1999b).

Olson's (1999b) classification of *Anatalavis* was challenged by Dyke (2001b), who did not, however, include in his analysis all potential synapomorphies of *Anseranas* and *Anatalavis* listed by Olson (1999b). Revision and reanalysis of the data support a sister group relationship between *Anatalavis* and *Anseranas* (Mayr 2008f), although this hypothesis certainly needs to be bolstered with additional evidence. A pneumatic opening on the coracoid, for example, also occurs in the Anhimidae and some galliform birds, and is thus either plesiomorphic for Anseriformes or evolved several times independently within Galloanseres (in which case it would be a weak character). The sternal extremity of the furcula is further a thin sheet in *Anatalavis* but thickened and pneumatized in *Anseranas*. If *Anatalavis* is the sister taxon of *Anseranas*, it indicates that a duck-like beak was already present in the stem species of the clade (Anseranatidae + Anatidae).

Another putative anseranatid, *Anserpica kiliani* was described from the late Oligocene of France by Mourer-Chauviré et al. (2004). This species is only known from a coracoid which is very similar to that of *Geranopsis hastingsiae* Lydekker, 1891 from the late Eocene and early Oligocene of England, a presumed representative of the Gruoidea, with which it was not compared (see Sect. 9.3.4; Mayr 2005a).

The earliest Australian stem group representative of the Anseranatidae was reported by Worthy and Scanlon (2009) from the late Oligocene/early Miocene of the Riversleigh Formation. This new species was assigned to the taxon *Anseranas* and is represented by a coracoid and referred scapulae. It mainly differs from the extant *A. semipalmata* by its smaller size and the presence of pneumatic openings in the acrocoracoid process.

6.4.3 †Presbyornithidae

The Presbyornithidae are abundant birds in some early Paleogene fossil localities of the New World, and have a confusing history concerning both their taxonomy and their phylogenetic assignment. The first remains, a few isolated bones from the early Eocene of Utah, were described by Wetmore (1926) and assigned to the charadriiform Recurvirostridae (stilts and avocets; *Presbyornis*) and Alcidae (auks; "*Nautilornis*"). Howard (1955) subsequently described specimens from the Eocene (Casamayoran) of Patagonia as *Telmabates antiquus*. She tentatively referred this species to the Phoenicopteriformes, but also made comparisons with Charadriiformes and Mesozoic stem group representatives of Neornithes. It was not until Feduccia and McGrew (1974) reported new material of *P. pervetus* from the early Eocene of Wyoming that *Presbyornis* and *Telmabates* were classified in the same higher-level taxon.

Ericson (2000) revised the New World fossil record of the Presbyornithidae and confirmed validity of four species: the large Paleocene *P. isoni* Olson, 1994 (Olson 1994; Benson 1999), as well as the early Eocene *P. pervetus* Wetmore, 1926, *P. recurvirostra* (Hardy, 1959), and *T. antiquus*. Except for the latter, all of these species occur in North American sites. *T. howardae* Cracraft, 1970 from the Eocene (Casamayoran) of Argentina was excluded from the Presbyornithidae by Ericson (2000), who regarded the affinities of this poorly known species uncertain.

Remains of putative Presbyornithidae were also identified from the late Cretaceous of Mongolia (*Teviornis gobiensis* Kurochkin et al., 2002), but their classification needs to be confirmed by additional and more complete material (Kurochkin et al. 2002, see also Clarke and Norell 2004). Likewise presbyornithid affinities of *Proherodius oweni* Lydekker, 1891, whose fossil record consists of a poorly preserved sternum from the early Eocene London Clay, are not well based (Olson 1985; contra Harrison and Walker 1978).

Although the best-represented presbyornithid species, *P. pervetus*, is known from numerous bones, no articulated skeletons have as yet been found. *P. pervetus* combines a duck-like skull with very long legs, and its postcranial skeleton is quite different from that of extant Anseriformes. The caudal margin of the sternum exhibits two pairs of incisions, whereas there is only a single pair in all extant Anseriformes. Also unlike in all extant Anseriformes, the pneumotricipital fossa of the humerus is very shallow and lacks pneumatic foramina, and the ilia are not fused with the synsacrum. As evidenced by *T. antiquus*, the caudalmost thoracic vertebrae of presbyornithids are further opisthocoelous (Howard 1955), whereas they are heterocoelous in extant Anseriformes and most other neornithine birds.

As yet no detailed and comparative descriptions of the skull of presbyornithids have been published. However, it has been noted that these birds differ from crown group Anseriformes in proportionally shorter postorbital processes, the absence of a caudal inflation of the ventral portion of the quadrate, and the presence of well-developed temporal fossae (Olson and Feduccia 1980a).

Presbyornithids were filter-feeding birds which probably nourished on planktonic organisms in shallow, saline lakes (Olson and Feduccia 1980a; Feduccia 1999). At least the taxon *Presbyornis* may have been sexually dimorphic in size (Ericson 2000), and judging from mass mortality layers with thousands of bones, mainly at Lake Gosiute of the Green River Formation, appears to have been highly gregarious (Olson 1985; Ericson 2000). Trackways from the Green River Formation of eastern Utah which were allocated to *P. pervetus* by earlier authors were described as *Presbyorniformipes feduccii* [sic] by Yang et al. (1995). If correctly identified, they provide evidence not only for the presence of fully webbed anterior toes and a long hallux in *Presbyornis*, but, through the presence of dabble marks, also for the feeding behavior of this species. Eggshells of *Presbyornis* were reported by Leggitt and Buchheim (1997).

Like few other fossil birds, presbyornithids were cited as "missing links" to support phylogenetic hypotheses. Before the skull was discovered, they were considered to be most closely related to either charadriiform birds (Wetmore 1926) or the Phoenicopteriformes (Howard 1955; Feduccia and McGrew 1974; Feduccia 1976). Feduccia (1976) hypothesized that the skeletal morphology of presbyornithids constitutes evidence for a close relationship between the Phoenicopteriformes (flamingos) and Charadriiformes (shorebirds). Anseriform affinities of presbyornithids were assumed by Harrison and Walker (1976a, 1979a) and became widely recognized through the publication of Olson and Feduccia (1980a), who cited the mosaic character distribution displayed by *Presbyornis* in order to establish a charadriiform ancestry of the Anseriformes.

Olson and Feduccia (1980a, p. 22) considered presbyornithids to represent “a charadriiform grade of morphology”, and Olson (1985) listed them as “transitional shorebirds.” By contrast, the Presbyornithidae resulted as a sister taxon of the Anatidae in cladistic analyses of Ericson (1997) and Livezey (1997). Ericson (1997) identified only a single character as a possible apomorphy of a clade including the Presbyornithidae and Anatidae, the presence of a pneumatic foramen on the medial process of the mandible. Livezey (1997) did not list the character evidence for his phylogeny, but mentioned that fully webbed anterior toes, whose presence can be inferred for *Presbyornis* from the above-mentioned trackways, are a synapomorphy of the Presbyornithidae and Anatidae.

Most likely, the long legs of presbyornithids are an autapomorphic feature, and certain peculiarities in which presbyornithids differ from other Anseriformes may be related therewith. In particular, this seems to be true for the morphology of the caudal margin of the sternum and the large cnemial crests of the tibiotarsus (Mayr 2008f).

6.4.4 Anatidae (Ducks, Geese, and Swans)

Most extant anseriform species belong to the Anatidae, which are widespread in all kinds of aquatic and semiaquatic environments. Anatids typically are short-legged birds. The crown group representatives are characterized by the reduction of the foramen for the supracoracoideus nerve on the coracoid, which in some extant representatives of early diverging lineages still forms a notch in the medial margin of the bone. The Paleogene fossil record of duck- or goose-like birds is very incomplete. The earliest unambiguously identified taxa are from late Eocene deposits of Europe. No representatives of the Anatidae are as yet known from the Paleogene of Africa.

Eonessa anaticula Wetmore, 1938 from the middle Eocene (Uinta Formation) of Utah is based on wing bones and was assigned to the Anatidae by Wetmore (1938a); this classification was disputed by Olson and Feduccia (1980a). Likewise, identification of “*Anas*” *benedeni* Sharpe, 1899 from the early Oligocene of Belgium as an anseriform was regarded incorrect by Brodkorb (1962); the material referred to this species consists of several incomplete bones of unknown whereabouts, including a humerus, an ulna, and a tibiotarsus.

Cygnopterus affinis (van Beneden, 1883) is known from several bones of a single individual from the early Oligocene (MP 23–24; Mlíkovský 2002) of Belgium. These were described by Lambrecht (1931a), who considered the fairly large species to be a representative of the Cygnini (swans). Another Paleogene species of *Cygnopterus*, *C. lambrechti* Kurochkin, 1968 from the late Oligocene (*Indricotherium* Beds) of Central Kazakhstan, whose holotype is the distal end of a humerus (Kurochkin 1968a), was synonymized with the phoenicopteriform bird “*Agnopterus*” *turgaiensis* Tugarinov, 1940 from the late Oligocene of Kazakhstan (Mlíkovský and Švec 1986). Mlíkovský and Švec (1986, p. 266) hypothesized that *Cygnopterus* may be a representative of the Phoenicopteriformes, and I also consider the phylogenetic affinities of the taxon to be uncertain and in need of a revision. Humerus, scapula, and coracoid of *C. affinis* are very similar to the corresponding bones of the coeval and similarly sized presumptive phoenicopteriform ?*Agnopterus hantoniensis* (Chap. 10; Mayr and Smith 2002a; Mayr 2005a, 2008f). The femur of *C. affinis* is, however, more slender than that of the Phoenicopteriformes and differs from a femur referred to ?*A. hantoniensis* in the low trochanteric crest.

The earliest unambiguously "duck-like" anseriform is *Romainvillia stehlini* Lebedinsky, 1927 from the late Eocene (MP 20; Mourer-Chauviré 1996) of France. Lebedinsky (1927) based the description of this species on a coracoid, furcula, carpometacarpus, and tarsometatarsus, but the material from the type locality also includes humeri that were not mentioned in the original description (Mayr 2008f). *R. stehlini* was a small species, the size of the extant Silver Teal (*Anas versicolor*), and is classified into the taxon Romainvilliinae. A record of *Romainvillia* sp. was also reported from the early Oligocene of Belgium (Mayr and Smith 2001). *Paracygnopterus scotti* Harrison and Walker, 1979, from the early Oligocene of England, is a further representative of the Romainvilliinae (Fig. 6.6; Mayr 2008f).

The coracoid of *R. stehlini* is distinguished from that of crown group Anatidae in that it still exhibits a small foramen for the supracoracoideus nerve, and in that the articulation facet for the furcula is ovate, essentially flat and in line with the medial margin of the coracoidal shaft (Fig. 6.6). The tip of the omal extremity of the furcula differs from that of crown group Anatidae in being wider and blunt. The elongate humerus is similar to that of the Presbyornithidae; as in the latter, the pneumotricipital fossa is very shallow and lacks pneumatic foramina. The short tarsometatarsus of *R. stehlini* is distinguished from that of crown group Anatidae in the shape of the trochlea for the second toe, which is mediolaterally narrow and lacks a proximally extending crest. The differences in the shape of the tarsometatarsal trochlea possibly suggest that *Romainvillia* was less adapted to a swimming way of living than extant Anatidae, which while paddling bring the toes together when moving the feet forward (Mayr 2008f).

Mlíkovský (2002) and Olson (1999b) assumed that *R. stehlini* belongs to the Anseranatidae, but a phylogenetic analysis supported the clade (*Romainvillia* + Anatidae), whose sister taxon are the Presbyornithidae (Mayr 2008f). Derived characters shared by *Romainvillia* and extant Anatidae but absent in the Presbyornithidae include the lack of a tarsometatarsal fossa for the first metatarsal, which indicates that the hallux was small as in extant Anatidae.

A putative anatid, *Palaeopapia eous* (Harrison and Walker, 1976), is known from a sternal fragment and a referred coracoid from the late Eocene and early Oligocene of England (Harrison and Walker 1976a, 1979a). The earliest modern-type anatids are from the earliest Oligocene of Belgium (Mayr and Smith 2001) and were tentatively assigned to *Paracygnopterus* in the original description. This identification is no longer upheld and the specimens are now regarded as indeterminate Anatidae (Mayr 2008f).

Crown group representatives of the Anatidae were reported from the late Oligocene of France and assigned to *Mionetta blanchardi* (Milne-Edwards, 1863) and *M. natator* (Milne-Edwards, 1867) (Hugueney et al. 2003). According to

Livezey and Martin (1988: 196), *Mionetta* “diverged from the rest of the Anatidae after *Dendrocygna* but before *Stictonetta*,” but an analysis by Worthy and Lee (2008) resulted in a sister group relationship between this taxon and a clade including *Stictonetta*, *Malacorhynchus*, and *Oxyura*.

The holotype and only known specimen of the alleged swan *Cygnavus formosus* Kurochkin, 1968a from the early Oligocene of Kazakhstan is the distal end of a tibiotarsus. Because this bone is damaged in *C. senckenbergi* Lambrecht, 1931, the early Miocene type species of the taxon *Cygnavus*, identification of the Kazakh specimen is arguable. Kurochkin (1968a) further assigned a distal ulna from the late Oligocene (*Indricotherium* Beds) of Kazakhstan to the extant taxon *Somateria*, but this assignment is likewise poorly founded. There is a greater possibility that the fragmentary bone belongs to one of the other taxa described by Kurochkin (1968a).

Louchart et al. (2005) detailed that *Guguschia nailiae* Aslanova and Burchak-Abramovich, 1968 from the Oligocene of Azerbaijan is not a swan (Cygnini), as that it was originally described (Aslanova and Burchak-Abramovich 1968). The species is known from wing remains, including a nearly complete humerus, and needs to be restudied. It is well possible that it is conspecific with the pelagornithid *Caspiodontornis kobystanicus* from the same locality (Aslanova and Burchak-Abramovich 1999; see Sect. 6.5).

In contradiction to Olson’s (1989) assumption that the Anatidae originated in the Southern Hemisphere, the Southern Hemisphere fossil record of duck-like birds is rather scarce in the Southern Hemisphere and restricted to the late Oligocene. *Teleornis impressus* Ameghino, 1899 from the Deseadan of Patagonia (Argentina) was assumed to be a member of the Tadornini (shelducks) by Agnolin (2004). However, this species is represented by a distal humerus only, and although it indeed seems to be an anseriform, possibly even an anatid, additional specimens are required to establish its exact affinities. Agnolin (2004) also assigned to the Anseriformes another species from the Deseadan of Patagonia, *Aminornis excavatus* Ameghino, 1899, which is based on the omal extremity of a coracoid and was previously considered to be a representative of the Aramidae (limpkins; Sect. 9.3.4). The affinities of this species also have to be established with further material.

Worthy (2009) described crown group representatives of the Anatidae from the late Oligocene Etadunna Formation and Namba Formation of Australia. These were assigned to new taxa of the Oxyurini (stiff-tailed ducks) and Tadornini (shelducks), and are represented by many well-preserved limb bones.

6.5 †Pelagornithidae (Bony-Toothed Birds)

These large to very large marine birds are characterized by the possession of irregular spiny projections along the tomia of the long beak, extremely thin walled bones, and a highly derived morphology of the humerus. They occur in late Paleocene to Pliocene deposits, and appear to have already achieved a global distribution in the early Paleogene.

Among the earliest and most substantial Paleogene remains of bony-toothed birds are three-dimensionally preserved bones, which Bourdon (2005, 2006) reported from the late Paleocene/early Eocene of the Ouled Abdun Basin in Morocco. Bourdon (2006) distinguished three species of *Odontopteryx* from this locality, one of which she referred to *O. toliapica* Owen, 1873; the other two represent undescribed new species.

Harrison (1985) described a partial mandible from the late Paleocene of England as *Pseudodontornis tenuirostris*, and another jaw fragment from the latest Paleocene of Kazakhstan was described as *Pseudodontornis tshulenis* by Averianov et al. (1991). Although these specimens are clearly from pelagornithid birds, their taxonomic distinctness is questionable, since little is known on the intraspecific variability of the "bony teeth" in pelagornithids.

Bony-toothed birds are comparatively abundant in the early Eocene London Clay of the Isle of Sheppey, and the first specimens of pelagornithids were actually found in this locality. Unfortunately, a revision of the London Clay Pelagornithidae by Harrison and Walker (1976b) resulted in formidable taxonomic confusion. Although these authors identified several wrongly classified fossils from the Isle of Sheppey as bony-toothed birds, altogether they distinguished six species in five "genera" and three "families" for the pelagornithids from this locality. This result was rightly considered "completely unrealistic" by Olson (1985, p. 195), so much the more so as many species were based on noncomparable skeletal elements. In fact, all London Clay pelagornithids can probably be assigned to three species (Fig. 6.7): the smallest of these is *O. toliapica*, which is the first bony-toothed bird recognized as such (Owen 1873). A somewhat larger species was described as *Macrodontopteryx oweni* by Harrison and Walker (1976b) (see also Owen 1880), but may actually also belong to *Odontopteryx* (Warheit 2002, p. 53). Finally, there is a very large species, more than twice the size of *O. toliapica*, with a complicated taxonomic history. This species is known from various skeletal elements, virtually all of which were assigned to different species by Harrison and Walker (1976b, 1977). As shown by Mayr (2008g), all of these specimens should be classified as *Dasornis emuinus* (Bowerbank, 1854), with *Dasornis londinensis* Owen, 1870, *Argillornis longipennis* Owen, 1878, the alleged procellariiform *Neptuniavis miranda* Harrison and Walker, 1977, and possibly also *Pseudodontornis longidentata* Harrison and Walker, 1976 being junior synonyms of this species.

Remains of medium-sized Pelagornithidae were further found in the middle Eocene of Belgium (Mlíkovský 1996c; personal observation). The putatively gruiform *Zheroia kurochkini* Nessov, 1988, which is based on a worn distal tibiotarsus from the late Eocene of Kazakhstan, may also be a representative of the Pelagornithidae, of which partial mandibles were found in the type locality of *Z. kurochkini* (Nessov 1992).

From the middle Eocene of Nigeria, a very large fragmentary sternum was described as *Gigantornis eaglesomei* by Andrews (1916). The pelagornithid affinities of this specimen were recognized by Harrison and Walker (1976b), but the exact phylogenetic affinities between *Gigantornis* and *Dasornis*, whose sternum is unknown, still need to be determined. Remains of a large pelagornithid species were also reported from the middle Eocene of Togo (Bourdon 2006).

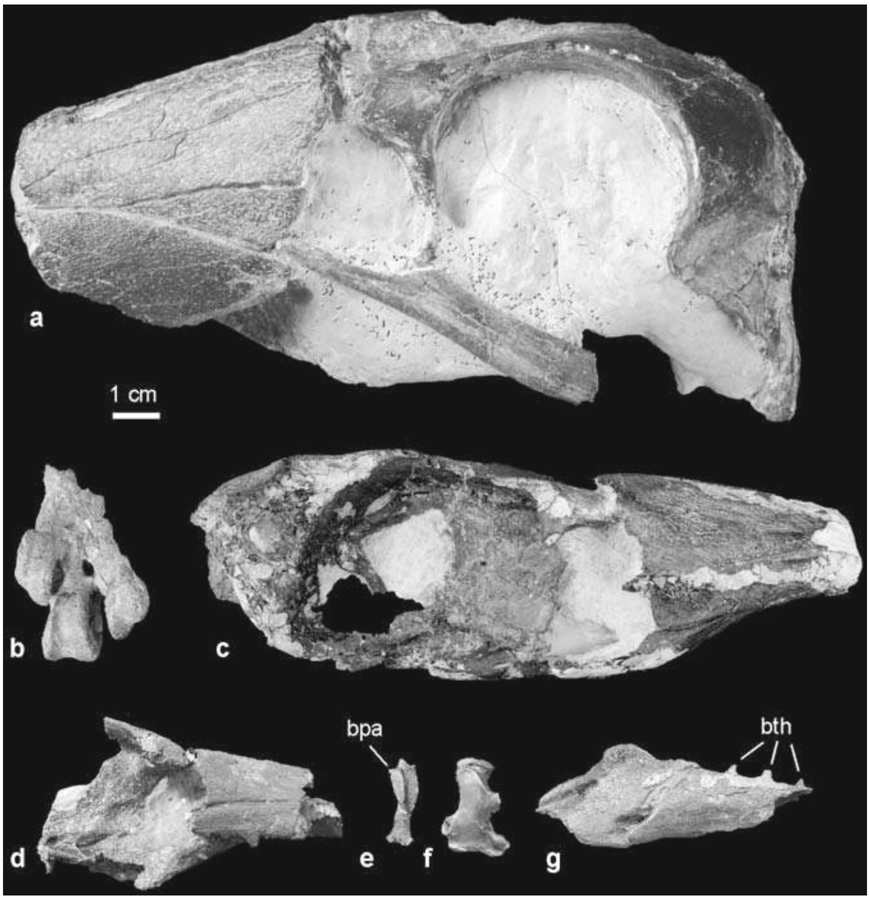

Fig. 6.7 Pelagornithidae from the early Eocene of the London Clay of the Isle of Sheppey. **a** Cranium of *Dasornis emuinus* (Bowerbank, 1854) (Staatliches Museum für Naturkunde Karlsruhe, Germany, SMNK-PAL 4017); **b** distal right tarsometatarsus of *D. emuinus* (Natural History Museum, London, UK, BMNH A 894; holotype of *Neptuniavis miranda* Harrison and Walker, 1977); **c** incomplete skull of *Macrodontopteryx oweni* Harrison and Walker, 1976 (holotype, BMNH A 1); **d** partial skull, **e** left pterygoid, **f** right quadrate, and **g** fragment of left mandible of *Odontopteryx toliapica* Owen, 1873 (holotype, BMNH A 44096). *bpa* articulation facet of basipterygoid process, *bth* tooth-like bony projection. All images to scale. (Photos by Sven Tränkner)

The earliest fossil record of a pelagornithid from the Pacific Basin is a fragmentary distal humerus from the middle Eocene of Mexico, which was tentatively referred to *Odontopteryx* (González-Barba et al. 2002). Olson (1999a) described remains of the Pelagornithidae from the early Eocene of Virginia, and Goedert (1989) reported specimens of giant pelagornithids from the late Eocene to early Oligocene of Oregon, which possibly belong to *Dasornis* (“*Argillornis*”).

Stilwell et al. (1998) further assigned a fragment of a humerus shaft from the middle Eocene of East Antarctica to the Pelagornithidae (see also Jones 2000). Pelagornithids are also known from the late Eocene of the La Meseta Formation of Seymour Island (Tonni and Tambussi 1985; Tambussi and Acosta Hospitaleche 2007).

Compared with this fairly extensive Eocene fossil record, few remains of the Pelagornithidae were found in Oligocene deposits. *Caspiodontornis kobystanicus* Aslanova and Burchak-Abramovich, 1982 from the "middle" Oligocene of Azerbaijan is based on a largely complete skull with a length of 30 cm (Aslanova and Burchak-Abramovich 1999). Aslanova and Burchak-Abramovich (1999) emphasized the fact the specimen is strongly flattened dorsoventrally, which is however likely to be an artifact of preservation. As noted in the preceding section, *C. kobystanicus* may be a junior synonym of *Guguschia nailiae* from the same locality, which was misidentified as a swan.

Remains of unnamed species of bony-toothed birds also occur in the Oligocene of Japan (Okazaki 1989, 2006). *Palaeochenoides mioceanus* Shufeldt, 1916 and *Tympanonesiotes wetmorei* Hopson, 1964 from the late Oligocene of South Carolina are further representatives of the Pelagornithidae (Olson 1985), but the exact taxonomic affinities of these species still need to be clarified.

Some peculiar skull features of pelagornithids are related to the unique bony projections along the tomia of the long beak. For example, there is a pair of distinct furrows along the ventral surface of the upper beak, which bear marked pits for reception of the "bony teeth" of the mandible. The high jugal bars and the strongly ventrally projecting palatine also seem to be functionally correlated with the specialized feeding technique of bony-toothed birds. Zusi and Warheit (1992) remarked that the mandible of these birds had an intraramal joint and lacked a fused mandibular symphysis. Pelagornithids probably captured their prey, larger fish or squid, near the water surface. Virtual endocasts of the skull of *Odontopteryx* were studied by Milner and Walsh (2009), who found the brain of this taxon to be similar to that of extant seabirds.

Despite the wide temporal and geographic distribution of pelagornithids, many aspects of their postcranial skeleton are still insufficiently known, because the fragile bones are often fragmentary or badly crushed. Much new information was gathered by Bourdon (2006), who studied one the most comprehensive samples of pelagornithid bones found to date. Still, however, the results of this study await formal publication. Pelagornithids had very long and slender wing bones and short legs. The proximal end of the humerus exhibits a peculiar morphology, which prohibited rotation of the bone, and is indicative of a highly specialized mode of wing movement not found in other avian taxa. According to Olson (1985) at least the very large Neogene species were not capable of sustained flapping flight. In *Gigantornis*, the tip of the sternal carina exhibits a large articulation facet for the furcula. Among extant birds a similar syndesmotic or synostotic joint between furcula and sternum mainly occurs in larger soaring birds (Mayr et al. 2008). The pelagornithid sternum is further characterized by a large, steep-walled opening in the cranial portion of the visceral surface, and a strongly vaulted body (Mayr et al. 2008).

Most earlier authors either assigned pelagornithids to the nonmonophyletic "Pelecaniformes" (Olson 1985; Olson and Rasmussen 2001) or classified them into the taxon Odontopterygiformes, which was considered closely related to both "Pelecaniformes" and Procellariiformes (Harrison and Walker 1976b). However, a cladistic analysis by Bourdon (2005) resulted in a sister group relationship between bony-toothed birds and the Anseriformes. Bourdon (2005) listed 12 apomorphies in order to support anseriform affinities of bony-toothed birds, including the presence of only two, instead of three, condyles on the mandibular process of the quadratum. As already remarked by Harrison and Walker (1976b), bony-toothed birds further possess the derived basipterygoid articulation of the Galloanseres. Moreover, the rostral furrow of the beak of pelagornithids is not homologous to that found in extant "Pelecaniformes" and Procellariiformes, and a position of bony-toothed birds outside Neoaves can be supported with the plesiomorphic absence of a ventral crest on the palatinum (Mayr 2008g). Comparisons with the Anseriformes were also made by previous authors (e.g., Spulski 1910), and at least one pelagornithid, i.e., *P. mioceanus*, was originally assigned to the Anseriformes (see Olson 1985); as noted above, this may also be true for the putative swan *Guguschia nailiae*. Anseriform affinities of the Pelagornithidae would be in line with the fact that the only other taxon with bony-tooth-like projections along the tomia is the moa-nalo *Thambetochen xanion*, an extinct goose-like duck that was described from the Holocene of Hawaii by Olson and James (1991). Certainly, however, more studies are needed to firmly establish the phylogenetic affinities of bony-toothed birds, so much the more so as Bourdon's (2005) analysis resulted in an unlikely (see Chap. 3) nonmonophyly of the Galloanseres.

Paleogene representatives of the Pelagornithidae cover a size range from medium-sized (*O. toliapica*) to very large (*D. emuinus*) species, which probably had a wingspan above 4 m. By contrast, all Neogene Pelagornithidae had a giant size, reaching wingspans of 5–6 m (Olson 1985). Most likely, giant size evolved only once within bony-toothed birds, and the large *Dasornis* is the sister taxon of the giant Neogene Pelagornithidae, which can be united on the basis of a derived humerus morphology (compare plates 6 and 10 in Harrison and Walker 1976b). Although a phylogenetic analysis by Bourdon (2005) resulted in a sister group relationship between *Dasornis* ("*Argillornis*") and *Odontopteryx*, only the fragmentary humeri and ulnae of *D. emuinus* were included in this analysis. The two characters listed as apomorphies of a clade including *Dasornis* ("*Argillornis*") and *Odontopteryx* (an elongated pneumatic foramen on the humerus and an elongated ulnar tubercle for the ventral collateral ligament; see the caption to Fig. 1 in Bourdon 2005) may well be plesiomorphic for the Pelagornithidae.

Chapter 7
Aquatic and Semiaquatic Taxa

I am aware that the title of this chapter conflicts with the fact that not all aquatic bird groups are included in it, but I was unable to find a more appropriate one. As outlined in Chap. 3, there is support for a clade including the nonmonophyletic "Pelecaniformes" except the Phaethontidae (tropicbirds), as well as the Sphenisciformes (penguins), Gaviiformes (loons), Procellariiformes (tubenoses), and the taxa of the nonmonophyletic "Ciconiiformes." The affinities of the Phaethontidae are uncertain, and the taxon is discussed in the present chapter for convenience only.

The fossil record of crown group representatives of the "waterbird clade" is among the oldest for Neoaves. Stem group Sphenisciformes date back to the Cretaceous–Paleogene boundary (Hansford 2008), and putative stem group Gaviiformes and Procellariiformes were reported from the late Cretaceous (Chap. 4). The early evolution and historical biogeography of these birds is, however, still poorly understood. The osteological features of early Eocene stem group representatives of, for example, the Threskiornithidae are trenchantly different from those of coeval Sphenisciformes, which indicates a long evolutionary separation of the lineages leading to these two taxa already by that time. Likewise it is uncertain where the stem species of the clade including the above-mentioned taxa lived, although this may well have been one of the southern continents.

A tentative hypothesis on the interrelationships of some of the taxa discussed in this chapter is depicted in Fig. 7.1.

7.1 Fregatidae (Frigatebirds) and Suloidea (Gannets, Boobies, Cormorants, and Anhingas)

Various phylogenetic analyses of different data congruently support a sister group relationship between the Fregatidae and Suloidea, i.e., a clade including the Sulidae, Phalacrocoracidae, and Anhingidae (Ericson et al. 2006; Mayr 2008b; Brown et al. 2008). Among others, these taxa share a greatly abbreviated tarsometatarsus, which is only about half of the length of the carpometacarpus, a distally protruding trochlea for the second toe, and a pectinate claw of the third toe (Mayr 2003a, 2008b). Within the Phalacrocoracidae the tarsometatarsal features are only

G. Mayr, *Paleogene Fossil Birds*, DOI: 10.1007/978-3-540-89628-9_7,

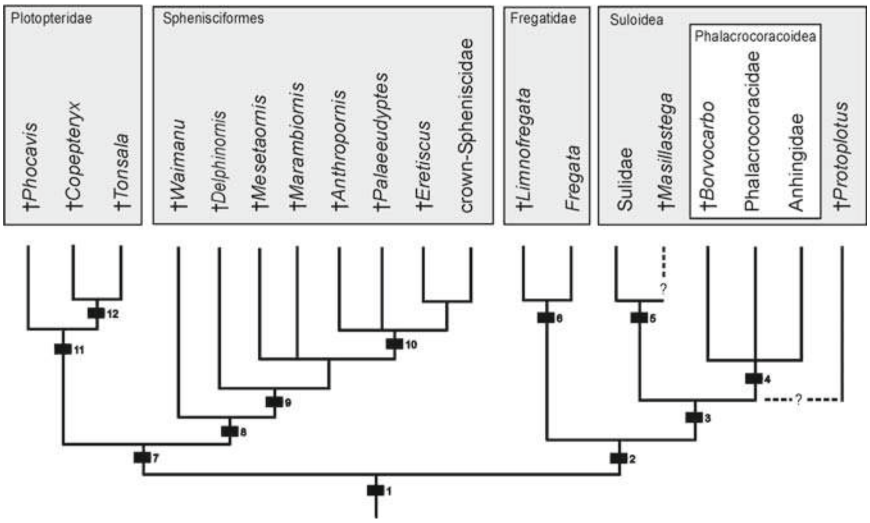

Fig. 7.1 Hypothesis on the phylogenetic relationships between Paleogene and extant representatives of the Plotopteridae, Sphenisciformes, Fregatidae, and Suloidea. Selected apomorphies: *1* tarsometatarsus greatly abbreviated, with distally protruding trochlea for the second toe; *2* palatine with well-developed caudolateral angle, dorsal tympanic recess greatly enlarged and situated rostrally to the articular facets of the quadrate (except in Phalacrocoracidae and Anhingidae), claw of the third toe distinctly pectinate on its medial side; *3* palatine flat horizontal plate, 13 or fewer sclerotic ossicles, orbital process of quadrate reduced; *4* interzygapophysial lacunae of caudal cervical vertebrae of the first section very shallow, costal processes of cervical vertebrae of the second section greatly elongated, cnemial crests of the tibiotarsus strongly proximally protruding; *5* upper beak and mandible dorsoventrally deep and with numerous impressions of blood vessels, marked dorsal tympanic recess; *6* tarsometatarsus measuring less than one third of the carpometacarpus, deltopectoral crest of the humerus triangular and protruding; *7* proximal end of the humerus deep and rounded, with ventrally directed humeral head, distal end of the humerus strongly flattened and ventrally protruding, scapulotricipital and humerotricipital sulci very deep and shifted toward the ventral margin of the humerus, scapula forming a thin, sheet-like, greatly expanded blade; *8* skull with marked supraorbital fossae for salt glands; *9* proximal vascular foramina of tarsometatarsus situated in very deep, elongate fossae on the dorsal surface of the tarsometatarsus; *10* distal vascular foramen of the tarsometatarsus lost; *11* acromion of the scapula greatly elongated and narrow (unknown for *Phocavis*); *12* distal vascular foramen of the tarsometatarsus lost. (After Mayr 2005b, 2007c, 2008b; phylogeny of Paleogene Sphenisciformes simplified after Ksepka et al. 2006, who did not list apomorphies of the nodes)

present in the small *Microcarbo* species, which are probably outside a clade formed by all other extant cormorants (Mayr 2007c).

7.1.1 †Protoplotidae

Protoplotus beauforti Lambrecht, 1931 is possibly among the earliest representatives of the Fregatidae/Suloidea clade. The species is based on a nearly complete skeleton from lacustrine sediments of Sumatra. The age of these deposits is debated, but they probably date from the Eocene or even the Paleocene (van Tets et al. 1989; Stidham et al. 2005).

P. beauforti is a small species, of a size similar to that of the extant Little Pied cormorant, *Phalacrocorax* (“*Microcarbo*”) *melanoleucos*. The tarsometatarsus is very short, and the trochlea for the second toe protrudes distally beyond those for the other toes. As in the stem group frigatebird *Limnofregata* (Sect. 7.1.2), the narial openings of *P. beauforti* are long and slit-like, whereas they are greatly reduced in extant Fregatidae and Suloidea. *Protoplotus* differs from *Limnofregata* in, for example, the shape of the mandible and the proportionally longer legs.

P. beauforti was originally described as a representative of the Anhingidae (Lambrecht 1931b). Van Tets et al. (1989) classified the species into a new taxon, Protoplotidae, and detailed that its anhingid affinities have not been well established. *P. beauforti* differs in many osteological features from crown group Anhingidae, for example, the mandibular rami are tightly joined in their rostral half (as in the stem group tropicbird *Prophaethon*; Sect. 7.11), the cervical vertebrae are proportionally shorter, and the limb elements have different proportions, with ulna and tarsometatarsus being relatively longer. Although the species more closely resembles the Anhingidae and Phalacrocoracidae in skeletal features than the Fregatidae and Sulidae, a closer relationship to the former two taxa has not yet been established with derived characters.

The holotype specimen of *P. beauforti* is remarkable because it preserves a dense accumulation of large gastroliths, which led Lambrecht (1931b) to hypothesize that the species was granivorous. By contrast, van Tets et al. (1989) assumed that it foraged under water and fed on small fish and invertebrates. These authors further noted that the gastroliths may have served as ballast to aid diving, whereas Zhou et al. (2004) argued that *Protoplotus* could have employed seasonal diet switching from fish to plant material.

7.1.2 Fregatidae (Frigatebirds)

The Fregatidae include five extant species, which occur in tropical and subtropical oceans worldwide. Frigatebirds are highly aerial birds and can neither walk on land nor swim. The only Paleogene fossil records of the group are two species of the taxon *Limnofregata*, which were found in the early Eocene Green River Formation (Olson 1977a; Olson and Matsuoka 2005). *Limnofregata azygosternon* Olson, 1977 and *L. hasegawai* Olson and Matsuoka, 2005 mainly differ in size and the proportions of the beak. Both species are known from several articulated skeletons, some of which exhibit feather remains. The smaller species, *L. azygosternon*, was about the size of the males of the Lesser Frigatebird (*Fregata ariel*), which is the smallest extant species (Olson 1977a). *Limnofregata* shares a greatly abbreviated tarsometatarsus, a triangular deltopectoral crest (humerus), and a short and wide pelvis with crown group Fregatidae. However, despite a similar overall morphology it distinctly differs in several presumably plesiomorphic features. Among others, the beak of *Limnofregata* is shorter and its tip less strongly hooked, the narial openings are long and slit-like and not greatly reduced as in extant Fregatidae (juvenile frigatebirds still have slit-like narial openings; see Fig. 9 in Olson 1977a), the hindlimbs are proportionately longer, and the coracoid is not fused with the sternum and furcula. Olson and Matsuoka (2005) further assumed that, in contrast to modern frigatebirds, *Limnofregata* was not sexually dimorphic in size.

Whereas extant frigatebirds are pelagic birds, the *Limnofregata* fossils were found in lacustrine deposits. According to Olson (1977a) and Olson and Matsuoka (2005), these Eocene frigatebirds may have occupied an ecological niche similar to that of extant Laridae (gulls).

7.1.3 Sulidae (Gannets and Boobies)

The extant species of the Sulidae are exclusively marine birds, which plunge-dive to capture fish or squid. All Paleogene fossils of the taxon were recorded from European fossil sites and mainly consist of fragmentary remains of uncertain affinities.

Masillastega rectirostris Mayr, 2002 from Messel is known from an isolated skull and was only tentatively identified as a stem group representative of the Sulidae (Mayr 2002c). *M. rectirostris* has a long, straight beak, which is deep in its proximal part and which, in contrast to the conical beak of extant Sulidae, has a slightly hooked tip (Fig. 7.2). The narial openings are strongly ossified. The dorsal surfaces of the mandibular rami are very wide mediolaterally and the tip of the mandible is truncated in lateral view. *M. rectirostris* shares with crown group Sulidae a deep

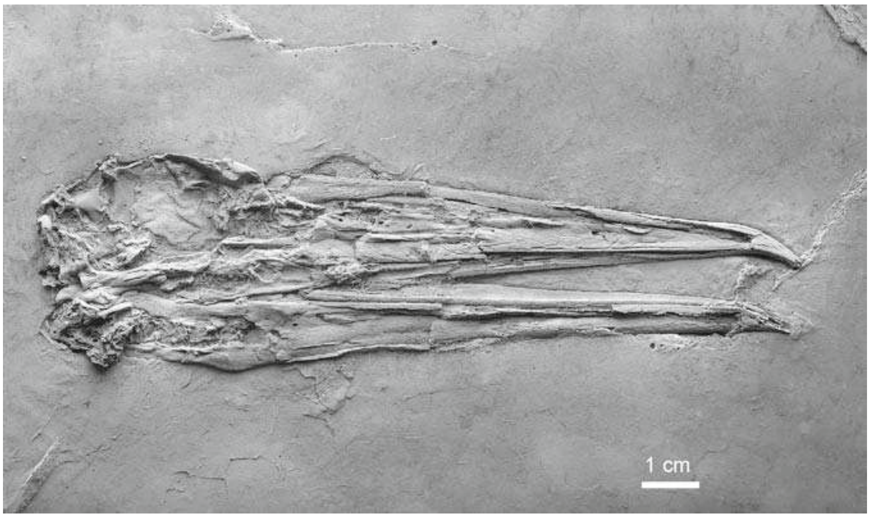

Fig. 7.2 Skull of *Masillastega rectirostris* Mayr, 2002 (?Sulidae) from the middle Eocene of Messel (holotype, Palaeontological Institute of Bonn University, Bonn, Germany, IPB 140b). Coated with ammonium chloride. (Photo by Sven Tränkner)

upper beak and mandible, which both bear numerous impressions of blood vessels, and the presence of a deeply excavated dorsal tympanic recess. If its assignment to the Sulidae can be confirmed by future specimens, the species indicates that stem lineage representatives of the taxon also occurred in limnic environments.

Eostega lebedinskyi Lambrecht, 1929 is based on an incomplete mandible from marine (Paratethyan) and putatively middle Eocene deposits of Romania, and was assumed to be closely related to extant Suloidea by Lambrecht (1929b). It was referred to the Sulidae by Mlíkovský (2002, 2007), but this assignment was due to overall similarity rather than unambiguous derived similarities. Mlíkovský (2007) further synonymized *Masillastega* with *Eostega*, an action whose validity needs to be evaluated by direct comparison of the specimens.

Prophalacrocorax ronzoni (Gervais, 1849) from the early Oligocene (MP 21; Mlíkovský 2002) lacustrine deposits of Ronzon in France is based on a fragmentary pelvis. The species was originally described as a merganser ("*Mergus ronzoni*"), i.e., a representative of the Anseriformes, but was transferred to the Sulidae by Milne-Edwards (1867–1871) ("*Sula ronzoni*"). It was then assigned to the taxon *Prophalacrocorax* by Harrison (1975a), who considered it to be a species of the Phalacrocoracidae. Without more material, its affinities probably cannot be determined (see also Olson 1985).

Empheresula arvernensis (Milne-Edwards, 1867) from the late Oligocene (MP 30; Mlíkovský 2002) lacustrine deposits of Gannat in France is also only known from an incomplete pelvis and a referred sternum (Milne-Edwards 1867–1871). As first noted by Olson (1985), the sternum of this species differs from that of crown group Sulidae in the presence of four incisions in the caudal margin. Its assignment to the Sulidae also needs to be established with additional material.

Remains of sulids were further reported from late Oligocene marine sediments of southern Germany (Darga et al. 1999, distal end of a humerus).

7.1.4 Phalacrocoracidae (Cormorants) and Anhingidae (Anhingas)

The piscivorous Phalacrocoracidae live in lacustrine and coastal habitats, and today have a global distribution. They are the sister taxon of the Anhingidae, which occur in tropical regions worldwide. Anhingas have no unequivocal Paleogene fossil record (see Sect. 7.1.1 concerning *Protoplotus*), and all Paleogene fossils of the Phalacrocoracidae stem from deposits in the Old World.

The earliest record of a cormorant-like bird is an incomplete upper beak from the late Eocene (MP 17; Mlíkovský 2002) of England, which was described as *Piscator tenuirostris* by Harrison and Walker (1976b). A similar rostrum from the early Oligocene of the Jebel Qatrani Formation of the Fayum in Egypt was assigned to the Phalacrocoracidae by Rasmussen et al. (1987). There also exists an undescribed skeleton of a cormorant-like bird from the early Oligocene of the Lubéron in France in a private collection (Roux 2002; own observation), and as yet undescribed remains of cormorants from an unknown horizon of the Quercy fissure fillings were listed by Mourer-Chauviré (1995a, 2006).

Borvocarbo guilloti Mourer-Chauviré et al., 2004 was established on the basis of a coracoid from the late Oligocene of France, which differs from the corresponding bone of extant Phalacrocoracidae and Anhingidae in the presence of a plesiomorphic, concave scapular articulation facet (Mourer-Chauviré et al. 2004). A foot and a nearly complete skeleton of a cormorant-like bird from the late Oligocene (MP 28) Enspel maar lake in Germany were tentatively assigned to *Borvocarbo*, and described as ?*Borvocarbo stoeffelensis* Mayr, 2007 (Fig. 7.3; Mayr 2001a, 2007c).

Fig. 7.3 Skeleton of ?*Borvocarbo stoeffelensis* Mayr, 2007 (Phalacrocoracoidea) from the late Oligocene of Enspel in Germany (holotype, Landesamt für Denkmalpflege Rheinland-Pfalz, Mainz, Germany, PW 2005/5022-LS). Coated with ammonium chloride. (Photo by Sven Tränkner)

This latter species was slightly larger than the extant Pygmy Cormorant (*Microcarbo pygmeus*), and has an overall morphology similar to that of extant cormorants. It exhibits derived characters of the Phalacrocoracidae which are absent in the Anhingidae, including a prominent nuchal sagittal crest on the skull and a very large patella (Mayr 2007c). Plesiomorphic features, such as the larger acromial process of the furcula, the absence of a proximal projection on the patellar crest of the tibiotarsus, and the less strongly protruding medial crest of the hypotarsus, support a position outside crown group Phalacrocoracidae. A phylogenetic assignment of ?*B. stoeffelensis* to the stem group of the Phalacrocoracidae is, however, not straightforward. At least two presumably plesiomorphic features, i.e., less prominent paroccipital processes (skull) and a shorter bicipital crest (humerus), even distinguish the fossil species from crown group representatives of the clade (Phalacrocoracidae + Anhingidae) (Mayr 2007c).

Limicorallus saiensis Kurochkin, 1968a is based on a distal humerus from the late Oligocene (*Indricotherium* Beds) of Kazakhstan. The species was originally described as a rail, but was rightly assigned to the Phalacrocoracidae by Mlíkovský and Švec (1986); *L. saiensis* was slightly smaller than the Pygmy Cormorant, which is the smallest extant cormorant.

7.2 †Plotopteridae

These large, flightless, and wing-propelled diving seabirds were found in late Eocene to early Miocene deposits of the northern Pacific, i.e., western North America and Japan. Most fossils come from deep-water strata which were deposited offshore (Goedert and Cornish 2002; see, however, Sakurai et al. 2008).

The earliest specimens assigned to the taxon belong to an as yet unnamed species from the late Eocene of Washington State (Goedert and Cornish 2002). They include a partial skeleton referred to as the "Whiskey Creek specimen" by Goedert and Cornish (2002), with which are associated three small pebbles that were interpreted as gastroliths by these authors. The earliest named species, *Phocavis maritimus* Goedert, 1988, is based on a tarsometatarsus from the late Eocene of Oregon (Goedert 1988). The tarsometatarsus of *P. maritimus* is less robust than that of later species and still exhibits a well-developed distal vascular foramen (Fig. 7.4). The presence of this plesiomorphic feature may suggest a sister group relationship between *P. maritimus* and the other plotopterid taxa whose tarsometatarsus is known.

Goedert and Cornish (2002) noted the presence of at least five different taxa of plotopterids in the late Eocene and early Oligocene of Washington State, which demonstrates a high diversity of these birds in the Northeastern Pacific during the Paleogene. The only named species from these deposits is the early Oligocene *Tonsala hildegardae*, whose original description by Olson (1980) was complemented by Goedert and Cornish (2002).

In the Paleogene of Japan, plotopterids have so far only been reported from late Oligocene deposits (Olson and Hasegawa 1979, 1996; Kimura et al. 1998; Sakurai

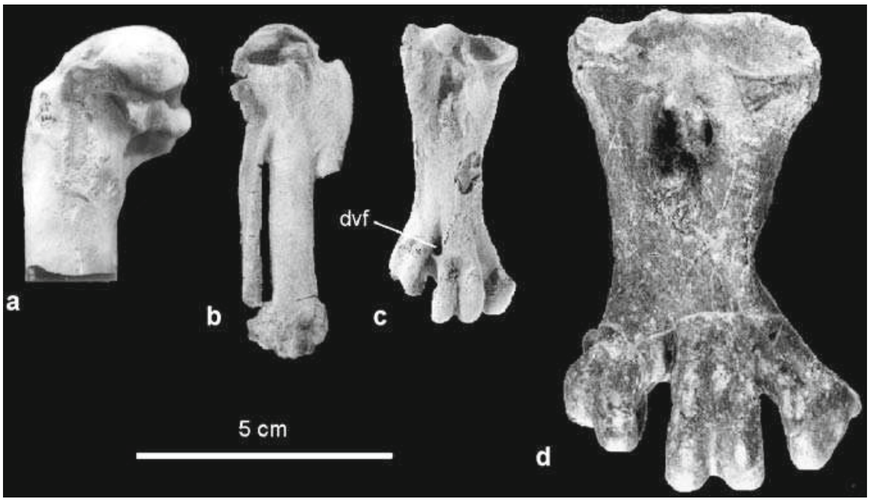

Fig. 7.4 Selected skeletal elements of the Plotopteridae. **a** Proximal left humerus of an unnamed species from the late Eocene or early Oligocene of Washington State, USA (Burke Museum of Natural History and Culture, University of Washington, Seattle, USA, UWBM 86871); **b** left carpometacarpus of the "Whiskey Creek specimen" from the late Eocene of Washington State, USA (UWBM 86869); **c** right tarsometatarsus of *Phocavis maritimus* Goedert, 1988 from the late Eocene of Oregon, USA (holotype, Natural History Museum of Los Angeles County, LACM 123897); **d** right tarsometatarsus of *Hokkaidornis abashiriensis* Sakurai et al., 2008 from the late Oligocene of Hokkaido, Japan (Ashoro Museum of Paleontology, Hokkaido, Japan, AMP 44). The humerus is from a species which was only slightly larger than *P. maritimus* (Goedert and Cornish 2002). *dvf* distal vascular foramen. All images to scale. (Photos courtesy of James Goedert)

et al. 2008), although Sakurai et al. (2008) mentioned unpublished specimens that possibly date from the late Eocene. Two species, *Copepteryx hexeris* and *C. titan*, were named by Olson and Hasegawa (1996). The former is known from partial skeletons, whereas of the latter only a femur was described, whose size suggests that *C. titan* is the largest diving bird as yet scientifically named (Olson 1985). An even larger species of the Plotopteridae, however, awaits its formal publication (Sakurai et al. 2008). Sakurai et al. (2008) described a fairly complete postcranial skeleton of a large plotopterid from the late Oligocene of Hokkaido as *Hokkaidornis abashiriensis*. This species was about the size of *C. hexeris*, from which it differed in several osteological features, including the shape of the coracoid and humerus.

Skull remains of the Plotopteridae were described by Hasegawa et al. (1979) and Goedert and Cornish (2002). According to Olson (1980), there were deep temporal fossae but no supraorbital fossae for salt glands. The mandible of *Tonsala hildegardae* is long, straight, and slender (Goedert and Cornish 2002).

The forelimbs of plotopterids are transformed into paddles and closely resemble those of penguins. As in the latter, the scapula is greatly expanded and sheet-like, and the radius and ulna are flattened. The humeri of plotopterids are also very similar to the peculiar humeri of penguins, and as noted by Olson (1980, p. 54) the proximal humerus of plotopterids has "a resemblance among known birds only to penguins" (compare Figs. 7.4, 7.5). The ulna bears a row of marked pits for the attachment of

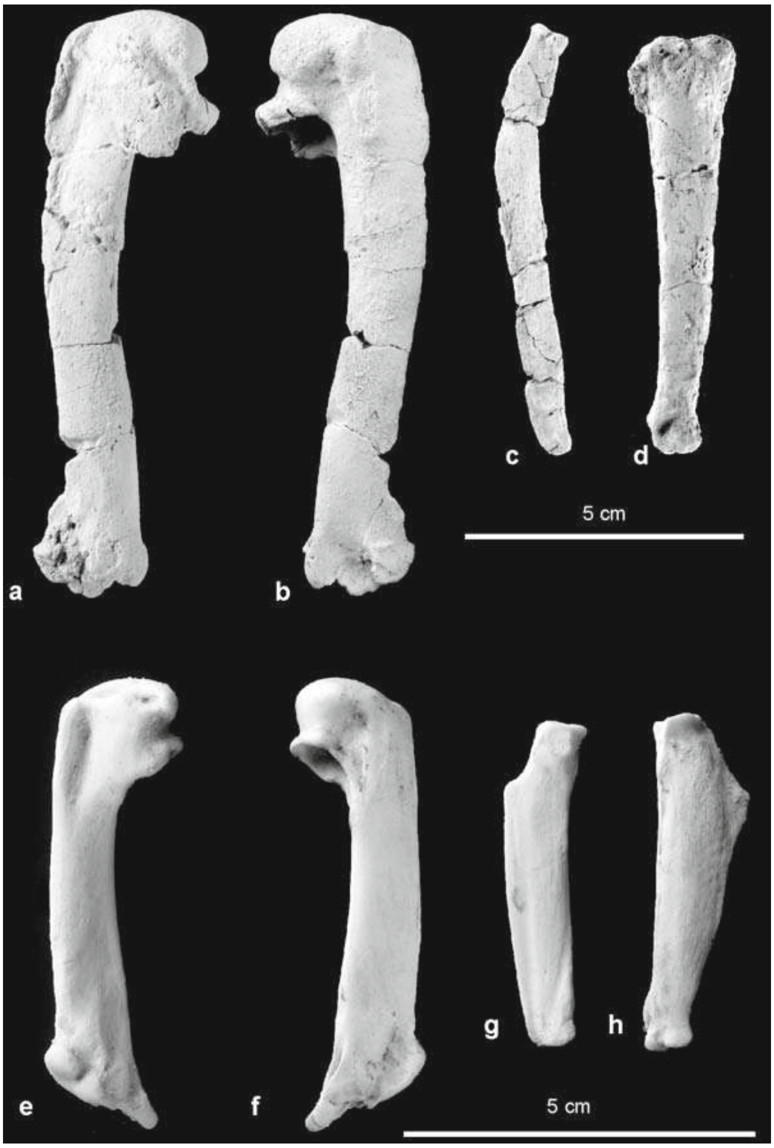

Fig. 7.5 **a–d** Wing bones of *Waimanu tuatahi* Ando, Jones and Fordyce, 2006 (Sphenisciformes) from the late Paleocene Waipara Greensand of New Zealand (holotype, Geology Museum, University of Otago, Dunedin, New Zealand, OU 12651); **e–h** wing bones of the extant Jackass Penguin (*Spheniscus demersus*). **a**, **b**, **e**, **f** Right humerus; **c**, **g** left radius; **d**, **h** left ulna. Same scale for **a–d** and **e–h**. (Photos of *W. tuatahi* courtesy of Ewan Fordyce, others by Sven Tränkner)

feather quills; similar structures otherwise only occur in the Sphenisciformes. As in penguins, the tarsometatarsus is very short. The similarities between plotopterids and penguins are especially evident if plotopterids are compared with stem group representatives of the Spheniscidae, such as the recently described Paleocene *Waimanu* (Sect. 7.3).

Plotopterids differ, however, from penguins and agree with the Suloidea in the presence of a distinct nasofrontal hinge, the absence of fossae for salt glands, the presence of a protruding furcular articulation facet for the acrocoracoid process of the coracoid, the very long acromion of the scapula, and the fact that the furcula articulates with the tip of the sternal carina. The similarities between Plotopteridae and Spheniscidae were attributed to convergence by Olson (1980) and Olson and Hasegawa (1979, 1996), who considered plotopterids to be most closely related to the Phalacrocoracidae and Anhingidae. By contrast, I proposed a sister group relationship between the Plotopteridae and the Sphenisciformes, and detailed that the derived similarities shared by plotopterids and taxa of the Suloidea do not necessarily contradict this hypothesis (Mayr 2005b). It was indicated in Chap. 3 that there exists morphological and molecular evidence in support of a sister group relationship between the Spheniscidae and the clade (Fregatidae + Suloidea) (Fig. 7.1). It is further known that several traits of the peculiar morphology of penguins, such as the incomplete fusion of the metatarsals, are of neotenic origin, and neoteny may account for the absence of derived characters in penguins, which are shared by plotopterids, Fregatidae, and Suloidea (Mayr 2005b). As noted in the following section, the earliest sphenisciforms are very similar to plotopterids, which further supports the hypothesis that the resemblances between these taxa are due to common ancestry rather than convergence.

7.3 Sphenisciformes (Penguins)

Extant Sphenisciformes occur on all continents of the Southern Hemisphere and include 17 species, whose standing height ranges from about 40 cm (Little Blue Penguin, *Eudyptula minor*) to slightly more than 1 m (Emperor Penguin, *Aptenodytes forsteri*). Owing to the fact that penguin bones are fairly robust, and because these birds live in an aquatic environment which offers favorable conditions for fossilization, their fossil record is very extensive and dates back into the Paleocene. Sphenisciformes were only briefly treated in earlier reviews of fossil birds (Olson 1985; Feduccia 1999), but in recent years several revisions were published. These greatly contribute to a clarification of the complicated taxonomy of Paleogene Sphenisciformes, and form the basis of the present account.

All penguin fossils were found in the Southern Hemisphere, and Paleogene remains of penguins are known from Antarctica, New Zealand, Australia, and South America. No Paleogene fossil penguins were described from South Africa, where the earliest penguins stem from late Miocene/early Pliocene deposits (Acosta Hospitaleche 2006). Most fossil species of the Sphenisciformes are based on humeri and tarsometatarsi, which are particularly robust bones and accordingly are dominant in the fossil record. There exist, however, also several partial skeletons, which provide further insight into the early evolution of penguins.

As yet undescribed late Cretaceous stem group Sphenisciformes were found on Chatham Island (Hansford 2008). The earliest published fossils come from the late Paleocene (58–61 Ma) of New Zealand and belong to the taxon *Waimanu*, which includes *W. manneringi* Jones, Ando and Fordyce, 2006 and the smaller and geologically slighter younger *W. tuatahi* Ando, Jones and Fordyce, 2006 (Fig. 7.5; Slack et al. 2006, see also Fordyce and Jones 1986, 1990). Substantial parts of the skeleton of *W. tuatahi* were discovered, including partial skulls. Comparisons between *Waimanu* and plotopterids have not yet been performed, but Slack et al. (2006, p. 1148) noted that "superficially, *Waimanu* is similar to geologically younger wing-propelled diving birds, such as the extinct Northern Hemisphere auk *Mancalla* and the diving plotopterid pelican [sic] *Copepteryx*."

The species of *Waimanu* had a standing height of 80–100 cm, and were already flightless, wing-propelled divers with an upright stance (Slack et al. 2006). In osteological details, however, they markedly differ from crown group Sphenisciformes. As in other Paleogene penguins, the beak is long and dagger-like. The scapula is not as greatly widened as in crown group Sphenisciformes, and according to Slack et al. (2006) the articular facet of the acrocoracoid of the furcula is projecting; this facet is well developed in the Suloidea but is absent in extant penguins. In contrast to those of crown group Sphenisciformes, the distal portions of the ulna and the radius of *Waimanu* are not flattened (Fig. 7.5). The tarsometatarsus is proportionally longer than in other Sphenisciformes and resembles that of the plotopterid *Phocavis*.

A sister group relationship between *Waimanu* and all other fossil and extant Sphenisciformes was supported by phylogenetic analyses of Ksepka et al. (2006) and Clarke et al. (2007). As far as this can be assessed from the published descriptions and figures, the taxon differs from the Plotopteridae in the presence of supraorbital fossae for the salt glands, a different shape of the coracoid, and a much shorter acromion of the scapula.

A high number of other sphenisciform taxa was reported from the late Eocene and Oligocene of New Zealand, and the following species are currently considered valid (Simpson 1971, 1975; Worthy and Holdaway 2002; Acosta Hospitaleche 2006): *Palaeeudyptes marplesi* Brodkorb, 1963 (late Eocene), *P. antarcticus* Huxley, 1859 [probably early Oligocene (Worthy and Holdaway 2002)], *Pachydyptes ponderosus* Oliver, 1930 (late Eocene), *Archaeospheniscus lopdelli* Marples, 1952 (late Oligocene), *A. lowei* Marples, 1952 (late Oligocene), *Duntroonornis parvus* Marples, 1952 (late Oligocene), *Platydyptes novaezealandiae* (Oliver, 1930) (late Oligocene), *P. amiesi* Marples, 1952 (late Oligocene), ?*P. marplesi* Simpson, 1971 (late Oligocene), and *Korora oliveri* Marples, 1952 (late Oligocene).

The standing height of these species varied from about 60 cm in the smallest (*Duntroonornis parvus*) to about 150 cm in the largest (*Pachydyptes ponderosus*), which reached twice the size of the largest extant penguin and had an estimated weight of about 100 kg (Simpson 1971, p. 376).

By contrast, only three sphenisciform taxa were found in the Paleogene of Australia, i.e., *Anthropornis nordenskjoeldi* Wiman, 1905 (late Eocene), *Palaeeudyptes* sp. (Oligocene), and an undescribed smaller species (Vickers-Rich 1991).

All fossil penguins from Antarctica come from Seymour Island, where they were already very diversified in the early Paleogene. The earliest species is the late Paleocene (Cross Valley Formation) *Crossvallia unienwillia*, which was described by Tambussi et al. (2005). *C. unienwillia* is known from an incomplete humerus, femur, and tibiotarsus and had a large size, similar to that of *Waimanu manneringi*. Comparisons between *Waimanu* and *Crossvallia* were not made by Slack et al. (2006), and are still needed to firmly establish the distinctness of these coeval taxa.

Several thousand penguin bones, which accumulated in the vicinity of former rookeries, were collected from the Eocene deposits of the La Meseta Formation of Seymour Island. Myrcha et al. (2002) briefly reviewed the collection history of these specimens and distinguished the following taxa on the basis of their tarsometatarsi: *Anthropornis nordenskjoeldi* Wiman, 1905, *A. grandis* (Wiman, 1905), *Palaeeudyptes gunnari* (Wiman, 1905), *P. klekowskii* Myrcha et al., 1990, *Delphinornis larseni* Wiman, 1905, *D. gracilis* Myrcha et al., 2002, *D. arctowskii* Myrcha et al., 2002, *Mesetaornis polaris* Myrcha et al., 2002, *Marambiornis exilis* Myrcha et al., 2002, and *Archaeospheniscus wimani* Marples, 1952.

Jadwiszczak (2006a) identified other postcranial elements of these species, and Ksepka and Bertelli (2006) reported cranial remains, which could, however, not be assigned to particular taxa. Tambussi et al. (2006) further described humeri from the La Meseta Formation as *Tonniornis mesetaensis* and *T. minimum*, but these identifications were disputed by Jadwiszczak (2006b). Tambussi et al. (2006) also assumed the presence of *Archaeospheniscus lopdelli* and *Palaeeudyptes antarcticus* in the Eocene of Seymour Island. These two species are otherwise only known from the Oligocene of New Zealand. Their identification in the fossil record of Seymour Island was likewise questioned by Jadwiszczak (2006b), who also commented on some penguin specimens from the early Eocene of the La Meseta Formation. Jadwiszczak (2008) described a new but as yet not named small sphenisciform species from the late Eocene of the La Meseta Formation, which is represented by a fragment of the proximal tarsometatarsus.

The earliest South American fossil Sphenisciformes are *Perudyptes devriesi* Clarke et al., 2007 from the middle Eocene of Peru and an unnamed species from the late middle Eocene of Tierra del Fuego (Argentina) (Clarke et al. 2003, 2007). *P. devriesi* was about the size of the extant King Penguin (*Aptenodytes patagonicus*) and is known from a partial skeleton including substantial parts of the skull, whereas the equally large Argentinian specimen consists of portions of the pelvis and hindlimb elements, including a complete femur.

Icadyptes salasi Clarke et al., 2007 from the late Eocene of Peru is based on a nearly complete skull and associated wing elements (Fig. 7.6; Clarke et al. 2007; Ksepka et al. 2008). This species was very large, with a minimum standing height of 1.5 m (Clarke et al. 2007); in contrast to extant penguins, it seems to have had a free alular wing phalanx (Ksepka et al. 2008). Other Paleogene South American Sphenisciformes were discovered in the Argentinian part of Patagonia and, according

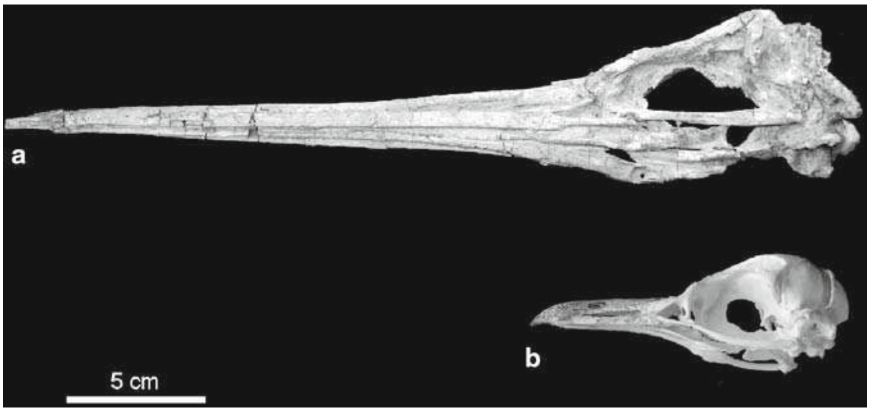

Fig. 7.6 **a** Skull of *Icadyptes salasi* Clarke et al., 2007 (Sphenisciformes) from the late Eocene of Peru (Museum of San Marcos University, Lima, Peru, MUSM 897); **b** skull of an extant Jackass Penguin (*Spheniscus demersus*). (Photo of *Icadyptes* courtesy of Dan Ksepka)

to Acosta Hospitaleche (2006) and Acosta Hospitaleche et al. (2004), include the late Eocene/early Oligocene *Arthrodytes andrewsi* (Ameghino, 1901) and *Paraptenodytes robustus* (Ameghino, 1895), as well as the late Oligocene/early Miocene *Eretiscus tonnii* (Simpson, 1981), which is among the smallest species of Paleogene Sphenisciformes.

As already noted by Simpson (1975), Paleogene penguin faunas were much more diversified than the extant ones, and ten to 14 sympatric species coexisted in the late Eocene of Seymour Island alone (Tambussi and Hospitaleche 2007). The Eocene penguins from Seymour Island show a remarkable variation in size, from small species the size of the extant Macaroni Penguin, *Eudyptes chrysolophus*, to the largest known penguin, the giant *Anthropornis nordenskjoeldi*, which reached an estimated standing height of about 1.7 m (Jadwiszczak 2001). *A. grandis* and the species of *Palaeeudyptes* were also much larger than extant penguins, and the large size range spanned by these species may have facilitated coexistence of so many taxa in a geographically restricted area (Ksepka et al. 2006).

It is further remarkable that, if the above lists reflect the true taxonomic composition of Paleogene Sphenisciformes, the South American species appear to have been quite distinct from those of Antarctica and New Zealand which share at least some "genera" (Simpson 1975; Acosta Hospitaleche et al. 2004).

Another outstanding peculiarity of Paleogene penguins is the very large size of many species, with representatives of the taxa *Anthropornis*, *Pachydyptes*, *Icadyptes*, *Palaeeudyptes*, and *Archaeospheniscus* having been distinctly larger than the extant Emperor Penguin. According to a phylogenetic analysis of Clarke et al. (2007), giant size, i.e., a standing height of about 1.5 m or more, evolved only once within Sphenisciformes, in the early Eocene, and persisted into the Oligocene, across the Eocene–Oligocene climate transition which marks the onset of global cooling. Ksepka et al. (2006) further alluded to the fact that attainment of a large body size must have occurred rapidly in the early evolution of penguins, as even the Paleocene species *Waimanu manneringi* and *Crossvallia unienwillia* were as large as or even larger than the Emperor Penguin.

Concerning extant penguins, the large *Aptenodytes* species occur in the extreme south, whereas the small forms are found in New Zealand, southern Australia and Africa, and the Galapagos Islands. It was thus suggested by earlier authors that there is a correlation between size and latitude in penguins, in accordance with Bergmann's rule, which states that within clades of endothermic animals the species in colder climates are larger than closely related ones that live in warmer areas. However, the validity of this rule in the case of Sphenisciformes was questioned by Simpson (1971). In fact, the average size of penguins seems to have become smaller over the Cenozoic global cooling (Clarke et al. 2007), and fossils of the giant *Pachydyptes ponderosus* were found associated with warm-water foraminiferans (Clarke et al. 2007; see also Tambussi et al. 2006).

From the occurrence of the large *Icadyptes* in near-equatorial fossil deposits, Clarke et al. (2007) concluded that giant size in Paleogene penguins is not correlated with either cooler temperatures or higher latitudes, but may be due to increased ocean productivity. However, to explain the body size of these early Sphenisciformes, it may be more appropriate not to ask why there were such large species in the past, but why there are none today (see Sect. 17.3.3.2).

The phylogenetic affinities between Paleogene Sphenisciformes are incompletely understood, and only very recently more comprehensive phylogenetic analyses were performed (Ksepka et al. 2006; Clarke et al. 2007). The tarsometatarsi of *Waimanu*, *Delphinornis*, *Marambiornis*, and *Mesetaornis* still exhibit a distal vascular foramen, which is lost in other sphenisciform taxa. A position outside crown group Sphenisciformes for these taxa and all other Paleogene penguins is also supported in the analyses of Ksepka et al. (2006) and Clarke et al. (2007). Among others, in most Paleogene Sphenisciformes the pneumotricipital fossa of the humerus is simple and not bipartite as in extant penguins, the tarsometatarsus is more elongated, the metatarsals are more strongly fused (Myrcha et al. 2002), and the hypotarsal crests are better developed (Jadwiszczak 2006b). In many Paleogene Sphenisciformes the distal margin of the sternal extremity of the coracoid is further convex rather than concave as in extant penguins (Simpson 1975; see Fig. 7 in Ksepka et al. 2006). The giant species were classified into the Palaeeudyptinae by Simpson (1971), but the analyses of Ksepka et al. (2006) and Clarke et al. (2007) did not support monophyly of this taxon.

Waimanu and other Paleogene Sphenisciformes have a very long and dagger-like beak (Olson 1985; Slack et al. 2006; Clarke et al. 2007). In its extreme, this presumably plesiomorphic morphology is displayed by *Icadyptes salasi*, whose beak measures about twice of the length of the cranium (Fig. 7.6; Clarke et al. 2007). Ksepka et al. (2008) confirmed the earlier hypothesis that the beak of these birds was probably used for spearing large prey items. These authors further detailed that the rhamphotheca of *Icadyptes* was considerably thinner than in extant penguins. If the identification of some fragmentary bill remains by Jadwiszczak (2006b) is correct, not all early Paleogene taxa had, however, such dagger-like beaks. Paleogene stem group Sphenisciformes further show strongly developed temporal fossae for a powerful adductor muscle complex, which indicates that they may have been more specialized toward feeding on fish than on planktonic prey (Ksepka and Bertelli 2006; Ksepka et al. 2006).

Glaciation of the Antarctic continent resulted from formation of the circum-Antarctic current after the late Eocene (about 36 Ma) opening the Drake Passage, which separates South America from Antarctica (Woodburne and Case 1996). The origin of Pan-Sphenisciformes clearly predates this event (Myrcha et al. 2002; Tambussi et al. 2005). Baker et al. (2006) assumed an origin of crown group Sphenisciformes in the Eocene of Antarctica, and further hypothesized that climatic cooling had a major impact on their subsequent evolution. However, Clarke et al. (2007) found no evidence for a correlation between major events in penguin evolution and either formation of the circum-Antarctic current or onset of Cenozoic global cooling. The same conclusion was reached by Ksepka et al. (2006), who noted that geographic events, such as changes in marine currents and emergence of islands, may have had a greater impact on penguin evolution than climatic cooling itself (see also Sect. 17.3.3.2).

7.4 Gaviiformes (Loons)

The five extant species of the Gaviiformes are foot-propelled diving birds of the Northern Hemisphere which breed in northern freshwater sites but winter along sea costs in temperate areas. Loons are among the few neornithine birds with a putative late Cretaceous fossil record (Chap. 4). Whereas these Cretaceous remains stem from deposits of the Southern Hemisphere, all Paleogene fossils are from fossil sites in Europe and, possibly (see below), North America.

The earliest described Northern Hemisphere species of the Gaviiformes is *Colymboides anglicus* Lydekker, 1891 from the late Eocene (MP 17; Mlíkovský 2002) of England, which is represented by a coracoid, a referred humerus, and a portion of the frontal bones of the skull (Harrison 1976; Harrison and Walker 1976a).

The fossil record of ?*Colymboides metzleri* Mayr, 2004 from early Oligocene (Rupelian) marine sediments of Germany is more substantial, and consists of an incomplete disarticulated skeleton (Mayr 2004b). This species is smaller than *C. anglicus* and is only about half of the size of the smallest extant loon, the Red-throated Diver (*Gavia stellata*). It is distinguished from the similarly sized early Miocene *C. minutus* Milne-Edwards, 1867 in a more protruding and narrower process formed by the cnemial crests of the tibiotarsus, and a proportionally shorter femur and longer tarsometatarsus. These presumably derived features are shared with extant Gaviidae, for which reason ?*C. metzleri* may actually be more closely related to *Gavia* than to *Colymboides* (Mayr 2004b). In the holotype specimen of ?*C. metzleri* stomach content is preserved. It consists of numerous fish bones and shows Paleogene loons to have been piscivorous like their modern relatives.

Another Paleogene species of *Colymboides*, *C. belgicus* Mayr and Smith, 2002, was described from lacustrine sediments from the earliest Oligocene of Belgium, and is based on a proximal carpometacarpus and a distal ulna (Mayr and Smith 2002b). *C. belgicus* was only slightly smaller than *G. stellata*, but in the Brussels Natural History Museum there are remains of another as yet undescribed and very small gaviiform from Rupelian deposits (personal observation).

An undescribed leg of a small gaviiform bird has also been found in the late Oligocene (MP 28) of the Enspel maar lake in Germany (personal observation). Kurochkin (1976) further noted the presence of *Colymboides* in the late Oligocene of Kazakhstan.

An allegedly Paleogene North American species assigned to the Gaviiformes is *Gaviella pusilla* (Shufeldt 1915), whose holotype consists of a proximal carpometacarpus from an unknown locality and horizon in Wyoming. Wetmore (1940) assumed that the specimen comes from Oligocene deposits, and, because of its morphological distinctness, classified it into a monotypic taxon, Gaviellinae.

The fossil record shows that Paleogene stem group representatives of the Gaviiformes occurred in limnic environments with a subtropical paleoclimate, but the factors which largely restricted the inland distribution of loons to the northern latitudes are unknown.

7.5 Procellariiformes (Tubenoses)

All Procellariiformes are pelagic birds, which mainly feed on squid or fish and are characterized by the possession of tubular nostrils. The extant species are classified into four taxa, the Hydrobatidae (storm-petrels), Diomedeidae (albatrosses), Procellariidae (fulmars, petrels, shearwaters), and Pelecanoididae (diving-petrels). There is, however, evidence from morphological and molecular studies that the Procellariidae are not monophyletic but encompass the Pelecanoididae; likewise, monophyly of the Hydrobatidae, i.e., a clade including the Oceanitinae (southern storm-petrels) and Hydrobatinae (northern storm petrels), is not well based (Forbes 1882; Kennedy and Page 2002; Hackett et al. 2008). The distal humerus of the Diomedeoididae and Procellariidae bears a very prominent dorsal supracondylar process; this process is much smaller in the Hydrobatidae and in the Pelecanoididae (the humerus of the latter is modified owing to its use for underwater propulsion).

Although the main distribution of extant Procellariiformes is in the Southern Hemisphere, most Paleogene taxa were found in European and North American fossil sites. This may be an artifact of the superior fossil record of the Northern Hemisphere, but it is notable that procellariiform birds are absent or very rare in Southern Hemisphere fossil localities which yielded numerous penguin bones.

An incomplete humerus from the latest Cretaceous or earliest Paleocene Hornerstown Formation of New Jersey was named *Tytthostonyx glauconiticus* by Olson and Parris (1987), who tentatively assigned it to the Procellariiformes, within a monotypic taxon, Tytthostonychidae. The fossil resembles the humerus of extant

Procellariiformes in most features, but has a very small supracondylar process. Its affinities are uncertain and Bourdon et al. (2008b) considered it to be more similar to the Prophaethontidae (Sect. 7.11).

All remains of putative procellariiform birds from early Paleogene deposits are also very fragmentary. *Eopuffinus kazachstanensis* Nessov, 1986 from the late Paleocene of Kazakhstan was described on the basis of a cranium fragment, which bears distinct, *Puffinus*-like fossae for salt glands (Nessov 1992). Presumptive procellariiform birds were also reported from the London Clay (Harrison and Walker 1977), but these specimens, a distal end of a humerus described as *Primodroma bournei* Harrison and Walker, 1977 and a fragmentary beak and proximal end of a carpometacarpus which form the holotype of the fairly large *Marinavis longirostris* Harrison and Walker, 1977, are too incomplete for a reliable identification (see also Steadman 1981; Mlíkovský 2002).

Feduccia and McPherson (1993) described a distal tibiotarsus from the late Eocene of Louisiana (USA), which they considered to be most similar to that of the extant taxon *Pterodroma* (Procellariidae). *Argyrodyptes microtarsus* Ameghino, 1905 from the late Eocene/early Oligocene of Argentina is based on the distal portions of a tibiotarsus and a femur, and was assigned to the Procellariidae by Agnolin (2007a), who thus confirmed earlier identifications of this fossil (e.g., Tonni 1980). "*Larus*" *raemdonckii* van Beneden, 1871 from the early Oligocene (Rupelian) of Belgium is known from an incomplete humerus that bears a large dorsal supracondylar process. The species was transferred from the charadriiform Laridae to the Procellariiformes by Brodkorb (1962), who proposed a classification into the extant taxon *Puffinus*; procellariiform affinities of "*L.*" *raemdonckii* were also assumed by Miller and Sibley (1941). As yet undescribed remains of procellariiform birds from the late Oligocene of North America were mentioned by Olson (1985).

The Diomedeidae have no unambiguous published Paleogene fossil record. Panteleyev and Nessov (1987) described a putative albatross from the middle Eocene of Uzbekistan as *Murunkus subitus*. This species is much smaller than any extant albatross and is based on a carpometacarpus only. Without further material its phylogenetic affinities probably cannot be assessed, but it is more likely that *M. subitus* belongs to the Diomedeoididae (see below) than to the Diomedeidae. An incomplete tarsometatarsus from the late Eocene La Meseta Formation of Seymour Island (Antarctica), which has not yet been figured, was considered to be from a representative of the Diomedeidae by Tambussi and Tonni (1988).

The material assigned to *Manu antiquus* Marples, 1946 from the late Oligocene of New Zealand consists of a furcula and tentatively referred incomplete femora. This albatross-sized species was assigned to the Diomedeidae by Marples (1946), from which the furcula is, however, clearly distinguished in the much more expanded shafts. I consider this classification to be unjustified, and the specimens may belong to the Pelagornithidae, whose furcula is still unknown. Olson (1985) mentioned an as yet undescribed specimen of the Diomedeidae from the late Oligocene of South Carolina.

The only Paleogene procellariiform birds with a substantial fossil record are the Diomedeoididae, which are known from isolated bones and articulated skeletons from marine Oligocene deposits of Germany, France, Belgium, and Iran [Cheneval 1995; Fischer 1983a, 1985, 1997, 2003; Peters and Hamedani 2000; Mayr et al. 2002; Merle et al. 2002 (erroneously assigned to the Pelecaniformes; C. Mourer-Chauviré, personal communication)]. Three species are currently recognized, i.e., *Diomedeoides lipsiensis* (Fischer, 1983) and the smaller *D.* ("*Frigidafons*") *brodkorbi* (Cheneval, 1995) from the Oligocene of Europe, as well as *D. babaheydariensis* (Peters and Hamedani, 2000) from the Rupelian of Iran. Diomedeoidids were further reported from the early Miocene of Germany (Cheneval 1995; Mayr et al. 2002).

All fossils of the Diomedeoididae were found in marine sediments, and these birds are actually the most common seabirds in the Rupelian of Europe. Mayr et al. (2002) showed that some remains were misidentified by earlier authors and that the name *Diomedeoides* is likely to be a junior synonym of *Rupelornis*. The latter taxon was originally proposed by van Beneden (1871) for *Rupelornis definitus*, a species based on a distal tibiotarsus from the Rupelian of Belgium. From the published illustrations, I further conclude that "*Vanellus*" *selysii* van Beneden, 1871, which is represented by a distal humerus from the Rupelian of Belgium, is also a representative of the Diomedeoididae and probably conspecific with *R. definitus*. An incomplete proximal humerus, which was assigned to the Anseriformes by van Beneden (1871, Fig. 4), may also belong to the Diomedeoididae, and there are many further undescribed diomedeoidid bones in the collection of the Brussels Natural History Museum (personal observation).

The Diomedeoididae are best characterized by their highly peculiar feet, whose greatly widened and flattened toes with "nail-like" ungual phalanges are strikingly similar to those of the extant Polynesian Storm-petrel *Nesofregetta fuliginosa* (Oceanitinae) (Fig. 7.7; see Fig. 5 in Mayr et al. 2002). Within extant Oceanitinae, widened phalanges also occur in *Fregetta* and *Pelagodroma*, but are absent in *Garrodia* and *Oceanites*.

The legs of the Diomedeoididae are very long as in the extant Oceanitinae, but in other skeletal features they are clearly distinguished from southern storm-petrels. The wing proportions are like those of extant Procellariidae, whereas the wing of the Oceanitinae is proportionally much shorter. Apart from being considerably larger, *Diomedeoides* further differs from all extant Hydrobatidae in its longer and more slender beak, the much more marked temporal fossae, the presence of incisions in the caudal margin of the sternum (which is entire in all extant Hydrobatidae), and the morphology of the hypotarsus (Cheneval 1995). Of these features, at least the entire caudal margin of the sternum is a derived character, which is shared by *Nesofregetta* and other Oceanitinae but is absent in *Diomedeoides*. The tip of the beak of diomedeoidids is further less hooked than that of extant Procellariiformes.

Mainly owing to the lack of morphology-based phylogenies of the extant taxa, the phylogenetic affinities between the Diomedeoididae and other procellariiform birds are uncertain. However, the dorsal supracondylar process of the humerus of *Diomedeoides* is proportionally much smaller than in extant Procellariidae and Diomedeidae (Fig. 7.7). This presumably plesiomorphic feature supports a position of the fossil taxon at least outside a clade including the Procellariidae, Pelecanoididae, and Diomedeidae, which is obtained in recent phylogenetic analyses (Kennedy and

Fig. 7.7 Selected skeletal elements of the procellariiform taxon *Diomedeoides* (Diomedeoididae) and extant Procellariiformes. **a** Right foot of *D. brodkorbi* (Cheneval, 1995) from the early Oligocene of Wiesloch-Frauenweiler in Germany (Staatliches Museum für Naturkunde, Karlsruhe, Germany, SMNK-PAL.3812); **b** left tarsometatarsus of *D. lipsiensis* (Fischer, 1983) from the early Oligocene of Espenhain near Leipzig, Germany (Museum für Naturkunde, Berlin, Germany, MB.Av.896); **c** left tarsometatarsus of the extant Bonin Petrel (*Pterodroma hypoleuca*); **d** incomplete right humerus of *D. lipsiensis* from the early Oligocene of Steendorp in Belgium (Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich, Germany, BSP 1973 VII 226); **e** right humerus of *P. hypoleuca*. The specimen in **a** was coated with ammonium chloride. *sup* dorsal supracondylar process. All images to scale. (Photos by Sven Tränkner)

Page 2002; Hackett et al. 2008). Possibly the Diomedeoididae were less adapted to sustained gliding but rather employed flap-gliding like extant Oceanitinae (Pennycuick 1982). The feet may not only have served as a brake for rapid stops when the bird caught sight of prey near the water surface, but, immersed in the water, may have also facilitated a stationary position against strong winds.

7.6 Scopidae (Hamerkop), Balaenicipitidae (Shoebill), and Pelecanidae (Pelicans)

The Scopidae include a single African species and have no Paleogene fossil record. The Balaenicipitidae likewise contain a sole extant representative, the Shoebill (*Balaeniceps rex*), which lives in remote swamps of east-central Africa. The only Paleogene fossil species that was assigned to the taxon is *Goliathia andrewsi* Lambrecht, 1930 from the Jebel Qatrani Formation of Egypt (Rasmussen et al. 1987). This species is known from an ulna, which lacks exact stratigraphic data, and a referred incomplete distal tarsometatarsus from early Oligocene sediments.

The Pelecanidae occur on all continents except Antarctica, but their position within a clade which otherwise only includes the Balaenicipitidae and Scopidae may indicate an origin in Africa. Such an assumption would explain the fact that pelicans have no unequivocal Paleogene fossil record in the Northern Hemisphere, but occur in essentially their modern form in early Neogene deposits of Europe (Olson 1985). *Protopelicanus cuvieri* Reichenbach, 1852 from the late Eocene Paris Gypsum is founded on a femur and its affinities are probably indeterminate without further material. Whereas Brunet (1970) considered the species to be a pelican, it was classified into the Sulidae by Harrison (1979a), and compared with the Pelagornithidae by Olson (1985).

7.7 Ardeidae (Herons)

Hackett et al.'s (2008) analysis of nuclear gene sequences strongly supported a sister group relationship between the Ardeidae and the clade including the Balaenicipitidae, Scopidae, and Pelecanidae. Because the stem species of the last two groups probably lived in Africa (see Sect. 7.6), the Ardeidae may also have originated on this continent.

Indeed, the oldest unambiguous fossils of the Ardeidae stem from the early Oligocene Jebel Qatrani Formation of Egypt. A tarsometatarsus from this locality was assigned to the extant taxon *Nycticorax* (night herons) by Rasmussen et al. (1987), but the authors themselves considered the possibility that the morphology of this bone in *Nycticorax* may be primitive for the Ardeidae. Rasmussen et al. (1987) further described a second, slightly larger and also unnamed species of the Ardeidae from the Jebel Qatrani Formation, which is represented by an incomplete rostrum and a few referred bones.

Another Paleogene heron, *Proardea amissa*, was reported by Milne-Edwards (1892) from an unknown horizon and locality of the Quercy fissure fillings. As yet undescribed remains of this species were found in the late Oligocene (MP 28) Quercy locality Pech Desse (C. Mourer-Chauviré, personal communication, and own observation). Mlíkovský and Švec (1989) further noted that "*Anas*" *basaltica* Bayer, 1883 from the "middle" Oligocene of the Czech Republic is a representative of the Ardeidae. Kurochkin (1976) mentioned the presence of as yet undescribed Ardeidae in the early Oligocene of Mongolia.

Olson (1985) found the holotypic distal humerus of *Gnotornis aramiellus* Wetmore, 1942 from the early Oligocene (Whitneyan) of South Dakota to be very similar to that of herons. If further material confirms ardeid affinities of this species, it would constitute the earliest New World fossil record of the Ardeidae.

7.8 †Xenerodiopidae

This taxon includes a single species, *Xenerodiops mycter* Rasmussen et al., 1987, from the early Oligocene of Egypt, which was established on the basis of a rostrum and a tentatively referred humerus. Whether these bones indeed belong to the same taxon cannot be definitely shown, but as noticed by Rasmussen et al. (1987) there exists a possibility that they do. *X. mycter* was slightly smaller than the extant Abdim's Stork, *Ciconia abdimii*. The humerus shows some overall similarity to that of extant Ardeidae, but the pneumotricipital fossa lacks pneumatic openings (Rasmussen et al. 1987). The rostrum exhibits weak lateral furrows, which occur in many of the taxa discussed in the present chapter, and a completely ossified ventral surface. Humerus morphology also suggests that *X. mycter* is probably most closely related to the birds united here, but its phylogenetic affinities are best considered unresolved. I agree, however, with Rasmussen et al. (1987) that this species represents a distinctive taxon, and it is to be hoped that future specimens shed more light on its relationships.

7.9 Threskiornithidae (Ibises)

The earliest unambiguous representative of the Threskiornithidae is *Rhynchaeites messelensis* Wittich, 1898 from Messel, of which more than a dozen partial or complete skeletons have been found (Fig. 7.8). *R. messelensis* was originally assigned to the charadriiform Rostratulidae (painted snipes) by Wittich (1898) and was also misidentified as a charadriiform bird by Hoch (1980). Its threskiornithid affinities were recognized by Peters (1983), and the species was classified in the monotypic taxon Rhynchaeitinae by Mayr (2002d). Derived similarities shared by *R. messelensis* and extant Threskiornithidae include a long, decurved, and schizorhinal beak, and the presence of a notarium which consists of at least three fused thoracic vertebrae (Peters 1983). In many aspects of its skeleton, however, *R. messelensis* is very different from extant ibises. Most notably, the legs are much shorter than in crown group Threskiornithidae. The tip of the upper beak lacks openings for sensory nerves, which are characteristic for extant ibises, and the Eocene taxon may thus have been a less tactile forager (Mayr 2002d). The sternum is proportionally much larger than that of extant Threskiornithidae and morphologically

Fig. 7.8 Postcranial skeleton of *Rhynchaeites messelensis* from the middle Eocene of Messel (Forschungsinstitut Senckenberg, Frankfurt am Main, Germany, SMF-ME 3577). Specimen coated with ammonium chloride. (Photo by Sven Tränkner)

it is very different: whereas the caudal margin of this bone bears two pairs of rather shallow incisions in modern ibises, there is only a single pair of very deep ones in *Rhynchaeites* (Mayr 2002d). As in the case of the long-legged *Presbyornis* (whose sternum resembles that of crown group Threskiornithidae) and the short-legged Anatidae (whose sternum is more similar to that of *Rhynchaeites*), these differences in sternum morphology may be due to the fact that the fossil taxon had much shorter legs than extant ibises (see Sect. 6.4.3). The coracoid still exhibits a plesiomorphic, cup-like articulation facet for the scapula.

As also noted by Peters (1983), *Actiornis anglicus* Lydekker, 1891 from the late Eocene (MP 17; Mlíkovský 2002) of England, whose identification as an ibis has been doubted by Olson (1981), was probably correctly assigned to the Threskiornithidae by Harrison and Walker (1976a). At least a humerus referred to this species closely matches the humerus of extant ibises (Fig. 7.9) and is quite different from the humerus of the Palaelodidae (contra Olson 1981). A postcranial skeleton of a representative of the Threskiornithidae was described by Roux (2002) from the early Oligocene of Céreste in France. This unnamed species also exhibits a proportionally shorter tarsometatarsus than modern ibises. Close comparisons between this fossil and the roughly contemporaneous but slightly larger *Actiornis anglicus* still have to be performed.

Outside Europe, the Paleogene fossil record of the Threskiornithidae is very scanty. On the basis of a distal tibiotarsus and a referred distal ulna, Hou (1982) described *Minggangia changgouensis* from the late Eocene of China as member of the Threskiornithidae. These specimens also need a critical reexamination and detailed comparisons with other Paleogene taxa. Stidham et al. (2005) further reported a distal tibiotarsus of a small ibis-like bird from the middle Eocene of Myanmar. The authors themselves noted, however, that an unambiguous identification

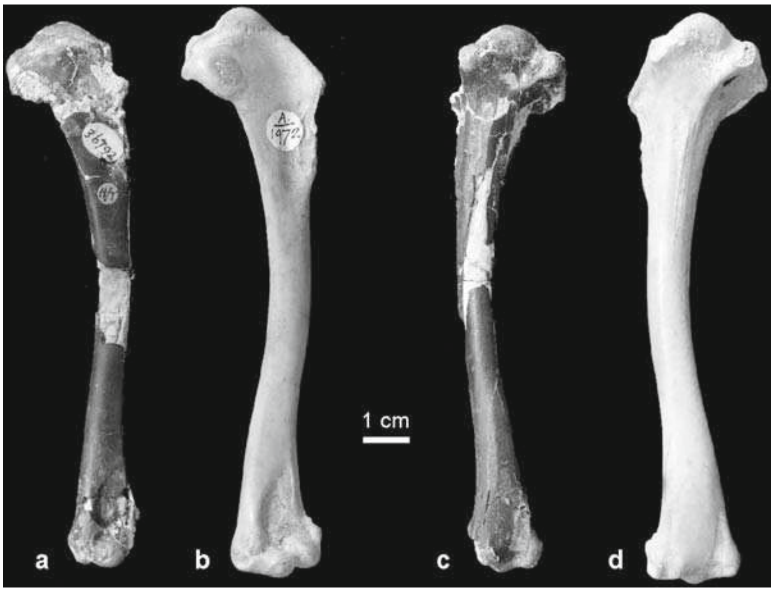

Fig. 7.9 **a**, **c** Referred left humerus of *Actiornis anglicus* Lydekker, 1891 (Threskiornithidae) from the late Eocene of Hampshire in England (Natural History Museum, London, UK, BMNH A 36792) in comparison with **b**, **d** a left humerus of the Sacred Ibis, *Threskiornis aethiopicus,* from the Pleistocene of Madagascar (BMNH A 1972). Images to scale. (Photos by Sven Tränkner)

of this bone is not possible and that there is a possibility that it belongs to the Geranoidiidae or Eogruidae (Sect. 9.3).

Jadwiszczak et al. (2008) published a note on an ibis-like partial beak from the late Eocene of Seymour Island, but univocal identification of this specimen also has to await the discovery of more material.

7.10 Ciconiidae (Storks)

Paleogene fossils of the Ciconiidae are only known from the Old World, where also most extant species occur. The putative ciconiid *Eociconia sangequanensis* Hou, 1989 from the middle Eocene of China is based on a fragmentary distal tarsometatarsus (Hou 1989, 2003). Although the specimen is of size and proportions similar to those of the tarsometatarsus of the extant *Ciconia*, its unambiguous identification requires additional fossils.

The earliest well-represented stork is thus *Palaeoephippiorhynchus dietrichi* from the early Oligocene of the Jebel Qatrani Formation of the Fayum in Egypt. This species was described by Lambrecht (1930) on the basis of a partial, three-dimensionally preserved skull, and was about the size of the extant Saddlebill (*Ephippiorhynchus senegalensis*). As in the extant taxa *Ephippiorhynchus* and *Jabiru* the tip of the beak is slightly upturned. Rasmussen et al. (1987) tentatively referred a distal tibiotarsus from the early Oligocene of the Jebel Qatrani Formation to *P. dietrichi*. Another distal tibiotarsus of a stork was reported from late Eocene deposits of this locality by Miller et al. (1997), who refrained from assigning it to *P. dietrichi* because of slight differences from the early Oligocene tibiotarsus.

Boles (2005b) described *Ciconia louisebolesae* from the late Oligocene/early Miocene of the Riversleigh Formation in Australia. The fossil material of this species, which was about the size of the extant White Stork (*C. ciconia*), consists of a partial skull and incomplete limb bones. The taxon *Ciconia* was also described from the Neogene of Australia, and it is unknown why it became extinct on the continent, where the only extant ciconiiform species belongs to *Ephippiorhynchus* (Boles 2005b).

7.11 †Prophaethontidae and Phaethontidae (Tropicbirds)

The Prophaethontidae occur in late Paleocene to middle Eocene marine localities of Europe, Asia, North Africa, and eastern North America. The taxon was originally established for *Prophaethon shrubsolei* Andrews, 1899 from the early Eocene London Clay of the Isle of Sheppey. The holotype of this species is a partial skeleton including a nearly complete skull (Fig. 7.10), a pelvis, as well as pectoral girdle and hindlimb elements (Andrews 1899; Harrison and Walker 1976c). Olson (1981) noted that a humerus fragment from the Isle of Sheppey, which was described as the putative ibis *Proplegadis fisheri* by Harrison and Walker (1971), more closely resembles the Phaethontidae; the bone is, however, too small to be from *P. shrubsolei* (own observation). Virtual endocasts of the skull of *P. shrubsolei* were examined by Milner and Walsh (2009).

Fig. 7.10 **a**, **c** Skull and **e** mandible of *Prophaethon shrubsolei* Andrews, 1899 (Prophaethontidae) from the early Eocene London Clay of the Isle of Sheppey (holotype, Natural History Museum, London, UK, BMNH A 683); **b**, **d** skull of the extant Red-tailed Tropicbird, *Phaethon aethereus* (Phaethontidae). Images to scale. (Photos by Sven Tränkner)

A second species of the Prophaethontidae, *Lithoptila abdounensis*, was reported by Bourdon et al. (2005) from late Paleocene and early Eocene strata of the Ouled Abdoun Basin in Morocco. Its original description was based on a well-preserved cranium, but abundant postcranial remains from the same locality, which were originally identified as bones of charadriiform birds (Bourdon 2006), belong to the same species (Bourdon et al. 2008b). Bourdon et al. (2008b) further showed that the humerus of *Lithoptila* is very similar to that of *Zhylgaia aestiflua* Nessov, 1988 from the late Paleocene of Kazakhstan. Accordingly, this species, which was originally also assigned to the Charadriiformes (Nessov 1988, 1992), was classified into the Prophaethontidae by Bourdon et al. (2008b). *L. abdounensis* is of size similar to *P. shrubsolei* and *Z. aestiflua*, and had a wingspan of about 1 m (Bourdon et al. 2008b).

A distal end of a humerus and an incomplete coracoid from the Paleocene of Maryland (USA) were assigned to the Prophaethontidae by Olson (1994), and a coracoid of a prophaethontid bird was reported from the middle Eocene of Belgium by Mayr and Smith (2002b).

Prophaethon shares with extant Phaethontidae and other representatives of the nonmonophyletic “Pelecaniformes” a derived articulation facet for the furcula on the sternal carina, and a distinct nasofrontal hinge. A sister group relationship between the Prophaethontidae and Phaethontidae resulted from a cladistic analysis by Bourdon et al. (2005) and, among others, is supported by a very large dorsal tympanic recess. The skull of *Prophaethon* is similar to that of living tropicbirds, but differs in the presence of long and slit-like narial openings (Fig. 7.10). In contrast to that of extant Phaethontidae, the pelvis of *Prophaethon* is much more elongated and narrower, and the tibiotarsus bears strongly projecting cnemial crests. The tarsometatarsus of *Prophaethon* is unknown, but that of *Lithoptila* differs from the corresponding bone of extant Phaethontidae in being proportionally longer and less dorsoventrally flattened.

Bourdon et al. (2008b) assumed that the long-winged prophaethontids were offshore or pelagic feeders. The features of the pelvis and tibiotarsus indicate that these birds had better diving and swimming capabilities than extant Phaethontidae (Andrews 1899).

Bourdon et al. (2008a) tentatively assigned a proximal humerus from the early Eocene of the Ouled Abdoun Basin in Morocco to the Phaethontidae. The specimen was assigned to a new species, *Phaethusavis pelagicus*, but its actual distinctness from the Prophaethontidae still needs to be verified by additional material.

Chapter 8
Charadriiformes (Shorebirds and Allies)

Extant Charadriiformes are a diversified and speciose group of birds and occupy many different habitats, from the open sea and coastal shores to semideserts. Molecular data provide a robust framework for the interrelationships of the various groups, which fall into three clades, the Lari, Charadrii, and Scolopaci (Paton and Baker 2006; Baker et al. 2007; Fain and Houde 2007).

Crown group Charadriiformes share an unusually slow motility of the enzyme malate dehydrogenase (Kitto and Wilson 1966), but because some taxa exhibit a highly aberrant morphology, it is more difficult to characterize the group with derived osteological features. Most charadriiform birds lack pneumatic foramina in the pneumotricipital fossa of the humerus (except Stercorariidae), which may be a plesiomorphic feature. In many taxa the humerus further exhibits a marked dorsal supracondylar process (except in Jacanidae, Burhinidae, Alcidae, and Turnicidae), and the coracoid likewise has a characteristic derived morphology with a strongly ventromedially protruding acrocoracoid process.

The late Cretaceous/early Paleocene "Graculavidae," which were considered "transitional shorebirds" by Olson (1985) and Feduccia (1999), were discussed in Chap. 4 and cannot be convincingly assigned to the Charadriiformes on the basis of derived features. This is also true for various early Paleogene taxa that were considered representatives of the "Graculavidae." *Dakotornis cooperi* Erickson, 1975 from the late Paleocene of North Dakota, for example, was originally described as an ibis-like bird, but was assigned to the "Graculavidae" by Benson (1999), who referred further fragmentary bones from the late Paleocene of North Dakota to this taxon. None of these exhibit features which would unambiguously support a classification into the Charadriiformes, and the same is true for fragmentary remains of putative "Graculavidae" from the early Eocene Tingamarra Local Fauna in Australia (Boles 1999; see Chap. 10).

Kievornis rogovitshi Averianov et al., 1990 from the late Eocene of the Ukraine was likewise referred to the "Graculavidae" in the original description. This small species, which is known from an incomplete humerus and an ulna (Averianov et al. 1990), needs to be restudied. The published illustrations suggest that it is more similar to the Procellariiformes or Phaethontidae than to the Charadriiformes.

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A representative of the Charadriiformes was identified in the middle Eocene of Messel (Mayr 2000c), but the specimen consists of wing bones only and cannot be assigned to any extant charadriiform taxon with confidence.

8.1 Lari (Gulls, Auks, and Allies)

The Lari comprise the Dromadidae (crab plover), Stercorariidae (skuas), Alcidae (auks), Laridae (gulls), Sternidae (terns), Rynchopidae (skimmers), and Glareolidae (pratincoles and coursers). With the exception of some Glareolidae, all of these birds live in aquatic environments. The Turnicidae (buttonquails) are the sister taxon of the above-mentioned taxa (Paton et al. 2003; Paton and Baker 2006; Fain and Houde 2007).

The earliest fossil Alcidae come from North American deposits, which may indicate that the early evolution of these birds was restricted to the northern Pacific, where most extant species of auks occur (Olson 1985). *Hydrotherikornis oregonus* Miller, 1931 from the late Eocene of Oregon is based on a distal tibiotarsus. This specimen was assumed to possibly be from a procellariiform bird by Warheit (2002), but Chandler and Parmley (2003) reported a distal end of an alcid humerus from the late Eocene of Georgia, which further substantiates the presence of auks in the late Eocene of North America. There is no unambiguous Paleogene fossil record of auks outside North America. A partial skeleton from late Oligocene (MP 30; Mlíkovský 2002) marine deposits of Austria was described as *Petralca austriaca* by Mlíkovský and Kovar (1987), who assigned it to the Alcidae, within a new subtaxon Petralcinae. The authors did not detail the reasons for their identification of the fossil, and on the basis of the published photographs I consider it more likely that it constitutes a representative of the Gaviiformes. The distal humerus does not exhibit the characteristic derived morphology found in extant Alcidae, and in all characters listed by Mlíkovský and Kovar (1987) in which *Petralca* differs from the Alcidae (shape of proximal humerus and coracoid), it matches gaviiform birds, with which it was not compared (see also Warheit 2002). The carpometacarpus is, however, proportionally longer than in the Paleogene loon *Colymboides*.

The Laridae and Sternidae are unknown from pre-Oligocene deposits, and all Paleogene fossils are from sediments of lacustrine origin. Kurochkin (1976, p. 78) mentioned an as yet undescribed "fragment of skull belonging to a large representative of the suborder Lari" from the early Oligocene of Mongolia, which "has no exact parallels among the recent families of that group." "*Larus*" *elegans* Milne-Edwards, 1868 and "*L.*" *totanoides* Milne-Edwards, 1868 occur in late Oligocene lacustrine deposits of France (Hugueney et al. 2003; Mourer-Chauviré et al. 2004). Both species have an abundant fossil record in early Miocene French fossil sites of lacustrine origin and are very small, the size of small terns, with fairly long legs. They were classified into the new taxon *Laricola* by Mlíkovský (2002), but the exact phylogenetic affinities of these birds with respect to extant Laridae and Sternidae still need to be determined.

On the basis of several postcranial elements, Mayr and Smith (2001) described two charadriiform species from the early Oligocene of Belgium as *Boutersemia belgica* and *B. parvula*, and tentatively assigned them to the Glareolidae. The coracoid exhibits a foramen for the supracoracoideus nerve, and the presence of a distinct tarsometatarsal fossa for the first metatarsal indicates that a hallux was present. *Boutersemia* shares with extant Glareolidae, Charadriidae, and Jacanidae a large distal vascular foramen of the tarsometatarsus; this presumably derived feature is absent in other extant charadriiform taxa. Compared with extant Glareolidae, *Boutersemia* most closely resembles the taxa *Stiltia* and *Glareola* (Glareolinae), whereas in *Rhinoptilus* and *Cursorius* (Cursoriinae) the hallux is reduced and the distal vascular foramen smaller; *Cursorius* further lacks a foramen for the supracoracoideus nerve.

Stem group representatives of the Turnicidae were reported from the early Oligocene of France and Germany. These fossils belong to the taxon *Turnipax* and the tentatively referred *Cerestenia pulchrapenna* Mayr, 2000. *Turnipax dissipata* Mayr, 2000 was described from the Lubéron in France. A second, slightly larger species, *T. oechslerorum* Mayr and Knopf, 2007, occurred in the early Oligocene of Wiesloch-Frauenweiler in Germany. *Turnipax* can be assigned to the stem group of the Turnicidae because of the unique, derived morphology of the coracoid, which agrees with the morphology of extant buttonquails in the presence of an unusually broad procoracoid process that almost meets the articulation facet for the furcula, and a markedly excavated impression for the sternocoracoideus muscle on the sternal extremity. The skeleton of *Turnipax* combines derived characteristics of crown group Turnicidae with a plesiomorphic and more typically charadriiform overall morphology (Mayr 2000c; Mayr and Knopf 2007a). Crown group Turnicidae are omnivorous birds, which take seeds and other plant matter as well as various invertebrates. The presence of gastroliths in the holotype of *Turnipax oechslerorum* indicates an at least facultatively granivorous diet of this species (Mayr and Knopf 2007a). *C. pulchrapenna* and extant Turnicidae lack a hallux. Its presence in *Turnipax* suggests that the habitat and way of living of this fossil taxon differed from that of crown group Turnicidae, which mainly inhabit open grasslands and arid scrub, and probably did not diversify before the spread of open habitats toward the Neogene (Mayr and Knopf 2007a).

8.2 Charadrii (Plovers and Allies)

The Charadrii encompass the Chionididae (sheathbills), Pluvianellidae (Magellanic plover), Charadriidae (plovers and allies), Haematopodidae (oystercatchers), Recurvirostridae (stilts and avocets), Ibidorhynchidae (ibisbill), and Burhinidae (thick-knees). Except for the Chionididae, these birds are characterized by the loss of the hallux.

The Paleogene fossil record of the Charadrii is very poor. Assignment of fossils to the Recurvirostridae is based on very fragmentary remains whose identification is doubtful. "*Recurvirostra*" *sanctaenebulae* Mourer-Chauviré, 1978 from the late Eocene of France is known from the proximal end of an ulna (Mourer-Chauviré 1978), and its identification needs to be substantiated with additional bones. Even if this species belongs to the Recurvirostridae, it is unlikely that it can be classified in the extant taxon *Recurvirostra*. Another putative recurvirostrid, which was described by Harrison (1983) from the early Eocene of Portugal, is based on an incomplete femur and cannot even be reliably assigned to the Charadriiformes, let alone Recurvirostridae (see also Mlíkovský 2002). The same is true for reputed Recurvirostridae and Burhinidae, which were reported by Harrison and Walker (1976a) from the late Eocene (MP 14–16/MP 17; Mlíkovský 2002) of England.

Hou and Ericson (2002) described a humerus from the middle Eocene of China as *Jiliniornis huadianensis* and tentatively assigned the species to the Charadriidae. This assignment was, however, not established with derived features, and the authors themselves considered the possibility that the shared similarities may be plesiomorphic for a more inclusive clade. The correct identification of "*Charadrius*" *sheppardianus* Cope, 1880 from the late Eocene Florissant shales of Colorado was questioned by Olson (1985). The holotype of this species was not figured by Cope (1880) and awaits restudy. Bessonat and Michaut (1973) briefly described a charadriiform bird from the early Oligocene of the Lubéron area in southern France. The exact affinities of this specimen, which has the size of a stone-curlew (*Burhinus oedicnemus*) and is now in a private collection in France, have not been determined. Judging from the overall morphology of the skeleton and the absence of a hallux, it may well be a representative of the Charadrii. Boles (2001b) mentioned the presence of undescribed Burhinidae in the late Oligocene Etadunna Formation of Australia.

8.3 Scolopaci (Sandpipers and Allies)

The Scolopaci include the Jacanidae (jacanas), Rostratulidae (painted snipes), Pedionomidae (plains wanderer), Thinocoridae (seed snipes), and Scolopacidae (sandpipers, snipes, and allies). Among others, these birds share the presumably derived absence of a foramen for the supracoracoideus nerve on the coracoid.

Olson (1999a) described remains of putative Scolopaci from the early Eocene of the Nanjemoy Formation of Virginia. Owing to the fragmentary nature of these specimens (incomplete humerus and distal tarsometatarsus), their identification needs further substantiation. *Paractitis bardi* Weigel, 1963 from the late Eocene (Chadronian) of Canada is based on the omal extremity of a coracoid, which was assigned to the Scolopacidae because of the absence of a foramen for the supracoracoideus nerve. As noted above, this feature is characteristic for all representatives of the Scolopaci.

A well-preserved postcranial skeleton of an unnamed species of the Scolopacidae from the early Oligocene of the Lubéron area in France was described by Roux (2002). Apart from the proportionally longer tarsometatarsus, this specimen was about the size of the Eurasian Woodcock (*Scolopax rusticola*). The humerus bears a well-developed dorsal supracondylar process, and a short hallux is present. Assignment of this specimen to the Scolopacidae was mainly based on the shape of the acrocoracoid process of the coracoid. Although this classification would be in line with the overall morphology of the fossil, it has not yet been established with derived characters. A fragmentary coracoid of a representative of the Scolopaci was also reported from the early Oligocene of Belgium (Mayr and Smith 2001).

"*Totanus*" *edwardsi* Gaillard, 1908 from an unknown horizon of the Quercy fissure fillings awaits restudy and an assessment of its affinities within the Scolopaci. A tentative record of the Phalaropodinae (phalaropes), consisting of the omal extremity of a coracoid, comes from the late Oligocene of France (Mourer-Chauviré et al. 2004).

The Jacanidae today occur in the tropic regions of all continents and are assumed to be the sister taxon of the Rostratulidae (Paton and Baker 2006; Fain and Houde 2007). These quite aberrant Charadriiformes have the proportionally longest toes of all modern birds, which enable them to walk on floating vegetation. The only Paleogene fossil records are three species from the late Eocene and early Oligocene of the Jebel Qatrani Formation in Egypt. All are known from distal tarsometatarsi only and were described by Rasmussen et al. (1987) as *Nupharanassa bulotorum*, *N. tolutaria*, and *Janipes nymphaeobates*. A derived feature shared with extant Jacanidae is the large distal vascular foramen, which opens dorsally in a very wide fossa. The early Oligocene *N. bulotorum* and *J. nymphaeobates* are distinctly larger than extant Jacanidae, whereas the late Eocene *N. tolutaria* falls within the size range of the modern species (the latter species was also considered to be of early Oligocene age in the original description, but see Rasmussen et al. 2001).

Chapter 9
"Core-Gruiformes" (Rails, Cranes, and Allies)

The traditional "Gruiformes" constitute a polyphyletic taxon (Chap. 3), but current analyses congruently support a sister group relationship between the Ralloidea and Gruoidea, i.e., the clades (Rallidae + Heliornithidae) and (Psophiidae + (Aramidae + Gruidae)) (Livezey 1998; Cracraft et al. 2004; Ericson et al. 2006; Fain et al. 2007; Harshman 2007; Mayr 2008b). These taxa are referred to here as "core-Gruiformes." Mainly because of the apomorphic morphology of the aquatic Heliornithidae, it is difficult to characterize this clade with morphological apomorphies. However, most of its representatives exhibit supraorbital processes (skull), a very narrow sternum, and a derived pelvis morphology (Mayr 2008b). The "core-Gruiformes" have a comparatively rich Paleogene fossil record, but many species are based on fragmentary remains, which do not allow a reliable identification.

9.1 †Messelornithidae and †*Walbeckornis*

With over 500 specimens (Morlo 2004), the Messelornithidae (Messel rails) are the most abundant avian group in Messel, and these birds are also fairly common in the Green River Formation (Hesse 1990; Weidig 2003). The four species currently included in the taxon are *Messelornis cristata* Hesse, 1988 from Messel, *M. nearctica* Hesse, 1992 from the Green River Formation, *M. russelli* Mourer-Chauviré, 1995 from the Paleocene of France, and *Itardiornis hessae* Mourer-Chauviré, 1995 from the late Eocene and early Oligocene (MP 17–23) of the Quercy fissure fillings (Hesse 1988a, 1990, 1992; Mourer-Chauviré 1995b).

Messelornis cristata, the best known species of the Messelornithidae, was the size of a Common Moorhen (*Gallinula chloropus*), and had long legs and a rather short beak (Fig. 9.1). The species epithet "*cristata*" refers to the fact that in one specimen Hesse (1988a, 1990) identified the remains of what she assumed to be a fleshy crest (see p. 242 in Feduccia 1999). However, after my own examination of this specimen, I am not convinced of this interpretation and rather assume that the "crest" is an artifact of organic matter lying under the beak.

M. cristata was a rather generalized terrestrial bird, which according to Hesse (1990, p. 115) had only moderate flight capabilities. In several specimens the feathering

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Fig. 9.1 Skeleton of *Messelornis cristata* Hesse, 1988 (Messelornithidae) from the middle Eocene of Messel (Forschungsinstitut Senckenberg, Frankfurt am Main, Germany, SMF-ME 3551). Specimen coated with ammonium chloride. (Photo by Sven Tränkner)

is well preserved, and it can be observed that the species had a long tail (Hesse 1990, plate 2, Fig. 5). The species appears to have been sexually dimorphic in size. Morlo (2004) described a skeleton of *M. cristata* which is preserved with the remains of the percoid fish *Rhenanoperca minuta* Gaudant and Micklich, 1990 in the area of the esophagus. The gut contents of other specimens of this species consist of seeds (Hesse 1990).

Fossils of *M. cristata* constitute about half of all avian remains discovered in Messel. Many specimens have exact stratigraphic data and can be assigned to particular horizons of the Messel deposits. Hesse and Habersetzer (1993) assumed that there exists evidence for an evolution toward increased perching capabilities during the sedimentation period of the Messel oilshale in the position and relative size of the hallux of the numerous specimens of *M. cristata*. However, this hypothesis has to be viewed with caution, as it is very difficult to reliably assess such subtle differences in Messel skeletons, many of which are considerably flattened and crushed.

The Quercy messelornithid *I. hessae* is represented by most major limb bones. As in the species of *Messelornis*, the proximal end of the tarsometatarsus exhibits an ossified supratendinal bridge (arcus extensorius). *I. hessae* was, however, larger than *M. cristata* and *M. nearctica*, from which it is further distinguished in that the scapular articulation facet of the coracoid is shallow and not cup-like as in *Messelornis*.

Messel rails were considered to be most closely related to the South American Eurypygidae by Hesse (1988b, 1990) and Livezey (1998). However, this hypothesis conflicts with the fact that they lack several of the derived characters shared by the Eurypygidae and their sister taxon, the Rhynochetidae (Chap. 3), most notably schizorhinal nostrils, a notarium, and a deep, U-shaped incision in the caudal margin of the pelvis (Mayr 2004c). In contrast to that of extant Eurypygidae and Rhynochetidae, the coracoid of messelornithids further exhibits a foramen for the supracoracoideus nerve (Fig. 9.2), and a sister group relationship between messelornithids and the clade (Heliornithidae + Rallidae) is better supported by the current morphological evidence. Derived characters shared by these taxa include the absence of pneumatic foramina in the proximal end of the humerus and a derived morphology of the coracoid and hypotarsus (Mayr 2004c).

M. russelli from the Paleocene of the Reims area in France is based on two incomplete/poorly preserved humeri. Owing to its fragmentary fossil record, identification of this species is not uncontroversial. Although the humerus resembles that of *M. cristata*, it is also very similar to the humerus of *Walbeckornis creber* Mayr, 2007 from the Paleocene of Walbeck in Germany (Fig. 9.3). This latter species is the most abundant bird in the locality and is known from numerous three-dimensionally preserved bones, which represent all major limb elements (Mayr 2007a). In particular, the humerus and coracoid of *W. creber* are very similar to the corresponding bones of the Messelornithidae, but the phylogenetic affinities of the species are unresolved (Mayr 2007a). *W. creber* has a much shorter tarsometatarsus than *Messelornis*, but there appears to be a second, unnamed species of *Walbeckornis* in the Walbeck material with a long tarsometatarsus (Mayr 2007a). As in *Messelornis*, the proximal end of the humerus lacks pneumatic foramina, although in contrast to that of *Messelornis* the hypotarsus does not enclose a canal for the tendon of the flexor digitorum longus muscle.

The distal tibiotarsus and proximal tarsometatarsus of *W. creber* show some similarity to the corresponding bones of *Wanshuina lii* Hou, 1994 from the Paleocene of China (Hou 2003). The fossil record of this species, which I overlooked

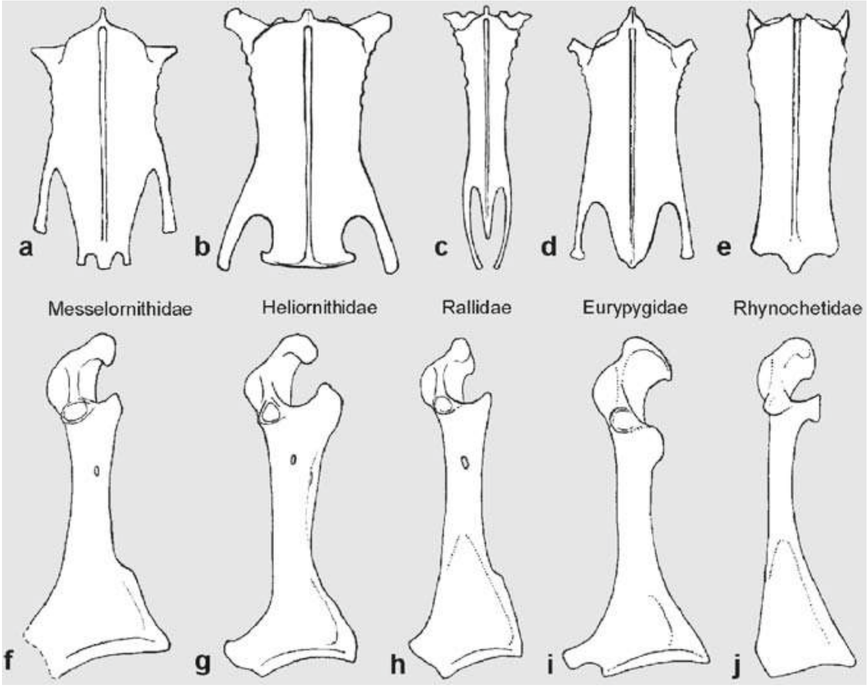

Fig. 9.2 Comparison of the sternum (**a**–**e**) and coracoid (**f**–**j**). **a**, **f** *Messelornis cristata* Hesse, 1988 (Messelornithidae); **b**, **g** *Heliornis fulica* (Heliornithidae); **c** *Pardirallus maculatus* (Rallidae); **d**, **i** *Eurypyga helias* (Eurypygidae); **e**, **j** *Rhynochetos jubatus* (Rhynochetidae); **h** *Aramides saracura* (Rallidae). Not to scale. (After Mayr 2004c)

in the description of the Walbeck species (Mayr 2007a), consists of a humerus shaft, a distal tibiotarsus, and a proximal tarsometatarsus, and was assigned to the Rallidae by Hou (1994). Direct comparisons would, however, be needed to evaluate the possibility of a closer relationship between *Walbeckornis* and *Wanshuina*.

9.2 Ralloidea (Finfoots and Rails)

The Rallidae are most closely related to the Heliornithidae (Cracraft et al. 2004; Ericson et al. 2006; Fain et al. 2007), and an analysis by Hackett et al. (2008) even showed them to be paraphyletic with respect to the latter. Extant rails are globally distributed and include ecologically diversified taxa, such a crakes (*Crex*, *Porzana*) and coots (*Fulica*). As an adaptation to their habitat, mainly dense clutter of reeds, they have a mediolaterally compressed body, which is reflected osteologically by a very narrow sternum and pelvis. The three modern species of the Heliornithidae are

Fig. 9.3 Selected skeletal elements of *Walbeckornis creber* Mayr, 2007 from the late Paleocene of Walbeck in Germany. **a** Right coracoid (Institut für Geologische Wissenschaften of Martin-Luther-Universität Halle-Wittenberg, Halle/Saale, Germany, IGWuG WAL39.2007); **b** right humerus (IGWuG WAL102.2007); **c** left carpometacarpus (IGWuG WAL221.2007); **d** distal left humerus (IGWuG WAL162.2007); **e** right femur (IGWuG WAL372.2007); **f** left tibiotarsus (IGWuG WAL385.2007); **g** distal left tibiotarsus (IGWuG WAL390.2007); **h** right tarsometatarsus (holotype, IGWuG WAL472.2007). Specimens coated with ammonium chloride. All images to scale. (Photos by Sven Tränkner)

foot-propelled aquatic birds, which occur in Africa south of the Sahara and in the tropical areas of South America/Central America and Asia.

Finfoots have no Paleogene fossil record, and the earliest specimen is from the middle Miocene of North America (Olson 2003). Although many early Paleogene fossils were identified as rails, virtually all of these consist of very fragmentary or poorly preserved fossils. Without further material and before detailed comparisons with, for example, the Messelornithidae have been performed, they are of indeterminate affinities. In particular, this is true for several species of putative Rallidae from early and middle Eocene deposits of North America and England (Olson 1977b; Harrison and Walker 1979b; Harrison 1984a). The same applies to *Ibidopsis hordwelliensis* Lydekker, 1891 from the late Eocene (MP 17; Mlíkovský 2002) of England, which was classified into the Rallidae by Harrison and Walker (1976a). This fairly large species is known from an incomplete coracoid and a distal tibiotarsus (Fig. 9.4). Although it seems to be a representative of the "core-Gruiformes," its assignment to the Rallidae is weakly based, and the coracoid likewise resembles the corresponding bone of the Messelornithidae (Sect. 9.1) and Parvigruidae (Sect. 9.3.1)

Quercyrallus arenarius (Milne-Edwards, 1892) and "*Quercyrallus*" *quercy* Cracraft, 1973 are represented by incomplete humeri from unknown horizons of the Quercy fissure fillings and are of uncertain affinities, just as "*Rallus*" *adelus*

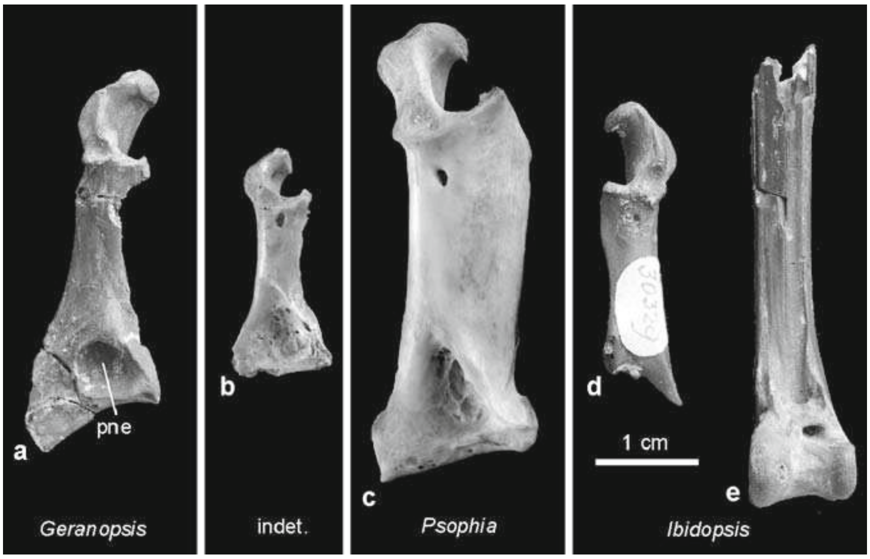

Fig. 9.4 **a** Left coracoid of *Geranopsis hastingsiae* Lydekker, 1891 from the late Eocene of England (Natural History Museum, London, UK, BMNH A 30331); **b** left coracoid of a *Psophia*-like bird from an unknown locality of the Quercy fissure fillings in France (Muséum National d'Histoire Naturelle, Paris, France, MNHN QU 16929); **c** left coracoid of the extant Grey-winged Trumpeter, *Psophia crepitans* (Psophiidae); **d** referred right coracoid of *Ibidopsis hordwelliensis* Lydekker, 1891 (BMNH A 30329); **e** distal right tibiotarsus (holotype, BMNH A 36793) of *I. hordwelliensis* from the late Eocene of England. *pne* pneumatic opening. All images to scale. (Photos by Sven Tränkner)

Oberholser, 1917 (="*Quercyrallus ludianus*" Brodkorb, 1963) from the late Eocene of the Paris Gypsum, a long-beaked species which is based on an incomplete and poorly preserved skeleton (Cracraft 1973a; Olson 1977b). "*Quercyrallus dasypus*" (Milne-Edwards, 1892) was synonymized with the galliform *Palaeortyx gallica* by Mourer-Chauviré (1992a). *Megagallinula harundinea* Kurochkin, 1968 (proximal ulna) from the late Oligocene (*Indricotherium* Beds) of Kazakhstan (Kurochkin 1968a) and *Palaeorallus alienus* Kurochkin, 1968 (distal tibiotarsus) from the "middle" Oligocene of Mongolia (Kurochkin 1968b) were excluded from the Rallidae by Cracraft (1973a).

Songzia heidangkouensis Hou, 1990 from the early Eocene of Songzi County (Hubei Province) of China is known from a partial skeleton, consisting of the skull, both hindlimbs, and an incomplete wing, and was classified in the monotypic taxon Songziidae (Hou 1990). Although the specimen is rather poorly preserved, its proportions are rail-like, and a close relationship to the Rallidae was also assumed by Hou (1990). In particular, the tarsometatarsus of this small species is long and slender, the ulna is short, and the hallux and other toes are very long (Hou 2003). Nevertheless, proportions are a weak indicator of relationships of an Eocene bird, and the holotype specimen would certainly benefit from further preparation.

Accordingly, the earliest well-represented Rallidae are two species of *Belgirallus*, *B. oligocaenus* Mayr and Smith, 2001 and *B. minutus* Mayr and Smith, 2001, which are based on diagnostic postcranial bones from the earliest Oligocene of Belgium (MP 21). A partial skeleton of a rail from the early Oligocene of Germany corresponds well with *B. oligocaenus* in size and morphology (Mayr 2006c). This specimen is from a medium-sized species, about the size of the extant Water Rail, *Rallus aquaticus*, and closely resembles extant rails in its osteological features. The elongated toes allow an assignment to the Rallinae (all Rallidae except the African Nkulengu Rail, *Himantornis haematopus*), but a further classification within that taxon is not possible.

Most other Oligocene Rallidae are known from a few bones only and tell us little apart from the presence of rails in European and African deposits of that geological period. This applies to a distal tarsometatarsus of an unnamed rail from the early Oligocene of the Jebel Qatrani Formation (Fayum) in Egypt (Rasmussen et al. 1987) and *Rallicrex kolozsvarensis* Lambrecht, 1933 from the "middle" Oligocene of Romania (distal tarsometatarsus). Remains of *Paraortygometra porzanoides* (Milne-Edwards, 1869) were reported from the late Oligocene of France by Mourer-Chauviré et al. (2004).

Boles (2001b) indicated that rails were also found in the late Oligocene Etadunna Formation, and Boles (2005a) described a flightless rail in the extant taxon *Gallinula*, *Gallinula disneyi*, from late Oligocene to early Miocene deposits of the Riversleigh Formation in Australia. This species apparently existed over a time span of about 15 million years, and the fossil material consists of remains of most major wing and leg bones. Its flightlessness was inferred from the proportions of the limb elements. Whereas extant rails include several flightless insular species, flightlessness in the continental *G. disneyi* is more unusual, as the species coexisted with marsupial carnivores. If correctly assigned to *Gallinula*, this species would be the earliest known crown group representative of the Rallidae. Boles (2005a) even assumed that it may be on the stem lineage of the extant flightless Tasmanian Native-hen (*G. mortierii*).

9.3 Gruoidea (Trumpeters, Limpkins, and Cranes)

The Psophiidae, Aramidae, and Gruidae share pneumatic openings on the sternal extremity of the coracoid, a notarium, and a prominent tubercle near the supratendinal bridge of the tibiotarsus. As detailed in Chap. 3, a clade including these three taxa was congruently obtained in recent phylogenetic analyses of molecular data.

The South American Psophiidae have no Paleogene fossil record. Mayr and Mourer-Chauviré (2006a) described a trumpeter-like coracoid from an unknown horizon of the Quercy fissure fillings, which agrees with the corresponding bone of modern Psophiidae in the presence of a marked crest along the medial side of the shaft and pneumatic openings on the sternal extremity (Fig. 9.4). The specimen is, however, from a species which was much smaller than any extant trumpeter, and cannot be referred to this group of birds with confidence.

9.3.1 †Parvigruidae

One of the best represented Paleogene species of the Gruoidea belongs to the early Oligocene Parvigruidae and is known from a complete skeleton from the Lubéron in France. This species, *Parvigrus pohli* Mayr, 2005, is a chicken-sized bird with rather short legs. Its assignment to the Gruoidea is supported by the elongated and narrow sternum which lacks deep incisions in its caudal margin, and the presence of a medially protruding projection on the proximal end of the first phalanx of the fourth toe (Mayr 2005c). As in the Rallidae, Gruidae, and Aramidae, the caudal end of the mandible bears a hook-like retroarticular process. The beak is of proportions similar to those of the Psophiidae, but with longer narial openings. The length proportions of the limb bones are "rail-like," i.e., the ulna is shorter than the humerus, the femur is as long as the humerus. The toes are proportionally longer than those of the Gruidae but are less elongated than in the Aramidae.

In the original description (Mayr 2005c), *P. pohli* was considered to be the sister taxon of the Grues, i.e., the clade (Aramidae + Gruidae), because it agrees with the latter and differs from the Psophiidae in the greatly elongated narial openings, the plantarly deflected trochlea for the second toe, and the presence of ossified tendons along the hindlimbs. I did then, however, not recognize that *Rupelrallus saxoniensis* Fischer, 1997 from the early Oligocene of Germany is probably another representative of the Parvigruidae. This species is based on several bones of a single individual, including a fragmentary furcula and coracoid, a complete carpometacarpus, and distal ends of the tibiotarsus and tarsometatarsus. *R. saxoniensis* was assigned to the Rallidae in the original description (Fischer 1997), but differs from rails in the much wider sternal extremity of the furcula and the longer lateral process of the coracoid. The species is also larger than any extant species of rails and closely resembles the contemporaneous, slightly smaller *Parvigrus pohli* in the preserved skeletal elements (Mayr 2006c).

The distal tibiotarsus of *R. saxoniensis* lacks a tubercle at the supratendinal bridge and is similar to the distal tibiotarsus of extant Rallidae. The sternal extremity of the coracoid bears a marked depression, but judging from the published figures and description it lacks pneumatic foramina. The latter two features, which for reasons of preservation cannot be discerned in the holotype of *P. pohli*, distinguish the Parvigruidae from extant Gruoidea and indicate that these birds are the sister taxon of the Gruoidea, rather than the Grues as assumed previously (Mayr 2005c). This revised phylogenetic position is also in better agreement with the fact that the caudal margin of the sternum of *P. pohli* exhibits a pair of shallow incisions, whereas it is entire in extant Gruoidea.

9.3.2 †Geranoididae

This poorly known North American taxon was originally erected for *Geranoides jepseni* Wetmore, 1933, a species represented by a distal tibiotarsus and an associated incomplete, long and slender tarsometatarsus from the early Eocene Willwood Formation of Wyoming (Wetmore 1933a). Cracraft (1969, 1973a) included six further species in the Geranoididae, which are also based on hindlimb elements, i.e., *Paragrus prentici* (Loomis, 1906) (distal tibiotarsus, distal femur, pedal phalanges), *P. shufeldti* Cracraft, 1969 (distal ends of tibiotarsus and tarsometatarsus), *Eogeranoides campivagus* Cracraft, 1969 (distal tibiotarsus and proximal tarsometatarsus), *Palaeophasianus meleagroides* Shufeldt, 1913 (distal tibiotarsus, incomplete femur and tarsometatarsus), *P. incompletus* Cracraft, 1969 (fragmentary distal tarsometatarsus), and *Geranodornis aenigma* Cracraft, 1969 (distal tibiotarsus). Except for *G. aenigma*, which stems from the middle Eocene Bridger Formation, all of these species come from the Willwood Formation. Remains of *P. meleagroides* were found in both the Willwood Formation and the Bridger Formation.

The species included in the Geranoididae are large, crane-sized birds. An assessment of their phylogenetic affinities is hampered by the fact that they are only known from fragmentary hindlimb bones (more complete specimens were mentioned by Olson 1985 on p. 159, but still remain undescribed). Neither has the validity of all of the above-mentioned taxa been convincingly established, nor a clade including all of them. As also noted by Cracraft (1969), the bones of the well-represented taxa most closely resemble those of the late Eocene and Oligocene Eogruidae of Central Asia (Sect. 9.3.3). Cracraft (1973a), however, considered the Geranoididae to be most closely related to the Bathornithidae and Idiornithidae, i.e., to taxa of the Cariamae (Chap. 13). I agree with Olson (1985) that Cracraft's earlier hypothesis is probably the correct one, and that the Geranoididae are most closely related to the Eogruidae. As in the latter and extant Gruoidea, but in contrast to that of the taxa of the Cariamae, the distal tibiotarsus of the Geranoididae exhibits a prominent tubercle lateral of the supratendinal bridge. Also as in the Eogruidae, the hypotarsus encloses a bony canal, presumably for the tendon of the flexor digitorum longus muscle, whereas the hypotarsus of most Cariamae is simple and block-like (some taxa in the Bathornithidae are exceptions).

Future studies will have to concentrate on the identification of other bones of the Geranoididae among the specimens from the Willwood Formation and the Bridger Formation. For example, it is possible that a large coracoid and associated bone fragments (including a fragmentary tarsometatarsus) from the Willwood Formation, which were described as *Calcardea junnei* by Gingerich (1987), belong to one of the above-mentioned taxa. Gingerich (1987) considered *C. junnei* to be a member of the Ardeidae. This identification is not supported by the morphology of the specimen, which among others exhibits a foramen for the supracoracoideus nerve, a feature invariably absent in the Ardeidae.

9.3.3 †Eogruidae

Large, long-legged birds are comparatively abundant in the late Eocene and early Oligocene of Central Asia, and were assigned to the taxa Eogruidae and Ergilornithidae by earlier authors (e.g., Kurochkin 1976; Olson 1985). However, Clarke et al. (2005a) noted that the Eogruidae are likely to be paraphyletic with respect to the Ergilornithidae, and I follow their proposition to subsume the latter in the taxon Eogruidae, which has taxonomic priority.

The first eogruid species was described as *Eogrus aeola* by Wetmore (1934) on the basis of hindlimb elements from the middle Eocene of Inner Mongolia (China). Olson (1985) recognized that a coracoid from the same locality, which Wetmore (1934) assigned to the Accipitridae, most likely also belongs to *Eogrus*. Further material of *E. aeola* was described by Clarke et al. (2005a) from the late Eocene of Mongolia. Two other species of *Eogrus*, *E. crudus* Kurochkin, 1981, and *E.* ("*Progrus*") *turanicus* (Bendukidze, 1971), are known from the late Eocene of Mongolia and Kazakhstan, respectively. From the early Oligocene of Mongolia, *Ergilornis rapidus* Kozlova, 1960, *E.* ("*Proergilornis*") *minor* (Kozlova, 1960), and *Sonogrus gregalis* Kurochkin, 1981 were described (Kurochkin 1976, 1981, 1982; Olson 1985).

Eogruids were cursorial birds with a very long and slender tarsometatarsus, which bears a distinct crest along the lateral side of its plantar surface. Kurochkin (1976) considered the possibility that they were sexually dimorphic in size. Within the taxon a progressive reduction of the tarsometatarsal trochlea for the second toe can be recognized. This trochlea was already somewhat reduced in the late Eocene *Eogrus*, was very small in the early Oligocene *Ergilornis* and *Sonogrus*, and was almost completely lost in the Neogene *Amphipelargus* ("*Urmiornis*"), which existed until the middle Pliocene in Western Asia and Europe (Olson 1985).

Whereas many hindlimbs elements of Paleogene eogruids have been discovered, little is known about other aspects of their skeleton. According to Kurochkin (1976) the morphology of an incomplete humerus of *Ergilornis* from the early Oligocene of Mongolia indicates that this taxon was flightless. Concerning *Eogrus*, however, Clarke et al. (2005a) noted that a referred proximal phalanx of the major wing digit does not show indications of flightlessness.

Olson (1985) hypothesized that eogruids are stem group representatives of the palaeognathous Struthionidae, but apart from the reduction of the tarsometatarsal trochlea for the second toe, there exists no evidence in support of this hypothesis. Wetmore (1934) assumed that these birds were related to the Gruidae, and they were considered to be the sister taxon of the Gruoidea by Cracraft (1973a, Fig. 46). In a cladistic analysis of Clarke et al. (2005a), eogruids resulted as a sister taxon of the clade (Aramidae + Gruidae). In this study a single character was optimized as an apomorphy of a clade including the Eogruidae, Psophiidae, Aramidae, and Gruidae (notched distal rim of the medial condyle of the tibiotarsus), and another one supported a sister group relationship to the Grues (tarsometatarsal trochlea for the second toe subequal in distal projection to that for the fourth toe). None of these characters are, however, restricted to the taxa in question. If Olson's (1985) identification of the *Eogrus* coracoid is correct (see above), the bone differed from the coracoid of extant Gruoidea in the absence of pneumatic openings in the dorsal surface of the sternal extremity, and its morphology would conflict with a sister group relationship between the Eogruidae and Grues.

9.3.4 Aramidae (Limpkins) and Gruidae (Cranes)

The extant representatives of these two taxa have a complementary distribution, with the Aramidae occurring in South America and Central America, and the Gruidae on all other continents. A putative member of the Aramidae from the early Oligocene (Brule Formation) of South Dakota was described as *Badistornis aramus* by Wetmore (1940). This species is known from a nearly complete tarsometatarsus, which resembles that of extant Aramidae in the strongly plantarly deflected trochlea for the second toe. Its classification into the Aramidae was also accepted by Cracraft (1973a), but the fossil record may be too incomplete to be confident about the phylogenetic affinities this species. Chandler and Wall (2001) described three eggs from the early Oligocene of the Brule Formation of South Dakota, which they assigned to *B. aramus*.

Loncornis erectus Ameghino, 1899 from the late Oligocene (Deseadan) of Argentina is based on a fragmentary distal femur. The species was classified into the Aramidae by Brodkorb (1967), but its affinities are indeterminate (Cracraft 1973a; Agnolin 2004).

Paleogene species of putative Gruidae are *Palaeogrus princeps* (Portis, 1884) from the middle Eocene (MP 11–13; Mlíkovský 2002) of Italy and *P. hordwelliensis* (Lydekker, 1891) from the late Eocene (MP 17; Mlíkovský 2002) of England, which are both based on distal tibiotarsi (Cracraft 1973a; Harrison and Walker 1976a). A smaller species, *Geranopsis hastingsiae* Lydekker, 1891, occurs in the late Eocene and early Oligocene of England, and is known from coracoids and a referred distal tibiotarsus (Fig. 9.4; Harrison and Walker 1976a, 1979a). As noted in Sect. 6.4.2, the coracoid of this species closely resembles that of the putative anseranatid *Anserpica* from the late Oligocene of France. Mourer-Chauviré (2006) further noted the presence of Gruidae in the Quercy fissure fillings.

The fossil record of cranes outside Europe is equally sparse. *Eobalearica tugarinovi* Gureev, 1949 from the middle Eocene Ferghana Basin of Uzbekistan is based on a distal tibiotarsus. The holotype and only known specimen is, however, poorly preserved, and its identification as a gruid was doubted by Cracraft (1973a). Rasmussen et al. (1987) assigned a distal tarsometatarsus from the early Oligocene Jebel Qatrani Formation of Egypt to the Gruidae. According to Olson (1985, p. 164, 1989, p. 2024), there further exist fossil cranes from the late Eocene (Chadronian) of North America.

Chapter 10

Phoenicopteriformes (Flamingos) and Podicipediformes (Grebes)

A sister group relationship between these two taxa was recognized only recently (Chap. 3), and the fossil record is still in need of a thorough revision in the light of this new hypothesis. Flamingos and grebes distinctly differ in many osteological features, and statements about character polarity are aggravated by the fact that the sister taxon of the clade (Phoenicopteriformes + Podicipediformes) is unknown.

Crown group Podicipediformes are rather short-legged, foot-propelled diving birds with a global distribution. They have no published Paleogene fossil record, although Kurochkin (1976) mentioned specimens from the late Oligocene of Kazakhstan. Vickers-Rich (1991) also indicated the existence of undescribed Podicipediformes from the late Oligocene or early Miocene of the Namba Formation of Australia. The earliest described grebe is *Miobaptus walteri* Švec, 1982 from the early Miocene of the Czech Republic (Švec 1982, 1984). Because this species already exhibited the highly derived osteological features of modern Podicipediformes, it indicates a Paleogene stem lineage which probably originated on one of the southern continents (see also Olson 1989).

Crown group Phoenicopteriformes are characterized by greatly elongated hindlimbs and a derived beak morphology. Both features constitute adaptations to filter-feeding in shallow saline lakes. Apart from some late Cretaceous remains of highly doubtful affinities (Olson and Feduccia 1980b), the earliest fossils that were assigned to the Phoenicopteriformes belong to the middle Eocene Juncitarsinae, which include two named species (Olson and Feduccia 1980b; Peters 1987a). *Juncitarsus gracillimus* Olson and Feduccia, 1980 from the Bridger Formation of Wyoming is known from a number of isolated bones, including a complete tarsometatarsus. *J. merkeli* Peters, 1987 is based on a fairly complete but rather poorly preserved skeleton from Messel; Peters (1987a) also tentatively assigned to this species hindlimbs from the Green River Formation. The distal humerus referred to *Juncitarsus* by Olson and Feduccia (1980b, Fig. 28) closely resembles that of a putative "graculavid" described by Boles (1999, Fig. 2) from the early Eocene Tingamarra Local Fauna of Australia. This specimen was compared with the Presbyornithidae by Boles (1999), from which it, however, differs in the shorter flexor process.

As evidenced by the Messel skeleton of *J. merkeli*, the beak of *Juncitarsus* was straight and very different from that of extant Phoenicopteriformes. Peters (1987a)

G. Mayr, *Paleogene Fossil Birds*, DOI: 10.1007/978-3-540-89628-9_10,

considered it to have been schizorhinal, in which case the beak morphology of *Juncitarsus* would even depart from that of both extant Podicipedidae and Phoenicopteridae, whose beaks are holorhinal. However, the bill of the holotype specimen is crushed and the exact caudal extent of the nostrils is difficult to ascertain. This leaves the possibility that the nostrils of *Juncitarsus* were just very long as in the Palaelodidae (see below). In concordance with extant Phoenicopteridae, the frontal bones of *Juncitarsus* exhibit fossae for salt glands (Olson and Feduccia 1980b), and the tarsometatarsus is extremely elongated and slender.

After recognition of a sister group relationship between the Phoenicopteriformes and Podicipediformes, the phylogenetic affinities of *Juncitarsus* are in need of revision. As shown by Mayr (2004a), the taxon lacks derived characters shared by extant Phoenicopteriformes and Podicipediformes. In particular, the proximal phalanx of the major wing digit is not as narrow, and the hallux is proportionally longer. Peters (1987a) further noted that the notarium of *Juncitarsus* consists of only two vertebrae, which would be a smaller number than in extant flamingos and grebes. Apart from the greatly elongated legs, no derived feature has been described which is exclusively shared by *Juncitarsus* and extant flamingos but absent in grebes. I thus consider it well possible that the taxon actually is a stem group representative of the clade (Podicipedidae + Phoenicopteridae).

Olson and Feduccia (1980b) remarked that the phylogenetic affinities of the putative phoenicopteriform *Elornis littoralis* Milne-Edwards, 1867 from the early Oligocene of France cannot be established, so much the more so as the whereabouts of the specimens, various crushed postcranial bones in slabs, is unknown. The material includes a very long and slender tarsometatarsus, which suggests that at least some of the bones may indeed belong to a phoenicopterifom bird. As noted by Mlíkovský (2002, p. 255), the figured tibiotarsus is, however, quite different from that of the Phoenicopteriformes.

Several late Eocene and early Oligocene specimens of putative Phoenicopteriformes were assigned to the taxon *Agnopterus*, which was originally established for *Agnopterus laurillardi* Milne-Edwards, 1867 from the late Eocene (MP 19) of the Paris Gypsum. The assignment of this species is based on an incomplete distal tibiotarsus (see also Brunet 1970). A coracoid from the late Eocene (MP 17; Mlíkovský 2002) of England was described as ?*Agnopterus hantoniensis* by Lydekker (1891), who tentatively referred it to the Phoenicopteriformes (Fig. 10.1). Harrison and Walker (1976a, 1979a) assigned humeri and a scapula from the late Eocene and early Oligocene of England to this species and classified it into the new taxon *Headonornis*, which they considered to be an Old World representative of the anseriform Presbyornithidae. Dyke (2001b) even concluded that the humeri referred to ?*A. hantoniensis* by Harrison and Walker (1979a) actually belong to *Presbyornis isoni* (Sect. 6.4.3). There is, however, no convincing reason to disassociate these bones from the coeval and similarly sized coracoids, and assign them to a species that lived some 20 million years earlier on a different continent (Mayr 2008f). Mlíkovský (2002) classified ?*A. hantoniensis* into the Anseranatidae. The coracoid is, however, very similar to the corresponding bone of the Palaelodidae (Fig. 10.1), and I consider ?*A. hantoniensis* to be a stem group representative of the Phoenicopteriformes.

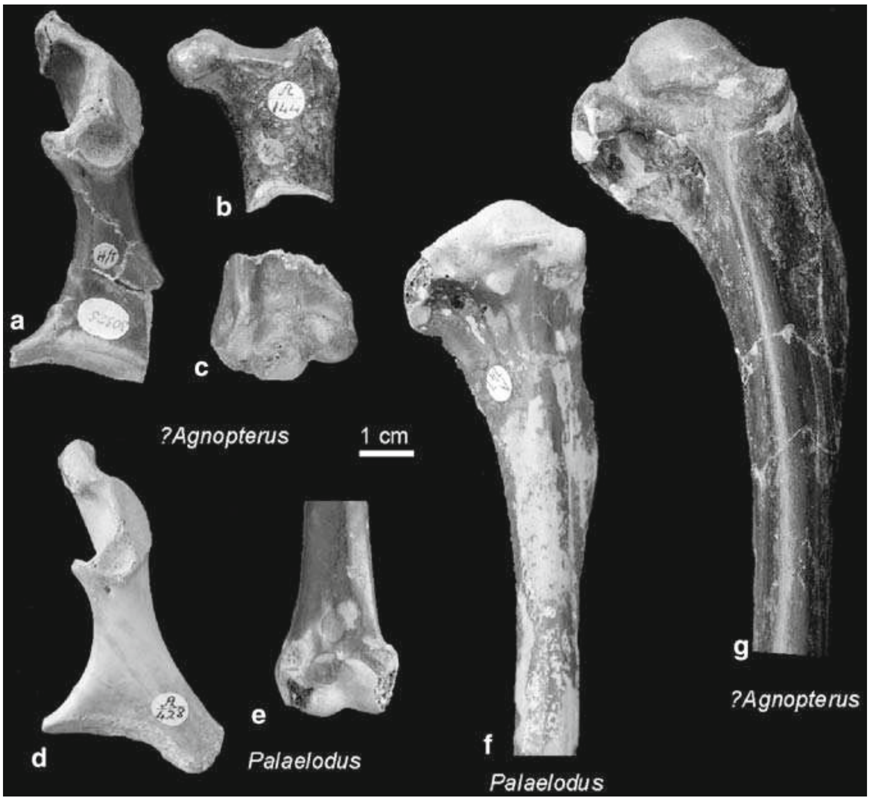

Fig. 10.1 Selected skeletal elements of ?*Agnopterus* (”*Headonornis*”) *hantoniensis* Lydekker, 1891 (**a–c**, **g**) from the late Eocene of England in comparison with *Palaelodus crassipes* Milne-Edwards, 1863 from the early Miocene of France (**d–f**). **a** Right coracoid (holotype, Natural History Museum, London, UK, BMNH A 30325); **b** cast of proximal left femur (BMNH A 144, holotype of *Gigantibis incognita* Harrison and Walker, 1976); **c** distal right humerus (BMNH A 5105); **d** right coracoid (BMNH A 428); **e** distal right humerus (BMNH A 747; reversed to facilitate comparisons); **f** proximal right humerus (BMNH A 747); **g** proximal right humerus (BMNH A 3686). All images to scale. (Photos by Sven Tränkner)

A proximal femur from the late Eocene type locality, which was described as a member of the Threskiornithidae (“*Gigantibis incognita*”) by Harrison and Walker (1976a), probably also belongs to ?*A. hantoniensis* (pro Lydekker 1891, contra Harrison and Walker 1976a). The same may be true for fragmentary remains of putative Phoenicopteriformes from the late Eocene of England (Harrison 1971).

Two further species which were classified into the taxon *Agnopterus* are *A. turgaiensis* Tugarinov, 1940 from the late Oligocene (*Indricotherium* Beds) of Kazakhstan (distal tibiotarsus and distal humerus; Mlíkovský and Švec 1986), and *A. sicki* Alvarenga, 1990 from the late Oligocene/early Miocene of the Taubaté

Basin in Brazil (distal end of a tibiotarsus; Alvarenga 1990). Although these seem to have been correctly assigned to the Phoenicopteriformes, the species are based on too fragmentary material for a reliable taxonomic assignment within the group.

From the late Oligocene or early Miocene of the Australian Etadunna Formation Miller (1963) described two species of the Phoenicopteridae as *Phoeniconotius eyrensis* and *Phoenicopterus novaehollandiae*. Both are known from leg bones and were assumed to have had a better developed hallux than extant Phoenicopteriformes, which also suggests a position outside the crown group.

Whereas the fossil record of the above species is quite limited, numerous bones of *Harrisonavis* ("*Phoenicopterus*") *croizeti* (Gervais 1852) were found in the late Oligocene and early Neogene of France. This species closely resembles crown group Phoenicopteridae, but the beak is still less downcurved than that of its extant relatives (Harrison and Walker 1976d).

Of particular interest with respect to the well-established sister group relationship between the Phoenicopteriformes and Podicipediformes are the Palaelodidae. These distinctive birds have long been recognized as stem group representatives of the Phoenicopteriformes, and markedly differ from the Juncitarsinae in limb proportions, most notably the much shorter tarsometatarsus. The earliest fossils assigned to the taxon come from the early Oligocene of Belgium (Mayr and Smith 2002a) and belong to a fairly large bird, which was described as *Adelalopus hoogbutseliensis* Mayr and Smith, 2002. Rasmussen et al. (1987) further reported bones of *Palaelodus*-like birds from the early Oligocene of the Jebel Qatrani Formation in Egypt. In the late Oligocene of France, three species of *Palaelodus* coexisted, which are very abundant in early Miocene deposits of Europe, i.e., *P. ambiguus* Milne-Edwards, 1863, *P. crassipes* Milne-Edwards, 1863, and *P. gracilipes* Milne-Edwards, 1863 (Hugueney et al. 2003; Mourer-Chauviré et al. 2004; whether Mlíkovský 2002 rightly regarded these as representatives of different size classes of a single species *P. ambiguous* needs to be scrutinized). Two species of *Palaelodus*, *P. wilsoni* and *P. pledgei*, were described by Baird and Vickers-Rich (1998) from the late Oligocene/early Miocene Etadunna Formation in Australia (see also Boles 2001b). Bones of *Palaelodus* cf. *ambiguus* were further identified in the late Oligocene/early Miocene of the Taubaté Basin in Brazil (Alvarenga 1990). Whereas early Oligocene remains of these birds are as yet only known from the Old World, palaelodids thus appear to have achieved a worldwide distribution in the late Oligocene.

Palaelodus has a short beak with a rounded tip, which was first misidentified as that of a representative of the Gruidae (see Cheneval and Escuillié 1992). The mandible is very deep, which suggests the existence of a thick tongue and a filter-feeding apparatus (Cheneval and Escuillié 1992). The tarsometatarsus is proportionally shorter than in extant Phoenicopteriformes and more mediolaterally compressed. In contrast to that in *Juncitarsus* and extant flamingos but in agreement with that in grebes, the hypotarsus further encloses canals for the digital flexor tendons. A presumably autapomorphic feature of the Palaelodidae is the presence of a marked cavity in the sternal extremity of the furcula, whose functional significance is unknown.

Palaelodids have been unanimously considered stem group representatives of the Phoenicopteriformes, but recognition of a sister group relationship between the Phoenicopteriformes and Podicipediformes calls for a reinterpretation of the phylogenetic significance of some of their features. In combining the deep mandibular rami of extant flamingos with leg bones that "show many similarities with those of a foot-propelled diving bird such as *Podiceps*" (in Cheneval and Escuillié 1992, p. 218) palaelodids provide a morphological link between the Phoenicopteriformes and Podicipediformes. It is, however, not straightforward to tell the character polarity of these features, i.e., which represent the plesiomorphic condition for the Phoenicopteriformes/Podicipediformes clade, and which are derived within that clade. Although palaelodids were regarded as specialized "swimming flamingos" by earlier authors (see, e.g., p. 209 in Feduccia 1999), it now appears more likely that the swimming adaptations, in particular the mediolaterally compressed tarsometatarsus, are plesiomorphic for the Phoenicopteriformes. Because both grebes and palaelodids are aquatic birds, which use their hindlimbs for propulsion in the water, it is most parsimonious to assume that the stem species of Pan-Phoenicopteriformes was also a rather short-legged bird, which utilized its feet for aquatic locomotion (Mayr 2004a). Species in the stem lineage of the Phoenicopteridae may then have entered a new ecological zone, as filter-feeders in shallow waters.

Admittedly, the morphology of the long-legged *Juncitarsus* conflicts with this interpretation. If this taxon is indeed a stem group representative of the clade (Phoenicopteriformes + Podicipediformes) (see above), an alternative interpretation of the fossil record, which was not yet considered, would be a sister group relationship between the Palaelodidae and the Podicipedidae. In this case the phoenicopteriform features of the Palaelodidae, such as the deep mandible which is absent in *Juncitarsus*, would be plesiomorphic for a clade (Podicipediformes + Phoenicoptrifo rmes) excluding *Juncitarsus*, and subsequently lost in the Podicipedidae.

Chapter 11
Columbiformes (Doves and Sandgrouse), Cuculiformes (Cuckoos), and Other Neoavian Taxa of Uncertain Affinities

This chapter includes taxa which cannot even be tentatively assigned to any of the groups discussed in the preceding and following chapters. Columbiformes, Opisthocomiformes, Eurypygidae, Rhynochetidae, and Mesitornithidae are part of Fain and Houde's (2004) "Metaves" (Chap. 3).

11.1 Columbiformes (Doves and Sandgrouse)

There exists congruent morphological and molecular evidence that the Columbidae and Pteroclidae are sister taxa (Mayr and Clarke 2003; Cracraft et al. 2004; Ericson et al. 2006; Livezey and Zusi 2007). The closest extant relatives of the clade including these two taxa are, however, unknown. The Pteroclidae only occur in Africa and Eurasia, whereas the Columbidae are globally distributed.

Stem group representatives of the Pteroclidae were found in the Quercy fissure fillings (Mourer-Chauviré 1992b, 1993). The specimens of the three species of *Archaeoganga*, *A. larvatus* (Milne-Edwards, 1892), *A. validus* (Milne-Edwards, 1892), and *A. pinguis* Mourer-Chauviré, 1992, lack stratigraphic data, whereas *Leptoganga sepultus* (Milne-Edwards, 1869) occurs in late Oligocene (MP 28) deposits. The *Archaeoganga* species are represented by humeri, coracoids, and tarsometatarsi, which closely resemble the corresponding bones of extant Pteroclidae (especially *Pterocles* spp., whereas the species of *Syrrhaptes* exhibit a more derived morphology). Of *Leptoganga* also an intertarsal sesamoid bone was described, whose presence is a derived feature of the Pteroclidae (Mourer-Chauviré 1993).

Like their modern counterparts, these Paleogene Pteroclidae lived in an open and arid habitat (Mourer-Chauviré 1993). Whereas *A. larvatus* was the size of the extant Black-bellied Sandgrouse (*Pterocles orientalis*), *A. pinguis* was about twice as large and thus distinctly exceeded any extant species of Pteroclidae in size. Feduccia (1999, p. 225) erroneously stated that this species was 3 times larger than the largest extant sandgrouse, as Mourer-Chauviré's (1992b) comments pertained to its weight and not size.

The fossil record suggests that the Columbidae evolved in the Southern Hemisphere and did not arrive in the Northern Hemisphere before the Neogene

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(Olson 1989). There is no published Paleogene fossil record, but Boles (2001b) noted the presence of Columbidae in the late Oligocene Etadunna Formation in Australia. The earliest named species is from the early Miocene of Florida and was classified into the extant taxon *Columbina* (Becker and Brodkorb 1992). The alleged columbiform *Microena goodwini* Harrison and Walker, 1977 from the early Eocene London Clay is based on a tarsometatarsus, which lacks the trochlea for the fourth toe. Without additional material, the affinities of this species are indeterminable, but I consider affinities to some of the "Coraciiformes" or a position within the "Caprimulgiformes"/Apodiformes clade most likely.

11.2 Opisthocomiformes (Hoatzin)

The Opisthocomiformes include a single extant species, the Hoatzin, *Opisthocomus hoazin*, of northern South America, and have no Palaeogene fossil record. *Onychopteryx simpsoni* from the Eocene (Casamayoran) of Argentina was described by Cracraft (1971a) within the monotypic taxon Onychopterygidae, and was considered to be most closely related to extant Opisthocomiformes. However, the holotype specimen, a small tarsometatarsus fragment, was already rightly considered to be of indeterminate affinities by Brodkorb (1978).

11.3 †Foratidae

This taxon likewise comprises a single species, *Foro panarium* Olson, 1992, which is based on a complete and well-preserved skeleton from the early Eocene Green River Formation (Olson 1992b). *F. panarium* was about the size of a medium-sized phasianid, had rather short wings, and long legs. As shown by Olson (1992b), the skull is similar to that of *Opisthocomus Hoatzin* in its overall proportions, but differs, among others, in the shape of the beak, the much larger nostrils, and the deeper mandibular rami. As in the Hoatzin, the mandible exhibits retroarticular processes. *F. panarium* is, however, distinguished from extant Opisthocomiformes in most aspects of its postcranial skeleton, such as the absence of a notarium, the much longer legs, and the morphology of the sternum and pectoral girdle. The pelvis exhibits distinct praeacetabular tubercles, which among extant neognathous birds are equally well developed in the Galliformes, Musophagiformes, and some Cuculiformes only.

Olson (1992b) considered *F. panarium* to be most similar to extant Musophagiformes and Opisthocomiformes. However, its phylogenetic affinities were "refined mainly by the absence of derived characters" (Olson 1992b, p. 129), which is a problematic approach in the case of early Paleogene fossils, as it is to be expected that stem group representatives of extant taxa lack derived features of their modern relatives. The phylogenetic affinities of *Foro* are thus uncertain, and the well-preserved holotype would probably repay efforts of a detailed character analysis.

11.4 Musophagiformes (Turacos)

The extant species of this taxon are arboreal, frugivorous birds with a semizygodactyl foot and only occur in Africa south of the Sahara. Musophagiformes were considered to be most closely related to the Cuculiformes by earlier authors, but current analyses do not yield congruent results concerning their affinities (Ericson et al. 2006). The earliest fossils were recorded from the early Oligocene of Egypt (Rasmussen et al. 1987). These specimens, the distal ends of a tarsometatarsus and humerus, are very similar to the corresponding bones of the extant taxon *Crinifer*. The as yet unnamed species to which they belong was larger than any modern musophagiform taxon except *Corythaeola*.

A proximal end of a humerus from the late Oligocene (Chattian) of southern Germany was assigned to the Musophagiformes by Ballmann (1970). This fossil comes from a bird which was larger than ali extant species of turacos, from which it also differs in several morphological features (Ballmann 1970). I consider it more likely that it is from a representative of the Idiornithidae (Sect. 13.2), probably of the taxon *Idiornis* itself. Musophagiformes should thus be expunged from the Oligocene fossil record of Europe, with which Ballmann (personal communication) agrees.

11.5 Cuculiformes (Cuckoos)

Although the zygodactyl Cuculiformes have a worldwide distribution today, their evolutionary history is virtually unknown and the fossil record is very poor. A putative cuckoo, *Dynamopterus velox* Milne-Edwards, 1892, is based on a humerus from an unknown horizon of the Quercy fissure fillings (Mourer-Chauviré 2006). Its identification needs to be confirmed by additional skeletal elements, as this fairly large bone, which is here figured for the first time (Fig. 11.1), is distinguished in a number of features from the humerus of extant Cuculiformes. From the late Eocene (Chadronian) of Canada, Weigel (1963) described *Neococcyx mccorquodalei*. The holotype of this species is a distal humerus of a bird the size of the extant Yellow-billed Cuckoo (*Coccyzus americanus*). Identification of this fossil as a cuckoo may be correct, but the specimen has not been compared with the coeval *Eocuculus cherpinae.* This latter species was reported by Chandler (1999) from the late Eocene of the Florissant Fossil Beds of Colorado, and a very similar fossil from the early Oligocene of the Lubéron area in France was classified as *E.* cf. *cherpinae* by Mayr (2006d, 2008a). Both records consist of postcranial skeletons. *Eocuculus* is possibly a stem group representative of the Cuculiformes, with which it shares, in addition to a similar overall shape of most bones, a strongly cranially protruding tip and markedly convex cranial margin of the sternal carina. Further, the ulna is as long as the humerus, whereas it is longer than this bone in most extant "higher land birds." As in extant Cuculiformes, the furcula has a well-developed apophysis

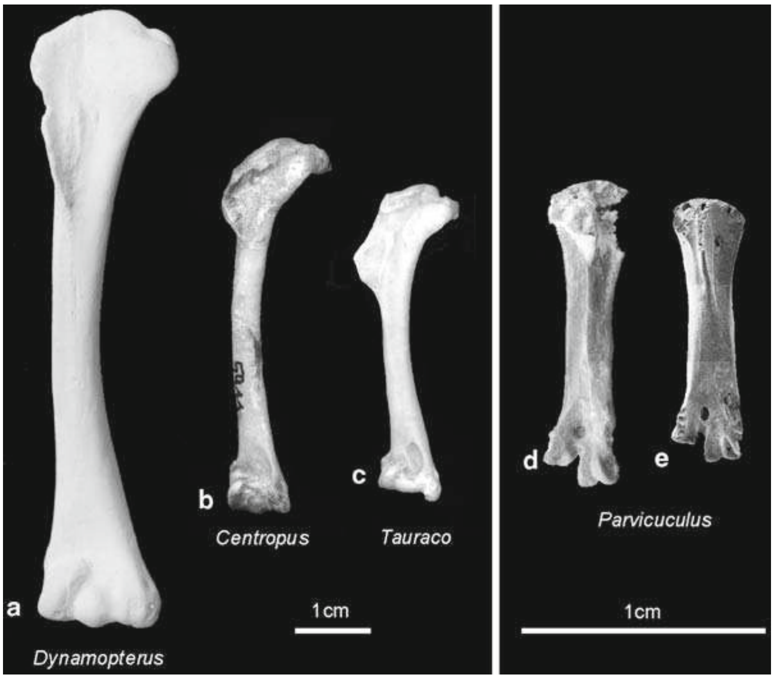

Fig. 11.1 **a** Right humerus of *Dynamopterus velox* Milne-Edwards, 1892 from an unknown horizon of the Quercy fissure fillings (cast of the holotype in the Natural History Museum, London, UK, BMNH A 5336); **b** right humerus of the Goliath Coucal, *Centropus goliath* (Cuculiformes); **c** right humerus of the Red-crested Turaco, *Tauraco erythrolophus* (Musophagiformes); **d** left tarsometatarsus of *Parvicuculus minor* Harrison and Walker, 1977 from the early Eocene London Clay (holotype, BMNH A 4919); **e** left tarsometatarsus of *Parvicuculus* cf. *minor* from the early Eocene of Condé-en-Brie, France (Muséum National d'Histoire Naturelle, Paris, France, MNHN-CB-17345). Same *scale bars* for **a–c** and **d** and **e**. (**e** Courtesy of Cécile Mourer-Chauviré, other photos by Sven Tränkner)

(Mayr 2008a). However, and in addition to other differences (Mayr 2006d), the tarsometatarsal trochlea for the fourth toe does not bear a large accessory trochlea, and in contrast to extant Cuculiformes, *Eocuculus* thus probably only had semizygodactyl feet (Mayr 2006d).

11.6 †*Pumiliornis* and †*Morsoravis*

Pumiliornis tessellatus Mayr, 1999 is a tiny, wren-sized species, of which two skeletons were found in Messel (Fig. 11.2; Mayr 1999c, 2008a). It exhibits a very unusual morphology in combining a long, probably schizorhinal beak with short and robust feet with a well-developed hallux. Other peculiar features include a far caudally positioned sternal keel, and the absence of an ossified supratendinal bridge on the distal end of the tibiotarsus. The bodies of the thoracic vertebrae bear marked lateral depressions. The proximal phalanx of the fourth toe is very wide and flat; in fact, this phalanx is much wider than the corresponding tarsometatarsal trochlea, which precluded arrangement of the fourth toe in an anterior position and indicates the presence of an at least semizygodactyl foot. Although the phylogenetic affinities of *Pumiliornis* are unresolved, it shares several characteristics with *Eocuculus* (Sect. 11.5; Mayr 2008a).

Even greater are the similarities between *Pumiliornis* and a small bird from the early Eocene of the Danish Fur Formation, which was described by Bertelli et al. (2009). The exceptionally well preserved skeleton of the latter species was first studied by Kristoffersen (2002a) and lacks the wings, pectoral girdle, and sternum (see also Fig. 7 in Dyke and van Tuinen 2004, who introduced the nomen nudum "*Morsoravis sedile*" for this bird). The Danish bird agrees with *P. tessellatus* in the presence of a schizorhinal beak, lateral excavations on the body of the thoracic vertebrae, a fairly long tibiotarsus, the morphology and proportions of the tarsometatarsus, and the robust feet with a wide and flat proximal phalanx of the fourth toe (Kristoffersen 2002a). Unlike in *Pumiliornis*, there is, however, an ossified supratendinal bridge on the distal tibiotarsus of the Danish fossil. The Fur Formation fossil was assigned to the Charadriiformes by Kristoffersen (2002a), Dyke and van Tuinen (2004), and Bertelli et al. (2009), but the evidence therefore is weak and the shared similarities (e.g., the vertebral excavations) may well be plesiomorphic. In addition to the presence of an at least semizygodactyl foot, the bird from the Fur Formation shares an unusually low number of scleral ossicles with extant Cuculiformes (Bertelli et al. 2009). Because some current analyses support a close relationship between the Cuculiformes and core-Gruiformes (Ericson et al. 2006; Hackett et al. 2008), the possibility that *Pumiliornis* and the Danish fossil are early stem group representatives of the Cuculiformes with plesiomorphic "charadriiform" and "gruiform" features should be scrutinized in future studies.

11.7 †Parvicuculidae

Parvicuculus minor was described by Harrison and Walker (1977) on the basis of a tarsometatarsus from the London Clay. The bone is short and stout, and exhibits a distinctive morphology in that there is a well-developed medianoplantar crest, a large distal vascular foramen, and a plantarly projecting wing-like flange on the trochlea for the fourth toe (Fig. 11.1). Further specimens of *Parvicuculus* are known from the early Eocene of France and North America (Mayr and Mourer-Chauviré 2005), but also consist of tarsometatarsi only. *Parvicuculus* was considered to be a representative of the Cuculiformes by Harrison and Walker (1977) and Harrison (1982a). Clearly, however, there are no morphological features which convincingly support this assumption, and cuculiform affinities of *Parvicuculus* were disputed by

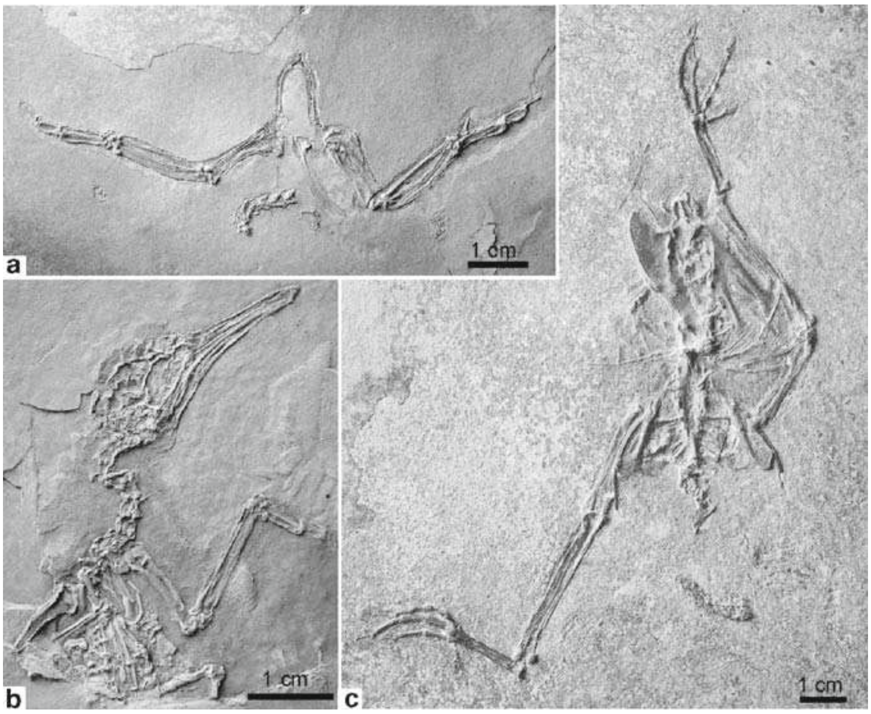

Fig. 11.2 **a** Wings and pectoral girdle elements of ?*Eocuculus* sp. from the early Oligocene of the Lubéron in France (Forschungsinstitut Senckenberg, Frankfurt am Main, Germany, SMF Av 424); **b** skeleton of *Pumiliornis tessellatus* Mayr, 1999 from the middle Eocene of Messel (holotype, SMF-ME 2092A); **c** legs and pelvic girdle of *Eocuculus* cf. *cherpinae* Chandler, 1999 from the early Oligocene of the Lubéron in France (SMF Av 425). The specimen in **b** was coated with ammonium chloride. (Photos by Sven Tränkner)

subsequent authors (Olson and Feduccia 1979; Martin and Mengel 1984; Baird and Vickers-Rich 1997; Mlíkovský 2002; Mayr and Mourer-Chauviré 2005). Assessment of the true affinities of this taxon thus requires the discovery of additional material.

11.8 Otididae (Bustards), Eurypygidae (Sunbittern), Rhynochetidae (Kagu), and Mesitornithidae (Mesites)

These four taxa are traditionally classified in the nonmonophyletic "Gruiformes." Eurypygidae and Rhynochetidae are sister taxa (Chap. 3), but their closest relatives are unknown, as are those of the Otididae and Mesitornithidae. According to Kurochkin (1976), as yet undescribed remains of the Otididae were found in late Oligocene deposits of Kazakhstan. Mourer-Chauviré (2006) also lists Otididae from an unknown horizon of the Quercy fissure fillings.

Olson (1989) and Weidig (2003) considered a specimen from the Green River Formation, which was figured by Grande (1980, Fig. III.23), to be a representative of the Eurypygidae, whose single extant species is restricted to South America. The New Caledonian Rhynochetidae and the Madagascan Mesitornithidae have no Paleogene fossil record.

Chapter 12
"Caprimulgiformes" and Apodiformes (Nightjars and Allies, Swifts, and Hummingbirds)

As noted in Chap. 3, molecular data congruently support a clade including the paraphyletic "Caprimulgiformes" and the Apodiformes, which share a greatly elongated leg (crus longum) of the ulnar carpal bone. Morphological characters further support a clade including the Caprimulgidae, Nyctibiidae, Aegothelidae, and Apodiformes, for which the name Cypselomorphae has been introduced (Fig. 12.1; Mayr 2002b). Among others (Mayr 2002b), the palatine bones of cypselomorph birds bear well-developed rostral processes (Fig. 12.2). The Steatornithidae exhibit a number of plesiomorphic features, which indicate a sister group relationship to a clade including the other "caprimulgiform" and apodiform taxa (Figs. 12.1, 12.2). The Aegothelidae are the sister taxon of the Apodiformes (Mayr 2002b; Mayr et al. 2003; Cracraft et al. 2004; Ericson et al. 2006).

The taxa of the "Caprimulgiformes" are crepuscular or nocturnal birds. On the basis of the phylogeny in Fig. 12.1, it is most parsimonious to assume that there was a single origin of dark-activity in the stem lineage of the "Caprimulgiformes"/Apodiformes clade, and a reversal to a diurnal way of living in the stem lineage of the Apodiformes (Mayr 2002b). A less parsimonious but possibly more plausible alternative explanation is a fourfold origin of dark-activity in the stem lineages of the Steatornithidae, Caprimulgidae/Nyctibiidae, Podargidae, and Aegothelidae. The origin of dark-activity in these aerial insectivores may well have been correlated with the evolution of nocturnal insects in the early Paleogene, such as the lepidopteran Noctuoidea ("owl"-moths), whose earliest unambiguous fossil records stem from that period (Kristensen and Skalski 1999).

Despite the small size of its representatives, the "Caprimulgiformes"/Apodiformes clade has a fairly extensive Northern Hemisphere Paleogene fossil record, which includes stem group representatives of most extant groups.

12.1 †Fluvioviridavidae

The Fluvioviridavidae include two species, *Fluvioviridavis platyrhamphus* Mayr and Daniels, 2001 from the Green River Formation (Fig. 12.3) and *Eurofluvioviridavis robustipes* Mayr, 2005 from Messel. The holotype of *F. platyrhamphus* was figured

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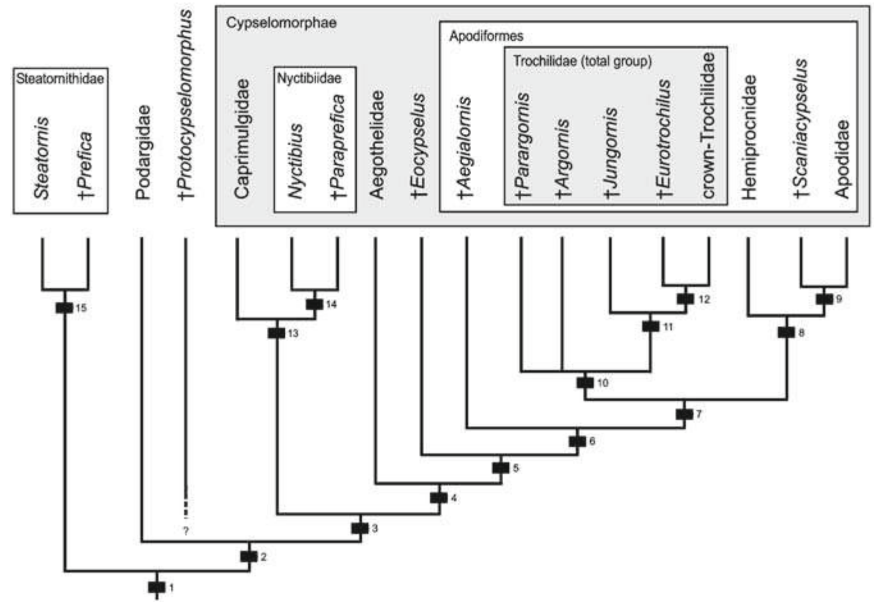

Fig. 12.1 Hypothesis on the phylogenetic relationships between Paleogene and extant representatives of the "Caprimulgiformes" and Apodiformes. Selected apomorphies of the nodes: *1* long leg (crus longum) of ulnar carpal bone greatly elongated; *2* palatine with strongly protruding caudolateral angle, 18 or fewer presacral vertebrae (except in *Protocypselomorphus*); *3* palatine with a distinct rostral process (except in Nyctibiidae), orbital process of quadrate strongly reduced; *4* splenius capitis muscle with cruciform origin, coracoid with foramen for supracoracoideus nerve; *5* humerus abbreviated and stocky; *6* internal index process of proximal phalanx of major wing digit greatly elongated; *7* sternal manubrium reduced, sternal articulation facets for coracoid saddle-shaped or slightly convex, ratio length of humerus to width of shaft in midsection less than 7.0, cnemial crests of tibiotarsus reduced; *8* ventral supracondylar tubercle of humerus elongated and narrow, distal end of radius with marked tubercle on ventral side of shaft, opposite to carpal tubercle of ulna, tarsometatarsus with deep sulcus on dorsal surface proximal to distal vascular foramen, outermost primaries greatly elongated, measuring at least 2.5 times the length of the longest secondaries, salivary glands greatly enlarged; *9* dorsal supracondylar process of humerus greatly enlarged (also in Trochilidae and Aegialornithidae); *10* ventral cotyla of ulna with weakly pronounced ventroproximal edge, olecranon elongated and narrow, deep fossa on the caudal surface of proximal end of ulna (unknown for *Parargornis*); *11* humerus head with marked distal protrusion; *12* beak greatly elongated and narrow (unknown for *Argornis* and *Jungornis*); *13* palatines extremely widened, cone-like bony protrusion at caudal margin of foramen for optic nerve, mandible with intraramal joint and unusually small proximal end; *14* tarsometatarsus greatly abbreviated, tibiotarsus without ossified supratendinal bridge; *15* temporal fossae well developed, tibiotarsus and tarsometatarsus of about equal length, tarsometatarsus extremely abbreviated. (After Mayr 2002b, 2003c, 2005f)

by Olson (1985, p. 126), who subsequently erroneously assigned it to the oilbird *Prefica nivea* Olson, 1987 (Olson 1987; Mayr and Daniels 2001; see Sect. 12.2). Undescribed *Fluvioviridavis*-like birds also occur in the London Clay of Walton-on-the-Naze (Mayr and Daniels 2001). An incomplete skeleton from the Green

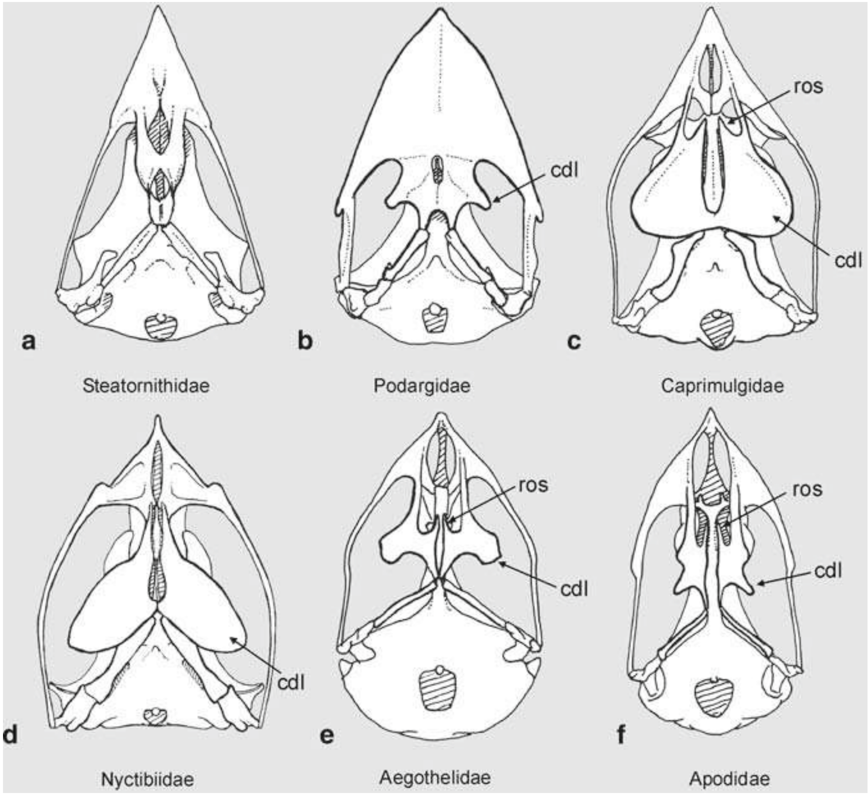

Fig. 12.2 Comparison of skulls of extant "caprimulgiform" and apodiform birds (ventral view). **a** Oilbird, *Steatornis caripensis* (Steatornithidae); **b** Tawny Frogmouth, *Podargus strigoides* (Podargidae); **c** Common Nighthawk, *Chordeiles minor* (Caprimulgidae); **d** Common Potoo, *Nyctibius griseus* (Nyctibiidae); **e** Australian Owlet-nightjar, *Aegotheles cristatus* (Aegothelidae); **f** common swift, *Apus apus* (Apodidae). Not to scale. *cdl* caudolateral angle of palatine bone, *ros* rostral process of palatine bone

River Formation which was figured by Davis and Briggs (1998, Fig. 3C) may also belong to this group of birds.

F. platyrhamphus was a small, presumably insectivorous bird with a wide beak, long wings, and short feet. The coracoid has a cup-like articulation facet for the scapula and a foramen for the supracoracoideus nerve, and both the alular and major wing digits bear ungual phalanges. The caudal margin of the sternum exhibits two pairs of shallow incisions. The long hallux reaches nearly the length of the tarsometatarsus. *Eurofluvioviridavis* is distinguished from *Fluvioviridavis* by its much stronger feet, and certainly occupied an ecological niche different from that of its North American relative (Mayr 2005e).

Fig. 12.3 Skeleton of *Fluvioviridavis platyrhamphus* Mayr and Daniels, 2001 (Fluvioviridavidae) from the early Eocene Green River Formation (holotype, Staatliches Museum für Naturkunde Karlsruhe, Germany, SMNK-PAL.2368a). (Photo by Sven Tränkner)

Assignment of fluvioviridavids to a clade including the Steatornithidae, Podargidae, and Cypselomorphae is tentative and is mainly based on overall similarity, including the presence of a wide beak and short legs. Likewise, classification of *Eurofluvioviridavis* into the Fluvioviridavidae is not strongly based. As noted previously (Mayr 2005e), the short and stout tarsometatarsus of *Eurofluvioviridavis* resembles that of the Eocene Quercypsittidae (Sect. 16.3.2) in the shape of the large trochlea for the second toe and the presence of a wing-like flange on the trochlea for the fourth toe. However, judging from the morphology of the large accessory trochlea, quercypsittids appear to have been fully zygodactyl (i.e., the fourth toe was permanently retroverted), whereas *Eurofluvioviridavis*, as evidenced by the position of the feet of the holotype skeleton, was at best facultatively zygodactyl or semizygodactyl (i.e., the fourth toe either was spread laterally or could be turned forward and backward).

Fluvioviridavis resembles *Palaeopsittacus georgei* from the London Clay of Walton-on-the-Naze, which was described as a parrot by Harrison (1982b). The type specimen consists of a nearly complete coracoid and several fragmentary bones (Fig. 12.4). Mayr and Daniels (1998) described additional specimens of *P. georgei* from the type locality Walton-on-the-Naze, and Mayr (2003b) tentatively referred a postcranial skeleton from Messel to this species (Fig. 12.4). Assignment of *P. georgei* to the Psittaciformes is disproved by these new specimens, which show that the species lacks a zygodactyl foot. Although the new fossils substantially contribute to a better understanding of the skeletal morphology of *P. georgei*,

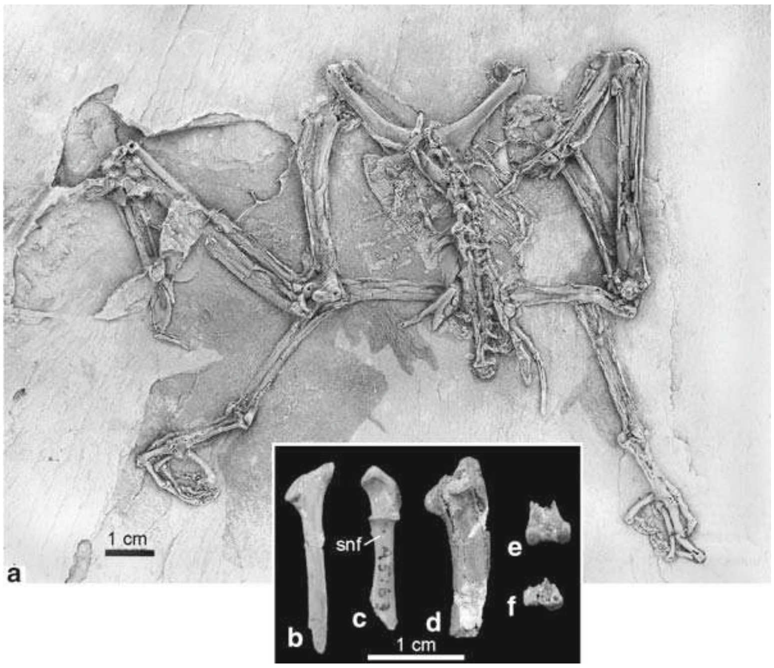

Fig. 12.4 **a** Postcranial skeleton of *Palaeopsittacus* cf. *georgei* Harrison, 1982 from the middle Eocene of Messel (Staatliches Museum für Naturkunde Karlsruhe, Germany, SMNK-PAL.3834a); **b**–**f** holotype of *P. georgei* from the early Eocene London Clay of Walton-on-the-Naze (Natural History Museum, London, UK, BMNH A 5163). **b** Incomplete left scapula; **c** incomplete right coracoid; **d** proximal right ulna; **e** distal right tibiotarsus; **f** proximal right tarsometatarsus. *snf* foramen for supracoracoideus nerve. (Photos by Sven Tränkner)

its phylogenetic affinities remain uncertain. As in *Fluvioviridavis*, the coracoid of *Palaeopsittacus* exhibits a foramen for the supracoracoideus nerve.

12.2 Steatornithidae (Oilbirds)

The Steatornithidae include a single extant species, the frugivorous Oilbird, *Steatornis caripensis*, which occurs in the northern part of South America. On the basis of a skeleton from the Green River Formation, a fossil stem group representative was described as *P. nivea* by Olson (1987); as noted in Sect. 12.1, a second specimen from the Green River Formation was misidentified. Olson (1999a) further tentatively assigned the distal and proximal ends of a humerus from the early Eocene of the Nanjemoy Formation in Virginia to *Prefica*. An earlier tentative identification of oilbirds in the Quercy fissure fillings (Mourer-Chauviré 1982) was based on a cranial portion of a sternum from a late Oligocene deposit. I consider it likely that this specimen belongs to a species of the Archaeotrogonidae, whose sternum has not yet been described (own observation; see also Mourer-Chauviré 2006).

The skull of *P. nivea* is unknown, but the shape of its mandible is very similar to that of the extant *S. caripensis*. *P. nivea* further shares an extremely abbreviated tarsometatarsus and well-developed temporal fossae with the modern Oilbird; as in extant Steatornithidae, the tibiotarsus is only about as long as the carpometacarpus (Olson 1987; Mayr 2005d). *P. nivea* is smaller than *S. capensis* and differs in a number of presumably plesiomorphic features, including the presence of two pairs of notches in the caudal margin of the sternum and the lack of fusion between the ilium and the synsacrum. The fossil was classified in a monotypic taxon, Preficinae, by Olson (1987), who hypothesized that it already had a frugivorous diet similar to that of extant Steatornithidae.

12.3 Podargidae (Frogmouths)

Paleogene fossils of this group, which is today confined to Australasia, were reported from the late Eocene (MP 16) of the Quercy fissure fillings and from Messel (Mourer-Chauviré 1989; Mayr 1999b, 2001b). The French species, *Quercypodargus olsoni* Mourer-Chauviré, 1989, is known from tarsometatarsi and distal tibiotarsi. The species from Messel, *Masillapodargus longipes* Mayr, 1999, is based on articulated skeletons (Fig. 12.5), which show the characteristic wide, dorsoventrally flattened and broadly rounded bill of extant Podargidae. As in extant frogmouths, the ventral side of the upper beak seems to have been completely ossified. *M. longipes* has a somewhat narrower beak than crown group Podargidae and, among others (Mayr 1999b, 2001b), differs in the morphology of the coracoid and sternum. The legs are proportionally longer than in extant Podargidae, and the tarsometatarsus is also more slender than that of *Quercypodargus*.

Fig. 12.5 Partial skeleton of *Masillapodargus longipes* Mayr, 1999 (Podargidae) from the middle Eocene of Messel (Forschungsinstitut Senckenberg, Frankfurt am Main, Germany, SMF-ME 3362A). (Photo by Sven Tränkner)

12.4 †*Protocypselomorphus*

Protocypselomorphus manfredkelleri Mayr, 2005 is represented by a single skeleton from Messel (Mayr 2005f). The species is similar in overall size to the extant Common Swift (*Apus apus*), and also has a short, swift-like beak. Whereas, however, the forearm (carpometacarpus and distal phalanges) is very long as in apodiform birds, the humerus is not shortened. The sternum is elongate with a strongly cranially protruding sternal carina. The short tarsometatarsus is only one third of the length of the ulna. *P. manfredkelleri* agrees with the Steatornithidae but differs from all taxa included in this chapter in the plesiomorphic presence of 19 or 20 presacral vertebrae. The combination of a short, swift-like beak with long wings and short feet indicates that the species hawked insects on the wing. A phylogenetic analysis placed it as the sister taxon of the Cypselomorphae (Mayr 2005f), but still more data on the morphology of *P. manfredkelleri* have to be gathered for a strongly based classification.

12.5 †Archaeotrogonidae

These short-legged aerial insectivores are the most abundant small birds in the Oligocene deposits of the Quercy fissure fillings. Their taxonomy was revised by Mourer-Chauviré (1980), who recognized four species: *Archaeotrogon venustus* Milne-Edwards, 1892 (late Eocene to late Oligocene), *A. zitteli* Gaillard, 1908 (early to late Oligocene), *A. cayluxensis* Gaillard, 1908 (late Oligocene), and *A. hoffstetteri* Mourer-Chauviré, 1980 (from the old collections of unknown age).

A. venustus is the best known archaeotrogon and also has the largest temporal range, existing over a period of 15 million years. All major postcranial elements of this species have been found (Mourer-Chauviré 1980, 1995c). The humerus is quite stocky, with a wide proximal end and a double pneumotricipital fossa. As far as this can be inferred from the isolated bones and in contrast to the humerus of most other taxa included in the present chapter, the bone was only slightly shorter than the ulna. The extensor process of the short carpometacarpus forms a pointed spur (Fig. 12.6), which may have served for defense or intraspecific combats.

Archaeotrogons were collected by Michael Daniels from the early Eocene London Clay of Walton-on-the-Naze (see Table 4.1 in Feduccia 1999). I have examined these specimens, which were mentioned by Mourer-Chauviré (1995c), and can confirm their identification. Most notably, substantial portions of a swift- or goatsucker-like beak are preserved in one of the fossils. As in *Archaeotrogon*, there is a spur on the carpometacarpus.

Putative archaeotrogons are further known from Messel (Mayr 1998a, 2004d). The species from this locality, *Hassiavis laticauda* Mayr, 1998, was referred to the Archaeotrogonidae because of a similarly shaped humerus and tarsometatarsus, and similar wing proportions. *H. laticauda* has an owlet-nightjar-like beak, but owing to the rather poor preservation of the fossil specimens only limited comparisons with the species of *Archaeotrogon* are possible. The coracoid of the Messel species differs from that of *Archaeotrogon* in that the omal extremity has a hooked outline, whereas it is rounded in *Archaeotrogon*. The carpometacarpus does not bear a spur. Some specimens exhibit well-preserved feather remains and the tail resembles that of nightjars (Caprimulgidae) in its shape; in one fossil the tail feathers show a distinct barring (Fig. 12.6; Mayr 2004d).

As indicated by their name, archaeotrogons were originally considered to be representatives of the Trogonidae. However, in her revision of these birds,

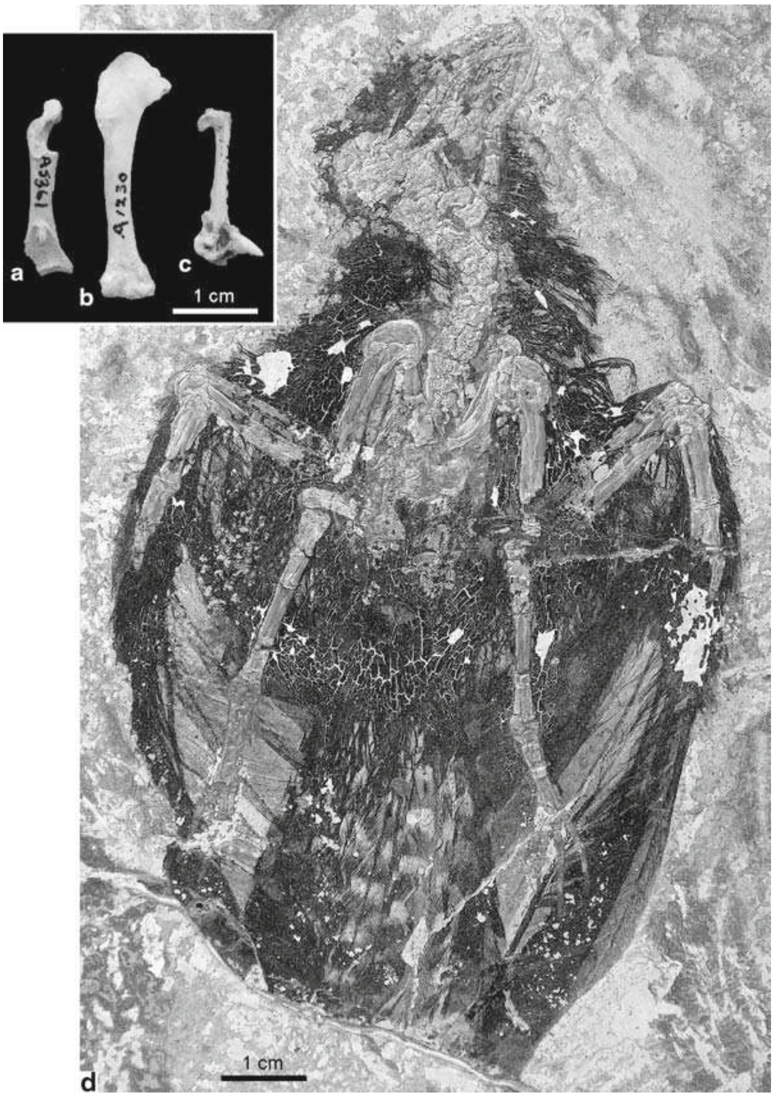

Fig. 12.6 **a–c** *Archaeotrogon* cf. *venustus* Milne-Edwards, 1892 (Archaeotrogonidae) from an unknown horizon of the Quercy fissure fillings; **d** skeleton of the putative archaeotrogonid *Hassiavis laticauda* Mayr, 1998 from the middle Eocene of Messel (Forschungsinstitut Senckenberg, Frankfurt am Main, Germany, SMF-ME 3545). **a** Left coracoid (Natural History Museum, London, UK, BMNH A 5361); **b** right humerus (BMNH A 1230); **c** right carpometacarpus (BMNH A 1228). (Photos by Sven Tränkner)

Mourer-Chauviré (1980) noted similarities to the Caprimulgidae. Cypselomorph affinities of archaeotrogons are confirmed by the above-mentioned London Clay specimens with a goatsucker-like beak (Mourer-Chauviré 1995c), but their position within that clade is unresolved.

12.6 Nyctibiidae (Potoos) and Caprimulgidae (Nightjars)

The nocturnal Nyctibiidae and Caprimulgidae share derived skull features, including a cone-like bony protrusion in the orbit, at the caudal margin of the foramen for the optic nerve, and extremely widened palatine bones (Fig. 12.2; Mayr 2002b). A clade including these two taxa is also supported by an analysis of mitochondrial genes (Brown et al. 2008), but is not retained in phylogenies based on nuclear sequence data, which do not conclusively resolve their affinities (Cracraft et al. 2004; Ericson et al. 2006).

12.6.1 Nyctibiidae

The seven extant species of the Nyctibiidae occur in forests of tropical Central America and South America. Osteologically, these birds are well characterized by a derived skull morphology with a very short beak and strongly bowed jugal bars (Fig. 12.2), and by a grotesquely abbreviated tarsometatarsus. Their first fossil record was a proximal humerus from an unknown horizon of the Quercy fissure fillings, which was described as *Euronyctibius kurochkini* by Mourer-Chauviré (1989). Complete skeletons of stem group Nyctibiidae were subsequently reported from Messel (Mayr 1999b, 2001b, 2005d), where two species, *Paraprefica major* Mayr, 1999 and *P. kelleri* Mayr, 1999, have been recognized (Fig. 12.7). As in extant Nyctibiidae, the palatine bones of *Paraprefica* are greatly enlarged, the tibiotarsus lacks an ossified supratendinal bridge, the tarsometatarsus is greatly abbreviated, and the tail feathers are fairly long. The carpometacarpus is, however, proportionally longer and more slender than that of extant potoos. *Paraprefica* was erroneously assigned to the Preficinae in the original description (Mayr 1999b), but the similarities to the latter are now considered to be plesiomorphic for the clade including "caprimulgiform" and apodiform birds (Mayr 2005d).

Although there seem to be minor differences in the shape of the humerus (Mayr 2005d), detailed comparisons between *Paraprefica* and *Euronyctibius* are limited by the incomplete fossil record of the latter.

12.6.2 Caprimulgidae

The modern representatives of this taxon have a worldwide distribution and include more than 80 species, but its Paleogene fossil record is very sparse. Olson (1999a) tentatively assigned to the Caprimulgidae some isolated bones (proximal humerus, carpometacarpus, and distal tarsometatarsus) from the early Eocene Nanjemoy Formation of Virginia, which belong to at least two different small species. The only other Paleogene specimens are two coracoids from the late Eocene of the Quercy fissure fillings, which were described as *Ventivorus ragei* by Mourer-Chauviré (1989). The identification of these fossils needs to be bolstered with more

Fig. 12.7 Skeleton of *Paraprefica kelleri* Mayr, 1999 (Nyctibiidae) from the middle Eocene of Messel (Forschungsinstitut Senckenberg, Frankfurt am Main, Germany, SMF-ME 3727A). (Photo by Sven Tränkner)

material (Feduccia 1999, p. 320, erroneously stated that *V. ragei* was assigned to the Archaeotrogonidae by Mourer-Chauviré 1989).

12.7 Aegothelidae (Owlet-Nightjars) and Apodiformes (Swifts and Hummingbirds)

There exists congruent evidence from multiple analyses of different data that the Australasian Aegothelidae are the sister taxon of apodiform birds (Mayr 2002b; Mayr et al. 2003; Cracraft et al. 2004; Ericson et al. 2006). Extant Apodiformes include the Southeast Asian Hemiprocnidae (tree swifts), the globally distributed Apodidae (true swifts), and the Trochilidae (hummingbirds), which today occur only in the New World. All representatives of the Apodiformes are small to very small birds with a highly specialized aerial locomotion. In all species the proximal wing bones (humerus and ulna) are strongly abbreviated and the hand is elongated, so the carpometacarpus is at least as long as the humerus.

The Aegothelidae have no Paleogene fossil record. An earlier tentative identification of owlet-nightjars in the Quercy fissure fillings (Mourer-Chauviré 1982) was based on a fragmentary sternum, which more likely belongs to a species of the Aegialornithidae (own observation and Mourer-Chauviré 2006). Apodiform-like birds were very diversified in the Paleogene of the Northern Hemisphere, and their fossil record dates back into the early Eocene. Although the published Eocene fossils are from European fossil sites, as yet undescribed apodiform birds were also reported from the Green River Formation (Feduccia 1999, p. 324; Weidig 2003). In virtually all earlier studies on Paleogene Apodiformes, the Trochilidae were omitted from comparisons, which led to a wrong placement of stem group Apodiformes into the crown group. In fact, most early Eocene species still belong to stem group Apodiformes (Mayr 2003c; see below).

The alleged swift *Laputavis robusta* (Dyke, 2001) from the London Clay of Walton-on-the-Naze is certainly not an apodiform bird (Mayr 2001c; contra Dyke 2001c, d). This species differs from all representatives of the clade including the Aegothelidae and Apodiformes in the absence of a coracoidal foramen for the supracoracoideus nerve. On the basis of comparisons with specimens from the type locality in the collection of Michael Daniels, which were figured by Mayr (1998b, plate 11), *L. robusta* appears to be a stem group representative of the Coraciidae/Brachypteraciidae (Sect. 16.7).

12.7.1 †Eocypselidae

This taxon of stem group Apodiformes (Mayr 2003c) was erected by Harrison (1984b) for *Eocypselus vincenti* from the early Eocene London Clay, whose holotype consists of wing and pectoral girdle bones (Fig. 12.8). The coracoid resembles the corresponding bone of the Aegothelidae and is distinguished from crown group Apodiformes in the proportionally smaller acrocoracoid process. The humerus is stouter than that of nonapodiform birds, including the Aegothelidae, but is still less abbreviated than the humerus of crown group Apodiformes. Together with the more slender ulna, the humerus proportions suggest a position of *E. vincenti* outside crown group Apodiformes (Mayr 2003c).

Two postcranial skeletons from the Fur Formation were assigned to *E. vincenti* (Kristoffersen 2002a; Dyke et al. 2004). These provide new information on the osteological features of *Eocypselus* and further support its position outside crown group Apodiformes. Most notably, the caudal margin of the sternum bears four incisions, deep lateral and shallow medial ones, whereas the bone lacks any incisions

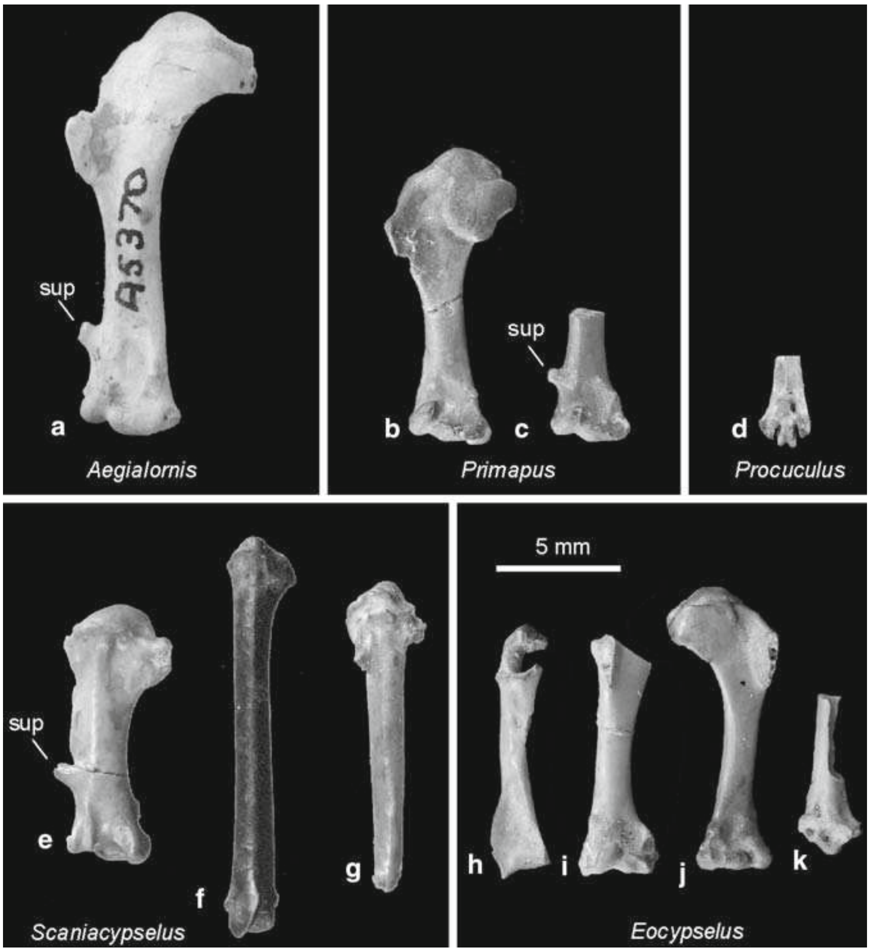

Fig. 12.8 Paleogene Apodiformes. **a** Right humerus of *Aegialornis gallicus* Lydekker, 1891 (Aegialornithidae) from an unknown horizon of the Quercy fissure fillings (Natural History Museum, London, UK, BMNH A 5370); **b**, **c** right humeri of *Primapus lacki* Harrison and Walker, 1975 (Aegialornithidae) from the early Eocene London Clay of Bognor Regis and the Isle of Sheppey (**b** holotype, BMNH A 2166; **c** referred specimen BMNH A 3710); **d** distal right tarsometatarsus of *Procuculus minutus* Harrison and Walker, 1977 from the early Eocene London Clay of Bognor Regis (holotype, BMNH A 4680); **e** left humerus, **f** right ulna, and **g** left carpometacarpus of *Scaniacypselus wardi* Harrison, 1984 (Apodidae) from the early Eocene Røsnæs Clay of Denmark (holotype, BMNH A 5430); **h** left coracoid, **i** right humerus, **j** left humerus, and **k** proximal left ulna of *Eocypselus vincenti* Harrison, 1984 (Eocypselidae) from the early Eocene London Clay of Walton-on-the-Naze (holotype, BMNH A 5429). *sup* dorsal supracondylar process. All images to scale. (Photos by Sven Tränkner)

in crown group Apodiformes. Also in contrast to the latter, the proximal phalanx of the major wing digit of *Eocypselus* bears only a small internal index process. This feature was not mentioned by Dyke et al. (2004), who likewise did not appreciate

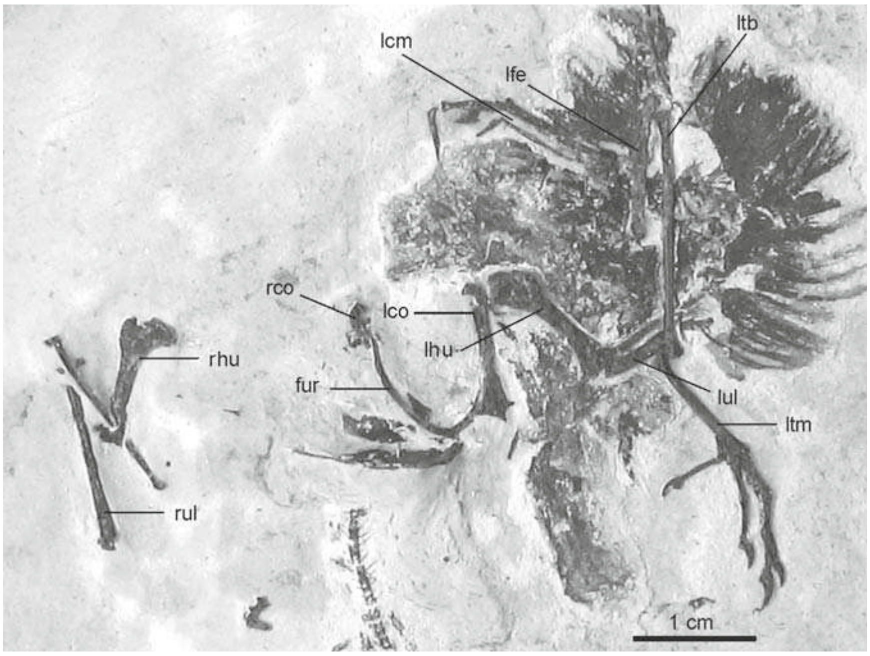

Fig. 12.9 Skeleton of *Eocypselus vincenti* Harrison, 1984 (Eocypselidae) from the early Eocene Fur Formation in Denmark (Geological Museum, Copenhagen, Denmark, MGUH 26729). *fur* furcula, *lco* left coracoid, *lcm* left carpometacarpus, *lfe* left femur, *lhu* left humerus, *ltb* left tibiotarsus, *ltm* left tarsometatarsus, *lul* left ulna, *rco* right coracoid, *rhu* right humerus, *rul* right ulna. (Photo courtesy of Bent Lindow)

another peculiarity of *Eocypselus* visible in the Danish specimens, i.e., that its legs are very long compared with those of most extant Apodiformes (Fig. 12.9). Although Dyke et al. (2004, p. 54) noted that the osteological traits displayed by the Fur Formation specimens of *Eocypselus* "may serve to confirm a basal placement for this taxon within Apodiformes," they erroneously classified it into the Hemiprocnidae.

12.7.2 †Aegialornithidae

The Aegialornithidae are among the most abundant small birds in late Eocene sites of the Quercy fissure fillings, but disappear toward the early Oligocene (Mourer-Chauviré 1978, 1980, 1988b). Four species were recognized in these deposits by Mourer-Chauviré (1988b), i.e., *Aegialornis gallicus* Lydekker, 1891, *A. broweri* Collins, 1976, *A. wetmorei* Collins, 1976, and *A. leehnardti* ("*leenhardti*") Gaillard,

1908. A humerus from the middle Eocene of the Geisel Valley (MP 12; Mayr 2002a) was assigned to *A. broweri* by Peters (1998), but was named *A. germanicus* by Mlíkovský (2002), who did not sufficiently justify this action. The alleged swift *Cypseloides mourerchauvireae* Mlíkovský, 1989 is a junior synonym of *A. gallicus* (Mayr 2003d).

Olson (1999a) assigned a tarsometatarsus from the early Eocene of the Nanjemoy Formation of Virginia to the Aegialornithidae. This specimen is stouter than the tarsometatarsus of *Aegialornis* and was assumed to be a representative of the Parvicuculidae (Sect. 11.7) by Mayr and Mourer-Chauviré (2005).

All major limb bones of aegialornithids are known. The humerus is less robust than in crown group Apodiformes, and there is a well-developed dorsal supracondylar process on its distal end (Fig. 12.8). The ulna is short and stout, but also less so than that of extant Apodiformes. The fenestrated proximal phalanx of the major wing digit bears a well-developed internal index process.

The Aegialornithidae were considered by earlier authors (e.g., Harrison 1975b, 1984b; Mourer-Chauviré 1988b; Karhu 1988, 1992) to be either closely related to the Hemiprocnidae or transitional forms between the Hemiprocnidae and the Apodidae. These hypotheses were, however, largely based on overall morphology and have not been well established. Plesiomorphic features which support a position of aegialornithids outside crown group Apodiformes include the morphology of the sternal articulation facets for the coracoid, which are not saddle-shaped or slightly convex as in crown group Apodiformes, the proportionally less abbreviated humerus, and the more strongly developed cnemial crests of the tibiotarsus (Mayr 2003c).

Primapus lacki from the early Eocene of the London Clay is known from humeri only (Fig. 12.8). The species was already assigned to the Aegialornithidae in the original description (Harrison and Walker 1975), and shares with *Aegialornis* the presence of a well-developed dorsal supracondylar process. Being much smaller than the late Eocene Aegialornithidae, *P. lacki* indicates that there was a size increase in the evolution of aegialornithids.

I agree with Olson (1985, p. 135) that the alleged cuculiform *Procuculus minutus* Harrison and Walker, 1977, which is based on the distal end of a tiny tarsometatarsus from the London Clay (Fig. 12.8), represents an apodiform bird, and this species may be a junior synonym of *P. lacki*.

12.7.3 Hemiprocnidae (Tree Swifts) and Apodidae (True Swifts)

After assignment of the Eocypselidae and Aegialornithidae to stem group Apodiformes (see Sects. 12.7.1, 12.7.2), the Hemiprocnidae have no Paleogene fossil record. The earliest stem group representatives of the Apodidae occur in the early and middle Eocene of Europe and belong to the taxon *Scaniacypselus*. *Scaniacypselus wardi* from the early Eocene (MP 8; Mlíkovský 2002) of Denmark was described by Harrison (1984b) and is known from wing bones of a single individual (Fig. 12.8). A second species, *S. szarskii* (Peters 1985), is represented by several skeletons from Messel and a humerus from the middle Eocene (MP 10/11) of the Quercy fissure fillings (Peters 1985; Mayr and Peters 1999; Mourer-Chauviré 2006). A record of *Scaniacypselus* sp. also comes from the late Eocene (MP 17) of Quercy (Mourer-Chauviré and Sigé 2006).

S. szarskii was erroneously assigned to the Aegialornithidae in the original description, from which it differs, among others, in the more abbreviated humerus and ulna (Mayr and Peters 1999). In fact, *S. szarskii* is quite similar to extant Apodidae in skeletal morphology, with whom it further shares a derived humerus morphology. Some Messel specimens of this species exhibit an excellent feather preservation, which gives a vivid impression of the external appearance of these birds in life (Fig. 12.10). In contrast to that of many extant Apodidae, the tail of *S. szarskii* was only slightly forked.

A proximal ulna of a true swift from the late Oligocene of France was assigned to *Procypseloides* cf. *ignotus* (Milne-Edwards, 1871) by Mourer-Chauviré et al. (2004). Boles (2001a) described a swiftlet (Collocaliini), *Collocalia buday*, from the late Oligocene/early Miocene of the Riversleigh Formation in Australia. This species is known from humeri, a coracoid, and a tarsometatarsus, and is larger than extant species of *Collocalia*. If correctly identified, this species would constitute the earliest record of crown group Apodiformes.

Fig. 12.10 Skeleton of *Scaniacypselus szarskii* (Peters, 1985) (Apodidae) from the middle Eocene of Messel (Forschungsinstitut Senckenberg, Frankfurt am Main, Germany, SMF-ME 3576A). (Photo by Sven Tränkner)

12.7.4 Trochilidae (Hummingbirds)

Although the nectarivorous Trochilidae are today among the most characteristic birds of the New World avifauna, Paleogene stem group representatives of this taxon were only found in fossil sites in Europe. Wing remains of a small hummingbird-like apodiform bird were first reported by Karhu (1988) from the early Oligocene of the Caucasus, who assigned these bones to the species *Jungornis tesselatus* within the new taxon Jungornithidae. Subsequently, Karhu (1999) also classified a second, slightly older and less derived species from late Eocene deposits of the Caucasus into the Jungornithidae. This bird was described as *Argornis caucasicus* and is likewise only known from wing and pectoral girdle elements. Karhu (1988, 1992, 1999) noted that *Jungornis* and *Argornis* share characteristic features with modern hummingbirds, including a derived morphology of the proximal ulna, and, in *Jungornis*, a protrusion on the humeral head, which is only found in hummingbirds and allows rotation of the humerus during hovering flight. He attributed these similarities to convergence, and considered *Argornis* and *Jungornis* to be aberrant swifts with hummingbird-like specializations. However, there are no derived morphological traits that are exclusively shared by *Argornis*, *Jungornis*, and swifts, and not also found in hummingbirds. Accordingly, analysis of the phylogenetic relationships between modern and fossil apodiform birds showed the "Jungornithidae" *sensu* Karhu (1999) to be paraphyletic, with *Argornis* being the sister taxon of a clade including *Jungornis* and crown group Trochilidae (Mayr 2003c). Another species of *Jungornis*, *J. geraldmayri*, was reported by Mourer-Chauviré and Sigé (2006) from the late Eocene (MP 17) of the Quercy fissure fillings, and is based on an almost complete humerus.

Argornis and *Jungornis* are only known from wing elements, but an *Argornis*-like bird, *Parargornis messelensis* Mayr, 2003, was described from Messel, and is represented by a complete skeleton with well-preserved feather remains (Fig. 12.11; Mayr 2003d). The beak of *P. messelensis* is short and swift-like, and as in all apodiform birds the humerus is strongly abbreviated. Most notably, however, the feathering of this species resembles that of owlet-nightjars and is very unlike the feathering of swifts and hummingbirds in that the wings are short and broad, and the tail is long. The peculiar wing morphology of *Parargornis*, i.e., the combination of a greatly abbreviated humerus with a short and broad wing, has no counterpart among extant birds and may represent an early stage in the evolution of hovering flight.

I have noted previously (Mayr 2003d, 2005a) that the humeri of *Parargornis* and *Argornis* are very similar to humerus of *Cypselavus gallicus* Gaillard, 1908 from the late Eocene and early Oligocene (MP 16–23) of the Quercy fissure fillings. This species was classified into the Hemiprocnidae by earlier authors (Harrison 1984b; Peters 1985; Mourer-Chauviré 1988b). The coracoid assigned to *C. gallicus* by Mourer-Chauviré (1978) was transferred to the Jungornithidae and was described as a new species, *Palescyvus escampensis*, by Karhu (1988). In fact, however, all skeletal elements of *Cypselavus* belong to a single species, which is also a stem group representative of the Trochilidae. Mourer-Chauviré (2006) classified

Fig. 12.11 Skeleton of *Parargornis messelensis* Mayr, 2003 (Trochilidae) from the middle Eocene of Messel (holotype, Hessisches Landesmuseum Darmstadt, Germany, HLMD-Be 163). The specimen in the large image was coated with ammonium chloride. (Photo by Sven Tränkner)

Parargornis, *Argornis*, and *Cypselavus* into the new taxon Cypselavidae, but there remains a possibility that the similarities between these birds are plesiomorphic.

Essentially modern-type stem group hummingbirds, which appear to have been nectarivorous and capable of sustained hovering flight, occur in the early Oligocene of Europe. The first described species is *Eurotrochilus inexpectatus* Mayr, 2004 from Wiesloch-Frauenweiler in Germany, which is known from partial skeletons of three individuals (Fig. 12.12; Mayr 2004e, 2007d). A second species of *Eurotrochilus*, *E. noniewiczi* Bocheński and Bocheński, 2008, was reported from the Flysh (about 31 Ma) of Poland (Bocheński and Bocheński 2008), and is also based on a partial skeleton. A complete skeleton of *Eurotrochilus* sp. was further discovered in the early Oligocene of the Lubéron in France (Louchart et al. 2008).

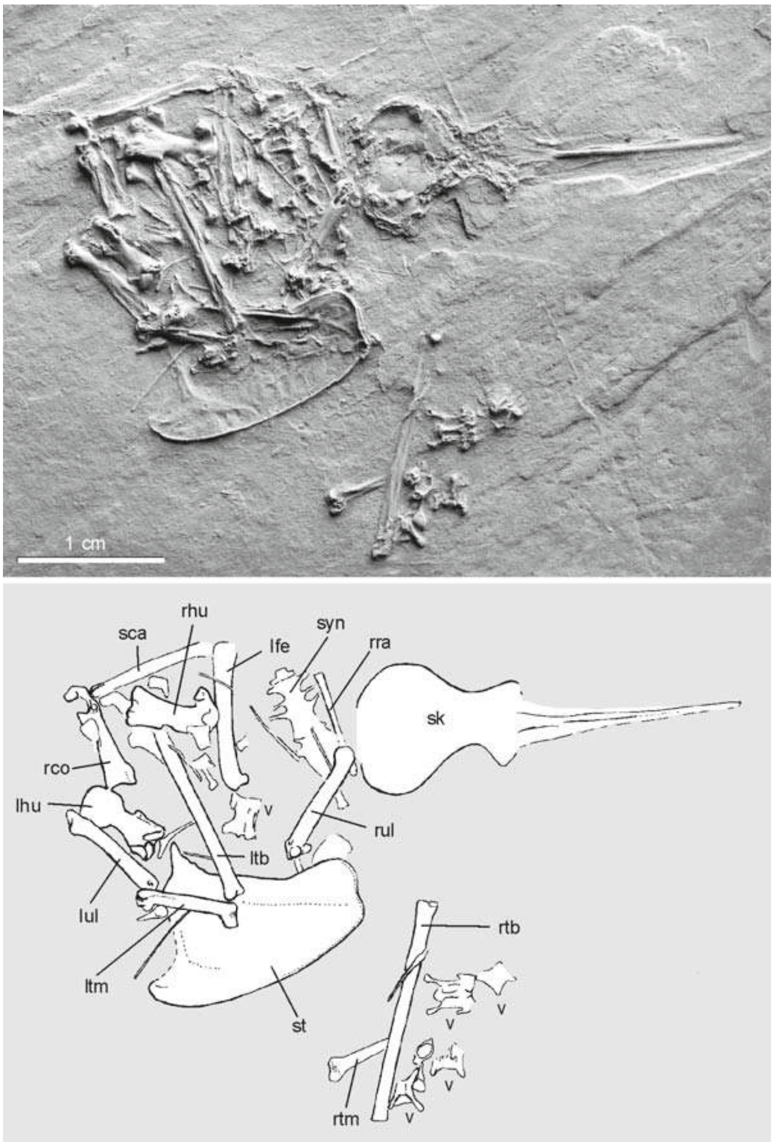

Fig. 12.12 Skeleton of *Eurotrochilus inexpectatus* Mayr, 2004 (Trochilidae) from the early Oligocene of Wiesloch-Frauenweiler in Germany with interpretative drawing (counter slab of holotype, Staatliches Museum für Naturkunde, Karlsruhe, Germany, SMNK-PAL.5591). *lfe* left femur, *lhu* left humerus, *ltb* left tibiotarsus, *ltm* left tarsometatarsus, *lul* left ulna, *rco* right coracoid, *rhu* right humerus, *rra* right radius, *rtb* right tibiotarsus, *rtm* right tarsometatarsus, *rul* right ulna, *sca* scapula, *sk* skull, *st* sternum, *syn* synsacrum, *v* vertebra. Coated with ammonium chloride. (Photo by Sven Tränkner)

Apart from a similar morphology of the bones, *E. inexpectatus* shares with extant Trochilidae a tiny size and greatly elongated beak, as well as a marked depression on the caudal surface of the proximal end of the ulna, and the presence of a distal protrusion of the humerus head (Mayr 2007d). The latter feature is more marked than in *Jungornis* and approaches the condition found in extant hummingbirds. As in crown group Trochilidae but in contrast to that of other apodiform birds, the ulna is further only slightly longer than the humerus. The feathering of *Eurotrochilus* was similar to that of some extant hummingbirds (Louchart et al. 2008).

These fossil hummingbirds nevertheless differ in a number of plesiomorphic features from their living relatives. They are thus outside crown group Trochilidae and do not have a bearing on the area of origin of the crown group, whose stem species unquestionably lived in South America or Central America. Whether Paleogene stem group Trochilidae also occurred in the New World is unknown but likely, given the great similarities in the early Oligocene avifaunas of North America and Europe (Chap. 17.1.1).

The long beak of *E. inexpectatus* indicates that the species was nectarivorous. The swift-like bill of *Parargornis*, by contrast, suggests that the stem species of Pan-Trochilidae was insectivorous. If interpretation of the wing morphology of *Parargornis* is correct (see above), capability for hovering flight evolved in the stem lineage of the Trochilidae before a nectarivorous feeding behavior, and may have enabled *Parargornis* to glean insects from the underside of leaves or around flowers (Mayr 2005g; Mayr and Manegold 2002).

The *Eurotrochilus* fossils are also of interest concerning the evolution of ornithophilous flowers in the Old World. Because hummingbirds are capable of sustained hovering flight, many extant hummingbird-pollinated plants differ from Old World ornithophilous plants in that they do not provide perches near the flower. Surprisingly, however, some Old World plants, which occur in areas without hovering avian pollinators, exhibit a flower morphology similar to that of those pollinated by hummingbirds in the New World. Examples therefore are the Himalayan *Agapetes* spp. (Ericaceae), the East African *Canarina eminii* (Campanulaceae), the South African *Tecomaria capensis* (Bignoniaceae), as well as the West African *Impatiens sakeriana* (Balsaminaceae), and *Sabicea speiosa* (Rubiaceae) (Mayr 2005g). It now seems possible that the flower traits of these plants may indeed primarily constitute an adaptation to pollination by hummingbirds, which after the disappearance of hummingbirds from the Old World may have been taken over by long-tongued bees and other insects (Mayr 2004e, 2005g).

Chapter 13
Cariamae (Seriemas and Allies)

Extant Cariamidae (seriemas) include two predominantly carnivorous species, which occur in semiopen, dry habitats of South America. Their classification into the "Gruiformes" by earlier authors has never been convincingly established, and molecular data congruently suggest a position of seriemas within a clade, which also includes the Strigiformes, "Falconiformes," Psittaciformes, and "higher land birds" (see Chap. 3).

Paleogene stem group representatives of the Cariamidae were very diversified and widely distributed over Europe and the Americas. These birds are usually united in the taxon Cariamae and include medium-sized to large, often cursorial species. They typically exhibit supraorbital processes on the skull, a short carpometacarpus with a wide intermetacarpal space, and a distinct, ventrally directed tubercle on the proximal end of the bowed minor metacarpal, as well as a block-like hypotarsus which does not enclose bony canals. Not all of these features are, however, present in every taxon included in this chapter, and some birds are discussed here only because they share a similar overall morphology with unambiguous Cariamae.

Even if only those groups are considered whose close relationship to extant Cariamidae is well established, i.e., the Phorusrhacidae, Idiornithidae, and Bathornithidae, the historical biogeography of the Cariamae is not easily understood. These birds occurred in the Paleogene of South America, Europe, and North America. The most obvious hypothesis certainly is a dispersal from South America (Phorusrhacidae) to Europe (Idiornithidae) via North America (Bathornithidae), or vice versa (Mourer-Chauviré 1999b). As yet, however, no North American Cariamae are known before the late Eocene, whereas representatives of this taxon were already very diversified in the early Eocene of Europe and South America (see Sect. 17.2.1 concerning the similar distribution of Paleogene ratites).

13.1 †Phorusrhacidae

The Phorusrhacidae ("terror birds") are one of the most characteristic and best known avian groups from the Cenozoic of South America. Their taxonomy was revised by Alvarenga and Höfling (2003), who recognized five subtaxa, of which

G. Mayr, *Paleogene Fossil Birds*, DOI: 10.1007/978-3-540-89628-9_13,

only the Psilopterinae, Patagornithinae, and Brontornithinae have a Paleogene fossil record. The taxonomic allocation of the fossils assigned to the latter is, however, challenged by the fact that Agnolin (2007b) assumed that the early Neogene *Brontornis*, the type genus of the Brontornithinae, is actually a representative of the Anseriformes, and is more similar to the Gastornithidae and Dromornithidae (Sects. 6.2, 6.3). These conclusions were based on the morphology of a quadrate fragment assigned to this poorly known taxon, whose mandibular process only exhibits two condyles as in Galloanseres, instead of three as in most Neoaves. The ungual phalanges of *Brontornis* are further not raptor-like as in typical phorusrhacids. If Agnolin's hypothesis is confirmed by future studies, erection of a new taxon would be necessary for the Paleogene species classified into the Brontornithinae, which clearly exhibit a phorusrhacid-like morphology.

The earliest species assigned to the Phorusrhacidae is *Paleopsilopterus itaboraiensis* Alvarenga, 1985 from the late Paleocene of Itaboraí in southeastern Brazil, whose fossil record consists of a proximal tarsometatarsus and distal tibiotarsi (Alvarenga 1985a). *P. itaboraiensis* was classified in the Psilopterinae, which include rather small and gracile species with slender leg bones and a long and elongate tarsometatarsus. This assignment is, however, based on overall similarity and needs to be verified by additional specimens.

A proximal tarsometatarsus and an ungual phalanx of an unnamed species of the Psilopterinae were reported by Acosta Hospitaleche and Tambussi (2005) from the late Eocene (Mustersan) of Argentina. Another Paleogene species of the Psilopterinae is *Psilopterus affinis* (Ameghino, 1899) from the late Oligocene (Deseadan) of Argentina, which is based on an incomplete tarsometatarsus and is among the smallest phorusrhacids. Other taxa from the same formation, which were assigned to the Phorusrhacidae by earlier authors, were considered to be of undeterminable affinities and were excluded from the Phorusrhacidae by Alvarenga and Höfling (2003). Regarding these fossils, the authors noted, however, that "*Pseudolarus*" *guaraniticus* Ameghino, 1899 (known from a fragmentary proximal humerus) and *Smiliornis penetrans* Ameghino, 1899 (based on an omal extremity of a coracoid) may actually be synonymous with *P. affinis*. According to Agnolin (2006a), "*P.*" *guaraniticus* indeed belongs to *Psilopterus*, although it represents a larger species than *P. affinis*; Agnolin (2004) also assigned *S. penetrans* to the Cariamae. The coracoid of the latter species is of particular interest in that it shares with phorusrhacid birds the complete reduction of the acrocoracoid process, but still exhibits a well-developed and presumably plesiomorphic procoracoid process. Agnolin (2004) further classified the alleged ciconiiform *Ciconiopsis antarctica* Ameghino, 1899 into the Psilopterinae. This species is based on an incomplete carpometacarpus, which likewise comes from the Deseadan of Argentina, and may well also belong to a species of *Psilopterus*. *Riacama caliginea* Ameghino, 1899, which is known from the shaft and sternal extremity of a coracoid from the Deseadan of Argentina, was classified into the Cariamidae by Agnolin (2004). This species was assigned to the phorusrhacid Psilopterinae by earlier authors, but was considered to be of indeterminate affinities by Alvarenga and Höfling (2003), with whom I agree.

The species of the Patagornithinae are medium-sized phorusrhacids, with a long and slender mandibular symphysis and elongated tarsometatarsi (Alvarenga and Höfling 2003). Their only Paleogene representative is *Andrewsornis abbotti* Patterson, 1941 from the Deseadan of Argentina. Of this species an incomplete skull, fragments of the mandible, a femur, an incomplete coracoid, and pedal phalanges were described.

The Brontornithinae include the largest phorusrhacids, which reached a standing height of more than 2 m, given that the Neogene taxon *Brontornis* is indeed a phorusrhacid bird (see above). Brontornithines are more massively built than other phorusrhacids and have a much shorter and stouter tarsometatarsus. The earliest species is *Physornis fortis* Ameghino, 1895 from the Deseadan of Argentina, whose fossil record consists of mandible fragments and a few other incomplete bones. Much better documented is *Paraphysornis brasiliensis* (Alvarenga, 1982), which is based on a fairly complete skeleton from the late Oligocene/early Miocene of the Taubaté Basin of Brazil (Alvarenga 1982, 1993). This species was very large, with an estimated weight of about 180 kg (Alvarenga and Höfling 2003).

In addition to these South American specimens, an incomplete beak and associated bones (including a distal tarsometatarsus) from the late Eocene of Seymour Island (Antarctica) were tentatively assigned to the Phorusrhacidae (Case et al. 1987; Tambussi and Acosta Hospitaleche 2007). The fragmentary remains of the alleged phorusrhacid *Cunampaia simplex* Rusconi, 1946 from the late Eocene (Divisaderan) of Argentina are nonavian and probably belong to the Crocodylomorphae (Agnolin and Pais 2006).

Phorusrhacids show a significant variation in size, with representatives of the Psilopterinae being of size similar to that of the extant *Cariama cristata*, whereas *P. brasiliensis* approached the size of the early Miocene *Brontornis burmeisteri* Moreno and Mercerat, 1891, a species which had an estimated height of 175 cm “at the level of the back, and the head, when well raised, could have reached around 280 cm high” (Alvarenga and Höfling 2003, p. 59). All species whose skull is known had very large, mediolaterally compressed, raptor-like beaks (Fig. 13.1). In contrast to the skull of extant Cariamidae, that of phorusrhacids exhibits functional basipterygoid processes. Even in the early forms, the wings seem to be greatly reduced and the coracoid is long and slender, without an acrocoracoid process. As in other large flightless birds (e.g., the Gastornithidae and Dromornithidae), the ribs lack uncinate processes. The phylogenetic affinities between the various described forms are uncertain. There can be little doubt, however, that the small size and elongate leg bones of the taxa united in the Psilopterinae are plesiomorphic for the Phorusrhacidae.

It is generally assumed that phorusrhacids were among the top predators in the Cenozoic of South America, and a carnivorous diet of these birds is supported by the sharply hooked tip of the huge beak. The mediolaterally compressed pelvis and beak indicate that the body was very narrow, which led Alvarenga and Höfling (2003) to assume that phorusrhacids hunted in densely vegetated areas. Phorusrhacids greatly differ in the proportions of the limb bones, with the tarsometatarsus being very long and slender in psilopterines, patagornithines, and phorusrhacines but

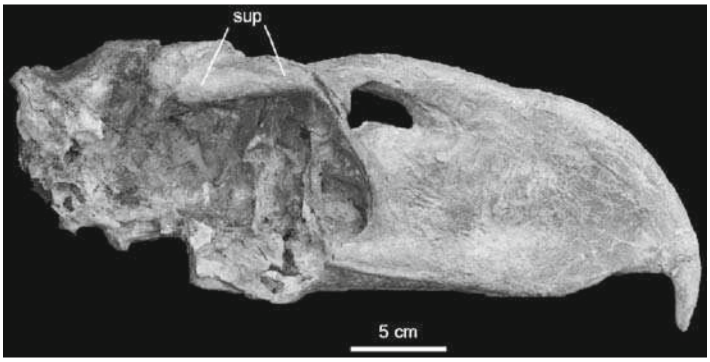

Fig. 13.1 Skull of the phorusrhacid *Patagornis marshi* Moreno and Mercerat, 1891 ("*Phorusrhacos inflatus*") from the early Miocene of the Santa Cruz Formation in Argentina (Natural History Museum, London, UK, BMNH A 516). *sup* supraorbital process. (Photo by Sven Tränkner)

short and stout in brontornithines. Certainly the latter were thus graviportal rather than cursorial birds, and Alvarenga and Höfling (2003) hypothesized that brontornithines may have been scavengers.

Whereas Tambussi and Acosta Hospitaleche (2007) assumed flight capabilities for the smaller Psilopterinae, all phorusrhacids were considered flightless by Alvarenga and Höfling (2003). These authors further noted that some phorusrhacids may have been sexually dimorphic in size and morphological features.

13.2 †Idiornithidae and †*Elaphrocnemus*

Most representatives of the Cariamae from the Paleogene of Europe were assigned to the Idiornithidae. These birds were first reported from the Quercy fissure fillings, where they constitute the most abundant medium-sized birds and occur in middle Eocene to late Oligocene deposits (Mourer-Chauviré 1983a, 2006). Idiornithids were also identified in the middle Eocene of Messel and the Geisel Valley in Germany (Peters 1995; Mayr 2000d, 2002a). Mourer-Chauviré (1999b, p. 85) further mentioned the presence of still undescribed idiornithid-like birds in the Paleocene of Brazil.

As currently recognized (Mourer-Chauviré 1983a, 2006), the Idiornithidae include the taxa *Idiornis*, *Elaphrocnemus*, *Oblitavis*, *Occitaniavis*, and *Propelargus*. Only the first two of these are well represented by numerous postcranial bones, and as detailed below, a clade including these five taxa still needs to be established with derived characters.

Mourer-Chauviré (1983a) distinguished the following six species of *Idiornis* in the Query material: *Idiornis cursor* (Milne-Edwards, 1892), *I. gaillardi* Cracraft, 1973, *I. gallicus* (Milne-Edwards, 1892), *I. gracilis* (Milne-Edwards, 1892), *I. minor* (Milne-Edwards, 1892), and *I. itardiensis* Mourer-Chauviré, 1983. The species from Messel were described as *Idiornis tuberculata* Peters, 1995 and *Idiornis* cf. *itardiensis*. The former is based on a largely complete but poorly preserved skeleton, and the latter on an isolated foot (Peters 1995; Mayr 2000d). The large ?*Idiornis anthracinus* Mayr, 2002 from the Geisel Valley is known from a tarsometatarsus.

The Quercy species of *Idiornis* greatly vary in size and most are smaller than extant Cariamidae, with the tarsometatarsus of the smallest species, *I. gracilis*, measuring less than one third of that of the extant *C. cristata*. The largest Quercy species, *I. itardiensis*, corresponds in size to *I. tuberculata* from Messel.

Osteologically, the taxon *Idiornis* is very similar to extant Cariamidae (Fig. 13.2). The small species were long-legged birds with gracile hindlimbs. As in extant Cariamidae the hypotarsus is block-like and does not enclose canals for the flexor tendons of the toes. The coracoid exhibits the characteristic derived morphology of that bone in modern seriemas, in that the acrocoracoid and procoracoid processes are connected, or at least nearly so, by an osseous bridge (Fig. 13.2). Likewise, the other limb bones closely correspond to those of extant Cariamidae.

The holotype specimen of *I. tuberculata* still constitutes the only articulated skeleton of an idiornithid. This species is also the only one in which a cranium is preserved, and is further most remarkable for the occurrence of numerous small bony tubercles on the cervical vertebrae and a few other bones. Similar vertebral tubercles were also reported from another as yet undescribed species from Messel and from an isolated cervical vertebra from Quercy, the latter possibly belonging to the Idiornithidae (Mayr 2007e). As evidenced by the *I. tuberculata* skeleton and in contrast to the hallux of extant Cariamidae, the hallux of *Idiornis* was well developed.

The tarsometatarsi of the middle Eocene Messel and Geisel Valley species (*I. tuberculata*, *I.* cf. *itardiensis*, and ?*I. anthracinus*) are stouter than the gracile ones of most idiornithid species from the Quercy fissure fillings. Accordingly, these species were probably less cursorial than the Quercy species of *Idiornis*, and the different proportions of the tarsometatarsi may reflect a different paleoenvironment of the fossil sites, which was forested in the German localities but more arid and open in the Quercy ones.

The species of *Elaphrocnemus* represent the most abundant medium-sized birds in the nineteenth century Quercy collections. Mourer-Chauviré (1983a) recognized three species, *E. phasianus* Milne-Edwards, 1892, *E. crex* Milne-Edwards, 1892, and *E. brodkorbi* Mourer-Chauviré, 1983, which mainly differ in size. She further noticed that the wing bones assigned to "*Filholornis*" by Milne-Edwards (1892) belong to the same taxon as the hindlimb elements described as *Elaphrocnemus* by that author (see also Olson 1985). New excavations have shown that *E. phasianus* occurs in late Eocene deposits, whereas *E. crex* is only known from Oligocene sites (Mourer-Chauviré 1983a). The few fossils of *E. brodkorbi* lack stratigraphic data.

The *Elaphrocnemus* species were rather small birds, the size of small to medium-sized phasianids. Some skeletal elements are very different from those of *Idiornis* and extant seriemas. Although the humerus, for example, is of similar

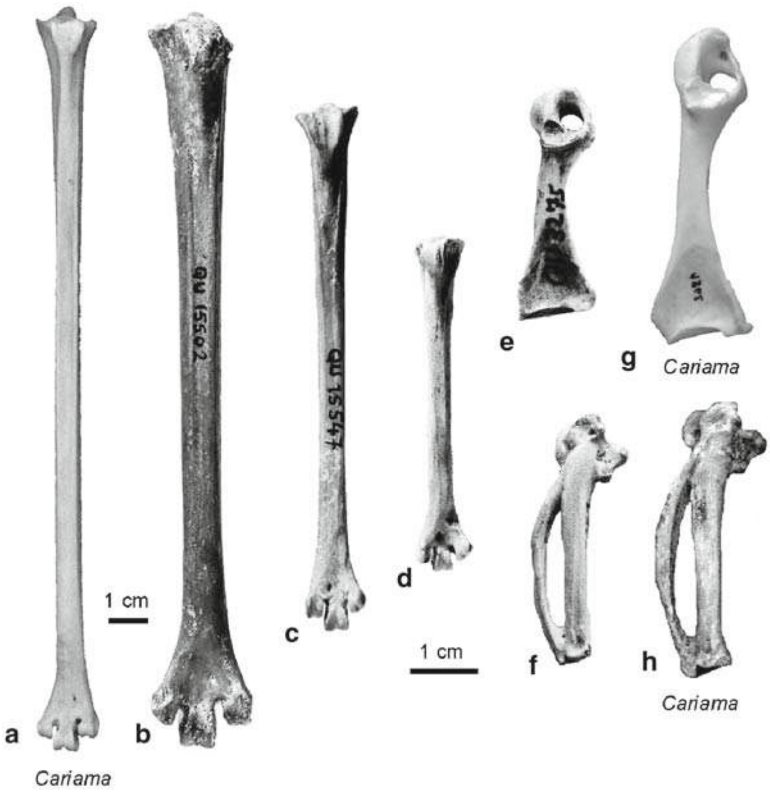

Fig. 13.2 Comparison of selected skeletal elements of some Idiornithidae from the Quercy fissure fillings in France (**b**–**f**) with the extant Red-legged Seriema, *Cariama cristata* (Cariamidae) (**a**, **g**, **h**). **a** Right tarsometatarsus; **b** right tarsometatarsus of *Idiornis gallicus* (Milne-Edwards, 1892) (Muséum National d'Histoire Naturelle, Paris, France, MNHN QU 15502 [3002]); **c** left tarsometatarsus of *I. minor* (Milne-Edwards, 1892) (MNHN QU 15547 [3047]); **d** left tarsometatarsus of *I. gaillardi* Cracraft, 1973 (MNHN QU 15534 [3034]); **e** left coracoid of *I. cursor* (Milne-Edwards, 1892) (MNHN QU 15775 [3275]); **f** right carpometacarpus of *I. cursor* (MNHN QU 15751 [3251]); **g** left coracoid; **h** right carpometacarpus. Same scale for **b**–**h**. (Photos of the idiornithid bones courtesy of Cécile Mourer-Chauviré)

overall proportions, it exhibits a strongly protruding, triangular deltopectoral crest. The scapula is peculiar in that it bears an extremely elongated acromion that serves to close the triosseal canal, which in *Idiornis* and extant Cariamidae is achieved by fusion of the procoracoid and acrocoracoid processes of the coracoid (Figs. 13.2, 13.3; Mayr and Mourer-Chauviré 2008). The tarsometatarsus is proportionally shorter than that of *Idiornis* and extant Cariamidae, and exceeds the femur only slightly in length. Mayr and Mourer-Chauviré (2006b) tentatively assigned a three-dimensionally preserved skull and several crania from an unknown locality and horizon of the Quercy fissure fillings to *Elaphrocnemus phasianus*. The skull

Fig. 13.3 Selected skeletal elements of the putative idiornithid *Elaphrocnemus phasianus* Milne-Edwards, 1892 from unknown horizons of the Quercy fissure fillings. **a** Skull (Muséum National d'Histoire Naturelle, Paris, France, MNHN QU 15688); **b** left coracoid (Naturhistorisches Museum Basel, Basel, Switzerland, NMB Q.D.242); **c** cranial extremity of left scapula (NMB Q.D.293); **d** left humerus (NMB Q.W.1755); **e** right femur (NMB Q.D.678); **f** right tibiotarsus (NMB Q.D.304/330); **g** left tarsometatarsus (NMB Q.H.158). All images to scale. (Photos by Sven Tränkner)

exhibits articulation facets for well-developed supraorbital processes, but in several features differs from that of extant Cariamidae, especially concerning the shape of the more slender beak (Fig. 13.3).

An assignment of *Elaphrocnemus* to the Cariamae can be established with the presence of well-developed supraorbital processes, and various derived similarities in the postcranial skeleton, in particular the humerus, ulna, and carpometacarpus (Mourer-Chauviré 1983a). The species of this taxon seem to have been less cursorial than those of *Idiornis*, the Phorusrhacidae, and extant Cariamidae, and probably had better flight capabilities. However, *Elaphrocnemus* lacks characters that are shared by *Idiornis* and modern Cariamidae, such as a well-developed procoracoid process and a hooked acrocoracoid process of the coracoid, as well as a block-like hypotarsus, and may be outside a clade including the latter two taxa (Mayr 2002e).

Mourer-Chauviré (1983a, 2006) identified three further taxa of the Idiornithidae among the avian material of the Quercy fissure fillings. These were classified into the species *Propelargus cayluxensis* Lydekker, 1891 (from an unknown horizon), *Occitaniavis elatus* (Milne-Edwards, 1892) (late Eocene), and *Oblitavis insolitus* Mourer-Chauviré, 1983 (unknown horizon). The material of the large *P. cayluxensis* consists of a distal tarsometatarsus and tibiotarsus, the equally sized *O. elatus* is based on a distal tibiotarsus, referred carpometacarpi, and a femur, and the smaller *O. insolitus* is known from humeri and a coracoid, which in contrast to that of other Paleogene Cariamae exhibits a foramen for the supracoracoideus nerve (see Figs. 9, 10 in Mourer-Chauviré 2003).

Gypsornis cuvieri Milne-Edwards, 1869 from the late Eocene of the Paris Gypsum was classified into the Rallidae by earlier authors (e.g., Brodkorb 1967; Brunet 1970), but was referred to the Idiornithidae by Cracraft (1973a). The fossil material of this species consists only of an incomplete tarsometatarsus and associated pedal phalanges. *G. cuvieri* is distinguished from the Idiornithidae in the presence of a hypotarsal canal. Its affinities are best considered uncertain until more material is found, but the species is probably a representative of the Gruoidea and may belong to the roughly coeval and similarly sized Parvigruidae (Sect. 9.3.1).

13.3 †Bathornithidae

All Paleogene North American Cariamae are classified in the Bathornithidae, which, following the revision of the North American biostratigraphy (Prothero 1994), occur in middle (?) Eocene to late Oligocene deposits. The first specimens of this group were described by Wetmore (1927) from the late Eocene of Colorado. After initial classification into the charadriiform Burhinidae, Wetmore (1933b) assumed that they are most closely related to the Cariamidae. The taxonomy and phylogenetic affinities of bathornithids were revised by Cracraft (1968, 1971b, 1973a) and Olson (1985). According to the former author, the taxon includes the following nine Paleogene species: *Eutreptornis uintae* Cracraft, 1971 from the middle Eocene (Uinta Formation) of Utah (distal tibiotarsus and proximal tarsometatarsus), *Bathornis cursor* Wetmore, 1933 from the late Eocene (Chadronian) of Wyoming (distal tarsometatarsus), *B. veredus* Wetmore, 1927 from the late Eocene/early Oligocene (Chadronian and Orellan) of South Dakota, Colorado, and Nebraska (distal tibiotarsi, tarsometatarsi, distal humeri), "*B.*" *celeripes* Wetmore, 1933 from the late Eocene/early Oligocene (Chadronian and Orellan) of Wyoming, Nebraska, and South Dakota (tarsometatarsi, tibiotarsi, distal humerus, carpometacarpi), "*B.*" *geographicus* Wetmore, 1942 from the early Oligocene (Brule Formation) of South Dakota (tarsometatarsus and tibiotarsus), *B. fricki* Cracraft, 1968 from the late Oligocene (Arikareean) of Wyoming (tibiotarsus), *Paracrax antiqua* (Marsh, 1871) from the early Oligocene (Orellan) of Colorado (distal humerus and proximal carpometacarpus), as well as *P. gigantea* Cracraft, 1968 (distal humerus and incomplete carpometacarpus) and *P. wetmorei* Cracraft, 1968 (postcranial bones of a single individual including ulna, humerus, coracoid, scapula, sternum, and pelvis) from the early Oligocene (Whitneyan) of South Dakota.

Olson (1985) further identified "*Neocathartes*" *grallator* (Wetmore 1944) from the late Eocene of Wyoming and "*Palaeocrex*" *fax* (Wetmore 1927) from the late Eocene (Chadronian) of Colorado as representatives of the Bathornithidae. He assumed that both species belong to the taxon *Bathornis*, and that *Bathornis fax* is possibly conspecific with *B. veredus*.

B. veredus was about one third larger than the extant *C. cristata* (Wetmore 1927). The humerus of *P. wetmorei* is about 1.5 times larger than that of *C. cristata* but is much stouter. The humerus of the largest species, *P. gigantea*, may have been twice as long as that of *C. cristata*, but judging from the stoutness of this bone, the actual size of *P. gigantea* was probably much more than twice that of *C. cristata*.

Monophyly of bathornithids has not been established, and even a diagnosis covering all currently recognized taxa does not exist. *E. uintae*, for example, differs from other bathornithids in the craniocaudally deeper and mediolaterally narrower distal end of the tibiotarsus. Its classification in the Bathornithidae was questioned by Olson (1985), who further detailed that the species assigned to *Bathornis* differ considerably in hypotarsus morphology. Whereas the hypotarsus of *B. veredus* is simple and block-like as in *Idiornis* and extant Cariamidae, that of "*Bathornis*" *celeripes* and "*B.*" *geographicus* is more complex and exhibits grooves and canals for the digital flexor tendons. As hypotarsus morphology usually shows little variation within closely related birds, the latter species are thus unlikely to be within the taxon *Bathornis* (Olson 1985).

Although Wetmore (1958) described a humerus of "*B.*" *celeripes* and Cracraft (1968) mentioned humeri of *B. veredus*, the published material of most species of *Bathornis* and the unnamed "*Bathornis*"-like taxon consists of hindlimb elements. Unfortunately, just the legs are unknown from *Paracrax*, which greatly aggravates meaningful comparisons between this taxon and the *Bathornis*-like birds. The holotype specimen of *Paracrax wetmorei* is coeval with "*B.*" *geographicus* and has been found in the same geographic area, and there is thus a possibility that both are conspecific. Likewise, the humerus and carpometacarpus of the smaller *P. antiqua* may well belong to one of the early Oligocene bathornithid species, which are known from leg elements only. At least judging from the published illustrations, I cannot discern any significant differences between the similarly sized humeri of *P. antiqua* (see Fig. 13 in Cracraft 1968) and "*B.*" *celeripes* (see plate 4 in Wetmore 1958).

The species of *Bathornis* had elongate hindlimbs, but detailed information on other parts of the skeleton is only available for *P. wetmorei* and *Bathornis* ("*Neocathartes*") *grallator*, which have not yet been compared with each other. *P. wetmorei* resembles idiornithids in the morphology of the wing bones. The sternum of this species exhibits a very bizarre morphology in that the sternal keel is greatly reduced in its midsection, similar to the condition found in the extant Opisthocomiformes. Unfortunately, sterna of idiornithids and other bathornithids were not yet found.

B. grallator was first described as a flightless species of the Cathartidae (New World vultures) by Wetmore (1944) and is represented by a partial skeleton including the skull. Although portions of the latter are damaged, it was considered to be very similar to that of New World vultures by Wetmore (1944). As in the Cathartidae but unlike in the Phorusrhacidae and extant Cariamidae, the prefrontal and frontal bones are fused and the former do not bear supraorbital processes. Owing to the little overlap of the preserved skeletal elements, only a few comparisons are possible between *B. grallator* and the species of *Paracrax*. However, from the illustrations in Wetmore (1944) it is evident that the humerus of *B. grallator* is more elongated than that of *P. wetmorei*, the scapula is much more curved and proportionally shorter, and the omal extremity of the coracoid is much smaller.

Concerning *B. veredus*, Wetmore (1933c, p. 214) noted that "on examination of the two specimens of *veredus* now available it appears to be definitely established that the first toe was missing," whereas *B. grallator* exhibits a well-developed hallux (Wetmore 1944). These differences were not mentioned by Olson (1985) and certainly more research is needed before the taxonomy and phylogenetic affinities of the various species currently classified in the Bathornithidae are fully understood.

13.4 †Ameghinornithidae

The Ameghinornithidae include presumably flightless, or nearly so, birds with a convoluted taxonomic history. The taxon was first established for a species from an unknown horizon of the Quercy fissure fillings. This was classified as "*Ameghinornis minor*" by Mourer-Chauviré (1981), who assigned to it a humerus, two coracoids, and two carpometacarpi. The holotypic humerus of "*A. minor*" was originally described as "*Strigogyps minor*" by Gaillard (1939), who before (Gaillard 1908) named another species of *Strigogyps*, *S. dubius*, which was based on a distal tibiotarsus. Gaillard (1908, 1939) compared these birds with extant Strigiformes and Accipitridae, but Mourer-Chauviré (1981) recognized the great similarity between the humerus of the Quercy species and that of the Phorusrhacidae. She considered "*A. minor*" to be an Old World representative of the Phorusrhacidae and the phylogenetic affinities of *S. dubius* to be uncertain.

A few years later, Peters (1987b) described another putative phorusrhacid bird from the middle Eocene of Messel. This species was named "*Aenigmavis sapea*" and is known from a postcranial skeleton and fragmentary remains of additional individuals (Fig. 13.4; Mayr 2005h). It was about the size of a male domestic chicken (*Gallus gallus*). The humerus of "*A. sapea*" closely resembles that of *S.* ("*Ameghinornis*") *minor* and the distal tibiotarsus exhibits the characteristic morphology of *S. dubius*, which lacks an ossified supratendinal bridge. The articulated Messel skeletons thus allow a revision of the taxonomic affinities of the Quercy specimens mentioned above. As detailed by Mayr (2005h), "*A. sapea*" is a representative of *Strigogyps*, and *S.* ("*Ameghinornis*") *minor* is most likely a junior

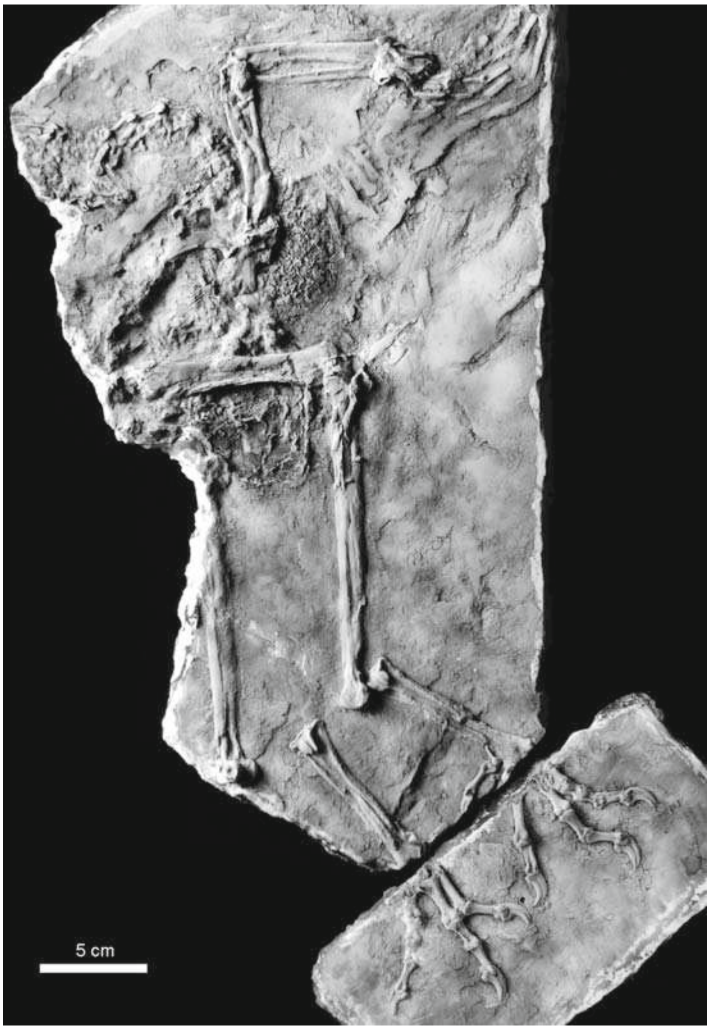

Fig. 13.4 Skeleton of *Strigogyps sapea* Peters, 1987 (Ameghinornithidae) from the middle Eocene of Messel (holotype, Forschungsinstitut Senckenberg, Frankfurt am Main, Germany, SMF-ME 1818). Specimen coated with ammonium chloride. (Photo by Sven Tränkner)

synonym of *S. dubius*. Peters (2007) accepted classification of *Strigogyps*, "*Ameghinornis*," and "*Aenigmavis*" into the Ameghinornithidae, but preferred their taxonomic separation, because the Quercy taxa are based on noncomparable skeletal elements. I do not concur with this conclusion (Mayr 2007f), and maintain allocation of the Quercy remains to a single species, *S. dubius*, to which these were also assigned by Mourer-Chauviré (2006).

A further representative of *Strigogyps* with an equally confusing taxonomic history occurs in the middle Eocene of the Geisel Valley, in a slightly younger stratigraphic level than Messel (Mayr 2002a). This species is somewhat larger than *S. sapea*, but morphologically is very similar (Mayr 2007f). The only known specimen consists of two partial skeletons on separate slabs, which were studied by Lambrecht (1935). The slab with the wing and shoulder girdle elements was described as "*Geiseloceros robustus*" and compared with the Bucerotidae (hornbills) by Lambrecht (1935). The slab containing the pelvis and hindlimb elements, which was found 2 m away from that of the wing bones, formed the holotype of the putative New World vulture "*Eocathartes robustus*." Peter Houde (in Olson 1985) first assumed that "*E. robustus*" and "*G. robustus*" represent a single species, and Olson (1985) noted that probably neither was correctly identified. The morphology of these fossils perfectly matches the characteristic osteological features of *Strigogyps sapea*, and the species is now classified as *Strigogyps robustus* (Mayr 2007f).

In summary, the Ameghinornithidae thus include three species, *S. dubius* (Quercy), *S. sapea* (Messel), and *S. robustus* (Geisel Valley). As yet undescribed remains of a species of *Strigogyps* were also found in the middle Eocene maar deposits of Eckfeld near Manscheid in Germany (own observation).

The skull of *Strigogyps* is very poorly known, as only small fragments are preserved in the holotype of *S. sapea*. The wing skeleton is highly characteristic in that the ulna is much shorter than the humerus, whereas the hand skeleton is fairly long. The humerus has a very small proximal end, which together with the short ulna indicates flightlessness, or at least very weak flight capabilities. The wing is, however, not as greatly reduced as in phorusrhacids. The pelvis is further not as narrow as is in phorusrhacid birds and the hallux not as strongly reduced. In the holotype of *S. sapea* stomach content is preserved, and consists of plant matter.

The robust coracoid and elongate carpometacarpus of *S. sapea* and *S. robustus* distinctly differ in their morphology from the corresponding bones, which were assigned to *S. dubius* ("*A. minor*") by Mourer-Chauviré (1981). These bones possibly belong to a flightless taxon of the Idiornithidae, such as the large *Propelargus*.

Strigogyps can be shown to be outside a clade including the Idiornithidae, Phorusrhacidae, and Cariamidae, because the hypotarsus does not exhibit the presumably derived morphology found in the latter taxa, in which it is block-like and without any distinct sulci and crests (in *Strigogyps* there are two well-developed crests). Phorusrhacid affinities of *Strigogyps* (i.e., "*Ameghinornis*" and "*Aenigmavis*") were also doubted by Alvarenga and Höfling (2003), but its true phylogenetic relationships have not yet been positively established.

13.5 †Salmilidae

The middle Eocene Salmilidae comprise a single species, *Salmila robusta* Mayr, 2000, whose description is based on three skeletons from Messel, two of which are exceptionally well preserved (Fig. 13.5; Mayr 2000e, 2002e). In the collection of Forschungsinstitut Senckenberg there is also an as yet undescribed skeleton of a juvenile bird, which may belong to this species (see Fig. 4 in Peters 1989).

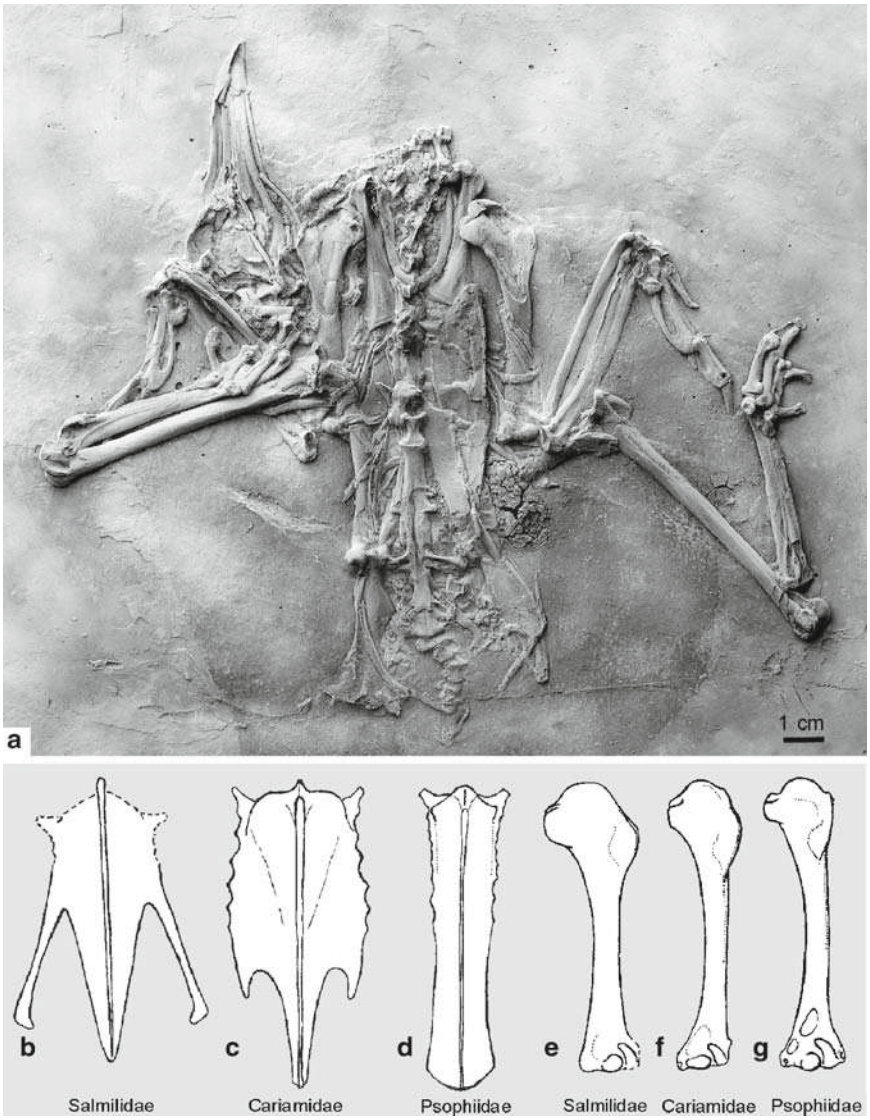

Fig. 13.5 **a** Skeleton of *Salmila robusta* Mayr, 2000 (Salmilidae) from the middle Eocene of Messel (Hessisches Landesmuseum Darmstadt, Germany, HLMD-Be 161); **b**–**d** comparison of sterna; **e**–**g** Comparison of humeri. **b**, **e** *S. robusta*; **c**, **f** Red-legged Seriema, *Cariama cristata* (Cariamidae); **d**, **g** Gray-winged Trumpeter, *Psophia crepitans* (Psophiidae). Fossil specimen coated with ammonium chloride. **b**–**g** Not to scale. (Photos by Sven Tränkner)

S. robusta reached about two thirds of the size of the extant Gray-winged Trumpeter (*Psophia crepitans*; Psophiidae), but had much shorter legs. Its phylogenetic affinities have not yet been convincingly established, and the species shares derived characters mainly with the Cariamae and the Psophiidae, whose limb bones are fairly similar. As in these extant taxa the carpometacarpus is short and with a bowed minor metacarpal, whose proximal end bears a small tubercle on the ventral margin. In contrast to the beak of extant Psophiidae and all Cariamae whose skull is known, however, the beak appears to have been schizorhinal. Unlike extant Cariamidae, the Phorusrhacidae, and *Elaphrocnemus*, it further lacks well-developed supraobital processes. The limb bones have a robust appearance, and apart from the more rounded deltopectoral crest, the proportions of the humerus are similar to those of *Elaphrocnemus*. The caudal margin of the sternum exhibits a single pair of very deep incisions and the bone is thus unlike the narrow sternum of the Gruoidea (Fig. 13.5). The distal tibiotarsus probably lacks an ossified supratendinal bridge (this is not clearly visible in the fossils), which, if confirmed by future specimens, may indicate affinities to the Ameghinornithidae (Sect. 13.4). The tarsometatarsus is rather short and indicates that in contrast to most Cariamae *S. robusta* was not a cursorial species. Also unlike most Cariamae, the hypotarsus is not block-like but exhibits a distinct sulcus, which separates two hypotarsal crests. As in the Gruoidea but unlike in extant Cariamidae the proximal phalanx of the fourth toe bears a large medially protruding projection. Two specimens with well-preserved feather remains allow the recognition of a long tail, similar to that of extant Cariamidae, whereas the tail of the Psophiidae is very short.

The postcranial osteological features of *S. robusta* correspond best with those of *Elaphrocnemus*, and a phylogenetic analysis resulted in a sister group relationship between *S. robusta* and a clade including *Elaphrocnemus*, *Idiornis*, Phorusrhacidae, and Cariamidae (Mayr 2002e). However, this analysis included a restricted character and taxon sampling and supported nonmonophyly of the Gruoidea, which can no longer be upheld (Chap. 3).

13.6 †*Gradiornis*

Another problematic taxon is *Gradiornis walbeckensis* Mayr, 2007, a species from the late Paleocene of Walbeck in Germany, which is represented by few bones only (humeri, coracoids, and tarsometatarsi; Mayr 2007a). The referred humeri resemble those of the Ameghinornithidae, and the distal ends of the tarsometatarsi are also similar to those of the Cariamae. The peculiar and characteristic morphology of holotypic coracoid, however, is not matched by that of any other avian taxon. The bone has a very straight shaft, lacks a foramen for the supracoracoideus nerve, and, in contrast to the bone in the Cariamae, exhibits a deeply excavated scapular articulation facet. *Gradiornis* further lacks the derived, block-like hypotarsus of the Cariamae, and its phylogenetic affinities are unresolved. A tentatively referred notarium consists of two fused thoracic vertebrae; if it indeed belongs to *Gradiornis* it would constitute another feature in which the taxon differs from the Cariamae. The elongate and robust tarsometatarsus indicates that *G. walbeckensis* was a terrestrial bird, and the humerus morphology suggests weak flight capabilities.

Chapter 14
“Falconiformes” (Diurnal Birds of Prey)

The traditional “Falconiformes” are probably not monophyletic, and whereas the Cathartidae, Sagittariidae, Pandionidae, and Accipitridae may form a clade, the affinities of the Falconidae are still unresolved (Chap. 3). A number of “falconiform” birds were discovered in late Eocene and Oligocene deposits, but unambiguous early Paleogene representatives have not yet been reported. This may be due to the fact either that these evolved in areas which yielded few fossils from this period, such as South America, Africa, and Australia, or that they displayed a plesiomorphic morphology which impedes correct identification.

14.1 Falconidae (Falcons)

The phylogenetic interrelationships of the modern species indicate that the Falconidae, which today have a worldwide distribution, originated in South America (Griffiths 1999). For this reason and because some molecular analyses provide support for a clade including the Cariamidae, Falconidae, Psittaciformes, and Passeriformes (Ericson et al. 2006; Hackett et al. 2008), it is tempting to speculate about possible affinities to the raptorial Phorusrhacidae, which are stem group representatives of the Cariamidae (Sect. 13.1; see also p. 108 in Olson 1985).

Unfortunately, the Paleogene fossil record of falcons is very poor, and includes no unambiguously identified specimens. Harrison (1982c) described a tiny distal tarsometatarsus with a few associated pedal phalanges from the London Clay of Walton-on-the-Naze as *Parvulivenator watteli*, and tentatively assigned the species to the Falconidae. The distal width of the tarsometatarsus is only about 3 mm, and its morphology does not suggest a closer relationship to falcons or any other diurnal bird of prey. I hypothesized that it may represent a coliiform bird (Mayr 2005a), but now rather think that its affinities are indeterminable without more material. A photo of the holotype is reproduced here for the first time (Fig. 14.1). As noted previously (Mayr 2005a), there is a second distal tarsometatarsus of this species,

G. Mayr, *Paleogene Fossil Birds*, DOI: 10.1007/978-3-540-89628-9_14,

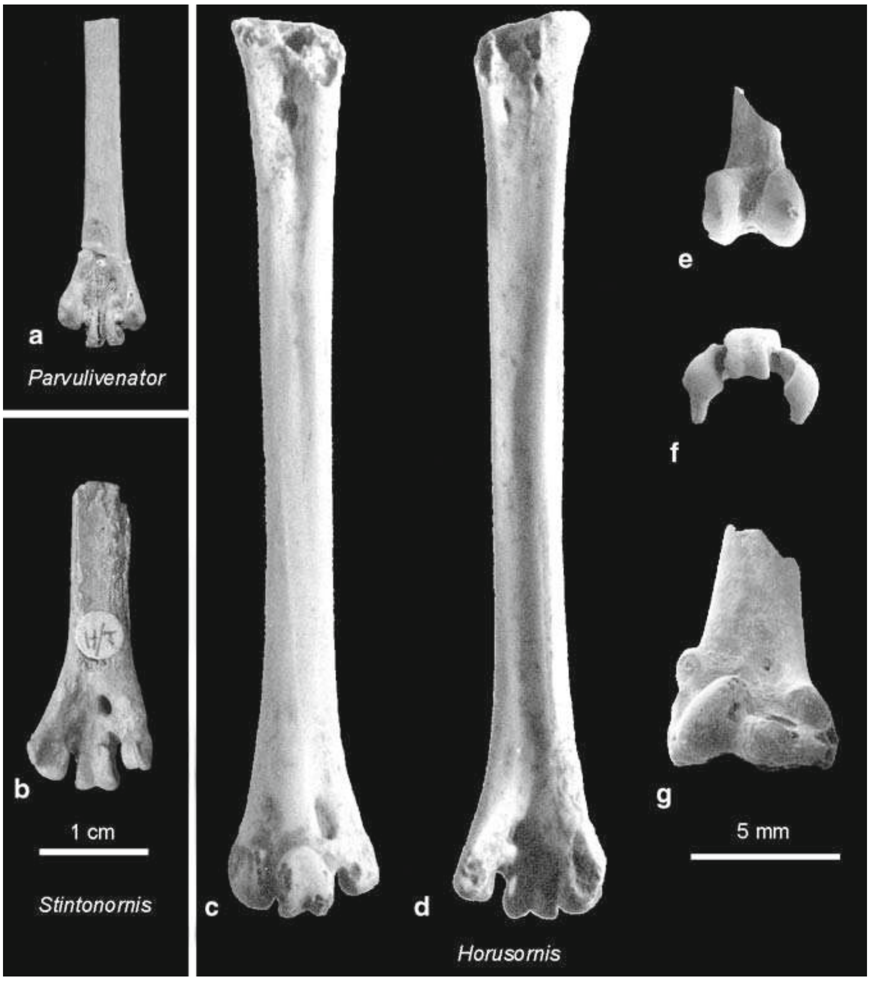

Fig. 14.1 **a** Right tarsometatarsus of *Parvulivenator watteli* Harrison, 1982 from the early Eocene London Clay of Walton-on-the-Naze (holotype, Natural History Museum, London, UK, BMNH A 5172); **b** right tarsometatarsus of *Stintonornis mitchelli* Harrison, 1984 from the London Clay of the Isle of Sheppey (holotype, BMNH A 5284); **c**–**g** selected skeletal elements of *Horusornis vianeyliaudae* Mourer-Chauviré, 1991 (Horusornithidae) from the late Eocene locality La Bouffie of the Quercy fissure fillings in France. **c**, **d** Left tarsometatarsus (holotype, Université des Sciences et Techniques du Languedoc, Montpellier, France, BFI 1974); **e** distal left tibiotarsus (BFI 1962); **f** distal left tarsometatarsus (BFI 1978); **g** distal right humerus (craniodistal view, BFI 1960). Same *scale bar* for all images except **b**. (Photos of *Horusornis* courtesy of Cécile Mourer-Chauviré, others by Sven Tränkner)

also from the London Clay, in the collection of the Natural History Museum. Another putative falconid from the London Clay of the Isle of Sheppey, *Stintonornis mitchelli* Harrison, 1984, is also based on the distal end of a tarsometatarsus

(Fig. 14.1). This specimen is more similar to extant Falconidae, but is also too fragmentary for a reliable identification. Mourer-Chauviré (2006) mentioned the presence of still undescribed Falconidae in the late Eocene and early Oligocene of the Quercy fissure fillings.

A distal tarsometatarsus from the middle Eocene of the La Meseta Formation of Seymour Island (Antarctica) was assigned to the Falconidae by Tambussi et al. (1995) and Tambussi and Acosta Hospitaleche (2007). This fossil comes from a species that was the size of the extant Crested Caracara (*Caracara plancus*), to which it was also considered morphologically similar. At least judging from the published figure (Tambussi and Acosta Hospitaleche 2007), however, the trochlea for the second toe does not reach as far distally as in extant Falconidae, and additional skeletal elements are needed to confirm identification of the specimen.

14.2 †*Masillaraptor*

Masillaraptor parvunguis Mayr, 2006 is known from two largely complete but poorly preserved skeletons from Messel (Fig. 14.2; Mayr 2006e). This species was considered to be possibly related to the falconid Polyborinae by Peters (1988a, Fig. 2; see also Peters 1991). Its long beak has an equal depth over most of its length and a straight culmen, which curves just before the tip. The legs are likewise quite long and the ungual pedal phalanges rather weak. As in the Falconidae, Sagittariidae, Pandionidae, and Accipitridae the two central phalanges of the fourth toe are abbreviated. In further concordance with the Pandionidae, Accipitridae, and Falconidae, the first phalanx of the second toe is shortened. Nevertheless, the phylogenetic affinities of *M. parvunguis* are difficult to establish because of the poor preservation of the fossil specimens and the unresolved relationships of extant raptorial birds. Its tentative assignment to the "Falconiformes" was based on the presence of a raptor-like beak and abbreviated pedal phalanges.

Mayr (2006e) assumed that *M. parvunguis* is closely related to *Coturnipes cooperi* Harrison and Walker, 1977 from the London Clay. The original description of this species was based on a distal tarsometatarsus, but Olson (1999a) reported fragmentary remains of similar birds from the early Eocene Nanjemoy Formation of Virginia, and mentioned a specimen of *C. cooperi* from the London Clay of Walton-on-the-Naze in the collection of Michael Daniels. I have also examined this latter specimen, and as already noted by Olson (1999a) the wing bones are reminiscent of those of the Falconidae, whereas the leg bones exhibit a quite generalized morphology unlike that of diurnal birds of prey. A tarsometatarsus from the Geisel Valley was tentatively assigned to *C. cooperi* by Mayr (2002a).

Fig. 14.2 Skeleton of *Masillaraptor parvunguis* Mayr, 2006 from the middle Eocene of Messel (Forschungsinstitut Senckenberg, Frankfurt am Main, Germany, SMF-ME 11042). Coated with ammonium chloride. (Photo by Sven Tränkner)

14.3 †Teratornithidae and Cathartidae (New Word Vultures)

The Teratornithidae are a group of New World birds of prey, which includes the largest known flying bird, *Argentavis magnificens* Campbell and Tonni, 1980 from the late Miocene of Argentina, whose wingspan has been estimated at 6–8 m (Campbell and Tonni 1983). Teratorns closely resemble the Cathartidae in many osteological features, and some bones were initially indeed mistaken for those of New World vultures (Miller 1910). Although most earlier authors (e.g., Brodkorb 1964) assumed a close relationship between teratorns and New World vultures, others (e.g., Campbell and Tonni 1980) emphasized the differences between these taxa and considered teratorns to be more closely related to "pelecaniform" birds. A sister group relationship between the Cathartidae and Teratornithidae is, however, well supported by derived skull features, most notably the fusion of the prefrontal, ectethmoid, and frontal bones (Miller 1909).

The only Paleogene fossil record of the Teratornithidae comes from the late Oligocene/early Miocene of the Taubaté Basin in Brazil and was described as *Taubatornis campbelli* by Olson and Alvarenga (2002). The species is only known from the distal end of a tibiotarsus and the proximal end of an ulna, and is the smallest representative of the Teratornithidae. As noted by Olson and Alvarenga (2002), *T. campbelli* supports the hypothesis that the Teratornithidae are of South American origin and did not reach North America until the late Neogene (Campbell and Tonni 1981).

A South American origin of the Teratornithidae suggests that the stem species of the Cathartidae also lived on this continent. However, two putative stem group representatives of this taxon, *Diatropornis ellioti* (Milne-Edwards, 1892) and *Parasarcoramphus milneedwardsi* Mourer-Chauviré, 2002, were reported from the Quercy fissure fillings (Cracraft and Rich 1972; Mourer-Chauviré 2002). Whereas several carpometacarpi and tarsometatarsi of *D. ellioti* were identified in middle and late Eocene (MP 16–17) deposits, *P. milneedwardsi* is only known from a single tarsometatarsus of unknown age (Mourer-Chauviré 1988a, 2002). The tarsometatarsus of *D. ellioti* closely resembles that of extant Cathartidae, but that of *Parasarcoramphus* has a more dorsally projecting trochlea for the fourth toe, which is more widely separated from the trochlea for the third toe, and bears a more markedly plantarly directed wing-like flange. A caveat that has to be placed on the classification of these birds is that comparisons were so far restricted to the Cathartidae. As the tarsometatarsus and carpometacarpus of teratorns closely resemble the corresponding elements of New World vultures, there remains a possibility that *Diatropornis* and *Parasarcoramphus* are actually stem group representatives of the clade (Teratornithidae + Cathartidae).

A putative New World vulture from the Paleogene of North America, *Phasmagyps patritus* Wetmore, 1927, is based on a distal tibiotarsus from the late Eocene (Chadronian) of Colorado. Another Paleogene New World record of the Cathartidae is *Brasilogyps faustoi* Alvarenga, 1985 from the late Oligocene/early Miocene of the Taubaté Basin in Brazil (Alvarenga 1985b). The fossil material assigned to this species consists of a distal tibiotarsus and an associated proximal tarsometatarsus. Olson (1985) further mentioned undescribed Cathartidae from the early Oligocene of Mongolia.

14.4 †Horusornithidae

The Horusornithidae (Fig. 14.1) occur in the late Eocene (MP 17) locality La Bouffie of the Quercy fissure fillings, and their fossil record includes most of the major limb elements (Mourer-Chauviré 1991). As yet undescribed remains also exist from the "early Oligocene" of the USA (Mourer-Chauviré 1991). The single named species of the taxon, *Horusornis vianeyliaudae* Mourer-Chauviré, 1991, was about the size of the Redfooted Kestrel, *Falco verspertinus*. Although the humerus, too, differs from that of extant "Falconiformes," the greatest peculiarities are found in the foot morphology of *H. vianeyliaudae*. The species is distinguished from other "falconiform" birds in the absence of an ossified supratendinal bridge on the distal tibiotarsus, whose condyles also exhibit a distinctive morphology in being proximodistally taller and less widely separated than in extant Accipitridae. The tarsometatarsus is elongated and the tip of the trochlea for the second toe more plantarly directed that in most extant Accipitridae. According to Mourer-Chauviré (1991) the morphology of the distal tibiotarsus indicates the presence of a hyperflexible intertarsal joint.

Among other features (Mourer-Chauviré 1991), horusornithids share with extant Pandionidae, Accipitridae, and Falconidae a derived morphology of the hypotarsus, which exhibits two marked crests that are separated by a wide sulcus, as well as a derived morphology of the coracoid and ungual phalanges. Their exact relationships to other "falconiform" birds are, however, unresolved.

14.5 Sagittariidae (Secretary Birds), Pandionidae (Ospreys), and Accipitridae (Hawks and Allies)

As detailed in Chap. 3 and in contrast to studies based on morphological data (Mayr et al. 2003; Mayr and Clarke 2003; Livezey and Zusi 2007), molecular analyses do not corroborate the traditional clade including the Falconidae, Pandionidae, and Accipitridae, but support a sister group relationship between the Sagittariidae and the clade (Pandionidae + Accipitridae).

14.5.1 Sagittariidae

The single extant species of this taxon is the long-legged Secretary Bird, *Sagittarius serpentarius*, which occurs in sub-Saharan Africa and predominantly feeds on snakes. *Pelargopappus schlosseri* (Gaillard, 1908), a stem group representative from the early and late Oligocene of the Quercy fissure fillings, is smaller than *S. serpentarius*, and is based on hindlimb elements and a referred ulna. It has greatly elongated legs and also otherwise resembles extant Sagittariidae in the morphology of the known bones. However, the tarsometatarsus has a more strongly developed trochlea for the second toe and a more pronounced medial hypotarsal crest, which by outgroup comparisons with the Pandionidae and Accipitridae probably represents the plesiomorphic condition for the Sagittariidae (Mayr 2005a).

14.5.2 Accipitridae and Pandionidae

The fossil record indicates that the divergence between the accipitrid and pandionid lineages took place before the Oligocene. Extant ospreys have a nearly global distribution, but all Paleogene fossils stem from Old World sites. The earliest specimen is an ungual phalanx from the late Eocene of England (Harrison and Walker 1976a). Although isolated ungual phalanges of birds can seldom be reliably identified, those of ospreys exhibit a characteristic derived morphology, which is related to their specialized mode of foraging, i.e., feet-first plunges into water bodies from considerable heights (Mayr 2006f). Harrison and Walker (1976a) referred the above-mentioned fossil to *Palaeocircus*, following Brunet's (1970) identification of *Palaeocircus cuvieri* Milne-Edwards, 1871 from the late Eocene Paris Gypsum as an osprey. However, *P. cuvieri* is only known from a carpometacarpus and there are thus no skeletal elements in common with the British specimen. Correct identification of *P. cuvieri* as an osprey was further doubted by Olson (1985). An ungual phalanx of an osprey was described by Mayr (2006f) from the early Oligocene (Rupelian) of Germany. Rasmussen et al. (1987) reported a distal humerus and a tentatively referred incomplete carpometacarpus of a stem group representative of the Pandionidae from the early Oligocene of the Jebel Qatrani Formation in Egypt.

The fossil record of the Accipitridae also dates back to the late Eocene/early Oligocene. The oldest representative may be *Milvoides kempi* Harrison and Walker, 1979 from the late Eocene of England, a species known from an incomplete distal tarsometatarsus, which resembles the corresponding bone of extant accipitrids (Harrison and Walker 1979b). Mayr and Smith (2002a) tentatively assigned a distal tarsometatarsus from the early Oligocene of Belgium to the Accipitridae. Two accipitrid species were further described from unknown localities and horizons of the Quercy fissure fillings: "*Aquila*" ("*Aquilavus*") *hypogaea* Milne-Edwards, 1892 is based on a femur, whereas the holotype of "*A.*" *corroyi* Gaillard, 1939 is a tarsometatarsus, which resembles the corresponding bone of extant kites (*Milvus* spp.) in its proportions. Because of the lack of overlap of skeletal elements, the affinities between these species cannot be established, and their classification in the same genus-level taxon (either "*Aquila*" as in the original descriptions or "*Aquilavus*" as per Brodkorb 1964) is conjectural. As first recognized by Mourer-Chauviré (see p. 110 in Olson 1985), the alleged cuculiform *Dynamopterus boulei* Gaillard, 1939 is a species of the Accipitridae, and may well be a junior synonym of *A. corroyi*, with which it corresponds in size. *Palaeohierax gervaisii* (Milne-Edwards, 1863) from the late Oligocene of France is also based on a tarsometatarsus and was nearly twice as large as the kite-sized *A. corroyi*.

From the "middle" Oligocene of Mongolia, Kurochkin (1968b) described three species of putative Accipitridae as *Buteo circoides* Kurochkin, 1968 (distal ulna), *Venerator* ("*Tutor*") *dementjevi* (Kurochkin, 1968) (distal humerus), and *Gobihierax edax* Kurochkin, 1968 (fragmentary distal humerus). The former two species were assigned to the Buteoninae, the latter species to the Accipitrinae. Because of their fragmentary representation, identification of all of them needs to be verified with additional material. From the early Oligocene of Mongolia, Kurochkin (1976, p. 78) further mentioned "several rather large femora resembling the recent Aegypiinae … in a number of important characteristics." Kurochkin (1976) also noted the presence of an accipitrid ("*Aquilavus*") in the late Oligocene (*Indricotherium* Beds) of Kazakhstan.

A distal tarsometatarsus of a large accipitrid from the late Eocene of the Jebel Qatrani Formation (Fayum) in Egypt resembles that of modern eagles of the taxon *Haliaeetus* (Rasmussen et al. 1987).

Several species of the Accipitridae were described from the Oligocene of North America. "*Buteo*" *grangeri* Wetmore and Case, 1934 and "*B.*" *fluviaticus* Miller and Sibley, 1942 occur in the White River Formation of Colorado. The latter is based on a distal tarsometatarsus, whereas of the former only the skull is known; Miller and Sibley (1942) noted that these specimens may be from the same species. "*B.*" *antecursor* Wetmore, 1933 from the early Oligocene Brule Formation of Wyoming is represented by a tarsometatarsus. Assignment of all of these species to the extant taxon *Buteo* is based on overall similarity, which may well be plesiomorphic for the Accipitridae.

Also from the early Oligocene (Poleslide Member of the Brule Formation) of Wyoming comes *Palaeoplancus sternbergi* Wetmore, 1933, the holotype of which consists of a partial skeleton including the skull. This roughly Osprey sized species is very close in its osteological features to modern Accipitridae, and judging from the published illustrations its tarsometatarsus resembles that of the similarly sized *P. gervaisii*. *P. sternbergi* was classified in the monotypic taxon Palaeoplancinae by Wetmore (1933d). The species agrees with the Sagittariidae and Pandionidae but differs from all extant Accipitridae in the long and slender acromial process of the furcula, a presumably plesiomorphic feature which suggests a position outside crown group Accipitridae.

On the basis of distal tarsometatarsi, three accipitrid species were described from the late Oligocene (early Arikareean) of Nebraska, i.e., "*Geranoaetus*" *ales* Wetmore, 1926, *Palaeastur atavus* Wetmore, 1943, and *Promilio efferus* (Wetmore, 1923) (see Brodkorb 1964).

Agnolin (2006b) and earlier authors (e.g., Brodkorb 1964) assigned *Climacarthrus incompletus* Ameghino, 1899 from the late Oligocene (Deseadan) of the Santa Cruz Province in Argentina to the Accipitridae. The species is based on a very fragmentary and badly preserved distal tarsometatarsus, and its definite identification has to await the discovery of more complete specimens. The same is true for *Cruschedula revola* Ameghino, 1899, also from the Deseadan of Argentina, whose holotype is the cranial extremity of a scapula. *C. revola* was classified into the Cladornithidae (Sect. 16.11) by Ameghino (1899), but was assigned to the Accipitridae by Brodkorb (1964), Tonni (1980), and Agnolin (2006b). I do not consider it possible to reliably establish the phylogenetic affinities of this fragmentary bone.

Pengana robertbolesi Boles, 1993 from the late Oligocene/early Miocene of Riversleigh in Australia is represented by a distal tibiotarsus. The specimen exhibits mediolaterally very narrow condyles, which permitted "a much greater degree of both anteriorposterior and mediolateral flexion than in other species of the Accipitridae" (Boles 1993, p. 19). Within extant Accipitridae a similar morphology is found in the South American *Geranospiza* and the African *Polyboroides*, which are, however, considerably smaller than *Pengana*. The two extant taxa are probably neither closely related to each other nor to the fossil taxon (Boles 1993), and use their feet to capture prey in hollows inaccessible to other predatory birds. Despite a presumed similar function of the intertarsal joint, the tibiotarsus of *Pengana* is very different from that of the Horusornithidae (Sect. 14.4) in, for example, the more accipitrid-like shape of the condyles and the presence of a supratendinal bridge.

Chapter 15
Strigiformes (Owls)

Crown group Strigiformes are divided into the Tytonidae (barn owls) and Strigidae (true owls). The latter have a worldwide distribution, whereas barn owls are absent from the northern parts of Asia and North America. All owls possess semizygodactyl feet and most extant species are crepuscular or nocturnal. The osteological features of owls are distinctive and allow an unambiguous identification of the major postcranial bones.

The fossil record of strigiform birds goes back into the Paleocene and is quite extensive in Eocene and Oligocene deposits of the Northern Hemisphere. Most notably, however, there is as yet no Paleogene fossil record of owls from the Southern Hemisphere. Although a great number of fossil strigiform taxa has been distinguished in European and North American fossil sites, their interrelationships are still poorly understood. The two known Paleocene taxa are trenchantly different, and whereas one (the North American *Ogygoptynx*) is quite similar to crown group Strigiformes, the other (the European *Berruornis*) is not. Apart from their proportionally shorter legs, late Eocene and Oligocene owls most closely resemble extant Tytonidae in overall morphology, but these similarities are likely to be plesiomorphic; there exists no unambiguous Paleogene fossil record of the Strigidae.

15.1 †*Berruornis* and †Sophiornithidae

The taxon *Berruornis* was established by Mourer-Chauviré (1994) for fossils from the late Paleocene of the Mont Berru area in France. The species from this locality, *Berruornis orbisantiqui* Mourer-Chauviré, 1994, is known from several tarsometatarsi and an incomplete distal tibiotarsus. A second species of *Berruornis*, *B. halbedeli* Mayr, 2007, occurs in the late Paleocene of Walbeck in Germany and is represented by a tarsometatarsus and a tentatively referred partial upper beak (Mayr 2002f, 2007a). According to Mourer-Chauviré (1994) a large phalanx of a strigiform-like bird, which was reported by Nessov (1992) from the late Paleocene of Kazakhstan, may also belong to *Berruornis*.

The species of *Berruornis* were very large, about the size of the extant Snowy Owl, *Nyctea scandiaca*. Their assignment to the Strigiformes can be established

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with the absence of a supratendinal bridge on the distal tibiotarsus, the morphology of the hypotarsus, which exhibits two widely separated crests, and the large tarsometatarsal trochlea for the second toe (Mourer-Chauviré 1994). The tarsometatarsus is very stout and the medial crest of the hypotarsus is pierced by a small foramen. The plantarly directing wing-like flange of the tarsometatarsal trochlea for the fourth toe is much less developed than in extant owls. If assignment of the Walbeck beak to *Berruornis* is correct, the taxon also had a more elongated and mediolaterally much narrower beak than crown group Strigiformes. The ventral surface of the rostral end of the premaxillary symphysis is further distinctive in that it bears two grooves along its sides, which among extant birds occur in the Falconidae and, albeit much less pronounced, in the Cathartidae.

Berruornis was assigned to the Sophiornithidae by Mourer-Chauviré (1994). This latter taxon was originally erected for *Sophiornis quercynus* Mourer-Chauviré, 1987, a likewise very large, *Bubo*-sized species, which is known from a tarsometatarsus, a distal humerus, and pedal phalanges from an unknown locality and horizon of the Quercy fissure fillings. Classification of *Berruornis* into the Sophiornithidae is, however, largely based on overall similarity, and as detailed by Mourer-Chauviré (1994), *Berruornis* and *Sophiornis* distinctly differ in several features. Most notably, and in contrast those in *Sophiornis*, the tarsometatarsal trochleae for the second and fourth toes are only weakly plantarly deflected in *Berruornis*, which may indicate a sister group relationship to all other strigiform birds. Compared with the tarsometatarsus of other owls from the Quercy fissure fillings, the tarsometatarsus of *Berruornis* more closely resembles that of *Palaeobyas*, which is equally stout, with only weakly deflected trochleae (Sect. 15.4).

15.2 †Protostrigidae

The Protostrigidae occur in the Eocene of North America and the early Oligocene of Europe, and comprise the taxa *Eostrix*, *Oligostrix*, and *Minerva*; as shown by Mourer-Chauviré (1983b), "*Protostrix*" is a junior synonym of the latter taxon.

Eostrix includes two small species from the early Eocene of Wyoming (Willwood Formation and Wind River Formation), *Eostrix mimica* (Wetmore, 1938) and *E. martinellii* Martin and Black, 1972, which are both based on hindlimb elements (distal tarsometatarsus and tibiotarsus for *E. mimica* and distal tarsometatarsus for *E. martinellii*; Wetmore 1938b; Martin and Black 1972). "*Eostrix*" *vincenti* Harrison, 1980 from the early Eocene of England is represented by a proximal tarsometatarsus and a pedal phalanx only (Harrison 1980). Mourer-Chauviré (1987, p. 122) noted that this species differs from the Protostrigidae and more closely resembles *Necrobyas* (Sect. 15.4).

According to Mourer-Chauviré (1983b), four species from the middle and late Eocene of North America can be recognized in the taxon *Minerva*: *Minerva antiqua* (Shufeldt, 1913), *M. leptosteus* (Marsh, 1871), and *M. saurodosis* (Wetmore, 1921) from the middle Eocene (Bridgerian) of Wyoming, as well as *M. californiensis*

(Howard, 1965) from the late Eocene of California. Whereas *M. antiqua* and *M. leptosteus* are based on hindlimb elements (Wetmore 1933e; Rich 1982; Mourer-Chauviré 1983b), the similarly sized *M. saurodosis* and *M. californiensis* are only known from humeri (Wetmore 1921; Howard 1965). It is thus well possible that *M. saurodosis* is a junior synonym of either *M. antiqua* or *M. leptosteus*, which have a similar temporal and geographic distribution.

In Europe, the Protostrigidae are represented by *Oligostrix rupelensis* Fischer, 1983, whose holotype is a distal tibiotarsus from the early Oligocene of Germany. *O. rupelensis* is the smallest species of the Protostrigidae, being about two thirds the size of the *Eostrix* species and only half of that of the large species of *Minerva* (Fischer 1983b).

Protostrigid owls are well characterized by a greatly widened medial condyle of the tibiotarsus and, possibly functionally correlated therewith, a strongly developed first and second toe (Mourer-Chauviré 1983b). The morphology of the ungual phalanx of the hallux of *Minerva* is peculiar in that the articular facet is markedly concave and the extensor process strongly proximally protruding (see Fig. 3 in Mourer-Chauviré 1983b). This morphology even led Wetmore (1933e) to erroneously assume that the ungual phalanges of *Minerva antiqua* are from an edentate mammal (see Mourer-Chauviré 1983b). The tarsometatarsal trochlea for the second toe of protostrigids is further proportionally shorter than in other strigiforms, which may constitute the plesiomorphic condition within Strigiformes. Another derived character shared by crown group Strigiformes but absent in the Protostrigidae is a medially situated tubercle for the tibialis anticus muscle on the proximal tarsometatarsus (see Fig. 2 in Mourer-Chauviré 1983b).

15.3 †Ogygoptyngidae

The single species classified into this taxon is *Ogygoptynx wetmorei* Rich and Bohaska, 1976, which is the earliest strigiform bird yet reported. *O. wetmorei* is represented by a tarsometatarsus from the late Paleocene (Tiffanian) of Colorado (Rich and Bohaska 1976, 1981). The bone is elongate and slender as in crown group Tytonidae, and more closely resembles the tarsometatarsus of extant owls than do the tarsometatarsi of *Berruornis* and the Protostrigidae. In particular, the enlarged trochlea for the second toe distally exceeds the trochlea for the third toe in length (contra Protostrigidae), and, in distal view, the trochleae are arranged on a markedly curved line (contra *Berruornis*). A presumably autapomorphic feature of *Ogygoptynx* concerns the shape of the proximal end of the tarsometatarsus, whose outline is, in proximal view, shaped like a parallelogram, not rectangular as in other Strigiformes. Despite being the earliest known strigiform, the far distally reaching trochlea for the second toe and the arrangement of the trochleae indicate that *O. wetmorei* is more closely related to crown group Strigiformes than are *Berruornis* and the Protostrigidae (Mourer-Chauviré 1987). However, although *Ogygoptynx* is likely to be outside crown group Strigiformes, the fossil material does not allow an unambiguous further assessment of its affinities.

Given that the age of *Ogygoptynx* has been correctly determined, this taxon significantly complicates our understanding of the early evolution of owls. Not only does the essentially modern appearance of its tarsometatarsus conflict with the presence of very different and apparently much more primitive owls in the Paleocene of Europe, but it also conflicts with the absence of similar "advanced" owls in later, i.e., Eocene, deposits of North America.

15.4 †Necrobyinae, †Palaeoglaucidae, and †Selenornithinae

These three taxa were named by Mourer-Chauviré (1987) for the inclusion of various modern-type Strigiformes from the Quercy fissure fillings, and were considered stem group representatives of the Tytonidae (see Fig. 8 in Mourer-Chauviré 1987). According to Mourer-Chauviré (1987, 2006), the Necrobyinae include the taxa *Necrobyas*, *Nocturnavis*, *Palaeobyas*, and *Palaeotyto*. All major limb bones of *Necrobyas* were described by Mourer-Chauviré (1987), and the following species were recognized in the taxon by Mourer-Chauviré (2006): *N. rossignoli* Milne-Edwards, 1892 (late Eocene), *N. harpax* Milne-Edwards, 1892 (early Oligocene), *N. edwardsi* Gaillard, 1939 (late Oligocene), and *N. medius* Mourer-Chauviré, 1987 (from deposits of unknown age). Mourer-Chauviré (2006) further listed *N. minimus* Mourer-Chauviré, 1987 (early Oligocene) in the Quercy avifauna, but this species was synonymized with *Prosybris antiqua* (Milne-Edwards, 1863) by Mlíkovský (1998a), an action with which Mourer-Chauviré (1999a) agreed. *P. antiqua* is otherwise known from the early Miocene of France, and a tentative record also comes from the early Oligocene of Belgium (Mayr and Smith 2002a).

The species of *Necrobyas* agree with the Tytonidae and differ from the Strigidae in that the coracoid has a wide procoracoid process and an acrocoracoid process without pneumatic foramina, the proximal end of the humerus bears a marked transverse groove, and the proximal end of the tarsometatarsus lacks an ossified supratendinal bridge (arcus extensorius) (Mourer-Chauviré 1987). All of these features are, however, likely to be plesiomorphic for the Strigiformes, and in contrast to the tarsometatarsus of crown group Tytonidae, that of *Necrobyas* is rather short and stout. *N. edwardsi* is about the size of a Southern Boobook (*Ninox boobook*); the other species are slightly smaller.

Two large owls from unknown localities of the Quercy fissure fillings were described as *Palaeotyto cadurcensis* and *Palaeobyas cracrafti* by Mourer-Chauviré (1987). The former is known from a coracoid, and the latter from a tarsometatarsus; Mourer-Chauviré (1987, p. 111) considered it possible that these bones actually belong to a single species. The coracoid of *Palaeotyto* is characterized by a straight acrocoracoid process which shows little medial deflection, and a long foramen for the supracoracoideus nerve. The tarsometatarsus of *Palaeobyas* is very robust and the distal end is only slightly curved across the trochleae; as noted in Sect. 15.1, the proportions of this bone resemble those of the tarsometatarsus of the Paleocene *Berruornis*. The taxonomic status of *P. cadurcensis* and *P. cracrafti* and their classification into the Necrobyinae need to be verified with further material.

A smaller species of the Necrobyinae from the late Eocene of the Quercy fissure fillings, *Nocturnavis incerta* (Milne-Edwards, 1892), is known from humeri only.

The Palaeoglaucidae include *Palaeoglaux perrierensis* Mourer-Chauviré, 1987, which is based on several limb and pectoral girdle bones from late Eocene (MP 17) deposits of the Quercy fissure fillings, and the middle Eocene *P. artophoron* Peters, 1992 from Messel, of which two postcranial skeletons were identified (Fig. 15.1).

Fig. 15.1 As yet undescribed skeleton of the strigiform *Palaeoglaux artophoron* Peters, 1992 from the middle Eocene of Messel (Forschungsinstitut Senckenberg, Frankfurt am Main, Germany, SMF-ME 10817a). Specimen coated with ammonium chloride. (Photo by Sven Tränkner)

The specimens of the Little Owl (*Athene noctua*) sized *P. artophoron* constitute the only articulated skeletons of Paleogene owls described so far, although Olson (1985, p. 131) mentioned "several complete and perfectly preserved skeletons of a small species of owl" from the "middle" Oligocene of Wyoming. The Quercy species *P. perrierensis* differs from the species of *Necrobyas* in a more globular ventral condyle of the humerus and the presence of pneumatic foramina in the acrocoracoid process of the coracoid. The latter feature is shared with crown group Strigidae. The Messel species *P. artophoron* is, however, distinguished from all crown group Strigiformes by the plesiomorphic absence of an osseous arch on the radius (see Fig. 4 in Peters 1992), whose presence is a characteristic derived feature of modern owls. The proximal phalanx of the second toe is not as strongly abbreviated as in strigid owls. Unfortunately, comparisons between the Messel owl and the Quercy specimens of *P. perrierensis* are limited owing to the fact that most bones of the *P. artophoron* specimens are crushed; whether this species is indeed a representative of *Palaeoglaux* thus needs to be verified by future specimens.

Peters (1992) noted "ribbon-like" feathers in the holotype of *P. artophoron*, which were assumed to be an autapomorphic feature of the species, possibly reflecting an ornamental plumage. However, a similar type of feather preservation is found in other birds from Messel and may possibly be caused by the fact that only the feather shafts are preserved.

The holotype and only known specimen of *Selenornis henrici* (Milne-Edwards, 1892) is a distal tibiotarsus from an unknown horizon of the Quercy fissure fillings. The species was assigned to the monotypic taxon Selenornithinae by Mourer-Chauviré (1987) and is of a size similar to *Necrobyas rossignoli*.

From the "middle" Oligocene of Mongolia, Kurochkin (1976, p. 79) mentioned a "complete tarsometatarsus of a small owl, differing markedly from all recent forms of Strigidae"; this specimen still awaits formal description. Pellets, which possibly stem from owls, were found in the late Oligocene of Enspel in Germany (Schweizer et al. 2006).

Chapter 16
Arboreal Birds

As are some of the preceding headings, that of the present chapter is a makeshift one, as not all taxa discussed in the following are arboreal, and others, which are, belong to groups not considered here. The taxa included here are probably further paraphyletic with respect to the Cariamae, "Falconiformes," and Strigiformes (Chap. 3; Ericson et al. 2006; Hackett et al. 2008). There exist osteological similarities between stem group representatives of the Coliiformes, Psittaciformes, and Passeriformes (Zygodactylidae), on the one hand, and between those of the Trogoniformes, nonleptosomid "Coraciiformes," and Piciformes, on the other. The Leptosomidae stand morphologically apart from the other taxa.

The fossil record of these birds dramatically increased in the last few years and includes numerous well-represented taxa. Still, however, the evolutionary significance of many of these is not fully understood.

16.1 Leptosomidae (Courols)

The single extant species of the Leptosomidae, the Courol or "Cuckoo-roller," *Leptosomus discolor*, is a carnivorous, forest-dwelling bird of Madagascar and the Comoro Islands. The phylogenetic affinities of this species are uncertain, but contrary to traditional classifications, it is not closely related to the Coraciidae (true rollers) and Brachypteraciidae (ground rollers) (see Chap. 3).

Fossil stem group representatives from the lower and middle Eocene of Europe and North America show that Pan-Leptosomidae had a wide distribution over the Northern Hemisphere in the early Paleogene. These fossils were classified into the taxon *Plesiocathartes*, which was assigned to the Cathartidae by earlier authors (Gaillard 1908; Cracraft and Rich 1972). Five species of *Plesiocathartes* have been named: *Plesiocathartes europaeus* Gaillard, 1908 from an unknown horizon of the Quercy fissure fillings, *P. geiselensis* Mayr, 2002 from the Geisel Valley, *P. kelleri* Mayr, 2002 from Messel, as well as *P. wyomingensis* Weidig, 2006 and *P. major* Weidig, 2006 from the Green River Formation (Mayr 2002a, g; Mourer-Chauviré 2002; Weidig 2006). As yet unnamed species occur in the London Clay (Mayr 2002g).

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The Messel and Green River specimens consist of complete articulated skeletons and are remarkably similar to the Courol in their osteological features (Fig. 16.1; Mayr 2002a, g, 2008c; Weidig 2006). As in extant Leptosomidae, the coracoid exhibits a foramen for the supracoracoideus nerve and a cup-like scapular articulation facet. These presumably plesiomorphic traits are absent in other "coraciiform" birds. *Plesiocathartes* further shares with the extant Courol a derived morphology

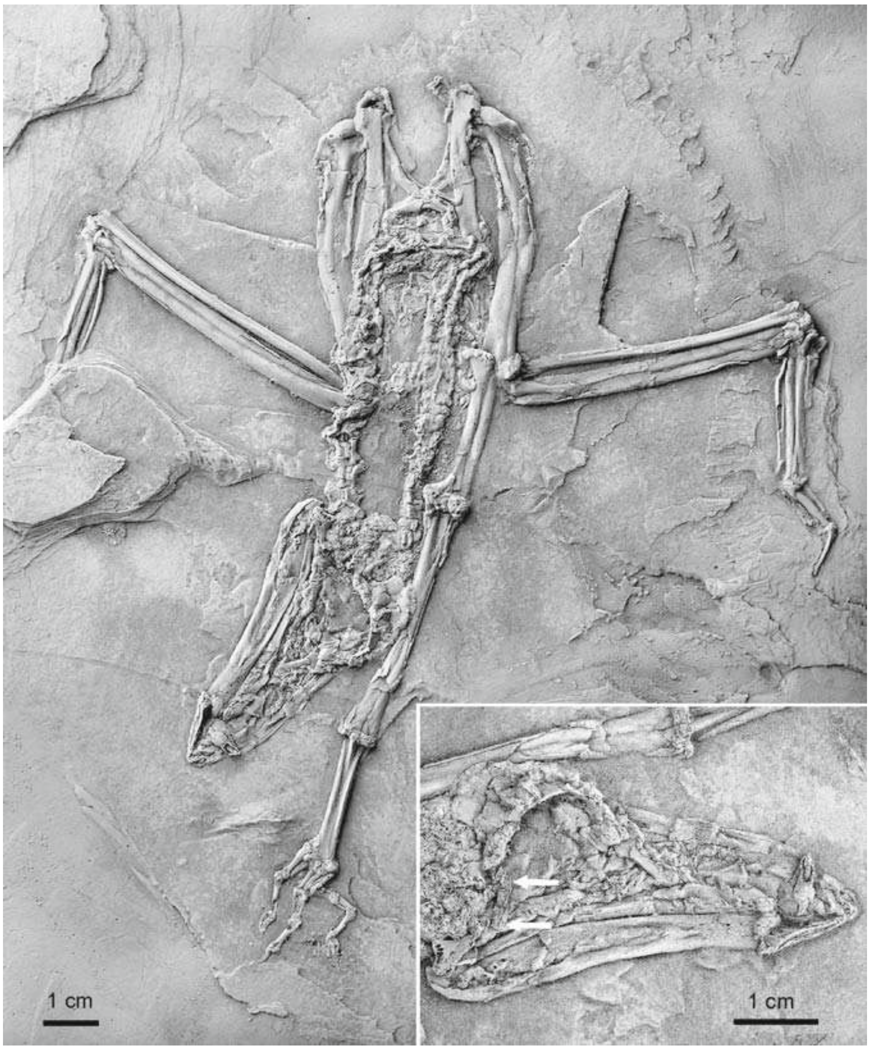

Fig. 16.1 Skeleton of *Plesiocathartes kelleri* Mayr, 2002 (Leptosomidae) from the middle Eocene of Messel (holotype, Forschungsinstitut Senckenberg, Frankfurt am Main, Germany, SMF-ME 3639). The *inset* shows an enlarged picture of the skull; the *arrows* indicate the postorbital process. Specimen coated with ammonium chloride. (Photos by Sven Tränkner)

of the tibiotarsus (condyles very low and widely separated) and tarsometatarsus (hypotarsus with two furrows which are closed to canals in *Leptosomus*, trochlea for the second toe reaching farther distally than that for the fourth toe; Mayr 2002a, g). As in extant Leptosomidae, the postorbital processes of the skull are greatly elongated (Fig. 16.1; this feature was not mentioned in the original description and was pointed out to me by Nikita Zelenkov).

These Eocene stem group Leptosomidae differ from *Leptosomus* in the morphology of the furcula, which has a smaller omal extremity, is more widely U-shaped, and whose shafts are not strap-like as in the Courol. They are further distinguished from *Leptosomus* by their proportionally longer legs, details of the pelvis morphology (the pubis is not reduced in its midsection and the obturator foramen is caudally open), and by the absence of an accessory tarsometatarsal trochlea for the fourth toe, which indicates that the feet were anisodactyl and not semizygodactyl as in the extant Courol.

All stratigraphically ranked specimens of fossil stem group representatives of the Leptosomidae come from Eocene deposits, and these birds may have already disappeared from the Northern Hemisphere toward the Oligocene.

16.2 Coliiformes (Mousebirds)

The Coliiformes include six predominantly frugivorous extant species, which occur in Africa south of the Sahara. They are sparrow-sized, long-tailed birds with a short, finch-like beak and a facultatively pamprodactyl and zygodactyl foot, i.e., the first and fourth toes can be turned forward and backward.

Among others (Mayr and Peters 1998), coliiform birds are further characterized by a very large dorsal cotyla of the ulna, the fact that both cnemial crests and the patellar crest of the tibiotarsus form a continuous ridge which circumscribes a groove on the cranial side of the bone, a thickened distal end of the femur with a large tubercle for the gastrocnemialis lateralis muscle, and, functionally correlated with the facultatively pamprodactyl foot, a tarsometatarsal fossa for the first metatarsal, which is situated on the medial surface of the tarsometatarsal shaft.

Mousebirds share a derived arrangement of the tendon of the extensor digitorum longus muscle with the Psittaciformes (Berman and Raikow 1982). Some analyses of morphological data support a sister group relationship between these two taxa (Mayr 2005i; Mayr and Clarke 2003), but others do not (e.g., Livezey and Zusi 2007). Likewise, molecular analyses do not yield congruent results concerning the phylogenetic affinities of the Coliiformes, and a sister group relationship to the Psittaciformes resulted from only one study of nuclear gene sequences (Chubb 2004).

The fairly extensive Paleogene fossil record of coliiform birds shows that the extant taxa are mere relicts of a once much more diversified group. All Paleogene specimens stem from fossil sites in Europe and North America. Whereas there are several archaic forms in the early and middle Eocene, only modern-type Coliiformes are known from the late Eocene on.

16.2.1 †Sandcoleidae

These morphologically distinct stem group representatives of the Coliiformes occur in the early and middle Eocene of North America and Europe. North American sandcoleids include the species *Sandcoleus copiosus* Houde and Olson, 1992 (early Eocene of the Willwood Formation) and *Anneavis anneae* Houde and Olson, 1992 (early Eocene of the Willwood Formation and the Green River Formation), as well as *Uintornis lucaris* Marsh, 1872, *U. marionae* Feduccia and Martin, 1976, *Botauroides parvus* Shufeldt, 1915, and *Eobucco brodkorbi* Feduccia and Martin, 1976 from the middle Eocene of the Bridger Formation. The fossil record of the latter four species consists of incomplete tarsometatarsi only, whereas the skeleton of *S. copiosus* and *A. anneae* is well known (Houde and Olson 1992).

In Europe, sandcoleids are represented by *Eoglaucidium pallas* Fischer, 1987, a species which was first described as an owl and occurs in Messel and the Geisel Valley (Fischer 1987; Mayr 2002a; Mayr and Peters 1998). *E. pallas* and a further unnamed sandcoleid species (Mayr 2000d) are known from complete articulated skeletons, and the former is among the most abundant medium-sized birds in Messel (Fig. 16.2). Sandcoleids also occur in the early Eocene of France (Mayr and Mourer-Chauviré 2004) and the London Clay (Daniels in Table 4.1 in Feduccia 1999).

The species of *Sandcoleus*, *Anneavis*, and *Eoglaucidium* are osteologically very similar and share robust feet and a thrush-like bill of generalized proportions. The caudal portion of the sternum exhibits a derived morphology in that the intermediate trabecles originate from the lateral ones, and the medial incisions are thus deeper than the lateral ones. In contrast to extant mousebirds, these fossil species still have a foramen for the supracoracoideus nerve on the coracoid. The tarsometatarsus has a characteristic shape, and, also in contrast to extant mousebirds, these species have a hypotarsus which bears two furrows for the deep flexor tendons of the toes, which may be closed to one or two canals (in extant Coliiformes there is only a single canal). The proximal phalanges of all anterior toes are abbreviated, whereas in extant Coliidae this is only true for the proximal phalanges of the fourth toe. The ungual pedal phalanges are very long and "raptor-like."

Some specimens of *A. anneae* and *E. pallas* are preserved with feather remains and allow the recognition of a long, staggered tail similar to that of extant mousebirds (Fig. 16.3). As in the latter, there seem to have been ten rectrices. In one Messel specimen of *Eoglaucidium* large seeds, probably from a species of the Annonaceae (custard apples), are preserved as stomach content (Fig. 16.2; Mayr and Peters 1998).

16.2.2 Coliidae

Mayr (2001d), Mayr and Peters (1998), and Mayr and Mourer-Chauviré (2004) showed that the putative sandcoleid *Chascacocolius oscitans* Houde and Olson, 1992 is actually more closely related to crown group Coliiformes than to the

Fig. 16.2 Skeleton of *Eoglaucidium pallas* Fischer, 1987 (Sandcoleidae) from the middle Eocene of Messel (Staatliches Museum für Naturkunde Karlsruhe, Germany, SMNK-PAL.553a). The *white circle* indicates a seed, probably from a species of the Annonaceae (custard apples). Specimen coated with ammonium chloride. (Photo by Sven Tränkner)

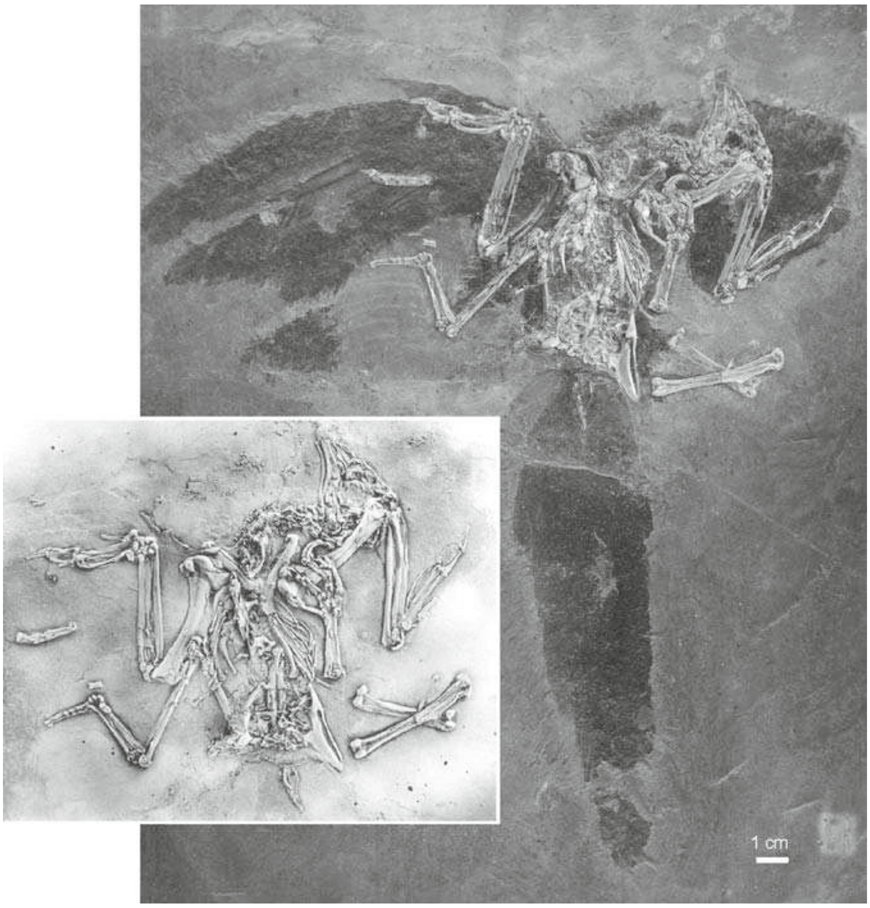

Fig. 16.3 Skeleton of *Eoglaucidium* sp. (Sandcoleidae) from the middle Eocene of Messel (Wyoming Dinosaur Center, Thermopolis, USA, WDC-C-MG 149). The small picture was taken after the specimen has been coated with ammonium chloride. (Photos by Sven Tränkner)

Sandcoleidae. This species occurs in the early Eocene of the Willwood Formation, and except for the skull and tarsometatarsus all major skeletal elements were found (Houde and Olson 1992). An incomplete wing from the Fur Formation was assigned to *Chascacocolius* cf. *oscitans* by Dyke et al. (2004), and an isolated skull from Messel was tentatively referred to *Chascacocolius* by Mayr (2005j), and described as ?*C. cacicirostris*.

Chascacocolius is characterized by the presence of very long retroarticular processes on the mandible (Fig. 16.4). These processes serve as the attachment site of the depressor mandibulae muscle and, by increasing its lever arm, enable gaping, i.e., opening of the beak within a substrate. The upper beak of *C. oscitans* is

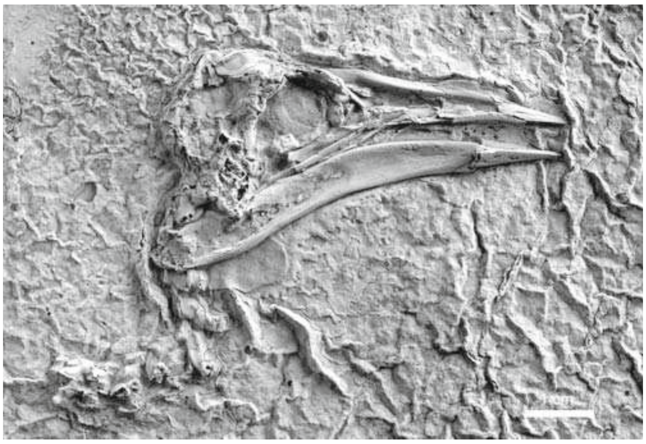

Fig. 16.4 Skull of ?*Chascacocolius cacicirostris* Mayr, 2005 (Coliidae) from the middle Eocene of Messel (holotype, Forschungsinstitut Senckenberg, Frankfurt am Main, Germany, SMF-ME 3790). Specimen coated with ammonium chloride. (Photo by Sven Tränkner)

unknown, but that of ?*C. cacicirostris* is very similar to that of extant passeriform caciques (*Cacicus* spp., Icteridae), who can forcefully open their bill within fruits (Mayr 2005j).

In its postcranial features, *Chascacocolius* resembles another early Eocene coliiform species, *Selmes absurdipes* Peters, 1999, which is known from two skeletons from Messel, a humerus from the Geisel Valley (Mayr 2001d), and a tentatively referred tarsometatarsus from an unknown locality of the Quercy fissure fillings (Mayr and Mourer-Chauviré 2004). *S. absurdipes* has an elongate and slender tarsometatarsus. The trochlea for the third toe is short and wide, and in the tentatively referred Quercy specimen the single proximal vascular foramen is close to the lateral margin of the tarsometatarsal shaft, whereas it is near its medial margin in extant Coliidae. In the holotype of *S. absurdipes* a dense package of as yet undetermined seeds is preserved as stomach content. Because the proximal phalanges of all three anterior toes are greatly abbreviated, *S. absurdipes* was classified into the Sandcoleidae by Peters (1999). However, the species also exhibits the characteristic derived morphology of the pygostyle of extant Coliidae (Mayr 2001d), and as in extant Coliidae the hypotarsus includes only a single canal (Mayr and Mourer-Chauviré 2004). Phylogenetic analyses by Mayr and Mourer-Chauviré (2004) and Ksepka and Clarke (2009) support its inclusion in a clade, which also includes crown group Coliidae but not the Sandcoleidae.

Masillacolius brevidactylus Mayr and Peters, 1998 is represented by two postcranial skeletons from Messel (Fig. 16.5). This species had the proportionally longest tarsometatarsus of all Coliiformes and unusually short tarsometatarsal trochleae. Judging from the position of the toes in the articulated Messel skeletons, the feet seem to have been fully pamprodactyl, i.e., the hallux was permanently directed

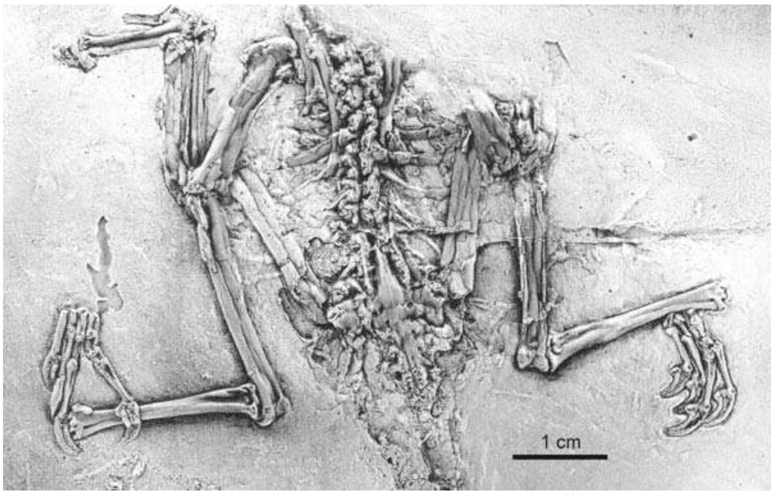

Fig. 16.5 Skeleton of *Masillacolius brevidactylus* Mayr and Peters, 1998 (Coliidae) from the middle Eocene of Messel (holotype, Hessisches Landesmuseum Darmstadt, Germany, HLMD-Me 10472). Specimen coated with ammonium chloride. (Photo by Sven Tränkner)

forward. Mayr and Peters (1998) assumed that *M. brevidactylus* was specialized for clinging to vertical surfaces, which also concords with its robust and stout ungual phalanges.

Eocolius walkeri Dyke and Waterhouse, 2001 from the London Clay is based on several isolated bones. The species lacks the enlarged dorsal condyle of the ulna, which is an apomorphy of the Coliiformes (Ksepka and Clarke 2009; contra Dyke and Waterhouse 2001). It is thus unlikely that it is a representative of the Coliiformes, from which it also differs in the shorter flexor process of the humerus.

Essentially modern-type stem group representatives of the Coliidae first occur in the middle Eocene. Among these are the two species of *Primocolius*, *P. sigei* and *P. minor*, which were described by Mourer-Chauviré (1988a) from the middle and late Eocene of the Quercy fissure fillings. These were the first Paleogene coliiform birds recognized as such, but both are known from a few bones only (humerus, tarsometatarsus, proximal carpometacarpus). A poorly preserved skeleton from the late Eocene deposits of the Paris Gypsum probably also belongs to *Primocolius* (Mayr 1998b, 2000g). Most surprisingly, essentially modern-type representatives of the Coliiformes were also present in the late Eocene of North America. *Palaeospiza bella* Allen, 1878 from the late Eocene of the Florissant shales of Colorado, which was originally described as a passeriform bird, closely resembles *P. sigei* in size, limb proportions, and morphological features, such as the presence of an enlarged intermetacarpal process (Mayr 2001d). Assignment of this species to the Coliiformes was also supported by Ksepka and Clarke (2009).

A fragmentary tarsometatarsus of an apparently modern-type mousebird was reported from the earliest Oligocene of Belgium (Mayr and Smith 2001). More substantial is the fossil record of a small coliiform bird from the early Oligocene of Wiesloch-Frauenweiler in Germany, which was described as *Oligocolius brevitarsus* by Mayr (2000g). This species is known from a disarticulated postcranial skeleton and has a proportionally more strongly developed wing and shorter tarsometatarsus than its modern relatives. In contrast to the ulna of other Coliiformes, that of *O. brevitarsus* distinctly exceeds the humerus in length, which may indicate that the species was adapted to a more sustained flight than extant mousebirds.

Primocolius, *Palaeospiza*, *Oligocolius*, and extant mousebirds form a clade, which is characterized by the derived presence of a well-developed intermetacarpal process on the carpometacarpus (Mourer-Chauviré 1988a; Mayr 2000g, 2001d).

16.3 Psittaciformes (Parrots)

Extant Psittaciformes are zygodactyl birds and are well characterized by a derived beak morphology, which enables them to get access to their prime food resource, the substantial content of hard-shelled seeds and nuts. As in other zygodactyl birds, the tarsometatarsal trochlea for the fourth toe bears a large accessory trochlea for the retroverted fourth toe.

Fossil Psittaciformes have been known for a long time from the Neogene of the Northern Hemisphere, and the specimens are morphologically very similar to extant parrots (Mlíkovský 1998b; Mayr and Göhlich 2004). Only in the last two decades, however, Paleogene stem group representatives were identified, all of which stem from European fossil sites. No representatives of crown group Psittaciformes are known from Paleogene fossil deposits. On the basis of a single humerus, Waterhouse et al. (2008) reported a presumptive psittaciform bird from the early Eocene of the Danish Fur Formation. This species, which was named *Mopsitta tanta*, is clearly distinguished from crown group Psittaciformes, which have a stouter humerus with a more elongated dorsal tubercle and ventral condyle (contra Waterhouse et al. 2008). Apart from vaguely similar overall proportions, which can be quite misleading in the case of Paleogene birds, I can see no reasons for an assignment of the Danish fossil to the Psittaciformes.

16.3.1 †Psittacopes and Allies

Unambiguous remains of early and middle Eocene stem group representatives of the Psittaciformes were reported from the London Clay and Messel (Mayr and Daniels 1998). The Messel species was named *Psittacopes lepidus* Mayr and Daniels, 1998, and is known from two skeletons. The London Clay remains belong to at least three different species, which are represented by three-dimensionally preserved skulls and bones of most major limb elements (Fig. 16.6; Mayr and Daniels 1998). All are very similar to the sparrow-sized *P. lepidus*, and closely resemble crown group Psittaciformes in their postcranial features. The slender tarsometatarsus exhibits an accessory trochlea for the retroverted fourth toe. As in the Quercypsittidae (Sect. 16.3.2) and extant Psittaciformes, but unlike in other zygodactyl birds except the Piciformes, this accessory trochlea is separated from the main trochlea by a distinct furrow (Mayr and Daniels 1998). The humerus of *Psittacopes* and its allies is less stout than that of crown group Psittaciformes and has a less protruding deltopectoral crest. The derived humerus morphology of extant parrots is functionally correlated to the large crop and weak furcula of these birds, and their ability for hovering flight over a short period of time (Stegmann 1964).

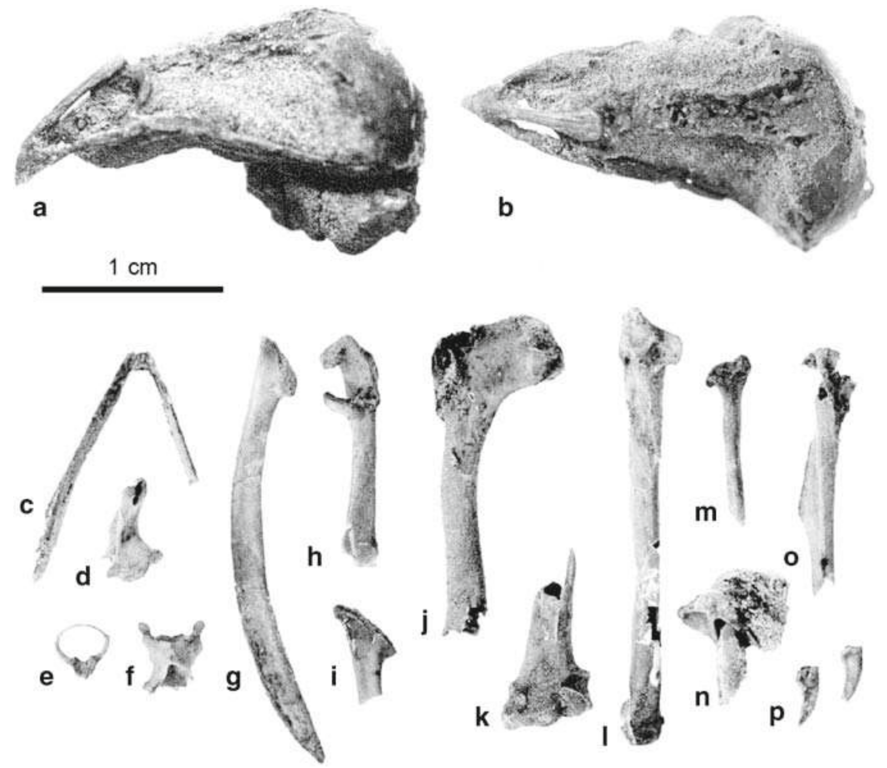

Fig. 16.6 Undescribed psittaciform bird from the early Eocene London Clay of Walton-on-the-Naze (collection of Paul Bergdahl, Kirby-le-Soken, UK, BC 8917A). **a**, **b** Skull (with matrix); **c** mandible; **d** right quadrate; **e** atlas; **f** cervical vertebra; **g** right scapula; **h** right coracoid; **i** omal extremity of left scapula; **j** proximal right humerus; **k** distal left humerus; **l** left ulna; **m** distal radius; **n** proximal left carpometacarpus (with matrix); **o** proximal tibiotarsus; **p** ungual phalanges. All images to scale. (From Mayr and Daniels 1998, modified)

These features seem to have been absent or at least much less developed in the Eocene stem group representatives.

The most significant differences between *Psittacopes*, the unnamed London Clay species, and extant Psittaciformes, however, concern the morphology of the beak. Although the upper beak is short and quite robust, expectedly for a stem group representative of the Psittaciformes, it is much less downcurved than in extant parrots, has much larger narial openings, and the mandible is not as deep and short (Fig. 16.6). The tarsometatarsus of *Psittacopes* and its London Clay relatives also exhibits a less derived morphology than that of extant parrots in that the accessory trochlea of the fourth toe is less elongated and the trochlea for the second toe is smaller. I have argued elsewhere (Mayr 2002h) that the highly specialized morphology of the beak and feet of crown group Psittaciformes are an example of synorganization, i.e., the concerted evolution of different parts of the body, which together form a functional unit. Extant parrots regularly use their feet to assist their husking food, and it is likely that their tarsometatarsal specializations constitute adaptations to increase the grasping capabilities of the foot. Because of the absence of the derived tarsometatarsus and skull features in the fossil species, *Psittacopes* and its London Clay relatives certainly had a feeding technique different from that of extant parrots, being rather generalized, possibly granivorous feeders.

16.3.2 †Quercypsittidae

Another taxon of early Paleogene stem group Psittaciformes are the Quercypsittidae, which occur in the late Eocene (MP 17) locality La Bouffie of the Quercy fissure fillings (Mourer-Chauviré 1992c) and the early Eocene London Clay (Mayr and Daniels 1998). Two species, *Quercypsitta ivani* Mourer-Chauviré, 1992 and *Q. sudrei* Mourer-Chauviré, 1992, were named from La Bouffie, and the described skeletal elements include an incomplete carpometacarpus, coracoids, distal tibiotarsi, tarsometatarsi, and pedal phalanges. Likewise, a distal tarsometatarsus from the middle Eocene (MP 11–13; Mlíkovský 2002) of England, which was referred to the nonpsittaciform *Palaeopsittacus georgei* (Sect. 12.1) in the original description, closely resembles that of *Quercypsitta* (Mayr and Daniels 1998).

After the recent discovery of abundant new fossils, including several tarsometatarsi, it became obvious that *Vastanavis eocaena* Mayr et al., 2007 from the early Eocene of the Vastan Lignite Mine in India is also a *Quercypsitta*-like psittaciform bird (personal observation). The original description of this species was based on coracoids and scapulae, and the former were erroneously likened to the Otididae (bustards; Mayr et al. 2007).

The short and stout tarsometatarsus of the Quercypsittidae is reminiscent of the corresponding bone of some extant parrots in its proportions. The accessory trochlea for the retroverted fourth toe is, however, less well developed than that of crown group Psittaciformes. The coracoid also strongly differs from that of modern parrots and exhibits a plesiomorphic, cup-like scapular articulation facet

(Mourer-Chauviré 1992c), which indicates a position of quercypsittids outside a clade including *Psittacopes* and crown group Psittaciformes. Ungual pedal phalanges preserved in a London Clay quercypsittid resemble those of strigiform birds (Mayr and Daniels 1998).

16.3.3 †Halcyornithidae ("Pseudasturidae")

Assignment of this taxon to stem group Psittaciformes is more controversial than that of the species discussed in Sect. 16.3.1, although its representatives are fairly abundant in the early and middle Eocene of Europe (Fur Formation, London Clay, Messel, Geisel Valley, and Egem in Belgium) and the early Eocene of the North American Green River Formation (Mayr 1998c, 2002a, h, 2007b; Dyke 2001e; Dyke and Cooper 2000; Kristoffersen 2002a; Waterhouse et al. 2008; see also Hoch 1988).

On the basis of a skeleton from the Green River Formation, the first species of this taxon was described as "*Primobucco*" *olsoni* by Feduccia and Martin (1976) and was assigned to the Primobucconidae, which were then considered to be piciform birds. The Primobucconidae are now assigned to the stem lineage of the Coraciidae/Brachypteraciidae, and the species of the type genus *Primobucco* are very different from "*P.*" *olsoni* (Sect. 16.7.1). More light was shed on the affinities of "*P.*" *olsoni* after recognition of several very similar species from the early and middle Eocene of Europe. In Messel, these birds are represented by complete and articulated skeletons that were assigned to *Pseudasturides* ("*Pseudastur*") *macrocephalus* (Mayr, 1998), *Serudaptus pohli* Mayr, 2000, and at least two other unnamed species (Fig. 16.7; Mayr 1998c, 2000d, 2004f). Isolated bones from the London Clay locality Walton-on-the-Naze were described as *Pulchrapollia gracilis* by Dyke and Cooper (2000), who assigned this species to the Psittaciformes but explicitly, and erroneously, did not consider it related to the *Pseudasturides*-like birds from Messel (Fig. 16.8). Specimens of *P. gracilis* from Walton-on-the-Naze were also figured by Mayr and Daniels (1998), and the species closely resembles "*Primobucco*" *olsoni*, with which it has not yet been directly compared (Mayr 2002h). Other remains from the London Clay were described from the Isle of Sheppey by Dyke (2001e) and Mayr (2007b), and include a partial skeleton which was assigned to *Pseudasturides* cf. *macrocephalus* (Mayr 2007b).

I introduced the taxon "Pseudasturidae" for these birds (Mayr 1998c). New cranial material from Messel has shown, however, that this name is a junior synonym of the taxon Halcyornithidae. The latter was erected by Harrison and Walker (1972) for the earliest named fossil bird, *Halcyornis toliapicus* Koenig, 1825, a species known from a cranium from the London Clay of the Isle of Sheppey (Fig. 16.8; Harrison and Walker 1972; Mayr 2007b).

Pseudasturides and its allies are very different from extant parrots in many osteological features. The skull exhibits very large supraorbital processes and well-developed temporal fossae. The humerus is elongated and slender. The coracoid

Fig. 16.7 *Pseudasturides macrocephalus* (Mayr, 1998) (Halcyornithidae) from the middle Eocene of Messel (Staatliches Museum für Naturkunde Karlsruhe, Germany, SMNK-PAL.2373a). Specimen coated with ammonium chloride. (From Mayr 1998c; photo by Sven Tränkner)

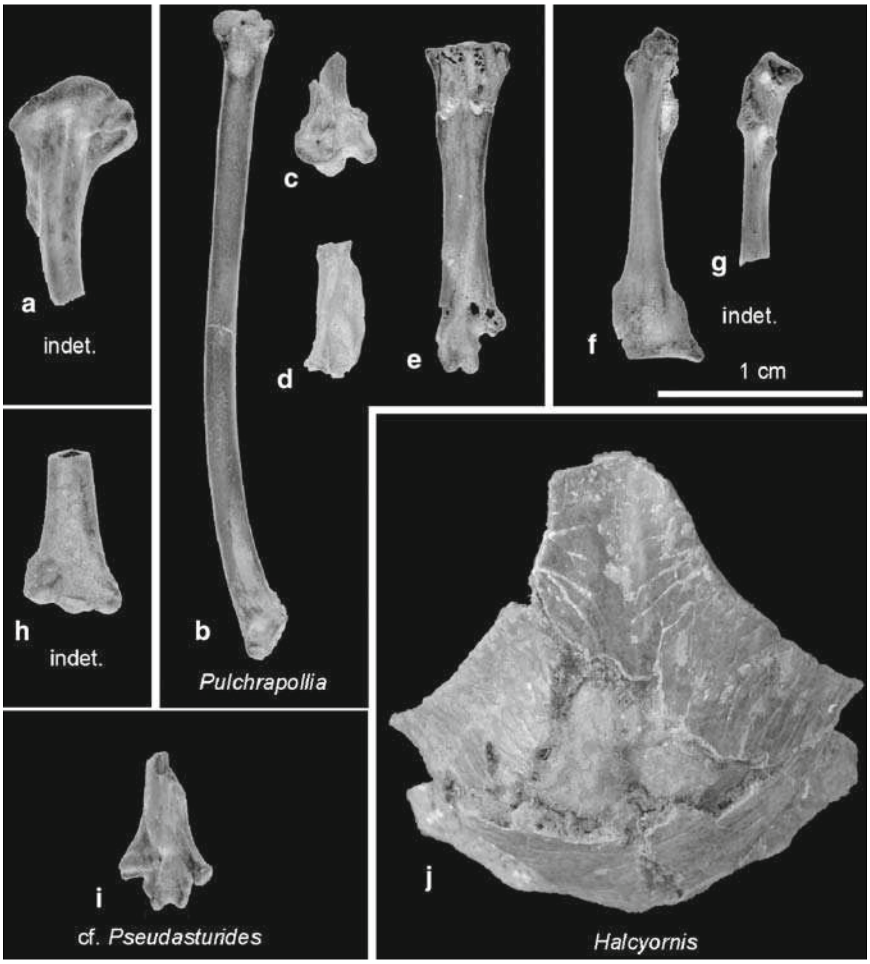

Fig. 16.8 Halcyornithidae from the early Eocene of the London Clay. **a** Proximal left humerus of an undetermined species from Warden Point, Isle of Sheppey (Natural History Museum, London, UK, BMNH A 3553, paratype of *Precursor parvus* Harrison and Walker, 1977); **b** right ulna; **c** proximal right carpometacarpus; **d** proximal phalanx of left major wing digit; and **e** right tarsometatarsus of *Pulchrapollia gracilis* Dyke and Cooper, 2000 from Walton-on-the-Naze (holotype, BMNH A 6207); **f** right and **g** left coracoid of an undetermined species from Walton-on-the-Naze (BMNH A 6218); **h** distal right humerus of an undetermined species from Warden Point, Sheppey, Kent, UK (BMNH A 6155); **i** distal left tarsometatarsus of ?*Pseudasturides* from Warden Point, Isle of Sheppey (BMNH A 6184); **j** cranium of *Halcyornis toliapicus* Koenig, 1825 from the Isle of Sheppey (holotype, BMNH A 130). All images to scale. (Photos by Sven Tränkner)

is similar to that of extant Strigiformes in overall morphology; in contrast to the coracoid of crown group Psittaciformes, *Psittacopes*, and the Quercypsittidae, it exhibits a foramen for the supracoracoideus nerve.

Initially (Mayr 1998c), I considered the phylogenetic affinities of *Pseudasturides* and its allies uncertain, but subsequently suggested that they are stem group representatives of the Psittaciformes (Mayr 2002h). Apart from the presence of fully zygodactyl feet, this assumption was based on derived similarities in the tarsometatarsal trochlea for the fourth toe (the presence of a furrow for the tendon of the flexor perforatus muscle of the fourth toe), the tibiotarsus (the presence of a ridge on the medial surface of the proximal end), and the thoracic vertebrae. The absence of a furrow between the accessory trochlea and the trochlea for the fourth toe supports a position of halcyornithids outside a clade including *Quercypsitta*, *Psittacopes*, and crown group Psittaciformes (contra Dyke and Cooper 2000 who assumed that *P. gracilis* is the sister taxon of crown group Psittaciformes). Regarding the presence of a coracoidal foramen for the supracoracoideus nerve and supraorbital processes on the skull, halcyornithids closely match the group discussed in the following section.

16.3.4 †Messelasturidae

The Messelasturidae include two named species, *Tynskya eocaena* Mayr, 2000 from the Green River Formation and *Messelastur gratulator* Peters, 1994 from Messel. The former is represented by a single skeleton, whereas of *M. gratulator* an incomplete skeleton and two skulls were identified (Peters 1994; Mayr 2000f, 2005i). *M. gratulator* was tentatively assigned to the Accipitridae in the original description (Peters 1994). The phylogenetic affinities of *T. eocaena* were considered uncertain (Mayr 2000f), but comparisons were made with raptorial birds and the Halcyornithidae (“Pseudasturidae”). A close relationship between *Tynskya* and *Messelastur* was assumed by Mayr (2005i), who established the taxon Messelasturidae for a clade including these birds.

Three-dimensionally preserved bones of multiple individuals of as yet undescribed, *Tynskya*-like species were collected by Michael Daniels in the London Clay of Walton-on-the-Naze, where they are among the more common avian remains. These birds are listed as owls in Feduccia (1999, Table 4.1; see also Mayr 2000f).

M. gratulator and the slightly smaller *T. eocaena* were about the size of the extant Scops-owl, *Otus scops*. Both species are similar in skeletal morphology, although the preservation of the fossil specimens prevents close osteological comparisons. *Messelastur* and *Tynskya* share the lack of pneumatic foramina in the pneumotricipital fossa of the humerus and a widely U-shaped furcula. The mandibular rami of *M. gratulator* are very deep. The foot of *Messelastur* is unknown, but the tarsometatarsus of *T. eocaena* exhibits a characteristic derived morphology (Mayr 2000f). The trochlea for the fourth toe is much shorter than that for the second and bears a plantarly projecting, wing-like flange, indicating the presence of at least facultatively zygodactyl feet. As in the Quercypsittidae, the ungual phalanges of the feet are owl-like. *M. gratulator* agrees with owls in the absence of a supratendinal bridge on the distal tibiotarsus (Mayr 2005i); however, if it is not an artifact of preservation or preparation, this feature seems to be an apomorphy of *Messelastur*, as the *Tynskya*-like London Clay specimens exhibit a supratendinal bridge (personal observation). The skull of *Messelastur* has large, caudally projecting supraorbital processes, similar to those found in extant Accipitridae and Falconidae. The presence of this feature cannot be established in the poorly preserved skull of the holotype of *T. eocaena*.

A cladistic analysis supported a sister group relationship between the Messelasturidae and strigiform birds (Mayr 2005i), but the results of this analysis were only weakly supported. As evidenced by the specimens in the Daniels collection, one of the two presumptive synapomorphies is absent in *Tynskya* (the lack of a supratendinal bridge), and the other is also present in the Halcyornithidae (the presence of a plantarly directed wing-like flange on the trochlea for the fourth toe).

After recently having had the opportunity to examine in detail the London Clay fossils in the Daniels collection, I am now convinced that messelasturids are close relatives of the Halcyornithidae, and thus most likely stem group Psittaciformes. In both messelasturids and halcyornithids, there are no pneumatic openings in the pneumotricipital fossa of the humerus, the tarsometatarsal trochlea for the second toe is very small, the coracoid exhibits a foramen for the supracoracoideus nerve, and the skull bears large supraorbital processes. A major difference between the Messelasturidae and the Halcyornithidae concerns the morphology of the hypotarsus, which bears a single wide furrow in the former but two narrower ones in the latter. Likewise, the beak is shorter and more raptor-like in the Messelasturidae.

16.4 †Zygodactylidae and Passeriformes (Passerines)

From analyses of morphological data, the closest extant relatives of the Passeriformes were considered to be either the Piciformes or taxa of the non-monophyletic “Coraciiformes” (Manegold 2005; Livezey and Zusi 2007). Recent analyses of nuclear gene sequences, by contrast, resulted in a clade including the Passeriformes and Psittaciformes (Ericson et al. 2006; Hackett et al. 2008). This hypothesis is as yet not supported by independent gene loci. It is, however, of particular interest because of the fact that the Passeriformes can be shown to be the sister group of the Zygodactylidae, which were among the most abundant small birds in the Paleogene of the Northern Hemisphere. Both the Psittaciformes and the Zygodactylidae have zygodactyl feet, and if future studies support a close relationship to parrots, passerines may thus have evolved from an at least semi-zygodactyl ancestor.

16.4.1 †Zygodactylidae

The taxon *Zygodactylus* was first described by Ballmann (1969a, b) from the early Miocene of Germany and the middle Miocene of France, and for a long time it was only known from distal tibiotarsi and tarsometatarsi. It took almost four decades until an articulated skeleton of *Zygodactylus* could be identified. This specimen comes from the early Oligocene of the Lubéron area in France and was described as *Zygodactylus luberonensis* (Fig. 16.9; Mayr 2008h). The osteological data that can be obtained from this fossil support earlier assumptions (Mayr 1998b; Feduccia

Fig. 16.9 Skeleton of *Zygodactylus luberonensis* Mayr, 2008 (Zygodactylidae) from the early Oligocene of the Lubéron in France (holotype, Forschungsinstitut Senckenberg, Frankfurt am Main, Germany SMF Av 519); note that the skull of this specimen has been inserted in the slab and can only be tentatively assigned to the species (Mayr 2008h). (Ultraviolet-induced fluorescence photograph by Sven Tränkner)

1999) that *Zygodactylus* is closely related to early Eocene birds, which were classified into the taxon "Primoscenidae." Accordingly, the latter taxon, which was established by Harrison and Walker (1977), was synonymized with the Zygodactylidae (Mayr 2008h).

These early Eocene zygodactylids (i.e., the "primoscenids") are known from many complete skeletons and isolated, three-dimensionally preserved bones (Figs. 16.10, 16.11). The first species was described by Harrison and Walker (1977) as *Primoscens minutus*, on the basis of an incomplete carpometacarpus from the London Clay (Fig. 16.10). Additional and much more complete London Clay specimens were collected by Michael Daniels from Walton-on-the-Naze (Fig. 16.11; Daniels 1994; Mayr 1998b; Daniels in Feduccia 1999, Table 4.1). Articulated skeletons were further identified in the early Eocene of Messel, the Green River Formation, and the Danish Fur Formation (Mayr 1998b; Kristoffersen 2002a; Weidig 2003). In Messel, zygodactylids are among the most abundant small birds, and the three currently recognized species, *Primozygodactylus danielsi* Mayr, 1998, *P. ballmanni* Mayr, 1998, and *P. major* Mayr, 1998, mainly differ in size and limb proportions.

Zygodactylids are small birds with a long and slender tarsometatarsus and long toes. As indicated by the taxon name, they had a permanently retroverted fourth toe. The tarsometatarsal trochlea for this toe exhibits a large accessory trochlea, which in *Zygodactylus* is distally elongated as in extant Psittaciformes and the piciform Pici. Otherwise, however, the distal tarsometatarsus of these two extant taxa markedly differs from that of *Zygodactylus*. The carpometacarpus is short and exhibits a very large intermetacarpal process, similar to that of extant Passeriformes and Piciformes. The beak of *Primozygodactylus* is thrush-like and neither very long nor very short. In some Messel specimens of *Primozygodactylus* long tail feathers are preserved, and it can be discerned that the two central rectrices are greatly elongated (Fig. 16.10; Mayr and Zelenkov 2009).

Ballmann (1969a, b) considered the phylogenetic affinities of *Zygodactylus* uncertain. The taxon was classified into the Zygodactylidae, within the piciform Galbulae (puffbirds and jacamars), by Brodkorb (1971), and Simpson and Cracraft (1981, p. 492) also tentatively placed *Zygodactylus* within the Pici. Piciform affinities of *Zygodactylus* were questioned by Olson (1983, 1985), who raised the possibility that its zygodactyl foot evolved independently from that of any of the extant taxa.

In contrast to the peculiar distal tarsometatarsus, the carpometacarpus of zygodactylids is very similar to that of passeriform birds, and Harrison and Walker (1977) and Harrison (1982a) indeed described *Primoscens* as the earliest fossil passerine. The high degree of derived similarity between the carpometacarpi of zygodactylids and passeriform birds is exemplified by the fact that these were twice independently assigned to the Passeriformes, by Harrison and Walker (1977) in the case of *P. minutus*, and by Ballmann (1969a) concerning *Zygodactylus ignotus* (Mayr 2008h). Likewise, the distal humerus of one of the London Clay zygodactylids in the Daniels collection exhibits a derived morphology which is otherwise only found in passeriform birds, in that the dorsal supracondylar process is very

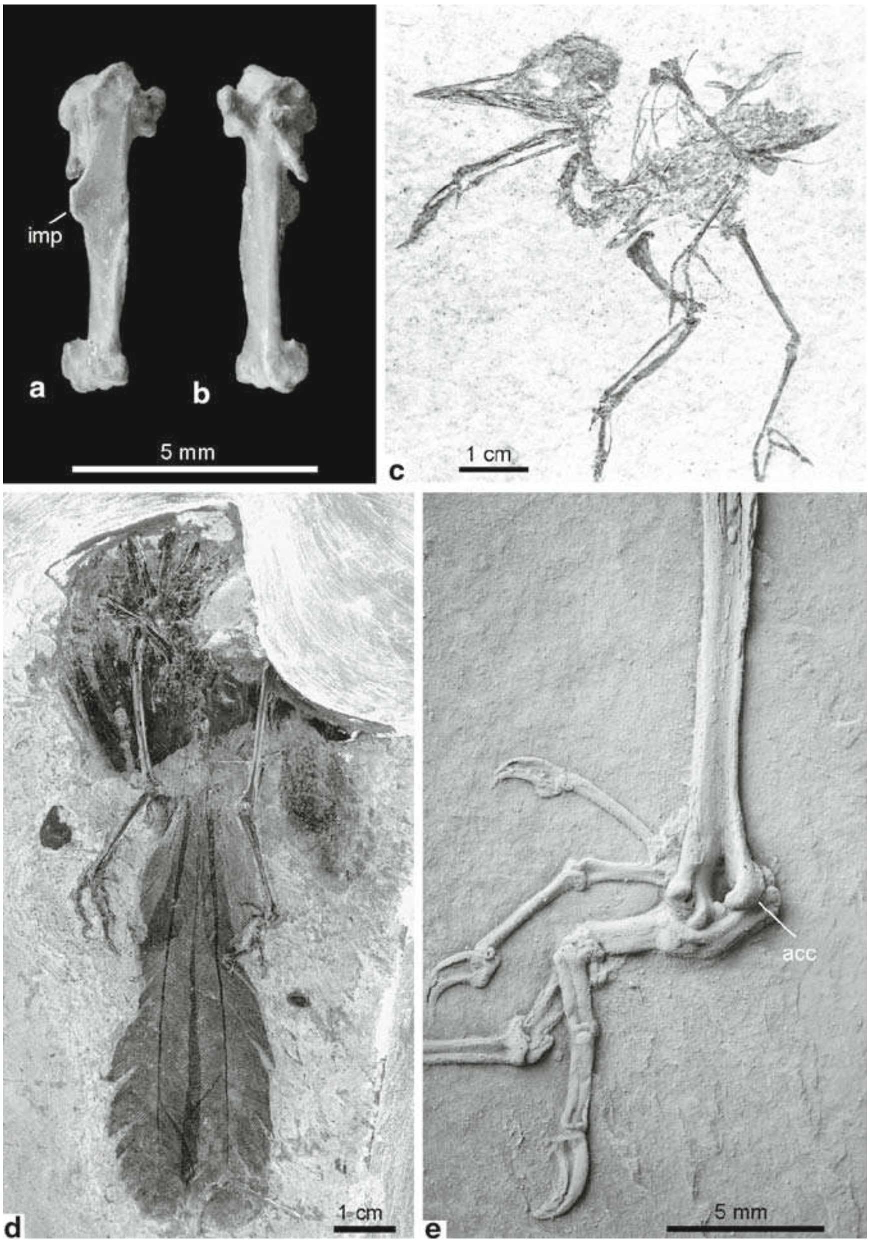

Fig. 16.10 Eocene Zygodactylidae. **a**, **b** Right carpometacarpus of *Primoscens minutus* Harrison and Walker, 1977 from the early Eocene London Clay of Bognor Regis (holotype, Natural History Museum, London, UK, BMNH A 4681); **c** skeleton of an undescribed species from the early Eocene Green River Formation (North American Museum of Ancient Life, Lehi, Utah, USA, NAMAL-2000–0217–004); **d** postcranial skeleton of *Primozygodactylus* sp. from the middle Eocene of Messel with well-preserved tail feathers (Forschungsinstitut Senckenberg, Frankfurt am Main, Germany, SMF-ME 1074); **e** distal end of right tarsometatarsus of the previous specimen. *acc* accessory trochlea for fourth toe, *imp* intermetacarpal process. The specimen in **e** was coated with ammonium chloride. (**c** Courtesy of Ilka Weidig; all other photos by Sven Tränkner)

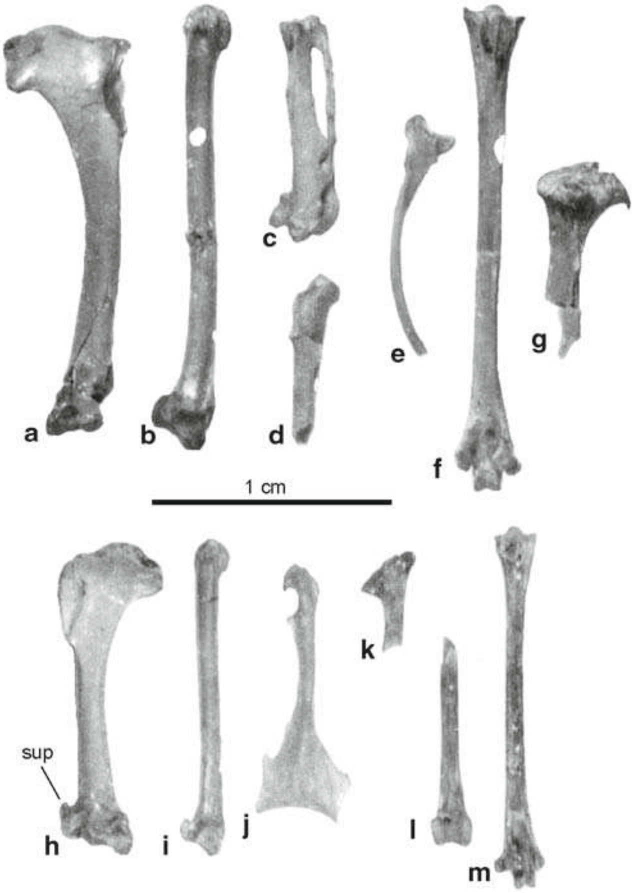

Fig. 16.11 Zygodactylidae from the early Eocene London Clay of Walton-on-the-Naze. **a**–**g** *Primozygodactylus* sp. (collection of Michael Daniels, Holland-on-Sea, UK, WN 88583A); **h**–**m** Zygodactylidae gen. et sp. indet. (WN 92747). **a** Left humerus; **b** left ulna; **c** right carpometacarpus; **d** omal extremity of left coracoid; **e** omal extremity of furcula; **f** right tarsometatarsus; **g** proximal right tibiotarsus; **h** right humerus; **i** left ulna; **j** left coracoid; **k** cranial extremity of left scapula; **l** distal left tibiotarsus; **m** left tarsometatarsus. *sup* dorsal supracondylar process. All images to scale. (From Mayr 1998b, modified)

large and in that there is a marked tubercle in the center of the cranial surface, above the dorsal condyle (Fig. 16.11; see Fig. 25A in Mayr 1998b).

Before recognition of the skeleton of *Z. luberonensis*, zygodact ylids (“primoscenids”) were assumed to be most closely related to either the Piciformes (Mayr 1998b) or the Passeriformes (Mayr 2004g). I now consider the derived similarities in the shape of the accessory tarsometatarsal trochlea of *Zygodactylus* and the Pici to be a striking example of convergence. Zygodactylids lack derived characteristics of crown group Piciformes, most notably a proximally directed process on the proximal phalanx of the major wing digit (Mayr 2004g, 2008h). As in passeriform birds, but unlike in the Piciformes, the hypotarsus exhibits a closed canal for the flexor hallucis longus muscle, and the tarsometatarsus is greatly elongated and bears a lateral plantar crest. A sister group relationship between the Zygodactylidae and Passeriformes was also supported by a phylogenetic analysis in which the new osteological data obtained from *Z. luberonensis* were included (Mayr 2008h).

The holotype of *Primozygodactylus major* is preserved with stomach content consisting of grape seeds (Vitaceae) (Mayr 1998b), and seeds are also found in the area of the intestinal tract of several other Messel zygodactylids.

The proportionally longer toes and larger accessory trochlea for the fourth toe indicate that *Zygodactylus* had a way of living different from that of early Eocene zygodactylids. The greater span width of the toes may indicate a more terrestrial way of living, possibly in a more open habitat (Mayr and Zelenkov 2009). The significance of the larger accessory trochlea is uncertain. I hypothesized (Mayr 2008h) that this feature may represent an adaptation for clinging to tree trunks, possibly for excavation of nesting cavities, but noted that downright trunk climbing can be excluded because of the morphology of the tarsometatarsal trochlea for the third toe.

16.4.2 Passeriformes

Crown group Passeriformes are osteologically fairly uniform birds and include more than half of all extant avian species. Molecular analyses provide a phylogenetic framework for the major clades, and according to these studies the Acanthisittidae (New Zealand wrens) are the sister taxon of all other extant passerines, the Eupasseres, which comprise the Suboscines and Oscines (Ericson et al. 2003; Barker et al. 2004). The Suboscines (tyrant flycatchers, antbirds, manakins, and allies) are mainly restricted to the New World, their sole Old World representatives being pittas (Pittidae), and broadbills and asities (Eurylaimidae). Phylogenies derived from molecular data indicate that the globally distributed Oscines, the most speciose passeriform group, originated on the Australian continental plate (Barker et al. 2002; Ericson et al. 2002).

Passeriform birds have an abundant Neogene fossil record, but only a few early Paleogene fossils have been identified. Two fragmentary bones, a proximal carpometacarpus and a distal tibiotarsus, from the early Eocene Tingamarra Local Fauna of Australia were assigned to the Passeriformes by Boles (1995, 1997c). As in extant passerines, the carpometacarpus exhibits a large intermetacarpal process. It differs, however, from that of modern passerines in the proportionally larger ventral portion of the carpal trochlea, and the fact that the depression between the major metacarpal and the pisiform process is shallower. Additional material is certainly needed for an unambiguous identification of these fossils, but from a biogeographic point of view it is well possible that they belong to stem group representatives of the Passeriformes (see below and Sect. 17.2.1).

All other Paleogene remains of passerines are from the Oligocene of Europe. The earliest fossils come from the early Oligocene of Germany and France, and the scarce record indicates that by this time Passeriformes were not yet the numerically dominant group among the small arboreal birds (Mayr 2005a). From the early Oligocene of Wiesloch-Frauenweiler in Germany, Mayr and Manegold (2004, 2006a) described a skeleton of a small passerine as *Wieslochia weissi*. This species lacks derived characteristics of crown group Oscines, such as a bifurcated acromion of the scapula, and shares with extant Suboscines the presence of a well-developed tubercle on the ulna for the ventral collateral ligament (tuberculum ligamenti collateralis ventralis). *Wieslochia* also resembles extant Suboscines in overall morphology, but some features may support its position outside crown group Eupasseres: the minor metacarpal of the carpometacarpus does not protrude as far distally as the articulation facet for the minor wing digit, the coracoid lacks a hooked acrocoracoid process, and the hypotarsus exhibits furrows instead of canals for the medial of the most plantar flexor tendons (Mayr and Manegold 2006a).

A wing fragment of a very small passeriform bird was reported from the early Oligocene of the Lubéron area in France (Mayr and Manegold 2006b). The well-preserved carpometacarpus of this specimen likewise most closely resembles that of extant Suboscines. The species to which it belonged was of a size similar to that of the Madagascan sunbird-asities (*Neodrepanis* spp.), the smallest extant Old World representatives of the Suboscines. Also from the Lubéron area, an as yet undescribed complete skeleton of a passeriform bird exists in a private collection in France (Roux 2002; own observation).

Passeriform birds were further identified in late Oligocene sites of France (Mourer-Chauviré et al. 1989) and Germany (Manegold 2008). Some of the French specimens were assigned to the Oscines (Mourer-Chauviré et al. 1989), but Mourer-Chauviré (2006) also noted the presence of a suboscine passerine in the late Oligocene (MP 26) of France. Manegold (2008) described a diverse assemblage of small passerines from the late Oligocene of Germany, in which he likewise identified representatives of both Oscines and Suboscines. It is noteworthy that all of these specimens belong to small species.

The fact that the earliest European Passeriformes already closely resemble their modern counterparts supports the hypothesis that passeriform birds dispersed on the Northern Hemisphere from one of the southern continents (Olson 1989; Ericson et al. 2003). All known early Oligocene passerines further do not belong to the Oscines, the only passeriform taxon which occurs in Europe today. The earliest European fossil record of oscine passerines is from the late Oligocene (Mourer-Chauviré et al. 1989; Manegold 2008), and nonoscine passerines thus seem to have colonized Europe before the arrival of the Oscines from the Australian continental plate.

16.5 Trogoniformes (Trogons)

The Trogoniformes are insectivorous or frugivorous arboreal birds which occur in the tropical and subtropical regions of continental Africa, Asia, and the New World. Trogons are the only avian group in which the second toe is permanently directed backward. This so-called heterodactyl foot is accompanied by a plantarly retroverted tarsometatarsal trochlea for the second toe.

Skeletal remains of several individuals of early Eocene trogons were collected by Michael Daniels in the London Clay of Walton-on-the-Naze. These as yet undescribed specimens were mentioned earlier (Mayr 1999a), and a completely preserved tarsometatarsus shows a plantarly deflected trochlea for the second toe. The earliest formally described specimen is a cranium from the Fur Formation in Denmark, which was assigned to the new species *Septentrogon madseni* by Kristoffersen (2002b). The cranium of *S. madseni* shares the presence of basipterygoid processes and a derived morphology of the zygomatic process with crown group Trogonidae, from which it differs in a proportionally narrower nasofrontal hinge.

A complete but poorly preserved skeleton of a trogoniform, ?*Primotrogon pumilio* Mayr, 2005, has also been identified in Messel (Mayr 2005k), and is likewise distinguished from crown group Trogoniformes in the shape of its narrower beak. The heterodactyl position of the toes is clearly visible in this specimen. Weidig (2003) reported a putative trogon from the Green River Formation, which would be the only Paleogene fossil record of this avian group in the New World.

Articulated skeletons of unambiguously identified early Oligocene trogons were described from Matt in Switzerland (Olson 1976) and the Lubéron in France (Mayr 1999a, 2001e). An isolated wing is also known from the early Oligocene of Wiesloch-Frauenweiler (Mayr 2005k). The Lubéron trogon, *Primotrogon wintersteini* Mayr, 1999, is represented by two skeletons which allow recognition of the heterodactyl foot. It was shown to be outside crown group Trogoniformes by its plesiomorphic skull morphology (the cranium and beak are narrower than in crown group Trogoniformes and the orbitae are proportionally smaller) and the absence of derived characters of the coracoid (Mayr 1999a, 2005k). Both *P. wintersteini* and ?*P. pumilio* are further smaller than their extant relatives.

The fossil record indicates that trogons underwent relatively little morphological changes during the past 50 million years, and suggests a Northern Hemisphere origin of the group and subsequent dispersal into South America during the Cenozoic.

16.6 Bucerotes (Hornbills, Hoopoes, and Woodhoopoes)

Extant Bucerotes comprise the Bucerotiformes (hornbills), which occur in Africa and Asia and have no Paleogene fossil record, and the Upupiformes, which include the African and Eurasian Upupidae (hoopoes) and the African Phoeniculidae (woodhoopoes) (Mayr 1998b; Mayr et al. 2003; Ericson et al. 2006; Livezey and Zusi 2007; Brown et al. 2008).

Stem group representatives of the Upupiformes were reported from the early Eocene London Clay and the middle Eocene of Messel and the Geisel Valley (Mayr

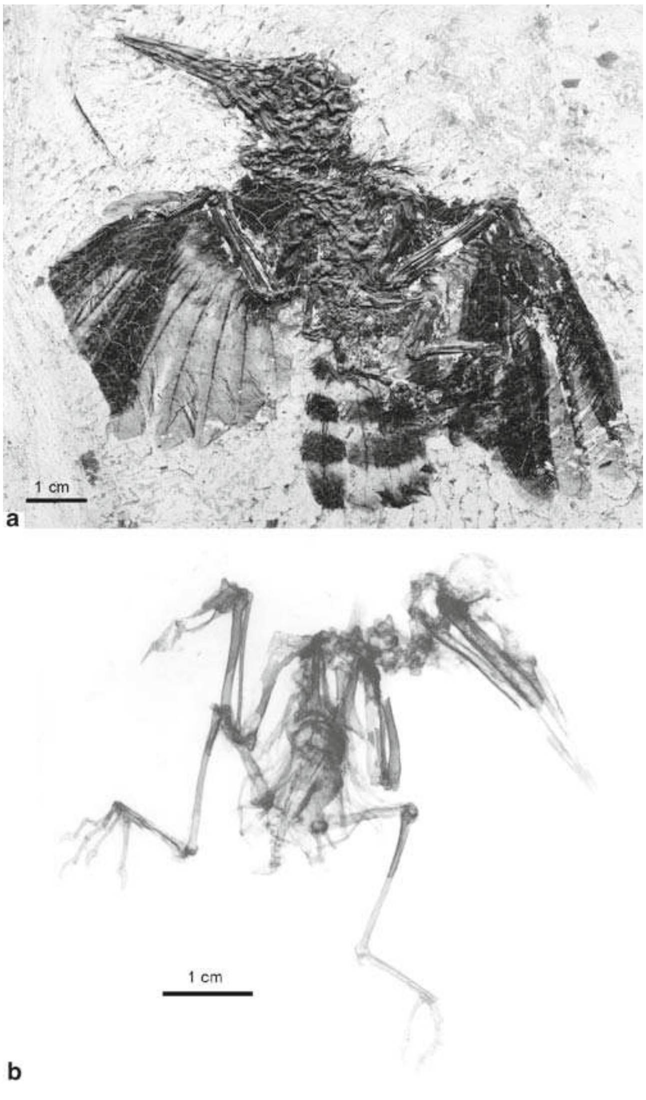

Fig. 16.12 Two specimens of the upupiform Messelirrisoridae from the middle Eocene of Messel. **a** *Messelirrisor grandis* Mayr, 2000 with well-preserved feathering (Hessisches Landesmuseum Darmstadt, Germany, HLMD-Be 178); **b** X-ray photograph of *M. halcyrostris* Mayr, 1998 (holotype, Forschungsinstitut Senckenberg, Frankfurt am Main, Germany SMF-ME 1883a + b). Note the distinct barring of the tail feathers of the specimen in **a**. (Photos by Sven Tränkner)

1998b, 2000h, 2006a). These fossils belong to the Messelirrisoridae, whose three named species, *Messelirrisor halcyrostris* Mayr, 1998, *M. parvus* Mayr, 1998, and *M. grandis* Mayr, 2000, mainly differ in size. Together with the Zygodactylidae, messelirrisorids are the most abundant small birds in Messel, and their fossil record consists of a fair number of well-preserved skeletons.

Messelirrisorids are small to tiny, long-beaked birds with a short tarsometatarsus and a very long hallux (Fig. 16.12). As in some extant Phoeniculidae, there seems to have existed a marked intraspecific variation in the length of the beak. In contrast

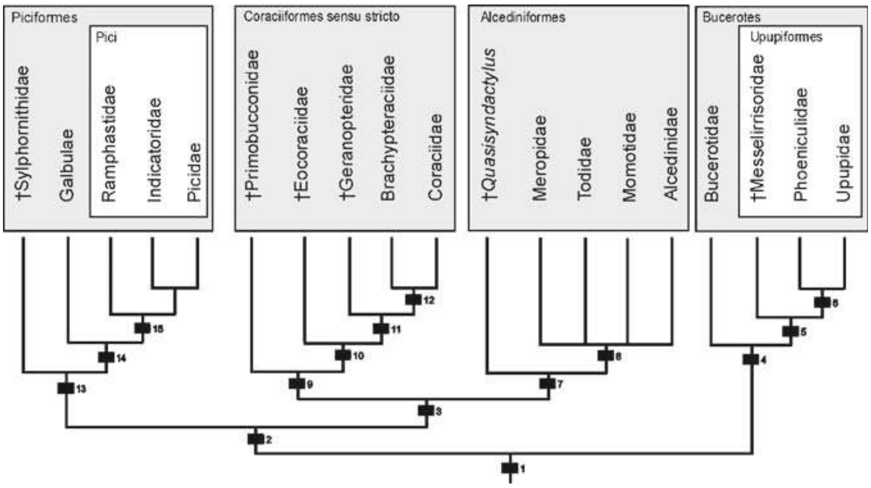

Fig. 16.13 Hypothesis on the phylogenetic relationships between Paleogene and extant representatives of the "Coraciiformes" (part) and Piciformes. Selected apomorphies of the nodes: *1* mandible of hatchling projecting beyond upper beak, greater ventral coverts of secondaries reduced; *2* acromion of scapula distinctly bifurcate (except Galbulae); *3* upper beak of nestling hooked; *4* mandibular symphysis rectangular, sternal manubrium with spina interna, femur with pneumatic foramen on craniolateral surface (except Messelirrisoridae); *5* mandible with large retroarticular processes, proximal end of ulna with projection on dorsal surface distal of dorsal cotyla, carpometacarpus with distinct ridge from caudal end of minor metacarpal to pisiform process; *6* sternal extremity of coracoid with marked medial projection; *7* proximal end of proximal phalanx of hindtoe with lateral projection, feet syndactyl; *8* sternal extremity of furcula very narrow; *9* minor metacarpal with ventrally protruding projection on ventral side of proximal end, distal interosseous canal (canalis interosseus distalis) of tarsometatarsus plantarly open; *10* postorbital process strongly elongated; *11* postorbital process with cranial projection, carpometacarpus with intermetacarpal process; *12* small foramen on ventral side of proximal part of minor metacarpal; *13* proximal phalanx of major wing digit with proximally protruding process (unknown for Sylphornithidae), humerus with far ventrodistally extending, large fossa for brachialis muscle which is situated on the far medial side of the bone and has a weakly developed ventral margin, carpometacarpus with well-developed intermetacarpal process which is fused with minor metacarpal, trochlea for fourth toe with plantarly projecting wing-like flange; *14* tarsometatarsal trochlea of fourth toe with well-developed accessory trochlea; *15* tarsometatarsus with large, distally elongated accessory trochlea and very small trochlea for second toe. (After Manegold 2005; Mayr 2004g, 2006a, 2008b; Mayr and Mourer-Chauviré 2000; Mayr et al. 2003).

to that in extant Upupiformes, the carpometacarpus bears an intermetacarpal process. Whereas crown group Upupiformes either forage on the ground (Upupidae) or are specialized toward trunk climbing (Phoeniculidae), messelirrisorids appear to have been perching birds (Mayr 1998b). In one specimen of *Messelirrisor* the tail feathers are distinctly barred, which may reflect the original color pattern, possibly through preservation of the melanosomes (Fig. 16.12; Vinther et al. 2008). In several other specimens of these birds from Messel fossilized uropygial gland waxes are preserved (Mayr 2006a)

A sister group relationship between the Messelirrisoridae and crown group Upupiformes (Fig. 16.13) is supported by a number of derived characters, including the presence of large, blade-like retroarticular processes on the mandible, a characteristic tubercle on the proximal shaft of the ulna, distal of the dorsal cotyla, and a distinct ridge from the caudal end of the minor metacarpal to the pisiform process (Mayr 1998b, 2006a). Messelirrisorids lack several derived characters shared by extant Bucerotes (Mayr 2006a), but their original identification as stem group representatives of the Upupiformes is supported by a phylogenetic analysis based on a comprehensive data set (Mayr 2006a).

An as yet undescribed skeleton from the Green River Formation, which was figured by Grande (1980, Fig. III.19) and Feduccia (1999, p. 335), also seems to be a member of the Bucerotes, as indicated by the very long hallux and the derived morphology of the carpometacarpus and distal tarsometatarsus. This specimen would constitute the first New World record of the taxon.

Mayr (1998b) noted that *Laurillardia longirostris* Milne-Edwards, 1871 and *L. munieri* Flot, 1891 from the late Eocene of the Paris Gypsum are stem group representatives of the Upupiformes. These species were before regarded as passeriform birds and assigned to the new taxon Laurillardiidae by Harrison (1979a). Small upupiform species were also found in the early Oligocene of the Lubéron; these fossils are in private collections (own observation).

16.7 Coraciidae/Brachypteraciidae (Rollers and Ground Rollers)

Extant rollers have an Old World distribution and include the Coraciidae (true rollers) and the more terrestrial, long-legged Madagascan Brachypteraciidae (ground rollers). They are characterized by very long postorbital processes of the skull. The minor metacarpal of the carpometacarpus further bears a pointed projection on the ventral side of its proximal end, and the distal interosseous canal (canalis interosseus distalis) of the tarsometatarsus is plantarly open, so there is a marked furrow between the trochleae for the third and fourth toes.

Three Paleogene stem group representatives of the Coraciidae/Brachypteraciidae were described, i.e., the Primobucconidae, Eocoraciidae, and Geranopteridae, and these are successive sister taxa of the crown group (Mayr and Mourer-Chauviré 2000; Mayr et al. 2004). Stem group representatives of the Coraciidae/

Brachypteraciidae are also known from the early Eocene of North America, where rollers do not occur today.

Extant rollers are almost exclusively carnivorous and feed on invertebrates and small vertebrates. It is thus notable that in the two known specimens of *Primobucco frugilegus* (Primobucconidae) and in one specimen of *Eocoracias brachyptera* (Eocoraciidae) seeds are preserved as stomach content (Mayr and Mourer-Chauviré 2000; Mayr et al. 2004). This indicates that stem group representatives of rollers may have been more generalized feeders than their modern relatives (Mayr et al. 2004).

16.7.1 †Primobucconidae

The Primobucconidae occur in early Eocene (MP 8/9–11) deposits of North America and Europe. The first species, *Primobucco mcgrewi*, was described by Brodkorb (1970) on the basis of a wing from the Green River Formation, and was considered to be the earliest representative of the Neotropical piciform puffbirds (Bucconidae). Feduccia and Martin (1976) classified *P. mcgrewi* in the taxon Primobucconidae, to which they also assigned other early Eocene fossils. The Primobucconidae *sensu* Feduccia and Martin (1976) are, however, polyphyletic (Houde and Olson 1989, 1992; Mayr and Peters 1998), and the taxon now only includes the species of *Primobucco*. As first recognized by Houde and Olson (1989), this latter taxon is a stem group representative of the Coraciidae/Brachypteraciidae.

Houde and Olson (1989) further identified a complete skeleton of *P. mcgrewi* from the Green River Formation. This fossil was studied in some more detail by Mayr et al. (2004), who described two very similar species from Messel as *P. perneri* and *P. frugilegus*. A three-dimensionally preserved tarsometatarsus of an unidentified species of the Primobucconidae was also reported from the early Eocene of France (Mayr et al. 2004). Specimens from the early Eocene of England, which were referred to the Primobucconidae by Olson and Feduccia (1979) and Harrison (1982a), have been wrongly identified (Mayr et al. 2004).

The species of *Primobucco* are short-legged birds and are much smaller than the representatives of the Eocoraciidae, Geranopteridae, and extant rollers. They are distinguished from the Eocoraciidae and Geranopteridae in the less robust beak and a proportionally shorter postorbital process. A presumably autapomorphic feature is the large distal vascular foramen of the tarsometatarsus.

16.7.2 †Eocoraciidae and †Geranopteridae

These two taxa are very similar to modern rollers in their skeletal morphology. *E. brachyptera* Mayr and Mourer-Chauviré, 2000 is known from articulated skeletons from Messel (Fig. 16.14). The fossils allow the recognition of greatly elongated

Fig. 16.14 Partial skeleton of *Eocoracias brachyptera* Mayr and Mourer-Chauviré, 2000 (Eocoraciidae) from the middle Eocene of Messel (Forschungsinstitut Senckenberg, Frankfurt am Main, Germany, SMF-ME 3364a). Specimen coated with ammonium chloride. (Photo by Sven Tränkner)

postorbital processes, and the tarsometatarsus is very short as in the extant taxon *Eurystomus* (Coraciidae). A number of plesiomorphic characteristics clearly distinguish *Eocoracias* from crown group rollers (Mayr and Mourer-Chauviré 2000). Some of the specimens exhibit excellent feather preservation, which shows that the short wings and the long and graduated tail of *E. brachyptera* resembled the feathering of the Brachypteraciidae, whereas the wing of the Coraciidae is more elongated and the tail more or less deeply forked. Outgroup comparisons with *E. brachyptera* thus suggest that the feathering of the Brachypteraciidae, which is suitable for agile maneuvering in a forested environment, is plesiomorphic for extant rollers. The elongated wing and forked tail of the Coraciidae are derived features, which allow a more rapid flight in the open habitats of true rollers (Mayr and Mourer-Chauviré 2000).

The Geranopteridae occur in the late Eocene of the Quercy fissure fillings, where they are represented by *Geranopterus alatus* Milne-Edwards, 1892, the smaller *G. milneedwardsi* Mayr and Mourer-Chauviré, 2000, and an unnamed species (Mayr and Mourer-Chauviré 2000; Mourer-Chauviré and Sigé 2006). Most major postcranial bones of *G. alatus* are known, and Mayr and Mourer-Chauviré (2000) also referred a partial skull to this species. The latter specimen shows that the postorbital process exhibits a small cranial projection, which is absent in *Eocoracias* but also occurs in extant Coraciidae and Brachypteraciidae. The carpometacarpus of *Geranopterus* further shares with that of the extant taxa the derived presence of a small intermetacarpal process, which is absent in the Primobucconidae and Eocoraciidae.

Cryptornis antiquus (Gervais, 1852), which is based on a largely complete but very poorly preserved skeleton from the late Eocene of the Paris Gypsum in France, appears to be closely related to, or even conspecific with, *G. alatus* (Mayr and Mourer-Chauviré 2000).

16.8 Alcediniformes (Bee-Eaters, Kingfishers, Todies, and Motmots)

Crown group Alcediniformes include the Alcedinidae (kingfishers) and Meropidae (bee-eaters), which predominantly (Alcedinidae) or exclusively (Meropidae) live in the Old World, and the Todidae (todies) and Momotidae (motmots), whose extant species are restricted to the New World. A clade including these four taxa can be supported by a derived morphology of the columella (Feduccia 1977). Because alcediniform birds dig earth tunnels for their nesting sites, they further have a syndactyl foot, in which the three anterior toes are tightly joined over much of their length.

Although the Todidae and Momotidae were traditionally assumed to be sister groups and share a derived morphology of the caudal end of the mandible (Olson 1976), molecular analyses support a clade (Todidae + (Momotidae + Alcedinidae)) whose sister taxon are the Meropidae (Ericson et al. 2006; Hackett et al. 2008).

All Paleogene Alcediniformes stem from European fossil sites. The earliest named species is *Quasisyndactylus longibrachis* Mayr, 1998 from Messel, which is a small bird and is comparatively abundant in the locality (Fig. 16.15). *Q. longibrachis* has a dorsoventrally flattened, very long, and remarkably tody-like beak. In contrast to that in crown group Todidae, however, the tarsometatarsus is rather short and the carpometacarpus lacks a well-developed intermetacarpal process. The proximal end of the first phalanx of the hindtoe bears a lateral projection, which is characteristic of crown group Alcediniformes. In all skeletons, the three anterior toes are further preserved in tight attachment, which indicates the former presence

Fig. 16.15 Skeleton of *Quasisyndactylus longibrachis* Mayr, 1998 (Alcediniformes) from the middle Eocene of Messel (Forschungsinstitut Senckenberg, Frankfurt am Main, Germany, SMF-ME 3543a). Specimen coated with ammonium chloride. (From Mayr 2004d; photo by Sven Tränkner)

of a syndactyl foot. Because of the presumably plesiomorphic morphology of the furcula, it has been hypothesized that *Q. longibrachis* is the sister taxon of crown group Alcediniformes (Mayr 1998b, 2004d).

Protornis glarniensis von Meyer, 1844 from the early Oligocene of Switzerland (Olson 1976) was assigned to the Momotidae by Olson (1976). The species is known from an incomplete skeleton. A second specimen referred to *P. glarniensis* by Peyer (1957) was identified as a trogon by Olson (1976). Among others, the proximal ends of the mandible of *P. glarniensis* exhibit marked incisions, which are a derived characteristic of extant Momotidae and Todidae. Except for the proportionally shorter symphysis, the wide and flat mandible of *Protornis* closely resembles that of the momotid taxa *Electron* and *Hylomanes*. Cracraft (1980) pointed out that Olson's (1976) assignment of *P. glarniensis* to the Momotidae was based on overall similarity and has not yet been established with derived characters. For biogeographic reasons he considered it more likely that *Protornis* is outside a clade including the Todidae and Momotidae. Whereas the former reservation is valid, the latter is only appropriate if one assumes a sister group relationship between Momotidae and Todidae and a New World stem species of the clade. As noted above, current molecular phylogenies do not support this assumption.

Moreover, stem group representatives of the Todidae, whose extant distribution is restricted to the Greater Antilles, also occur in the Paleogene of Europe. These fossils were assigned to the taxon *Palaeotodus*, which was originally erected by Olson (1976) for a species from the early Oligocene (Brule Formation) of Wyoming. The description of this North American species, *Palaeotodus emryi* Olson, 1976, was based on a skull and the proximal portion of a humerus, but there are undescribed postcranial remains of a second individual, which also comes from the Brule Formation (Mayr and Knopf 2007b). Because the humerus of *P. emryi* is proportionally larger than that of extant Todidae, Olson (1976) conjectured that Paleogene todies had better developed wings and dispersal capabilities than their extant relatives.

Two species of *Palaeotodus*, *P. escampsiensis* and *P. itardiensis*, were described by Mourer-Chauviré (1985) from the late Eocene (MP 19: *P. escampsiensis*) and early Oligocene (MP 23: *P. itardiensis*) of France. The description of *P. escampsiensis* is based on an incomplete humerus; of *P. itardiensis* a proximal ulna, distal tibiotarsus, and proximal tarsometatarsus were found. *P. itardiensis* is of size similar to that of *P. emryi* and is distinctly larger than extant todies, whereas *P. escampsiensis* is as small as the representatives of crown group Todidae.

A species of the Todidae which was identified as *Palaeotodus* cf. *itardiensis* also occurs in the early Oligocene of Wiesloch-Frauenweiler (Germany) and is known from a postcranial skeleton (Mayr and Knopf 2007b). This specimen shows that *Palaeotodus* agrees with extant Momotidae and Todidae in its long hindlimbs (the greatly elongated and slender tarsometatarsus is almost the length of the humerus) and the complete reduction of the procoracoid process of the coracoid. As in crown group Todidae, the carpometacarpus further bears a large intermetacarpal process. The distal end of the tarsometatarsus exhibits, however, a more plesiomorphic morphology than that of modern todies.

The extant Old World taxa of the Alcediniformes, i.e., the Meropidae and Alcedinidae, have no published Paleogene fossil record. Although Mourer-Chauviré (1982, 2006) tentatively identified both in the Quercy fissure fillings, the fragmentary remains have not yet been described and need to be substantiated by further material.

16.9 Piciformes (Jacamars, Puffbirds, Woodpeckers, and Allies)

The zygodactyl Piciformes comprise the Neotropic Galbulae (jacamars and puffbirds) and the Pici (barbets, toucans, honeyguides, woodpeckers and allies), which have a nearly worldwide distribution but do not occur in the Australian region and on Madagascar. In addition to a unique arrangement of the digital flexor tendons, piciform birds exhibit a derived morphology of the proximal phalanx of the major digit of the wing (Mayr et al. 2003; Manegold 2005).

The Paleogene fossil record of piciform birds is still quite scanty. Most notably, all known specimens are from very small species, some of which are even smaller than the smallest extant Piciformes. A very poorly known species with possible piciform affinities is "*Neanis*" *kistneri* Feduccia, 1973, a zygodactyl bird from the Green River Formation. "*N.*" *kistneri* was considered a piciform bird in the original description (Feduccia 1973) and was regarded as closely related to the Galbulae by Houde and Olson (1989). The latter authors also first recognized that it is not a congener of *N. schucherti* (see Sect. 16.10). The holotype of "*N.*" *kistneri* was meanwhile transferred on a resin slab, so additional osteological details are visible. A specimen from the Green River Formation that was figured by Davis and Briggs (1998, Fig. 2B) probably belongs to the same group of birds (Weidig 2003; own observation). The feet of "*N.*" *kistneri* exhibit a zygodactyl position and the trochlea for the fourth toe bears a well-developed accessory trochlea. The tarsometatarsus is shorter than that of the Zygodactylidae, and the procoracoid process of the coracoid is long and slender. However, despite some overall similarity to those of extant Galbulae, piciform affinities of "*N.*" *kistneri* have not yet been well based, and better preserved specimens are needed to firmly establish the phylogenetic affinities of this species.

16.9.1 †Sylphornithidae

The Sylphornithidae are tiny, long-legged birds, which were first described by Mourer-Chauviré (1988a) from the late Eocene (MP 16) locality Bretou of the Quercy fissure fillings. Of this French species, *Sylphornis bretouensis* Mourer-Chauviré, 1988, major portions of all limb bones are known (Mourer-Chauviré 1988a; Mayr 1998b). As noted by Mayr (1998b), the coeval and similarly sized *Palaegithalus cuvieri* (Gervais, 1848–1852) from the late Eocene of the Paris Gypsum, which was originally described as a passeriform bird, may also be a member of the Sylphornithidae. The very poor preservation of the only known skeleton of this species does, however, not allow a definitive assignment, and alternatively the fossil could be from a representative of the Zygodactylidae (Sect. 16.4.1). A further species, *Oligosylphe mourerchauvireae*, was described by Mayr and Smith (2002b) from the early Oligocene of Belgium and is based on a distal tarsometatarsus and tibiotarsus.

Sylphornithids are well characterized by an extraordinarily long and slender tarsometatarsus, whose distal end is very wide and bears short trochleae. The trochlea for the fourth toe exhibits a caudally directed wing-like flange, which indicates that the foot was at least facultatively zygodactyl. The carpometacarpus of *Sylphornis* bears a large intermetacarpal process similar to that of extant Piciformes and Passeriformes (Mayr 1998b). Sylphornithids differ from the equally long-legged Zygodactylidae not only in the absence of an accessory trochlea on the trochlea for the fourth toe, but also in the configuration of the other tarsometatarsal trochleae.

In further contrast to zygodactylids, in sylphornithids the hypotarsus does not enclose a canal for the tendon of the flexor hallucis longus muscle. Mourer-Chauviré (1988a) recognized similarities in the hypotarsus morphology of *Sylphornis* and the piciform Galbulae, and a cladistic analysis by Mayr (2004g) also supported piciform affinities of the Sylphornithidae, which resulted as sister taxon of either the Galbulae or the clade (Pici + Galbulae). It is, however, well possible that future findings may lead to a revision of the phylogenetic affinities of these enigmatic birds.

16.9.2 Pici

All Paleogene remains of the Pici come from Europe, and these fossils have a modern-type skeletal morphology. The earliest specimens, from the early Oligocene of Belgium and Germany, belong to species which are much smaller than any extant European Pici. A tarsometatarsus of a representative of the Pici was further reported from the late Oligocene of Germany (Mayr 2001f). The only named species, *Rupelramphastoides knopfi* Mayr, 2005, from the early Oligocene Wiesloch-Frauenweiler locality in southern Germany is represented by two partial skeletons, which constitute the most substantial remains of Paleogene Pici (Mayr 2005l, 2006g). *R. knopfi* is the smallest known species of the Pici, being smaller even than extant Picumninae. It is clearly identified as representative of the Pici by the presence of a very large and narrow accessory trochlea for the retroverted fourth toe, a very narrow tarsometatarsal trochlea for the second toe, and marked ulnar papillae for the attachment of the secondaries. In its proportions, the skull resembles that of the extant Scaly-throated Honeyguide, *Indicator variegatus* (Indicatoridae). A further phylogenetic assignment of *Rupelramphastoides* is, however, not straightforward. The tarsometatarsus is elongate as in many extant Ramphastidae, but the bill morphology shows that the fossil taxon is outside crown group Ramphastidae, which share smaller and more strongly ossified narial openings. The similarities between *Rupelramphastoides* and extant Ramphastidae may well be plesiomorphic for the Pici. Whereas the sternum of the fossil taxon exhibits a bifurcated manubrium, which is a derived characteristic of the Picidae, the plesiomorphic absence of an ossified extensor bridge (arcus extensorius) on the proximal tarsometatarsus supports a position outside a clade including the Indicatoridae and Picidae (Mayr 2005l, 2006g).

16.10 †Gracilitarsidae

This taxon was established for *Gracilitarsus mirabilis* Mayr, 1998, a tiny, long-legged bird, which is known from three skeletons from Messel (Fig. 16.16; Mayr 1998b, 2001g, 2005m). The limb proportions of this species have no counterpart

Fig. 16.16 Skeleton of *Gracilitarsus mirabilis* Mayr, 1998 (Gracilitarsidae) from the middle Eocene of Messel (Forschungsinstitut Senckenberg, Frankfurt am Main, Germany, SMF-ME 3547). Specimen coated with ammonium chloride. (Photo by Sven Tränkner)

among extant birds. The stout and short humerus and the very long forearm indicate that it may have been an aerial specialist, similar to Apodiformes and the passeriform Hirundinidae (swallows). Whereas, however, the latter have short legs, the tarsometatarsus of *Gracilitarsus* is very long and slender. Further, most unusually, the three anterior toes, which bear dorsoventrally deep ungual phalanges, are of nearly equal length owing to the fact that the proximal phalanges of the third and fourth toes are shortened. The alular phalanx of the wing exhibits an unusually well developed ungual phalanx.

As in the Sylphornithidae (Sect. 16.9.1), the minor metacarpal distinctly exceeds the major metacarpal distally. *Gracilitarsus* is, however, distinguished from the likewise tiny and long-legged *Sylphornis* in the more elongated carpometacarpus, the narrower distal end of the tarsometatarsus, and in that the trochlea for the third toe bears a deep furrow, as in some extant trunk-climbing birds.

According to the shape of its beak, which is of similar proportions to that of some short-billed passeriform Nectariniidae (sunbirds), *G. mirabilis* was probably either insectivorous or nectarivorous. Because of the lack of an extant analog, the peculiar foot morphology is difficult to interpret, but *Gracilitarsus* may have used its feet for clinging to vertical surfaces, possibly owing to a specialized feeding technique (Mayr 2001g). Given the fact that a similar foot structure, i.e., a greatly elongated tarsometatarsus with rather short anterior toes of subequal length, does not occur in extant birds, it is notable that the coliiform taxon *Masillacolius*, which also occurs in Messel (Sect. 16.2.2), exhibits a very similar foot morphology.

A phylogenetic analysis supported a clade including Gracilitarsidae, Sylphornithidae, and crown group Piciformes (Mayr 2005m), but this hypothesis is not yet well established. Gracilitarsidae and modern Piciformes exhibit a distinct notch on the medial side of the sternal end of the coracoid, which was hypothesized to be an apomorphy of Piciformes by Mayr et al. (2003). Manegold (2005) showed, however, that this character has a wider distribution among "higher land birds."

Mayr (2001g, 2005m) compared *Gracilitarsus* with two other Paleogene birds, *Eutreptodactylus itaboraiensis* Baird and Vickers-Rich, 1997 from the late Paleocene of Itaboraí in Brazil and *Neanis schucherti* (Shufeldt, 1913) from the early Eocene Green River Formation. *E. itaboraiensis* is known from a morphologically distinct tarsometatarsus. The bone has a strongly medially projecting trochlea for the second toe and a plantarly directed, wing-like flange on the trochlea for the fourth toe (Baird and Vickers-Rich 1997). The latter feature indicates the presence of semizygodactyl or facultatively zygodactyl feet. Whether or not this feature was present in *Gracilitarsus* cannot be discerned in the known specimens. However, the tarsometatarsus of *E. itaboraiensis* shares with that of *G. mirabilis* the presence of a marked furrow on the dorsal surface of the distal end, between the trochleae for the third and fourth toes, and is also similar in overall morphology. *E. itaboraiensis* was considered to be a representative of the Cuculiformes in the original description, but this hypothesis is only weakly supported by the morphology of the specimen.

N. schucherti is based on a wing and pectoral girdle elements from the Green River Formation. The wing shows similar proportions to that of *G. mirabilis* and the coracoid exhibits a notch in the medial margin of the sternal extremity. *N. schucherti* was originally described as a passeriform bird, but was considered to be an aerial specialist by Houde and Olson (1989). Although the remains of this species are very similar to the corresponding bones of *Gracilitarsus*, the discovery of hindlimb elements is needed to ultimately prove the hypothesis of a closer relationship.

16.11 †Cladornithidae

The phylogenetic affinities of few avian taxa are as enigmatic as those of *Cladornis pachypus* Ameghino, 1895. The holotype and only fossil record of this large species is an incomplete tarsometatarsus from the late Oligocene (Deseadan) of the

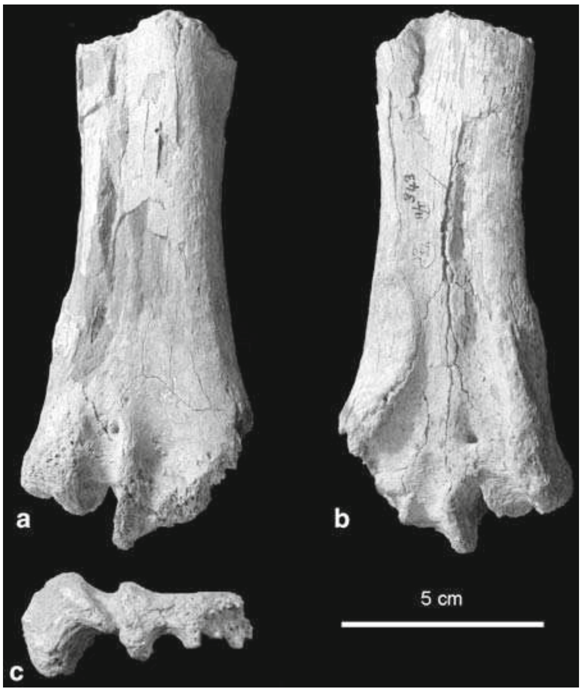

Fig. 16.17 Right tarsometatarsus of *Cladornis pachypus* Ameghino, 1895 from the late Oligocene of Patagonia (holotype, Natural History Museum, London, UK, BMNH A 589) in dorsal (**a**), plantar (**b**), and distal (**c**) views. (Photos by Sven Tränkner)

Argentinian part of Patagonia. Ameghino (1895) identified *C. pachypus* as a penguin-like aquatic bird, but Simpson (1946) rejected sphenisciform affinities of *Cladornis*. Olson (1985, p. 193) remarked that the bone "appears to be from some sort of very large and extremely weird land bird." The tarsometatarsus of *C. pachypus*, of which a photo is published here for the first time (Fig. 16.17), is very flat dorsoventrally and appears to have been quite short; although the proximal end is not preserved, the proportions of the shaft indicate that probably not more than about one quarter of the bone is missing. Judging from the presence of a very large articulation facet for the first metatarsal, *C. pachypus* had a well-developed hallux; the distal vascular foramen is very small. The rims of the trochlea for the third toe are separated by a marked furrow, and the trochlea for the fourth toe bears a plantarly directed flange, which led Olson (1985, p. 193) to assume that *C. pachypus* may have been "tending toward being zygodactyl." Placement of *Cladornis* in the present chapter is nevertheless largely by default. Although the taxon is highly distinctive, its phylogenetic affinities cannot be resolved without additional fossil material

Chapter 17
Paleogene Avifaunas: Synopsis of General Aspects

Probably owing to the formation of the circum-Antarctic current after separation of South America and Australia from Antarctica, the Paleogene witnessed global cooling (Berggren and Prothero 1992). Changes in continental geography owing to plate tectonics and sea-level fluctuations further influenced faunal interchanges between major geographic areas. A great number of publications have dealt with the effect of these events on mammalian evolution (e.g., Janis 1993; Cox 2000; Rose 2006), but their impact on Paleogene avifaunas is still poorly understood. Even fewer published data exist on ecological aspects of Paleogene bird communities, such as competition with mammals or between avian taxa. In the following sections some general aspects of the evolution of Paleogene avifaunas which pertain to these issues are outlined. The temporal distributions of major fossil taxa are summarized in the tables in the Appendix and form the basis of some of the subsequent notes.

17.1 Continental Avifaunas of the Northern Hemisphere

The pre-Oligocene avifauna of Europe and North America includes many archaic forms, which are morphologically clearly distinguished from modern bird groups. No crown group representatives of extant family-level taxa are known from Eocene or earlier fossil sites (Mayr 2005a), although some early Eocene taxa are morphologically very similar to their extant relatives, such as *Scaniacypselus* and crown group swifts (Apodidae), *Plesiocathartes* and the extant Courol (Leptosomidae), and *Eocoracias* and modern rollers (Coraciidae and Brachypteraciidae).

17.1.1 Biogeography

Europe and North America were connected by northern latitude land corridors via Greenland in the late Paleocene and early Eocene, whose existence was terminated by the opening of the North Atlantic (Smith et al. 1994). Until the early Oligocene,

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Europe was further separated from Asia by the Turgai Strait, an epicontinental sea which divided the Eurasian land mass. Whereas overland dispersal between Europe and Asia was thus aggravated in the early Paleogene, intermittent land connections via Beringia existed during the whole Cenozoic (Rose 2006).

Given the occurrence of similar mammalian taxa in the Paleocene of North America and Europe (Rose 2006), it would be very surprising if there were not also significant concordances in the avifaunas of that time. However, the known Paleocene nonmarine avifaunas of Europe and North America share few closely allied taxa. Although strigiform birds occur on both continents, with *Ogygoptynx* in North America and *Berruornis* in Europe, they represent morphologically very different lineages (Sects. 15.1, 15.3). Whether there were representatives of the Lithornithidae in the Paleocene of Europe is uncertain, as identification of the fragmentary Walbeck coracoid is only tentative (see Sect. 5.1). The Gastornithidae seem to have been restricted to Europe in the Paleocene, whereas Paleocene Presbyornithidae have so far only been recorded from North America. Admittedly, it has to be kept in mind that the Paleocene fossil record of birds is still much less known than that of contemporary mammals; therefore, general conclusions cannot yet been drawn and the picture may change with future discoveries.

There was a maximum interchange of mammalian faunas between Europe and North America in the early Eocene (Janis 1993; Rose 2006). Previous authors (e.g., Houde and Olson 1989; Peters 1991; Blondel and Mourer-Chauviré 1998) recognized that the early Eocene avifaunas of Europe and North America were also very similar. The occurrence of the flightless Gastornithidae in the early Eocene of North America and Europe actually provides direct evidence for the existence of a land connection by that time or shortly before (Andors 1992). Other avian groups which occur in the early/middle Eocene of both Europe and North America are the Lithornithidae, Gallinuloididae, Messelornithidae, Juncitarsinae, Messelasturidae, Primobucconidae, stem group Leptosomidae (*Plesiocathartes*), Sandcoleidae and other stem group Coliiformes (*Chascacocolius*), Fluvioviridavidae, Halcyornithidae ("Pseudasturidae"), and Zygodactylidae. The representatives of most of these taxa were forest-dwelling birds, which is in concordance with the existence of extensive paratropical forests in the early Eocene of at least the western part of the Northern Hemisphere (Blondel and Mourer-Chauviré 1998).

Several taxa were only found in the early and middle Eocene of either North America or Europe, but because some of the most productive fossil localities on these two continents represent different paleoenvironments (Chap. 2), there remains a possibility that this is an artifact of the incomplete fossil record. So far exclusively known from the early Eocene of North America are the frigatebird *Limnofregata*, unambiguous Presbyornithidae, the Foratidae, stem group representatives of the Steatornithidae, and the Geranoididae. Taxa which were only reported from European deposits include the Palaeotididae, Remiornithidae, Ameghinornithidae, Idiornithidae, Archaeotrogonidae, stem group Nyctibiidae and Trochilidae, as well as unambiguous representatives of the Aegialornithidae.

Opening of the North Atlantic after the early Eocene limited overland dispersal between Europe and North America to land connections via Beringia. Nevertheless, the early Oligocene avifaunas of Europe and North America were still remarkably similar. Taxa which were reported from the latest Eocene/early Oligocene of North America and Europe include stem group Todidae (*Palaeotodus*), the putative stem group cuculiform *Eocuculus*, and stem group representatives of the Coliidae (*Palaeospiza* in North America and *Primocolius* and *Oligocolius* in Europe). Again, the avifaunal congruencies seem to be greatest for forest-dwelling taxa, whereas the terrestrial avifaunas of Europe and North America already appear to have been more different in the early Oligocene. The Bathornithidae, for example, are only known from North America, where they are a common avifaunal element. The Idiornithidae, on the other hand, have not been reported from North American fossil sites.

Because Europe and Asia were separated by the Turgai Strait in the early Eocene, it is likely that the flightless Gastornithidae dispersed into Asia from western North America rather than Europe, where the group seems to have originated (Sect. 6.2). An exact stratigraphic correlation of the Asian and North American records of these birds would, however, be required to confirm this hypothesis. If the North American Geranoididae are indeed most closely related to the Asian Eogruidae (Sect. 9.3.2), a dispersal route from North America to Asia via Beringia may also have been used by a species in the stem lineage of the latter.

Closure of the Turgai Strait at the beginning of the Oligocene facilitated an exchange between European and Asian faunal elements. Immigration of new taxa from Asia was probably one of the major factors which led to a marked faunal turnover in Europe, known as the “Grande Coupure” (Prothero 1994; Hooker et al. 2004). Little has so far been published on the impact of this event on the European avifauna at the Eocene–Oligocene boundary, and all observations were made for the Quercy taxa (Mourer-Chauviré 1980, 1988b). As yet, only a few avian groups with an extensive early Paleogene fossil record are known that disappear at the Eocene–Oligocene boundary, i.e., the Quercymegapodiidae, Quercypsittidae, the putative idiornithid *Elaphrocnemus*, and the Aegialornithidae. In contrast, there are a fair number of taxa which have their earliest European fossil record in the latest Eocene/earliest Oligocene, including the Anatidae, Phasianidae, Phalacrocoracidae, Palaelodidae, Gaviiformes (*Colymboides*), Rallidae, Parvigruidae, Charadriiformes, Pici, and Passeriformes. Many of these latter groups are aquatic and semi-aquatic, so the Turgai Strait may not have formed an insurmountable barrier. Their occurrence in Europe thus cannot be convincingly ascribed to the disappearance of this epicontinental sea. The absence of some of these birds in earlier deposits may be an artifact of the fossil record, as most of our knowledge on late Eocene European avifaunas stems from the Quercy deposits, which mainly include terrestrial and arboreal forms. An immigration from Asia is, however, likely for the Passeriformes, which may well have originated in the Australian region (Sect. 17.2.1). Because extant Phasianidae and Pici have limited capabilities for crossing open sea, the occurrence of these taxa in the early Oligocene of Europe may also be due to immigration from Asia after closure of the Turgai Strait (see also Sect. 17.2.1).

17.1.2 Climatic Cooling and Avifaunal Turnovers

The early Eocene thermal maximum was followed by global cooling, with major temperature decreases in the early-middle Eocene (50–48 Ma), late Eocene (40–36 Ma), and early Oligocene (35–34 Ma) (Zachos et al. 2001). These climatic changes are temporally correlated with significant faunal extinction events at the end of the middle Eocene – the most severe of all prehuman Cenozoic mass extinctions – and in the earliest Oligocene (Prothero 1994).

As detailed in the preceding section and at least concerning European mammals, the early Oligocene extinction events are only indirectly related to climatic changes, but can be traced back to faunal exchanges owing to the disappearance of major geographic barriers. Concerning the Eocene extinctions, Lindow and Dyke (2006, p. 483) assumed that climatic changes did play a major role and that "deteriorations in climate beginning in the middle Eocene appear to be responsible for the demise of previously widespread avian lineages like Lithornithiformes and Gastornithidae." The factual basis for such generalized conclusions is still, however, rather slim. Unquestionably, there are many avian taxa which seem to have been widespread in the early and middle Eocene and have no unambiguous later fossil record. In addition to the Gastornithidae and Lithornithidae, these include the Presbyornithidae, Gallinuloididae, Prophaethontidae, Sandcoleidae, Halcyornithidae ("Pseudasturidae"), Messelasturidae, Primobucconidae, and Fluvioviridavidae. Other avian groups, such as the Leptosomidae, Nyctibiidae, and Steatornithidae, at least disappear from the Northern Hemisphere after the middle or late Eocene. At present, however, our knowledge of the exact stratigraphic occurrence of these taxa is simply too poor to correlate their extinctions with other biotic and abiotic events.

In the Northern Hemisphere, climatic cooling had a profound impact on the vegetation of North America, where paratropical rainforests were replaced by open and more arid woodlands toward the late Eocene and Oligocene. These environmental changes affected the diversity and composition of mammalian faunas and led to a decimation of arboreal species toward the Oligocene (Webb 1977; Janis 1993; Cox 2000). Likewise, they are probably responsible for the disappearance of many lineages of early Paleogene forest-dwelling birds from North America. The Zygodactylidae, for example, have no fossil record in North America after the early Eocene, but were still quite common in Europe in the early Neogene. Coliiform birds occurred in the early Eocene of Europe and North America, and during this period very similar species lived on both continents. Their latest record in North America is the late Eocene *Palaeospiza bella* (Sect. 16.2.2), whereas coliiform birds persisted into the Neogene in Europe (Ballmann 1969b). The same is true for stem group representatives of the Coraciidae/Brachypteraciidae, which are only known from the early Eocene of North America, but evolved into present day rollers in the Old World. The Protostrigidae may also have survived longer in Europe, where they were found in early Oligocene deposits, whereas all North American records are of Eocene age.

In Europe, the Tethys Sea had a moderating effect, so "European floras never reached the extremes of cooling or drying seen in North America" (p. 154 in

Prothero 1994). As yet, no convincing evidence has been presented that climatic cooling had a major impact on the demise of avian higher-level taxa in the Eocene of Europe (contra Lindow and Dyke 2006). Climatic cooling certainly explains today's absence of frugivorous and insectivorous birds with poor dispersal capabilities in natural higher-latitude habitats of the Northern Hemisphere, such as the Trogonidae, Coliidae, and Psittacidae. However, the Oligocene climate was still rather equable, and in Europe the taxa just mentioned persisted into the Neogene (Olson 1985; Feduccia 1999). Their extinction was probably not before further climatic cooling toward the Pliocene had led to the cold Northern Hemisphere winters with little food supply for nonmigrating insectivorous or frugivorous birds.

Concerning mammalian evolution, Alroy et al. (2000: 259) concluded that "over the scale of the whole Cenozoic, intrinsic, biotic factors like logistic diversity dynamics and within-lineage evolutionary trends seem to be far more important" than climatic changes. The same is also likely to be true in the case of birds, in particular those of the Eocene epoch.

17.2 Continental Avifaunas of the Southern Hemisphere

Despite their rather poor fossil record, the southern continents have played a significant role in discussions on the historical biogeography of modern avian groups. A number of extant higher-level taxa with species in the Northern Hemisphere further seem to have had their origin in the Southern Hemisphere. Such was assumed by Olson (1989) for the Anseriformes, Psittaciformes, Podicipedidae, Columbiformes, and Passeriformes. Stem group representatives of the first two of these groups are now known from the Paleogene of the Northern Hemisphere. In addition to the latter three taxa listed by Olson (1987), a Southern Hemisphere origin is, however, likely for Falconidae and Pelecanidae (see Sects. 7.6, 14.1).

17.2.1 Biogeography

Breakup of the Southern Hemisphere supercontinent Gondwana was largely completed at the beginning of the Paleogene (Smith et al. 1994). Africa separated from South America about 100 Ma, and Madagascar split from continental Africa in the middle to early-late Jurassic, about 155–160 Ma. Through the Lord Howe Rise, New Zealand was possibly connected to Australia until 75 Ma (Haddrath and Baker 2001). A land connection between South America and Antarctica may have persisted until the late Eocene, about 36 Ma, when the Drake Passage opened, and overland dispersal between Antarctica and Australia was possible at least until 64 Ma (Woodburne and Case 1996).

Cracraft (1973b) was among the first to discuss the extant distribution of birds in the light of the Mesozoic and Paleogene geography of the land masses. In particular, he assumed that the early divergences of several extant clades with Southern Hemisphere representatives were due to the breakup of the southern continents in the late Cretaceous. Cracraft (2001) further expounded this hypothesis of a vicariant origin of extant avian higher-level taxa, concluding that "trans-Antarctic distribution patterns" of several neornithine taxa indicate their origin in the Cretaceous of Gondwana. Similar hypotheses were also set up by molecular systematists for the initial divergences within some neoavian taxa, for example, crown group Psittaciformes (Miyaki et al. 1998) and Passeriformes (Ericson et al. 2002, 2003).

That such inferences based on the distribution of extant taxa can be profoundly misleading is, for example, shown by marsupial mammals, which are today restricted to Australia and the Americas, but originated in Asia (Rose 2006). Concerning birds, a comprehensible case for a diversification owing to the breakup of Gondwana can at best be made for the flightless ratites. If these constitute a monophyletic group, it is likely that their stem species was already flightless, so dispersal of the ancestors of the extant ratite lineages would have strongly depended on continental geography. The existence of supposed crown group representatives of ratites in the Paleocene of South America (*Diogenornis*) would further be in line with a diversification of crown group ratites in the late Cretaceous of the Southern Hemisphere.

As mentioned in the introduction to Chap. 5, however, analyses of nuclear DNA by Hackett et al. (2008) and Harshman et al. (2008) strongly supported paraphyly of ratites with respect to the Tinamidae. In the phylogenies proposed by these authors, flightlessness would have occurred at least three times independently in the stem lineages of the Struthionidae, Rheidae, and Apterygidae/Casuariidae. If the results of those analyses are confirmed by further studies, the stem species of the aforementioned ratite lineages would not have depended on land corridors for their dispersal (Harshman et al. 2008; see also Houde 1988; Briggs 2003).

In fact, all earlier hypotheses on ratite biogeography faced problems to fully match the paleogeography of the continents with the presumed pattern of ratite evolution. Proceeding from a flightless stem species of ratites, van Tuinen et al. (1998), for example, proposed two scenarios for the early diversification of palaeognathous birds (tinamous and ratites), one in which an African origin of the stem species was assumed, and another in which the stem species lived in South America. As long as no consensus exists on the interrelationships of extant ratites, such biogeographic considerations are afflicted with many uncertainties. As noted above, there probably existed overland dispersal routes between South America and Australia/New Zealand via Antarctica in the late Cretaceous, which could have been used by flightless stem species of the South American and Australian/New Zealand ratites. Apparently, however, the land connection between Antarctica and

Australia would have then acted as a filter route, and was not available for phorusrhacid birds, for example.

It is less straightforward to explain overland dispersal of a flightless stem species of the Aepyornithidae to Madagascar. Although there may have been a connection between Antarctica and Madagascar via the Kerguelen Plateau until 90 Ma (Masters et al. 2006), this date just overlaps with an age determination for the divergence of ratites from their sister taxon based on molecular clocks, which was estimated at 92.2 ± 18.9 Ma by Haddrath and Baker (2001) (van Tuinen et al. 1998 assumed that the earliest divergence between crown group ratites did not occur before about 90 Ma).

Ratites are known from the Paleocene of South America (*Diogenornis*) and Europe (*Remiornis*). The reconstruction of possible late Cretaceous/early Paleogene dispersal routes between these continents is another challenge in their historical biogeography, if ratites are monophyletic and descend from a flightless stem species. The existence of such dispersal routes is evidenced by the distribution of metatherian mammals, which also have a Paleocene fossil record in South America and the Northern Hemisphere (North America and Eurasia) (Rose 2006). As yet, however, there is no unambiguous evidence for a continuous land connection between South America and North America in the late Cretaceous or early Paleogene (Smith et al. 1994; Iturralde-Vinent and MacPhee 1999), and chance dispersal with flotsam via a proto-Antillean island chain is more easily envisioned for a small mammal than for a medium-sized ratite. Because no fossils of ratites were further found in Cenozoic deposits of North America, Peters and Storch (1993) suggested an alternative late Cretaceous dispersal route between South America and Europe via Africa.

The distributions of extant Megapodiidae (mainly Australian continental plate) and Cracidae (South America) have also been taken as evidence for a vicariant diversification of crown group Galliformes owing to the breakup of Gondwana in the late Cretaceous (Cracraft 1973b, 2001). This hypothesis conflicts, however, with the absence of crown group Galliformes in pre-Oligocene fossil deposits (Mayr and Weidig 2004). The earliest stem group representatives of the Galliformes were further reported from the Northern Hemisphere and are successively more closely related to crown group Galliformes. Moreover, the earliest galliform birds from South America also belong to the stem group (Sect. 6.1.4). The fossil record thus rather suggests a Northern Hemisphere origin of crown group Galliformes, whose stem species may have lived in the late Eocene/early Oligocene of Asia. From there, the Phasianidae dispersed into Europe after closure of the Turgai Strait in the early Oligocene, and a species in the stem lineage of the Megapodiidae could have reached Australia after northward drift brought this continent close to Asia in the Oligocene. The stem species of the Cracidae most likely dispersed into South America via North America, which was connected with Asia through Beringia during most of the Paleogene.

Current evidence for a diversification of neoavian lineages owing to the breakup of Gondwana is very weak. The traditional "Gruiformes," which were cited as an example of a neoavian taxon with a "trans-Antarctic distribution pattern" by

Cracraft (2001), constitute a polyphyletic assemblage (Chap. 3). Without knowledge of the exact interrelationships between these birds, a plausible reconstruction of biogeographic scenarios is not possible. Likewise the "Caprimulgiformes," another taxon listed by Cracraft (2001), are not monophyletic, and, except for the Aegothelidae, all extant representatives with a Southern Hemisphere distribution (Steatornithidae, Podargidae, and Nyctibiidae) have stem group representatives in the Northern Hemisphere. Although the Passeriformes probably originated in the Southern Hemisphere, an early diversification of the crown group due to the breakup of Gondwana is also not well supported (contra Cracraft 2001; Ericson et al. 2002, 2003). There is strong evidence for an origin of Oscines on the Australian continental plate (Barker et al. 2002; Ericson et al. 2002, 2003), but the area of origin of the Suboscines is less certain, and the distribution of the Acanthisittidae is restricted to New Zealand. Present data are in agreement with a Paleogene origin of crown group Passeriformes on the Australian continental plate. The Suboscines may have dispersed into South America via Antarctica only before the onset of glaciation of this continent, and the fossil record (Sect. 16.4.2) rather indicates dispersal over the Northern Hemisphere and a late, i.e., Neogene, arrival in South America and Africa.

Not many of the characteristic groups which occur in the early Paleogene of the Northern Hemisphere have been recorded from the Southern Hemisphere. With a few exceptions, such as the anseriform Presbyornithidae, the known Paleogene nonmarine avifauna of South America is clearly distinguished from that of other continents (see Tables A.1–A.6 in the Appendix). Taxa such as the Lithornithidae, Sandcoleidae, and Halcyornithidae have an abundant fossil record in the Eocene of Europe and North America, but have not yet been identified in Southern Hemisphere deposits. Campbell and Tonni (1981) noted that Cenozoic avifaunas of South America are characterized by the dominance of large carnivorous birds, most notably phorusrhacids and teratorns, which may be correlated with a low diversity of large mammalian carnivores (van Valkenburgh 1999). It is, however, remarkable, that no representatives of the Strigiformes have as yet been reported from the Paleogene of South America, whereas owls are among the more abundant avian taxa in the Paleogene of the Northern Hemisphere.

The late Eocene/early Oligocene avifauna of the Fayum in Egypt includes several higher-level taxa, which today still occur on this continent (see the Appendix). If the identifications of the often fragmentary remains from this locality are confirmed by future findings, some taxa are shared with contemporaneous avifaunas of Europe (e.g., Palaelodidae, Pandionidae). Others are, however, as yet unknown from the early Oligocene of Europe (e.g., Ciconiidae, Ardeidae), or seem to represent African endemics (Eremopezidae, Xenerodiopidae).

Virtually nothing can be said about the Paleogene avifauna of Africa south of the Sahara, and likewise our knowledge of the early Paleogene avifauna of Australia is far too incomplete for generalized conclusions.

17.2.2 Extant Southern Hemisphere "Endemics" in the Paleogene of the Northern Hemisphere

It has long been recognized that the distribution of many extant avian taxa is very different from that of their Paleogene stem group representatives (Mourer-Chauviré 1982; Olson 1989). Mourer-Chauviré (1982) pointed out that the closest living relatives of several bird groups found in the Quercy fissure fillings in France are today restricted to the Southern Hemisphere. In particular, there is a notably high number of birds in these localities and other Paleogene fossil sites of the Northern Hemisphere whose closest extant relatives only occur in Central America or South America (Mourer-Chauviré 1999b; James 2005; Mayr 2005a). Such is true for stem group representatives of the Cariamidae (middle Eocene to late Oligocene of Europe and late Eocene to late Oligocene of North America), Steatornithidae (early Eocene of North America), Nyctibiidae (Eocene of Europe), Trochilidae (middle Eocene to early Oligocene of Europe), Todidae (late Eocene/early Oligocene of Europe and North America), and, possibly (see the comments in Sects. 14.3, 16.8), the Momotidae and Cathartidae.

By contrast, the extant distribution of only two avian taxa with unambiguous Northern Hemisphere Paleogene stem group representatives is restricted to Africa south of the Sahara, i.e., the Coliidae (early Paleogene of North America and Paleogene and Neogene of Europe) and Sagittariidae (Oligocene and Neogene of Europe). Stem group representatives of the Madagascan Leptosomidae occurred in the early Eocene of Europe and North America.

With the possible exception of the Anseranatidae (Sect. 6.4.2), no taxa have been reported from the Paleogene of the Northern Hemisphere whose crown group representatives are restricted to Australia. Earlier identifications of stem group representatives of the Megapodiidae in the Paleogene of Europe (Mourer-Chauviré 1982) were preliminary, and these fossils are now assigned to stem group Galliformes (Quercymegapodiidae).

Many of the above-mentioned taxa probably had a wider distribution in the early Paleogene than the patchy fossil record currently documents. Because of the high degree of similarity of the early Eocene avifaunas of Europe and North America (see Sect. 17.1.1), stem group representatives of the Nyctibiidae and Trochilidae, for example, may also have occurred in the Paleogene of North America. These taxa could also have been present in the Paleogene of South America and other southern continents. Rather than there having been mere shifts in the area of distribution of the stem and crown group representatives of so many taxa, I assume that the distribution of their crown group representatives is relictual compared with that of the total group (pro Olson 1989; contra Cracraft 2001).

The extant representatives of the above-mentioned taxa with a South American or Central American distribution have very different ecological niches; therefore, and because the modern descendants of these groups do not occur in the Old World tropics, the disappearance of their stem group representatives from the Northern Hemisphere is not easily explained by climatic changes alone (Sect. 17.1.2). It is more likely that biotic factors played a major role in the extinction of these groups. South America was isolated from other continents during most of the Cenozoic (Smith et al. 1994). Until the formation of the Panamanian Isthmus at the end of the Pliocene, this "splendid isolation" aggravated the intrusion of both potential competitors and invasive species which had an impact on prevailing habitat structures. Therefore, certain avian taxa may have persisted in such isolated areas as South America and Madagascar, whereas related taxa succumbed to more competitive species in all other parts of their area of distribution.

Because the above-mentioned groups have very different ecological preferences, the ecological interactions which led to their extinction in the Northern Hemisphere must have been complex and multifactorial. Examples of such interactions were detailed by Cristoffer and Peres (2003), who hypothesized that, for example the higher density of large mammalian herbivores in Old World tropical rainforests is responsible for a lesser abundance of snails and butterflies, than in the New World tropics. Similarly, the much lower taxonomic diversity of placental mammals may have affected South American and Central American bird communities by the absence of key predators and potential competitors. Clearly, however, much more research has to be conducted to identify potential factors which ultimately affected the distribution of, for example, nectarivorous stem group Trochilidae as well as insectivorous and probably nocturnal stem group representatives of the Nyctibiidae in the same way.

17.3 Ecological Interactions

This section summarizes some considerations on possible ecological interactions which may have influenced the evolution of Paleogene avifaunas. I only focus on a few aspects concerning bird–mammal and bird–bird interactions. Coevolution with certain groups of insects and plants may have also played an important role in the early diversification of neornithine birds, but in most cases the data at hand do not even allow ad hoc hypotheses (see, however, Sect. 12.7.4).

17.3.1 Mammalian Evolution and Terrestrial Avifaunas

Mammals are among the main predators of birds, and it is well known from insular avifaunas that an environment with little or no predation pressure frequently led to the evolution of flightlessness in birds (Feduccia 1999; Steadman 2006). The Paleogene diversification of carnivorous mammals thus certainly had a significant impact on the evolution of birds, especially those with limited or no flight capabilities. Their evolutionary history was summarized by van Valkenburgh (1999) and Rose (2006), on whose surveys the following notes are based. The earliest carnivorous mammals of the Northern Hemisphere were the coyote-sized ungulate mesonychids, which first occur in the mid-Paleocene of North America and Europe. More specialized toward carnivory were the creodonts, which existed throughout the Eocene but had their greatest diversity in the early and middle Eocene. The first true stem carnivorans, the miacoids, probably arose in the mid-Paleocene of North America, from where they dispersed into Europe and Asia; the early representatives of this taxon also were only fox-sized animals. The earliest crown group carnivorans, i.e., caniforms, feliforms, and viverrids, occurred in the late Eocene. Caniforms evolved in North America and did not disperse into the Old World before the Neogene, whereas feliforms originated in Asia and appeared in Europe in the early Oligocene, just after the Grande Coupure.

After the extinction of dinosaurs in the late Cretaceous, several million years passed before the first specialized mammalian carnivores appeared (van Valkenburgh 1999). The absence of larger terrestrial predators in the early Paleocene may have licensed the evolution of flightlessness in various avian lineages, and it is probably no coincidence that the first occurrences of penguins, phorusrhacids, and gastornithids fall into this period. The former two taxa have an origin in the Southern Hemisphere, which correlates with the fact that no placental carnivorans occurred in the Paleocene and Eocene of this part of the earth (see p. 342 in Rose 2006). Whereas there already existed larger carnivorous marsupials in the early Paleogene of South America (Sparassodonta), only opossum-sized carnivorous mammals are known from the early Eocene of Antarctica (Goin et al. 1999). These dispersed into the continent from South America, and there may have been a predator-free period in the earliest Paleogene of the Antarctic region, which facilitated the evolution of flightless birds.

The origin of flightlessness in early Paleogene birds of the Northern Hemisphere is more poorly understood. Europe was largely isolated from other continents in the late Cretaceous and Paleocene (Smith et al. 1994). While it seems to be a plausible scenario that a species in the evolutionary lineage of the graviportal Gastornithidae lost its flight capability on this continent in the late Cretaceous/earliest Paleocene, the flightless ratites probably dispersed into Europe from one of the southern continents (Sect. 17.2.1). However, the same factor which may have licensed flightlessness in the Gastornithidae, i.e., isolation of Europe, would have aggravated dispersal of the flightless ratites.

The flightless Gastornithidae and Remiornithidae occur in the Paleocene of Europe, but have not been recorded from deposits of that period in North America. If this is not an artifact of the fossil record, it may indicate a lower predation pressure in the earliest Paleogene of Europe. There was still a high number of flightless birds in the early and middle Eocene of Europe, including the Gastornithidae, Palaeotididae, Ameghinornithidae, and possibly some large species of the Idiornithidae. Of these only the Gastornithidae, which owing to their large size were probably less susceptible to predation, were reported from North America, where their fossil record is restricted to the early Eocene.

No unambiguous evidence exists for the presence of flightless birds in the Oligocene of Europe and North America (see also Cracraft 1971b). It is thus likely that the early diversity of at least noncursorial flightless birds in the continental

Northern Hemisphere avifauna was strongly reduced, if not terminated, by the occurrence of larger carnivorans toward the late Eocene/early Oligocene. Owing to the isolation of the southern continents, flightless birds persisted longer in the Southern Hemisphere than in Europe and North America. In the extant (prehuman) avifauna, however, only cursorial ratites, which can outrun predators, coexist with large carnivorous mammals (Rheidae in South America, Struthionidae in Africa), whereas most other flightless birds are (were) restricted to areas free of larger mammalian predators (Australia, New Zealand, Madagascar, and isolated islands).

Mammals certainly not only had an impact on the evolution of birds as predators, but also as prey. The main extant avian predators of mammals are strigiform birds and diurnal birds of prey. The former include predominantly nocturnal species and have a significantly older fossil record, which dates back into the Paleocene. If most small mammals of that period were nocturnal, mammalian predation by owls may have preceded that by diurnal birds of prey. Alternatively, owls may have become nocturnal as a result of feeding competition with diurnal birds of prey, whose evolution was probably also intimately connected with that of mammalian prey.

17.3.2 The Impact of Passerines on the Diversity of Paleogene Avian Insectivores

Today, most small insectivorous or omnivorous birds belong to the Passeriformes, which also constitute the majority of perching birds. As noted in Sect. 16.4.2, there exist remains of presumptive passerines from the early Eocene of Australia. Outside this continent, passerines first occur in the early Oligocene of Europe, where they did not become the predominant group of small arboreal birds before the late Oligocene. Passerines have no Paleogene fossil record in the New World and Africa; in the latter continent they have not even been recorded in early Miocene deposits (Mourer-Chauviré 2003).

Both the phylogenetic relationships of the extant taxa and the fossil record are in concordance with an origin of Pan-Passeriformes in the Australian region (Sects. 16.4.2, 17.2.1). Dispersal of passerines into Europe seems to have been from Asia, and may have been correlated with the northward drift of the Australian continental plate in the mid-Paleogene and closure of the Turgai Strait in the early Oligocene.

It is likely that representatives of small nonpasserines had ecological niches before the Oligocene similar to those filled by modern passerines, and the occurrence of songbirds probably had a major impact on these birds (Harrison 1979b; Mayr 2005a). If Paleogene Passeriformes had feeding preferences similar to those of their extant relatives, it is to be expected that feeding competition with passeriform birds during periods of limited food availability would have had its greatest effect on small insectivorous taxa. Indeed, there seems to have been a greater diversity of aerial insectivores among the “caprimulgiform”/apodiform birds in the early

Paleogene. The crown group representatives of some taxa with putatively insectivorous or omnivorous Paleogene stem group representatives further exhibit feeding specializations or foraging strategies that are not, or are only rarely, found in passeriform birds (Mayr 2005a).

For example, crown group Upupiformes either forage on the ground (Upupidae) or are specialized toward trunk-climbing (Phoeniculidae), whereas the Messelirrisoridae, as evidenced by their foot structure, seem to have been perching birds (Mayr 1998b). Within crown group Pici, the Picumninae and Picinae are specialized toward trunk-climbing and wood-pecking, the Indicatoridae mainly feed on beeswax, and toucans and many other Ramphastidae mostly eat fruits. By contrast and according to its bill morphology, the early Oligocene piciform *Rupelramphastoides* appears to have been a rather generalized insectivorous or omnivorous bird (Mayr 2006g). The Coliiformes exhibited a great diversity in the Eocene and, judging from their bill shape, included omnivorous or insectivorous species by that time (Houde and Olson 1992; Mayr and Peters 1998; Mayr 2001d), whereas the six modern species of mousebirds are mainly frugivorous. The cacique-like beak of *Chascacocolius* (Sect. 16.2.2) is a particularly striking example for a passerine-like feeding adaptation in Paleogene non-Passeriformes. As indicated by their bill-shape, the Eocene stem group Psittaciformes of the taxon *Psittacopes* also appear to have been rather generalized feeders (Mayr and Daniels 1998), whereas extant parrots exhibit specialized feeding adaptations for various food sources which are used by few passerines (e.g., very hard-shelled seeds, roots, pollen, and nectar).

17.3.3 Marine Avifaunas

Major aspects of the evolution of marine avifaunas were summarized by Warheit (1992, 2002), although these reviews mainly concentrated on the Neogene fossil record. Among the most notable particularities of Paleogene marine avifaunas is the existence of giant soaring and diving birds without modern counterparts. Whereas the former (Pelagornithidae) already seem to have achieved a worldwide distribution in the early Eocene, the latter were restricted to the Southern Hemisphere (Sphenisciformes) and the North Pacific (Plotopteridae).

17.3.3.1 Pelagic Birds

Today, the Procellariiformes, Phaethontidae, Fregatidae, and some Charadriiformes (Stercorariidae, Laridae, Sternidae, and Alcidae) are the predominant taxa among the volant pelagic birds, i.e., those that regularly feed offshore. By contrast, the most abundant and widespread pelagic birds of the early Paleogene seem to have been the Prophaethontidae and Pelagornithidae, which are found together in several fossil sites, such as the early Eocene of the Ouled Abdoun Basin in Morocco and the London Clay.

Medium-sized pelagornithids coexisted with very large forms in the early Paleogene, but there appear to have been only giant representatives of this taxon in the Neogene. Concerning a trend toward gigantism, pelagornithids paralleled the Mesozoic pterosaurs, of which also only the giant forms survived into the late Cretaceous. In the case of pterosaurs, it has been hypothesized that competition with birds led to the extinction of the smaller species (Paul 2002). In analogy, ecological competition with other marine birds for food and/or breeding sites may have played a role in the extinction of smaller pelagornithids. Just because of their very large size, pressure of competition may have been lower for the giant species, although the extreme specializations of the flight and feeding apparatus of bony-toothed birds made them prone to environmental changes and ultimately proved to be an evolutionary dead end. Still, however, more data have to be gathered on the stratigraphic distribution of these birds to conclusively show whether extinction of the smaller pelagornithids was due to competition with other birds or whether the latter filled ecological niches left after extinction of the smaller bony-toothed birds.

It is notable that the earliest well-known representatives of the Procellariiformes, the Oligocene Diomedeoididae, had a highly specialized foot morphology (Sect. 7.5). The greatly widened pedal phalanges of these birds indicate that the feet were used as a brake for rapid stops or as an anchor to avoid drifting from strong winds. The evolutionary significance of this feature with regard to niche competition with other marine birds still needs to be addressed. A similar foot morphology is today only found in much smaller procellariiform species, whose distribution is mainly restricted to the Southern Hemisphere.

17.3.3.2 Giant Diving Birds

Even the earliest representatives of the Sphenisciformes and Plotopteridae were large compared with extant flightless diving birds (Sects. 7.2, 7.3). The giant penguins became extinct toward the late Oligocene (Clarke et al. 2007). Plotopterids also disappeared from North America toward the late Oligocene and only survived in Japan into the early Neogene. Similarly sized diving birds do not exist in late Neogene and extant avifaunas, and various factors have been suggested to explain their disappearance. Goedert (1988), in the case of plotopterids, and Vickers-Rich (1991, p. 748), concerning penguins, assumed that it may have been due to climatic reasons. Simpson (1971) considered it possible that the giant penguins succumbed to competition with pinnipeds and cetaceans, which was also assumed by Olson and Hasegawa (1979) in the case of plotopterids.

In the eastern North Pacific, plotopterids coexisted with odontocete cetaceans from at least the late Eocene on (Goedert and Cornish 2002), which makes it unlikely that competition with whales played a major role in their extinction. However, Warheit and Lindberg (1988) detailed that interference competition at breeding sites with land-based gregarious pinnipeds, such as elephant seals, has a significant impact on large flightless seabirds. They hypothesized that in New Zealand and Australian penguins this led to shifts to smaller body sizes, which temporally coincided with the first local appearance of gregarious pinnipeds (Warheit and Lindberg 1988). As further set forth by these authors, many extant penguins nest in hilly or rocky terrains that do not allow large aggregations of pinnipeds, or are fossorial, i.e., breed in earth tunnels, thus avoiding breeding competition with pinnipeds.

According to Goedert and Cornish (2002), the local extinction of plotopterids at the Oregon and Washington coastlines may have been further boosted by the demonstrable disappearance of offshore volcanic islands as potential breeding sites toward the late Oligocene.

Appendix

Table A.1 Temporal distribution of avian taxa in the Paleogene of Europe. Only taxa from stratigraphically dated localities, which are known from diagnostic parts of the skeleton, are listed. The sequence is as in the text and the *numbers* refer to the sections in which the taxa are discussed; extinct taxa are marked by a *dagger*. The *shaded fields* do not indicate an exact stratigraphic range but the mere presence of a taxon within a given temporal interval. *Light grey fields* have been extrapolated for hiatuses in the fossil record, or if taxa have a Neogene or extant fossil record in Europe. See the taxonomic sections for further information

	Paleocene	Eocene			Oligocene	
		Early	Middle	Late	Early	Late
5.1 †Lithornithidae	▓ ?	▓	▓			
5.2.1 †Palaeotididae			▓			
5.2.2 †Remiornithidae	▓					
6.1.1 †Gallinuloididae		▓	▓			
6.1.2 †Paraortygidae				▓	▓	▓
6.1.4 †Quercymegapodiidae			▓	▓		
6.1.6 Phasianidae					▓	▓
6.2 †Gastornithidae	▓	▓	▓			
6.4.2 Anseranatidae		▓ ?	░	░	░	▓ ?
6.4.4 Anatidae				▓	▓	▓
6.5 †Pelagornithidae	▓	▓	░	░	░	░
7.1.3 Sulidae			▓ ?	░	▓ ?	▓
7.1.4 Phalacrocoracidae						▓
7.4 Gaviiformes				▓	▓	░
7.5 Procellariiformes					▓	▓
7.7 Ardeidae						▓
7.9 Threskiornithidae		▓	▓	▓	▓	░
7.11 †Prophaethontidae		▓	▓			
8.1 Lari					▓	▓
8.3. Scolopaci					▓	▓

(continued)

Table A.1 (continued)

	Paleocene	Eocene			Oligocene	
		early	middle	late	early	late
9.1 †Messelornithidae	▓ ?	▓	▓	▓	▓	
9.1 †*Walbeckornis*	▓					
9.2 Rallidae				▓	▓	▓
9.3.1 †Parvigruidae					▓	
9.3.4 Gruidae				▓	▓	▓
10 Phoenicopteriformes			▓ ?	▓	▓	▓
11.1 Pteroclidae						▓
11.5 †*Eocuculus*					▓	
11.6 †*Pumiliornis*			▓			
11.7 †Parvicuculidae		▓				
12.1 †Fluvioviridavidae		▓				
12.1 †*Palaeopsittacus*		▓	▓			
12.3 Podargidae			▓			
12.4 †*Protocypselomorphus*			▓			
12.5 †Archaeotrogonidae		▓	▓	▓	▓	▓
12.6.1 Nyctibiidae			▓			
12.6.2 Caprimulgidae			▓ ?	░	░	░
12.7.1 †Eocypselidae		▓				
12.7.2 †Aegialornithidae		▓ ?	▓	▓		
12.7.3 Apodidae			▓	▓	░	▓
12.7.4 Trochilidae			▓	▓	▓	
13.2 †Idiornithidae			▓	▓	▓	▓
13.2 †*Elaphrocnemus*				▓	▓	▓
13.4 †Ameghinornithidae			▓			
13.5 †Salmilidae			▓			
13.6 †*Gradiornis*	▓					
14.3 Cathartidae			▓ ?	▓ ?		
14.4 †Horusornithidae				▓		
14.5.1 Sagittariidae					▓	▓
14.5.2 Pandionidae				▓	▓	░
14.5.2 Accipitridae				▓	▓	▓
15.1 †*Berruornis*	▓					
15.2 †Protostrigidae					▓	
15.4 †Palaeoglaucidae			▓	▓		
15.4 †Necrobyinae				▓	▓	▓

(continued)

Table A.1 (continued)

16.1 Leptosomidae		▓	▓			
16.2.1 †Sandcoleidae		▓	▓			
16.2.2 Coliidae			▓	▓	▓	░
16.3.1 †*Psittacopes*		▓	▓			
16.3.2 †Quercypsittidae		▓	░	▓		
16.3.3 †Halcyornithidae		▓	▓			
16.3.4 †Messelasturidae		▓	▓			
16.4.1 †Zygodactylidae		▓	▓	░	▓	░
16.4.2 Passeriformes					▓	▓
16.5 Trogoniformes		▓	▓	░	▓	░
16.6 Upupiformes		▓	▓	▓	░	░
16.7.1 †Primobucconidae		▓	▓			
16.7.2 †Eocoraciidae			▓			
16.7.2 †Geranopteridae				▓		
16.8 †*Quasisyndactylus*			▓			
16.8 Todidae				▓	▓	
16.9.1 †Sylphornithidae			▓	░	▓	
16.9.2 Pici					▓	▓
16.10 †Gracilitarsidae			▓			

Table A.2 Temporal distribution of avian taxa in the Paleogene of North America (see Table A.1 for further details)

	Paleocene	Eocene			Oligocene	
		Early	Middle	Late	Early	Late
5.1 †Lithornithidae	▓	▓	▓			
6.1.1 †Gallinuloididae		▓				
6.1.3 †*Procrax*				▓		
6.2 †Gastornithidae		▓				
6.4.2 Anseranatidae	▓ **?**					
6.4.3 †Presbyornithidae	▓	▓				
6.5 †Pelagornithidae		▓	░	░	░	▓
7.1.2 Fregatidae		▓				
7.2 †Plotopteridae				▓	▓	
7.4 Gaviiformes					▓ **?**	
7.5 Procellariiformes	▓ **?**	░	░	▓	░	░
7.11 †Prophaethontidae	▓					
8.1 Alcidae				▓	░	░
8.2 Scolopaci				▓	░	░

(continued)

Table A.2 (continued)

	Paleocene	Eocene			Oligocene	
		Early	Middle	Late	Early	Late
9.1 †Messelornithidae		■				
9.3.2 †Geranoididae		■	■			
9.3.4 Aramidae					■ ?	▒
10 Phoenicopteriformes		■ ?				
11.3 †Foratidae		■				
11.5 †*Eocuculus*				■		
11.7 †Parvicuculidae		■ ?				
12.1 †Fluvioviridavidae		■				
12.2 Steatornithidae		■				
12.6.2 Caprimulgidae		■ ?	▒	▒	▒	▒
12.7 Apodiformes		■				
13.3 †Bathornithidae			■ ?	■	■	■
14.4 †Horusornithidae					■	
14.5.2 Accipitridae					■	■
15.2 †Protostrigidae		■	■	■		
15.3 †Ogygoptyngidae	■					
16.1 Leptosomidae		■				
16.2.1 †Sandcoleidae		■	■			
16.2.2 Coliidae		■	▒	■		
16.3.3 †Halcyornithidae		■				
16.3.4 †Messelasturidae		■				
16.4.1 †Zygodactylidae		■				
16.5 Trogoniformes		■ ?				
16.7.1 †Primobucconidae		■				
16.8 Todidae					■	
16.9 †*Neanis*		■				

Table A.3 Temporal distribution of avian taxa in the Paleogene of Asia (see Table A.1 for further details)

	Paleocene	Eocene			Oligocene	
		Early	Middle	Late	Early	Late
6.1 Galliformes				▓	░	▓
6.2 †Gastornithidae		▓				
6.5 †Pelagornithidae					▓	
7.1.1 †Protoplotidae	▓ ?					
7.1.4 Phalacrocoracidae						▓
7.2 †Plotopteridae				▓ ?	░	▓
7.10 Ciconiidae		▓ ?				
7.11 †Prophaethontidae	▓					
9.2 Rallidae						▓
9.3.3 †Eogruidae				▓	▓	▓
10 Phoenicopteriformes						▓ ?
14.5.2 Accipitridae					▓ ?	▓ ?
16.3.2 †Quercypsittidae		▓				

Table A.4 Temporal distribution of avian taxa in the Paleogene of South America and Central America (see Table A.1 for further details)

	Paleocene	Eocene			Oligocene	
		Early	Middle	Late	Early	Late
5.4 Rheidae	▓	░	░	░	░	░
6.1.4 †Quercymegapodiidae						▓
6.4.1 Anhimidae						▓
6.4.3 †Presbyornithidae		▓				
6.4.5 ?Anatidae						▓ ?
6.5 †Pelagornithidae			▓			
7.3 Sphenisciformes			▓	▓	▓	▓
10 Phoenicopteriformes						▓
13.1 †Phorusrhacidae	▓	▓	▓	▓	▓	▓
14.3 Cathartidae						▓
14.3 †Teratornithidae						▓
14.5.2 Accipitridae						▓ ?
16.10 †*Eutreptodactylus*	▓					
16.11 †Cladornithidae						▓

Table A.5 Temporal distribution of avian taxa in the Paleogene of Africa (see Table A.1 for further details)

	Paleocene	Eocecne			Oligocene	
		Early	Middle	Late	Early	Late
5.3 †Eremopezidae				■		
6.5 †Pelagornithidae	■	■	■			
7.1.4 Phalacrocoracidae					■	░
7.6 Balaenicipitidae					■	░
7.7 Ardeidae					■	░
7.8 †Xenerodiopidae					■	
7.10 Ciconiidae				■	■	░
7.11 †Prophaethontidae	■	■				
8.3 Jacanidae				■	■	░
9.2 Rallidae					■	░
9.3.4 Gruidae					■	░
10 Phoenicopteriformes					■	░
11.4 Musophagiformes					■	░
14.5.2 Pandionidae					■	░
14.5.2 Accipitridae				■	░	░

Table A.6 Temporal distribution of avian taxa in the Paleogene of Australia (see Table A.1 for further details)

	Paleocene	Eocene			Oligocene	
		Early	Middle	Late	Early	Late
5.5 Casuariidae						■
6.1.5 Megapodiidae						■
6.3 †Dromornithidae		■ ?	░	░	░	■
6.4.5 Anatidae						■
7.3 Sphenisciformes				■	■	■
7.10 Ciconiidae						■
8.1.2 Burhinidae						■
9.2 Rallidae						■
10 †Palaelodidae						■
10 Phoenicopteridae						■
11.1 Columbidae						■
12.7.3 Apodidae						■
14.5.2 Accipitridae						■
16.4.2 Passeriformes		■ ?	░	░	░	■

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