The Paleogene fossil record of birds in Europe

Gerald Mayr

Forschungsinstitut Senckenberg, Sektion Ornithologie, Senckenberganlage 25, D-60325 Frankfurt am Main, Germany.
(Email: Gerald.Mayr@senckenberg.de)

ABSTRACT

The Paleogene (Paleocene–Oligocene) fossil record of birds in Europe is reviewed and recent and fossil taxa are placed into a phylogenetic framework, based on published cladistic analyses. The pre-Oligocene European avifauna is characterized by the complete absence of passeriform birds, which today are the most diverse and abundant avian taxon. Representatives of small non-passeriform perching birds thus probably had similar ecological niches before the Oligocene to those filled by modern passerines. The occurrence of passerines towards the Lower Oligocene appears to have had a major impact on these birds, and the surviving crown-group members of many small arboreal Eocene taxa show highly specialized feeding strategies not found or rare in passeriform birds. It is detailed that no crown-group members of modern 'families' are known from pre-Oligocene deposits of Europe, or anywhere else. The phylogenetic position of Paleogene birds thus indicates that diversification of the crown-groups of modern avian 'families' did not take place before the Oligocene, irrespective of their relative position within Neornithes (crown-group birds). The Paleogene fossil record of birds does not even support crown-group diversification of Galliformes, one of the most basal taxa of neognathous birds, before the Oligocene, and recent molecular studies that dated diversification of galliform crown-group taxa into the Middle Cretaceous are shown to be based on an incorrect interpretation of the fossil taxa used for molecular clock calibrations. Several taxa that occur in the Paleogene of Europe have a very different distribution than their closest extant relatives. The modern survivors of these Paleogene lineages are not evenly distributed over the continents, and especially the great number of taxa that are today restricted to South and Central America is noteworthy. The occurrence of stem-lineage representatives of many taxa that today have a restricted Southern Hemisphere distribution conflicts with recent hypotheses on a Cretaceous vicariant origin of these taxa, which were deduced from the geographical distribution of the basal crown-group members.

Key words: Aves, Paleogene, Europe, fossil record, biogeography, diversification of neornithine taxa.

CONTENTS

I. INTRODUCTION

Europe has the most complete and best studied Paleogene, i.e. Paleocene–Oligocene (65–24 million years ago), fossil record of birds, and some sites have yielded numerous well-preserved avian remains (Table 1). However, despite intensive study of these and other localities in the past decades, much uncertainty still exists on the exact composition of the Paleogene European avifauna.

Earlier identifications of isolated, fragmentary remains are often very doubtful, given the mosaic character distribution (e.g. Olson, 1977*a*) in Paleogene birds. Most problematic in this regard is the description of many species from the Eocene of England that are based on non-comparable elements of different parts of the skeleton (Harrison & Walker, 1976*c*, 1977, 1979*a*, *b*; see Steadman, 1981 and below). In addition, most earlier assignments of Paleogene birds to modern groups were not established with derived characters (e.g. Cracraft, 1980) but are based on overall similarity that, in the case of Paleogene taxa, can be quite misleading. If fossil birds are assigned to modern taxa, and especially if conclusions about the diversification time of these are drawn, it is further important to assess whether the fossil species are members of the crown-group (i.e. belong to a clade including the stem species of this modern taxon and all its descendants), or are stem-group representatives (i.e. are outside the crown-group). Unfortunately, such a distinction has also been made in recent years only.

The Paleogene avian record from Europe is in dire need of revision, as many new avian taxa have been described in the past decade, quickly outdating the existing earlier surveys (Olson, 1985; Mlíkovský, 1996*b*; Bocheński, 1997). A recently published catalogue by Mlíkovský (2002) is a valuable source for the species described until the date of its publication and the corresponding references. However, that study uses a very unorthodox and often evidently incorrect taxonomy and phylogeny (see Mourer-Chauviré, 2004 for a review), and numerous taxa are synonymized without first-hand examination of the specimens.

Here, I review the Paleogene avifauna of Europe and evaluate its paleobiogeographic relationships and implications for the timing of the origin of the modern taxa. This study is not intended to be a list of all Paleogene species that have been described so far, but a survey on those taxa that are known from sufficiently well-preserved remains to ascertain their distinctiveness. Based on published cladistic analyses, several recent and fossil taxa are placed into a phylogenetic framework and derived characters are listed that support the proposed phylogenies. The temporal distribution of the taxa is summarized in Table 2.

II. COMPOSITION OF THE PALEOGENE EUROPEAN AVIFAUNA

(1) Palaeognathae

Virtually all recent phylogenetic analyses support monophyly of the Palaeognathae, i.e. a clade including Tinamidae (tinamous) and the flightless ratites (see Sibley & Ahlquist, 1990; Livezey & Zusi, 2001; Mayr & Clarke, 2003). Palaeognathous birds today only occur in the Southern Hemisphere but are represented with several taxa in the Paleogene of Europe.

The Lithornithidae were reported from the Fur Formation, the London Clay, and the early Paleogene of North America (Houde, 1988; Kristoffersen, 1999, 2002*b*). Although clearly identified as palaeognathous birds by their palatal structure, the phylogenetic affinities between lithornithids and other palaeognathous birds are unresolved (Houde, 1988; Dyke & van Tuinen, 2004), which is in part due to the fact that even the exact composition of this taxon, which was considered paraphyletic by Houde (1986, 1988), is uncertain. Lithornithids are distinguished from all other palaeognathous birds by the plesiomorphic presence of a well-developed hallux. All named European species come from the London Clay, and include *Lithornis* Owen 1840 and a taxon that was tentatively referred to *Pseudocrypturus*

Table 1. *Major Paleogene European fossil localities that have yielded bird remains (see Mlíkovský, 1996 b for a complete list)*

Locality	Age	Kind of deposit	Selected references
Fur Formation, Denmark	Latest Paleocene/Lowermost Eocene	Marine	Kristoffersen (2002 b)
London Clay, England	Lower Eocene	Marine	Harrison & Walker (1977), Daniels in Feduccia (1999, p. 167)
Messel, Germany	Middle Eocene	Lake deposit	Schaal & Ziegler (1988), Peters (1988 a), Mayr (2000 f)
Geiseltal, Germany	Middle to Upper Eocene	Peatbogs and small lakes	Krumbiegel et al. (1983), Mayr (2002 f)
Quercy, France	Middle Eocene to Upper Oligocene	Fissure fillings	Mourer-Chauviré (1995 a, 1996)
Frauenweiler, Germany	Lower Oligocene	Marine	Trunkó & Munk (1998)
Céreste, France	Lower Oligocene	Lacustrine	Mourer-Chauviré (1996)

Houde 1988 by Houde (1988). Lithornithids and modern Tinamidae are the only known volant palaeognathous birds.

Lithornithids are unknown from Middle Eocene deposits of Europe where another palaeognathous taxon, the Palaeotididae, occurs. Well-preserved skeletons of the latter birds were discovered in the Geiseltal and in Messel (Houde & Haubold, 1987; Peters, 1988 b; Mayr, 2002 f). The Palaeotididae are distinguished from the Lithornithidae, and agree with a subclade of modern ratites, i.e. Struthionidae (ostrich), Rheidae (rheas), and Casuariidae (emus and cassowaries), in the presence of well-developed supraorbital processes, reduced sternal keel, presence of a scapulocoracoid, and loss of the hallux. Whereas Houde (1986) and Houde & Haubold (1987) considered a sister-group relationship between Palaeotididae and Struthionidae, Peters (1988 b) assumed a closer relationship with the Rheidae. However, evidence for neither hypothesis is convincing. Houde & Haubold (1987, p. 37) themselves indicated that their character evidence consists of 'trivial characters' and Peters (1988 b, p. 223) noted that, concerning his characters, 'there remain some doubts concerning the synapomorphic nature of these features'. Referring to an unpublished cladistic analysis, Dyke & van Tuinen (2004) considered the Palaeotididae to be the sister taxon of all modern ratites, but did not present the character evidence for this hypothesis.

The Remiornithidae are known from leg bones and few associated remains from the late Paleocene of France (Martin, 1992). The absence of an ossified supratendinal bridge on the distal tibiotarsus and the structure of the hypotarsus indicate palaeognathous affinities of these birds, but their relationships to other palaeognathous birds are uncertain pending on the discovery of more material.

A fragmentary large pelvis from the Middle Eocene of Switzerland was described as *Eleutherornis helveticus* by Schaub (1940), who considered it to be a ratite bird. This specimen formed the basis of the Eleutherornithidae Wetmore 1951, but the known fossils are too fragmentary to exclude the possibility that *Eleutherornis* belongs to the Palaeotididae, Remiornithidae, or the anseriform Gastornithidae.

(2) Neognathae

(a) *Galliformes* (landfowl)

Crown-group Galliformes comprise the Australian Megapodiidae (megapodes), the New World Cracidae (guans, chachalacas, and currasows), and the Phasianidae (grouse, quails, pheasants, and allies), which have a worldwide distribution and are the only galliform taxon that occurs in Europe.

Galliformes are well-represented and fairly diversified in the Paleogene of Europe and all sufficiently well-preserved pre-Oligocene taxa reported so far are stem-group representatives of this taxon (*contra* Mlíkovský, 2002; Dyke, 2003; Dyke & van Tuinen, 2004; van Tuinen & Dyke, 2004).

Paraortygoides Mayr 2000, the earliest European galliform bird (Fig. 1), was first described from Messel and belongs to the Gallinuloididae, a taxon that was originally erected for the Lower Eocene *Gallinuloides wyomingensis* Eastman 1900 from the North American Green River Formation. *Paraortygoides* and *Gallinuloides* are clearly identified as stem-group Galliformes by the cup-like scapular articulation facet on the coracoid that also occurs in Anseriformes, the sister taxon of Galliformes, and certainly is plesiomorphic within neornithine birds (Mayr, 2000 a; Mayr & Weidig, 2004; Fig. 1). Mlíkovský's (2002) synonymization of Gallinuloididae and modern Cracidae is thus without any foundation and incorrect. Mourer-Chauviré (1988 a) also assigned a distal tarsometatarsus from the Upper Eocene Quercy fissure fillings to the Gallinuloididae, in the genus *Taoperdix* Milne-Edwards 1871. As detailed by Mayr & Weidig (2004), the Upper Oligocene *Taoperdix pessieti* (Gervais 1862), the type species of the genus *Taoperdix*, is, however, not a member of the Gallinuloididae (*contra* Brodkorb, 1964), and the affinities of this taxon need to be restudied. My examination of the type specimens revealed that *Paraortygoides radagasti* Dyke & Gulas 2002 from the London Clay is probably a junior synonym of *Argillipes paralectoris* Harrison & Walker 1977 from the same locality, with which it was not compared by Dyke & Gulas (2002).

Table 2. Temporal distribution of avian taxa in major Paleogene European fossil localities. Only taxa that are known from substantial, diagnostic parts of the skeleton and dated localities are listed; extinct taxa are indicated by a dagger. Shaded fields indicate the temporal distribution of these taxa in Europe; shaded fields without locality entry are extrapolated from the minimum and maximum age (several taxa are known from Miocene or younger deposits). Correlation of the fossil localities with a Mammalian Paleogene (MP) level is after Mlíkovskỳ (1996 *b*) and Legendre & Lévêque (1997). Abbreviations of localities: **Au** – Austria; **Be** – Mont de Berru/Cernay les Reims, France; **Ce** – Céreste, France; **Eg** – England; **En** – Enspel, Germany; **Fl** – Flörsheim, Germany; **Fr** – Central France; **Fu** – Fur Formation, Denmark; **Fw** – Frauenweiler, Germany; **Ga** – Gaimersheim, Germany; **Ge** – Geiseltal, Germany; **Ha** – Hampshire, England; **He** – Herrlingen, Germany; **Ho** – Hoogbutsel/Boutersem, Belgium; **Le** – Leipzig area, Germany; **Lo** – London Clay, England; **Ma** – Matt, Switzerland; **Me** – Messel, Germany; **Mo** – Montmartre gypsum, France; **Ne** – Nederokkerzeel, Belgium; **Qu** – Quercy fissure fillings, France; **Si** – Siegsdorf, Germany; **Wa** – Walbeck, Germany

| | | Eocene | | | | Oligocene | |
| | | Lower | Middle | | Upper | Lower | Upper |
	Paleocene MP 1–6	MP 7–10	MP 11–13	MP 14–16	MP 17–20	MP 21–24	MP 25–30
PALAEOGNATHAE							
†**Lithornithidae**		Lo, Fu					
†**Palaeotididae**			Me, Ge				
†**Remiornithidae** (Palaeognathae inc. sed.)	Be						
NEOGNATHAE							
Galliformes: †Gallinuloididae		Lo	Me	?Qu			
†Quercymegapodiidae				Qu	Qu		
†Paraortygidae					Qu	Le, Qu	Qu
Phasianidae							Qu
Anseriformes: †Gastornithidae	Be, Wa	Lo	Me, Ge				
?Anseranatidae		Lo					Fr
Presbyornithidae					?Ha		
Anatidae					?Ha	?Ho	
Gaviiformes: †*Colymboides*					Ha	Fw, Ho	
Procellariiformes: †Diomedeoididae						Fw, Le	Fl
†**Pelagornithidae**	Eg	Lo					
Pelecaniformes: †Prophaethontidae		Lo	Ne				
Sulidae			?Me			Fr	Fr, Si
Phalacrocoracidae				Quercy, unknown horizon			En, ?Fr
Phoenicopteriformes: †Palaelodidae						Ho	Fr
Phoenicopteridae						Fr, ?Ho	Fr
†*Juncitarsus*			Me				
'**Ciconiiformes**': Threskiornithidae			Me			Ce	
Ardeidae							Qu
'**Gruiformes**': †Messelornithidae	Be		Me		Qu	Qu	
Rallidae					?Fr, Ha	Ho, Le	Fr
Gruidae					?Ha		
†*Elaphrocnemus*					Qu	Qu	Qu
†Idiornithidae			Me, Ge	Qu	Qu	Qu, ?Ho	Qu
†Salmilidae			Me				
†Ameghinornithinae			Me	?Qu		Qu	
Charadriiformes: †Turnipacidae						Qu	
?Glareolidae						Ce	
Scolopacidae						Ho	
Laridae						Ce	Fr
Alcidae							Fr
Columbiformes: Pteroclidae						Au	
'**Falconiformes**': Cathartidae				Qu			Qu
Sagittariidae						Qu	Qu
†Horusornithidae					Qu		
Accipitridae					?Ha	?Ho	Fr
Strigiformes: cf. †*Tynskya*, †*Messelastur*		Lo	Me				
†Sophiornithidae	?Be, ?Wa				Quercy, unknown horizon		
Protostrigidae		Lo				Le	
†Palaeoglaucidae			?Me		Qu		
Tytonidae					?Qu	?Qu	?Qu

Table 2. (*cont.*)

	Paleocene MP 1–6	Eocene Lower MP 7–10	Middle MP 11–13	MP 14–16	Upper MP 17–20	Oligocene Lower MP 21–24	Upper MP 25–30
Psittaciformes: †Pseudasturidae		Lo	Me, Ge				
†Quercypsittidae					Qu		
†*Psittacopes*		Lo	Me				
Musophagiformes							Ga
Coliiformes: †Sandcoleidae		?Fu	Me, Ge, Fr				
Coliidae			Me, Ge	Qu	Qu	Fw, Ho	
Trogoniformes		Lo, Fu	Me			Ce, Ma	
Caprimulgiformes s.s.: Nyctibiidae			Me		Quercy, unknown horizon		
Caprimulgidae				?Qu			
†Archaeotrogonidae		?Lo	Me		Qu	Qu	Qu
Podargidae			Me	Qu			
Apodiformes: †Eocypselidae		Lo, Fu					
†Aegialornithidae			Ge	Qu	Qu		
?Hemiprocnidae				Qu	Qu	Qu	
Apodidae			Me				Fr
Trochilidae			Me			Fw	
?Leptosomidae (†*Plesiocathartes*)		Lo	Me, Ge		Quercy, unknown horizon		
Coraciiformes s.s.: †Primobucconidae		Lo	Me				
†Eocoraciidae			Me				
†Geranopteridae					Qu		
Alcediniformes: †*Quasisyndactylus*			Me				
?Momotoidea					Qu	Qu, Ma	
Upupiformes: †Messelirrisoridae		Lo	Me, Ge				
†Laurillardiidae					Mo		
Piciformes: †Sylphornithidae				Qu	?Mo	Ho	
†Gracilitarsidae			Me				
Pici						Ho	He
†Primoscenidae		Lo, Fu	Me				
Passeriformes						Fw, Ce	Fr, Qu
Incertae sedis: †*Palaeopsittacus*		Lo	Me				
cf. †*Fluvioviridavis*[1]		Lo					
†*Pumiliornis*[2]			Me				

[1] See Mayr & Daniels (2001).
[2] See Mayr (1999*c*).

The Quercymegapodiidae and Paraortygidae are known from many well-preserved bones from the Middle to Upper Eocene and Oligocene, respectively, Quercy fissure fillings (Mourer-Chauviré, 1992*a*) and from the Lower Oligocene of Germany (Fischer, 1990, 2003). These two taxa are also identified as stem-group Galliformes by the plesiomorphic presence of a cup-like scapular articulation facet on the coracoid (Mourer-Chauviré, 1992*a*; Fig. 1), and Mlíkovský's (2002) synonymization of the Quercymegapodiidae with modern Megapodiidae again is incorrect. *Ludiortyx hoffmanni* (Gervais, 1852) from the Upper Eocene of Paris, classified into the Gallinuloididae by Brodkorb (1964) but considered to belong to the Rallidae (rails) by Brunet (1970) and Cracraft (1973), probably is a member of the Quercymegapodiidae with which it has not yet been compared (Mayr, 2000*a*).

Fragmentary remains of other putative Galliformes which were reported as 'Phasianidae' from the Paleogene of England by Harrison & Walker (1977, 1979*a*, *b*) need to be restudied and compared with the above taxa.

The earliest European crown-group galliform bird is the Upper Oligocene phasianid taxon *Palaeortyx* (Mourer-Chauviré, 1992). According to Ballmann (1969) this taxon most closely resembles the modern *Arborophila*, which is widespread in the tropical and subtropical regions of Africa and Asia, although these similarities may well be plesiomorphic within Galliformes and have not yet been evaluated in a cladistic context.

(*b*) *Anseriformes (waterfowl, incl. Gastornithidae)*

Crown-group Anseriformes include the South American Anhimidae (screamers), the Australian Anseranatidae (magpie goose), and the Anatidae (swans, geese, and ducks). Only the last group today occurs in Europe.
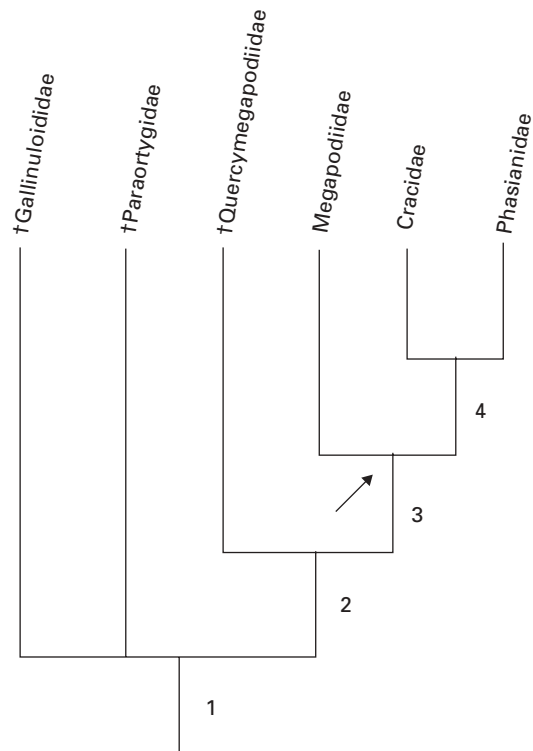
Fig. 1. Phylogenetic relationships between Paleogene and extant taxa of the Galliformes (after Mayr & Weidig, 2004), with a figure of *Paraortygoides messelensis* Mayr 2000 (Gallinuloididae) from the Middle Eocene of Messel in Germany (holotype specimen). Extinct taxa are indicated by a dagger, the arrow indicates the crown-group. The nodes are supported by the following diagnostic synapomorphies: **1** – humerus with markedly elongated tuberculum dorsale; tarsometatarsus, plantar side of articular surface of trochlea metatarsi III asymmetric with lateral ridge protruding farther proximally than medial ridge. **2** – Humerus with transversal ridge at beginning of incisura capitis (weakly developed in Quercymegapodiidae). **3** – Cotyla scapularis of coracoid shallow. **4** – Carpometacarpus with wide spatium intermetacarpale and strongly bowed os metacarpale minus.

The giant flightless Gastornithidae ('Diatrymidae' auct., see Buffetaut, 1997, and Mlíkovskỳ, 2002 who synonymized *Gastornis* Hébert 1855 and *Diatryma* Cope 1876) were shown to be the sister taxon of crown-group Anseriformes by Andors (1992). In Europe, gastornithids were reported from the Paleocene and Lower Eocene of England, France, and Germany (e.g. Fischer, 1962, 1978; Andors, 1992; Buffetaut, 1997). Gastornithidae also occur in the Lower Eocene of China (Hou, 1980) and North America, and are evidence for the existence of a land connection between Europe and North America by that time (Andors, 1992).

The extinct Presbyornithidae are abundant anseriform birds in the Paleogene of North America (Olson & Feduccia, 1980*a*) and were identified in Europe by Harrison & Walker (1976*c*, 1978) and Dyke (2001*e*).

From the London Clay, Olson (1999*b*) reported an anseriform species, *Anatalavis oxfordi* Olson 1999, that is represented by most of the cranial half of the skeleton including the skull. *A. oxfordi* was considered by Olson (1999*b*) to be most closely related to the Anseranatidae, but at least the large pneumatic foramen on the sternal end of the coracoid, which was listed as supporting evidence and also occurs in

the Anhimidae, may be plesiomorphic within Anseriformes (Livezey, 1986; it is equally parsimonious to assume that this foramen evolved in the stem species of Anseriformes and was reduced in the Anatidae, or that it convergently evolved in Anseranatidae and Anhimidae). A phylogenetic analysis by Dyke (2001*e*) resulted in a sister-group relationship between *A. oxfordi* and a clade including Presbyornithidae and Anatidae. However, this analysis is considerably flawed by the fact that only 22 of the 123 included characters could be coded for *A. oxfordi*, and that characters listed as evidence for anseranatid affinities of *Anatalavis* by Olson (1999*b*) were not included, e.g. concerning the morphology of the furcula that 'is absolutely distinctive in being V-shaped and having a long, broad symphysis, thus resembling only *Anseranas* among the Anseriformes' (Olson, 1999*b*, p. 241). *Anatalavis* was originally described from the Upper Cretaceous or early Paleocene of New Jersey (Olson & Parris, 1987, see Olson, 1994 for the age of this locality), and Mlíkovskỳ (2002) separated *A. oxfordi* in a new genus, *Nettapterornis*. I agree with Mourer-Chauviré (2004) that the known material does not justify this action. Mlíkovskỳ (1996*a*, 2002) and Olson (1999*b*) noted that another anseriform, *Romainvillia stehlini*

Lebedinsky 1927 from the Upper Eocene of France, may also belong to the Anseranatidae. So far, however, no derived characters have been presented which support this assumption, and the coracoid of *Romainvillia* lacks the pneumatic foramen which is characteristic for the coracoid of the Anseranatidae (Mayr & Smith, 2001). The plesiomorphic (Livezey, 1986; Olson, 1999*b*) presence of a foramen for the supracoracoideus nerve, however, shows *Anatalavis* and *Romainvillia* to be outside crown-group Anatidae. A further putative member of the Anseranatidae, *Anserpica kiliani*, has recently been reported from the Upper Oligocene of France (Mourer-Chauviré, Berthet & Hugueney, 2004).

The earliest European representative of crown-group Anatidae may be *Paracygnopterus scotti* Harrison & Walker 1979 from the early Oligocene of England. The coracoid of *Paracygnopterus* exhibits a distinct incision for the supracoracoideus nerve which is present in many recent Anserinae (swans and geese), but absent in Anatinae (ducks) and Dendrocygninae (whistling-ducks). Remains of *Paracygnopterus* were also tentatively identified in the Lowermost Oligocene of Belgium by Mayr & Smith (2001). Also from the Oligocene of Belgium, a large anseriform taxon was described as *Cygnopterus* by Lambrecht (1931), who considered it to be a swan. At least judging from the published illustrations, *Cygnopterus* is very similar to the presumed presbyornithid (Dyke, 2001*e*) *Headonornis* Harrison & Walker 1976 from the Upper Eocene of England, with which is has not yet been compared. *Mionetta* Livezey & Martin 1988, which occurs in the Upper Oligocene of France (Hugueney *et al.*, 2003), was shown to occupy a basal position within crown-group Anatidae by Livezey & Martin (1988).

(*c*) *Gaviiformes* (loons) *and Procellariiformes* (tubenoses and petrels)

In Europe, the earliest record of Gaviiformes is *Colymboides anglicus* Lydekker 1891 from the Upper Eocene of England (Storer, 1956). This species is represented by a coracoid, a referred humerus, and a referred frontal part of the skull (Harrison & Walker, 1976*c*). Another species of *Colymboides*, *Colymboides belgicus*, was described from the lowermost Oligocene of Belgium and is based on a proximal carpometacarpus and a distal ulna (Mayr & Smith, 2002*b*). Recently, a disarticulated skeleton of a new species of *Colymboides*, *C. metzleri* Mayr 2004, was also found in the Lower Oligocene of Frauenweiler (Mayr, 2004*a*). In this specimen stomach content is preserved, which shows Paleogene loons to be piscivorous like their modern relatives. Remains of *Colymboides* are also known from early Miocene deposits (Storer, 1956). Storer (1956, p. 423) noted that the hindlimbs of *Colymboides* were 'not as highly adapted for swimming rapidly and powerfully under water as are those of living loons', and that the 'morphological differences between *Colymboides* and *Gavia* are many and rather great, but they are largely one of size and degree of specialization' (p. 425).

The earliest European remains of putative procellariiform birds were reported from the London Clay (Harrison & Walker, 1977) but these, a distal end of a humerus described as *Primodroma bournei* Harrison & Walker 1977 and a fragmentary beak and proximal end of a carpometacarpus

described as *Marinavis longirostris* Harrison & Walker 1977, are too fragmentary for reliable identification (see also Steadman, 1981; Mlíkovskỳ, 2002, p. 259). The earliest European record of procellariiform birds thus is the Diomedeoididae which are known from abundant remains, including several complete skeletons, from the Lower Oligocene (Rupelian) of Germany, France, and Belgium, and the Upper Oligocene of Germany (Cheneval, 1995; Mayr, Peters & Rietschel, 2002). Diomedeoididae were further reported from the Oligocene of Iran (Peters & Hamedani, 2000). These birds are characterized by a peculiar foot structure with grotesquely widened phalanges, which are strikingly similar to those of the modern procellariiform *Nesofregetta* (Hydrobatidae, storm petrels). In other respects, however, the skeleton of the Diomedeoididae strongly differs from all Hydrobatidae, and their phylogenetic affinities to other procellariiform birds are uncertain (Mayr *et al.*, 2002).

'*Larus*' *raemdonckii* van Beneden 1871, known from an incomplete humerus from the Rupelian of Belgium, was placed in the genus *Puffinus* by Brodkorb (1962), but also needs to be compared with the Diomedeoididae.

(*d*) *Pelagornithidae* (bony-toothed birds)

The extinct, bony-toothed Pelagornithidae are fairly abundant and greatly diversified in Paleocene and Lower Eocene marine deposits of England (Harrison & Walker, 1976*b*, 1977; Harrison, 1985). However as noted by Olson (1985), the taxonomy of these birds, which at this locality are known from isolated remains only, is in dire need of revision and probably too many taxa are currently recognized. The large tarsometatarsi from the London Clay that were assigned to the alleged procellariiform *Neptuniavis* by Harrison & Walker (1977) almost certainly belong to one of the pelagornithid taxa from the same locality, of which the tarsometatarsus has not been described (Mayr *et al.*, 2002, see also Harrison & Walker, 1976*b*, p. 60). The systematic affinities of the Pelagornithidae are still uncertain and affinities to Procellariiformes and 'Pelecaniformes' were suggested (Harrison & Walker, 1976*b*; Olson, 1985). Pelagornithidae also occur in the Paleocene to early Oligocene of the former USSR (e.g. Averianov *et al.*, 1997; Aslanova & Burchak-Abramovich, 1999), the Eocene of Nigeria (see Rasmussen, Olson & Simons, 1987), and the Neogene of Europe, Japan, North and South America, Antarctica, and New Zealand (Olson, 1985; Ono, Hasegawa & Kawakami, 1985; Cheneval, 1993).

(*e*) '*Pelecaniformes*' (pelicans, cormorants, and allies)

The most completely preserved Paleogene 'pelecaniform' bird from Europe is *Prophaethon shrubsolei* Andrews 1899, the single named species of the extinct Prophaethontidae, of which a partial skeleton has been found in the London Clay (Harrison & Walker, 1976*a*) and a coracoid in Middle Eocene marine deposits of Belgium (Mayr & Smith, 2002*a*). Prophaethontidae were also tentatively identified in the Paleocene of North America (Olson, 1994), and exhibit a mosaic of derived characters of modern 'Pelecaniformes'

(e.g. presence of an articulation facet for the furcula on the sternal carina and a distinct naso-frontal hinge) and Procellariiformes (e.g. narrow pelvis and enlarged cnemial crests on tibiotarsus). Compared to modern birds, the Prophaethontidae most closely resemble the 'pelecaniform' Phaethontidae (tropicbirds), but their phylogenetic assignment is aggravated by the existing uncertainty regarding monophyly of the traditional 'Pelecaniformes' (e.g. Sibley & Ahlquist, 1990; van Tuinen *et al.*, 2001; Mayr, 2003*d*).

There is no Paleogene European record of Pelecanidae (pelicans), as *Protopelicanus cuvieri* Reichenbach 1852 was incorrectly identified (Olson, 1985, *contra* Brunet, 1970).

Phalacrocoracidae (cormorants) are known from the Upper Oligocene of Germany (Mayr, 2001*a*) and France (Mourer-Chauviré *et al.*, 2004) and were also reported from the Quercy fissure fillings (Mourer-Chauviré, 1995*a*). The Oligocene taxa appear to be outside crown-group Phalacrocoracidae (Mayr, 2001*a*). The coracoid of *Borvocarbo* Mourer-Chauviré *et al.*, 2004, from the Upper Oligocene of France, differs from that of extant Phalacrocoracidae and Anhingidae, their sister taxon, in the presence of a plesiomorphic, cup-like cotyla scapularis and *Borvocarbo* may thus even be outside the clade (Phalacrocoracidae + Anhingidae).

Sulidae (gannets and boobies) were reported from the Oligocene of Germany (Darga *et al.*, 1999) and France (Mourer-Chauviré, 1995*a*). *Masillastega* Mayr 2002 from Messel is known from an isolated skull only and was tentatively identified as a stem-group representative of the Sulidae (Mayr, 2002*d*).

(*f*) *Charadriiformes (shorebirds, incl. Turnicidae)*

Charadriiform birds have a scanty Paleogene record in Europe. Taxa that are unambiguously within crown-group Charadriiformes are not known from pre-Oligocene deposits. The Lower Eocene taxa that were reported from the London Clay consist of very fragmentary remains and are in need of revision; the paratypic humerus of the putative pratincole (Glareolidae) *Precursor parvus* Harrison & Walker 1977, for example, belongs to the psittaciform Pseudasturidae (Mayr, 2002*g*). A partial skeleton of an unnamed species of uncertain affinities within Charadriiformes was described from Messel (Mayr, 2000*e*), but is too incompletely preserved to allow detailed comparisons. Scolopacidae (sandpipers, snipes, and allies) were reported from the Lower Oligocene of Céreste (Roux, 2002), from an unknown horizon of the Quercy fissure fillings ('*Totanus*' *edwardsi* Gaillard 1908), and from the Upper Oligocene of France (Hugueney *et al.*, 2003). The two species of *Villetus* Harrison & Walker 1976 from the Upper Eocene of England are based on distal tibiotarsi and cannot be referred to the Scolopacidae with confidence (*contra* Harrison & Walker, 1976*c*).

An as yet unnamed charadriiform bird from the Lower Oligocene of Southern France was figured and briefly described by Bessonat & Michaut (1973). The affinities of this specimen, which is in a private collection in France, are uncertain, but judging from the apparently complete absence of a hallux it may belong within Charadriidae (plovers and allies). *Boutersemia* Mayr & Smith 2001 from the Lower

Oligocene of Belgium is known from several postcranial elements of two species and was tentatively assigned to the Glareolidae (pratincoles), but this assignment was based on a possibly plesiomorphic overall similarity (Mayr & Smith, 2001). Laridae (gulls) are known from the Upper Oligocene of France (Hugueney *et al.*, 2003; Mourer-Chauviré *et al.*, 2004; the putative gull *Gaviota lipsiensis* Fischer 1983 belongs to the procellariiform Diomedeoididae, see Mayr *et al.*, 2002). The earliest European record of Alcidae (auks) is a dissociated skeleton from the Upper Oligocene of Austria (Mlíkovskỳ, 1987).

The Turnipacidae were described from the Lower Oligocene of Céreste (Mayr, 2000*e*) and include *Turnipax* Mayr 2000 and the tentatively referred *Cerestenia* Mayr 2000. Mayr (2000*e*) assigned these birds to the Charadriiformes but noted similarities to the Turnicidae (buttonquails), including a highly derived coracoid morphology. If Turnicidae are indeed within crown-group Charadriiformes as assumed by Paton *et al.* (2003), the Turnipacidae may be on their stem-lineage and the similarities to charadriiform birds plesiomorphic for the clade including Charadriiformes and Turnicidae.

(*g*) *Columbidae (doves and pigeons) and Pteroclidae (sandgrouse)*

Columbidae have no Paleogene fossil record, even outside Europe, and I consider the Lower Eocene putative columbid *Microena* Harrison & Walker 1977 to be a member of the Cypselomorphae. Olson (1989) assumed that Columbidae evolved in the Southern Hemisphere and did not arrive in Europe before the Neogene. Pteroclidae, however, were found in the Quercy fissure fillings (Mourer-Chauviré, 1992*b*, 1993): *Archaeoganga* Mourer-Chauviré 1992 was reported from an unknown horizon and locality and *Leptoganga* Mourer-Chauviré 1993 from Upper Oligocene deposits. At least *Leptoganga* exhibits the peculiar intermetatarsal sesamoid bone that is characteristic of modern Pteroclidae (Mourer-Chauviré, 1993).

(*h*) *Threskiornithidae (ibises), Ardeidae (herons), and Ciconiidae (storks)*

The earliest substantial European fossil record of the Threskiornithidae is *Rhynchaeites messelensis* Wittich 1898 from Messel. This species is known from several complete and well-preserved skeletons and, among other characteristics, differs from its modern relatives in sternal morphology and a much more abbreviated tarsometatarsus (Peters, 1983; Mayr, 2002*a*). Roux (2002) further described an as yet unnamed species of the Threskiornithidae from the Lower Oligocene of Céreste, which also exhibits a proportionally shorter tarsometatarsus than modern ibises. All other Paleogene ibises are based on much too fragmentary remains for reliable identification (see Olson, 1981).

The only substantial Paleogene record of Ardeidae from Europe is *Proardea amissa* that was described from an unknown horizon and locality of the Quercy fissure fillings by Milne-Edwards (1892). New remains of *P. amissa* were found in the Upper Oligocene Quercy locality Pech Desse (C. Mourer-Chauviré, personal communication; G. Mayr,

personal observations). According to Mlíkovský & Švec (1989), 'Anas' basaltica Bayer 1883 from the Lower Oligocene of the Czech Republic is another member of the Ardeidae.

Ciconiidae (storks) have not been recorded from the Paleogene of Europe and their earliest record is from the Upper Eocene of Egypt (Miller, Rasmussen & Simons, 1997).

(i) Phoenicopteriformes (flamingos)

The phylogenetic affinities of the Phoenicopteriformes have long been debated (see reviews in Olson & Feduccia, 1980b and Sibley & Ahlquist, 1990). Recent molecular and morphological studies, however, provide strong evidence for a sister-group relationship to Podicipediformes (grebes) (van Tuinen et al., 2001; Chubb, 2004; Mayr, 2004b), which puts into a new light some fossil taxa that were assigned to the Phoenicopteriformes.

The earliest fossils classified into the Phoenicopteriformes belong to the Middle Eocene *Juncitarsus* that was originally described from North American deposits (Olson & Feduccia, 1980b), but subsequently also reported from Messel (Peters, 1987b). The phylogenetic position of *Juncitarsus* is in need of revision, as this taxon lacks most of the derived characters that support sister-group relationship between flamingos and grebes and thus could at best be the sister-group of a clade including the latter two taxa (Mayr, 2004b). *Kashinia* ('*Tenuicrus*') *magna*, from the Upper Eocene of England (Harrison & Walker, 1976c), was assigned to the Juncitarsinae by Mlíkovský (2002), but the coracoid of this species distinctly differs in its proportions from the corresponding bone of the Juncitarsinae as figured by Ericson (1999).

The Palaelodidae are an extinct taxon of phoenicopterid birds that is fairly abundant in the Upper Oligocene of France (Mourer-Chauviré, 1995a) and was also reported from the Lower Oligocene of Belgium (Mayr & Smith, 2002b). These aquatic birds provide a morphological link between Phoenicopteriformes and Podicipediformes, in combining the deep mandibular rami of modern flamingos with leg bones that 'show many similarities with those of a foot-propelled diving bird such as *Podiceps*' (Cheneval & Escuillié, 1992, p. 218). Palaelodids trenchantly differ, however, from modern flamingos in the plesiomorphic presence of a short and straight beak (Cheneval & Escuillié, 1992).

The earliest fossil assigned to the Phoenicopteridae, i.e. the most inclusive taxon to which modern flamingos but not the Palaelodidae belong, is *Elornis* Milne-Edwards 1867–71 from the Lowermost Oligocene of Ronzon in France. *Elornis* is too incompletely known to assess its exact phylogenetic position, but is likely to be outside crown-group Phoenicopteridae, as even early Miocene flamingos still exhibit a less derived bill morphology than their extant relatives (Feduccia, 1999, p. 202).

(j) 'Gruiformes' (cranes, rails, and allies)

Various fossil taxa have been assigned to the, almost certainly paraphyletic (e.g. Mayr & Clarke, 2003), 'Gruiformes'. An abundant group of these are the Messelornithidae, which are known from Paleocene to Lower Oligocene deposits of Germany and France (Hesse, 1990; Mourer-Chauviré, 1995c). These birds were considered to be most closely related to the South American Eurypygidae by earlier authors (Hesse, 1990; Livezey, 1998). However, this hypothesis has not been well established and I consider messelornithids to be the sister taxon of the clade (Heliornithidae + Rallidae), with which they share derived characters such as absence of pneumatic foramina on the proximal humerus and a derived morphology of the coracoid and hypotarsus (Mayr, 2004e). Messelornithidae are also known from the Lower Eocene of North America (Hesse, 1992).

Several putative true Rallidae (rails) were described from the London Clay (Harrison & Walker, 1977; Harrison, 1984b) but the identification of these fragmentary remains is questionable; specimens assigned to *Pediorallus* Harrison & Walker 1977 were identified as remains of the palaeognathous Lithornithidae by Houde (1988). *Ibidopsis* Lydekker 1891 from the Upper Eocene of England and *Quercyrallus quercy* Cracraft 1973 from the Quercy fissure fillings appear to have been correctly identified but are also known from few bones only (see Cracraft, 1973; Harrison & Walker, 1976c; Olson, 1977b). The earliest substantial records of Rallidae are *Rupelrallus* Fischer 1997 and *Belgirallus* Mayr & Smith 2001 from the Lower Oligocene of Germany and Belgium, respectively (Fischer, 1997; Mayr & Smith, 2001).

Gruidae (cranes) were reported from the Middle Eocene of Italy (*Palaeogrus princeps* Portis 1884) and the Upper Eocene of England [*Geranopsis hastingsiae* Lydekker 1891 and *Palaeogrus hordwelliensis* (Lydekker 1891)], but their identifications are based on fragmentary or poorly preserved remains and need to be confirmed by additional specimens. Judging from the illustrations, the coracoid of *Geranopsis hastingsiae* resembles that of the putative anseranatid *Anserpica* (see above).

A diverse group of 'gruiform' birds in the Paleogene of Europe are the Idiornithidae. These medium-sized to large cursorial birds are the sister taxon of a clade including the extinct New World Phorusrhacidae and the modern South American Cariamidae (seriemas) (Mourer-Chauviré, 1983a; Mayr, 2002c). Idiornithid remains are especially abundant in the Quercy fissure fillings (Mourer-Chauviré, 1983a) but were also reported from Messel and the Geiseltal (Peters, 1995; Mayr, 2000g, 2002f). As noted by Mayr (2002f), the putative hornbill *Geiseloceros* Lambrecht 1935 from the Geiseltal also belongs into the Idiornithidae. Of the idiornithid taxa currently recognized (Mourer-Chauviré, 1983a), *Elaphrocnemus* lacks derived characters that are shared by *Idiornis* and modern Cariamidae, such as the fusion of the procoracoid and acrocoracoid process of the coracoid and a block-like hypotarsus (Mayr, 2002c). The relationship of *Elaphrocnemus* need to be restudied, especially as Mourer-Chauviré (1983a) also noted similarities to the South American Opisthocomidae (hoatzin).

Alvarenga & Höfling (2003) recently showed convincingly that the alleged European 'Phorusrhacidae' (Mourer-Chauviré, 1981; Peters, 1987a) do not belong within Phorusrhacidae. Both species, from Quercy and Messel,

were recently assigned to the genus *Strigogyps* Gaillard 1908 (Mayr, 2005 *b*).

The enigmatic Middle Eocene Salmilidae Mayr, 2002 *c* are known from excellently preserved skeletons from Messel (Mayr, 2000 *d*, 2002 *c*) and share derived characters mainly with the Cariamae (to which the extant Cariamidae belong) and the Psophiidae (trumpeters). Their exact systematic affinities are however unknown, pending on a reliable phylogenetic framework of crown-group 'Gruiformes'.

(k) 'Falconiformes' (diurnal birds of prey)

As traditionally recognized (e.g. *sensu* Wetmore, 1960), crown-group 'Falconiformes' comprise Cathartidae (New World vultures), Sagittariidae (secretary bird), Falconidae (falcons), and Accipitridae (hawks and allies), but monophyly of this taxon is weakly supported and has been doubted by several recent authors (see discussions in Olson, 1985; Sibley & Ahlquist, 1990; Mayr, Manegold & Johansson, 2003).

Cathartidae were reported from the Quercy fissure fillings (Mourer-Chauviré, 2002) and include *Diatropornis* Oberholser 1899 and *Parasarcoramphus* Mourer-Chauviré 2002. *Oligocathartes* Harrison & Walker 1979 from the Lower Oligocene of England is based on such fragmentary remains (a distal tarsometatarsus lacking two trochleae) that a reliable identification is not possible, especially given the fairly undiagnostic morphology of the distal tarsometatarsus of the Cathartidae. *Plesiocathartes* Gaillard 1908 was removed from the Cathartidae (Mourer-Chauviré, 2002; Mayr, 2002 *b*) and probably is a stem-group Leptosomidae (cuckoo-rollers) (Mayr, 2002 *b*). The earliest New World record of the Cathartidae is from the late Oligocene of Brazil (Alvarenga, 1985).

Sagittariidae were reported from the Oligocene of France. The single known taxon, *Pelargopappus* Stejneger 1885, was considered to be 'too evolved to be the ancestor of recent Sagittariidae' (Mourer-Chauviré & Cheneval, 1983, p. 443). The more 'accipitrid'-like morphology of *Pelargopappus* (e.g. tarsometatarsus with a more strongly developed trochlea for the second toe and a more pronounced medial hypotarsal crest) may, however, turn out to represent the primitive condition in Sagittariidae, as some recent phylogenetic studies support a sister-group relationship between Sagittariidae and Accipitridae (Sibley & Ahlquist, 1990; Griffiths, 1994; Fain & Houde, 2004; *contra*, however, Mayr & Clarke, 2003).

An extinct taxon of 'falconiform' birds, the Horusornithidae Mourer-Chauviré 1991, occurs in the Upper Eocene Quercy fissure fillings and is known from numerous isolated postcranial bones (Mourer-Chauviré, 1991). Among other features (Mourer-Chauviré, 1991), horusornithids share with modern Accipitridae and Falconidae a derived morphology of the hypotarsus, which exhibits two marked crests that are separated by a wide sulcus. Horusornithidae and most Accipitridae further share a derived modification of the major metacarpal of the carpometacarpus (see Mourer-Chauviré, 1991), but differ from other 'falconiform' birds and agree with owls in the absence of an ossified supratendinal bridge on the distal tibiotarsus. Their exact relationships to other 'falconiform' birds still are uncertain.

Two species of the Accipitridae were further described by Milne-Edwards (1892) and Gaillard (1939) from unknown localities and horizons of the Quercy fissure fillings ('*Aquila*' *hypogaea* Milne-Edwards 1892 and '*Aquila*' *corroyi* Gaillard 1939), and Mayr & Smith (2002 *b*) tentatively assigned a distal tarsometatarsus from the Lower Oligocene of Belgium to the Accipitridae.

From deposits in England, the Lower Eocene *Parvulivenator* Harrison 1982 *a* and *Stintonornis* Harrison 1984 were assigned to the Falconidae (Harrison, 1982 *a*, 1984 *b*), the Upper Eocene *Milvoides* Harrison and Walker 1979 was considered to be a member of the Accipitridae. These three taxa are based on distal, partly fragmentary tarso-metatarsi, and at least the tiny *Parvulivenator* is almost certainly not a 'falconiform' bird. I identified a second specimen of *Parvulivenator watteli* Harrison 1984, also from the London Clay, in the collection of the Natural History Museum in London (specimen BMNH A 6161) and find this species to be more similar to Coliiformes (mousebirds). *Stintonornis* and *Milvoides* appear to have been correctly referred to the 'Falconiformes', but the fragmentary remains do not allow a reliable assignment to any subgroup within this taxon.

(l) Strigiformes (owls)

The fossil record of Strigiformes goes back into the Paleocene and is quite extensive in Eocene and Oligocene deposits of Europe, although the relationships between the fossil and the modern taxa (i.e. Tytonidae, barn owls, and Strigidae, true owls) are only insufficiently resolved.

The Sophiornithidae were originally erected for *Sophiornis* Mourer-Chauviré 1987, from an unknown locality and horizon of the Quercy fissure fillings. Subsequently, *Berruornis* Mourer-Chauviré 1994 from the Paleocene of Germany and France was also assigned to this taxon (Mourer-Chauviré, 1994; Mayr, 2002 *e*), as well as *Palaeotyto* Mourer-Chauviré 1987 and *Palaeobyas* Mourer-Chauviré 1987 from the Quercy (Mlíkovskỳ, 2002). Sophiornithidae were considered stem-group representatives of the Strigiformes by Mourer-Chauviré (1987, her Fig. 8).

The Protostrigidae, first reported from the Paleogene of North America (e.g. Wetmore, 1933; Martin & Black, 1972; Mourer-Chauviré, 1983 *b*), are represented in Europe by *Oligostrix* Fischer 1983 and *Eostrix* Harrison 1980 (Harrison, 1980; Fischer, 1983). The Protostrigidae are well-characterized by the derived presence of a greatly widened medial condyle of the tibiotarsus and, apparently functionally correlated therewith, a strongly developed first and second toe. The Protostrigidae were also considered to be outside crown-group Strigiformes by Mourer-Chauviré (1987, her Fig. 8) and derived characters shared by crown-group Strigiformes but absent in the Protostrigidae are the medially situated tubercle for the tibialis anticus muscle on the proximal tarsometatarsus (Mourer-Chauviré, 1983 *b*, her Fig. 2) and the unusually slender humerus (Howard, 1965).

An articulated postcranial skeleton of an owl from Messel was assigned to *Palaeoglaux* Mourer-Chauviré 1987 by Peters (1992), who considered the possibility that it 'represents the

Fig. 2. *Pulchrapollia gracilis* Dyke & Cooper 2000 (Psittaciformes, Pseudasturidae). Selected bones of a single individual from the Lower Eocene London Clay at Walton-on-the-Naze (private collection of M. Daniels, from Mayr & Daniels, 1998). Scale bar in millimeters.

first evidence of Eocene strigids' (p. 168). The Messel owl is, however, clearly distinguished from crown-group Strigiformes by the absence of an osseous arch on the radius, a derived feature of modern owls (Bock & McEvey, 1969; Fig. 4 in Peters, 1992).

All other Paleogene owls, which come mainly from Upper Eocene to Oligocene deposits of the Quercy fissure fillings, were assigned to the Tytonidae (Mourer-Chauviré, 1987; Mlíkovský, 1998). However, this assignment is based on the plesiomorphic absence of an ossified arcus extensorius on the proximal tarsometatarsus and a deep supracondylar fossa on the distal tibiotarsus. Thus some, if not all, Paleogene taxa that are currently assigned to the Tytonidae may well be stem-group representatives of either Strigiformes or Strigidae.

Tynskya eocaena was described by Mayr (2000*c*) from the Lower Eocene North American Green River Formation, and bones of a closely related species were also found in the London Clay. The tarsometatarsus of *T. eocaena* exhibits a derived morphology similar to that of strigiform birds in that the medial crest of the hypotarsus is markedly longer than the lateral crest, and the trochlea for the fourth toe much shorter than that for the second, bearing a plantarly projecting wing-like flange which is typical of semi-zygodactyl feet in which the fourth toe can be spread laterally. Contrary to owls however, *T. eocaena* lacks a derived enlarged trochlea for the second toe and the humerus is not as slender and elongated. *T. eocaena* was recently shown to be the sister taxon of *Messelastur gratulator* Peters 1994 (Mayr, in press), which was tentatively assigned to the Accipitridae by Peters (1994). An as yet undescribed, almost complete skeleton of *M. gratulator* shows that this species differs from all modern birds of prey and agrees with owls in the absence of a supra-tendinal bridge on the distal tibiotarsus (Mayr, in press). Cladistic analysis of 110 characters supports a sister-group relationship between *Messelastur* and *Tynskya,* and shows

Fig. 3. *Psittacopes lepidus* Mayr & Daniels 1998 (holotype), a small psittaciform bird from the Middle Eocene of Messel in Germany. Scale bar in millimeters.

both taxa to be the sister-group of strigiform birds (Mayr, in press).

(*m*) *Psittaciformes* (*parrots*)

In recent years, several stem-group Psittaciformes were described from Eocene deposits in England, Germany, and France that are successive sister taxa of crown-group Psittaciformes.

The most basal taxon of these are the Pseudasturidae (Fig. 2) that were reported from the London Clay, Messel, the Geiseltal, and the North American Green River Formation (Dyke & Cooper, 2000; Dyke, 2001*b*; Mayr, 2002*f, g*;). These birds distinctly differ from crown-group Psittaciformes and were originally considered to be of uncertain affinities (Mayr, 1998*a*), but especially the three-dimensionally-preserved London Clay specimens have allowed establishment of their psittaciform affinities (Mayr, 2002*g*).

Another taxon of stem-group Psittaciformes, *Psittacopes* Mayr & Daniels 1998 (Fig. 3), occurs in the London Clay
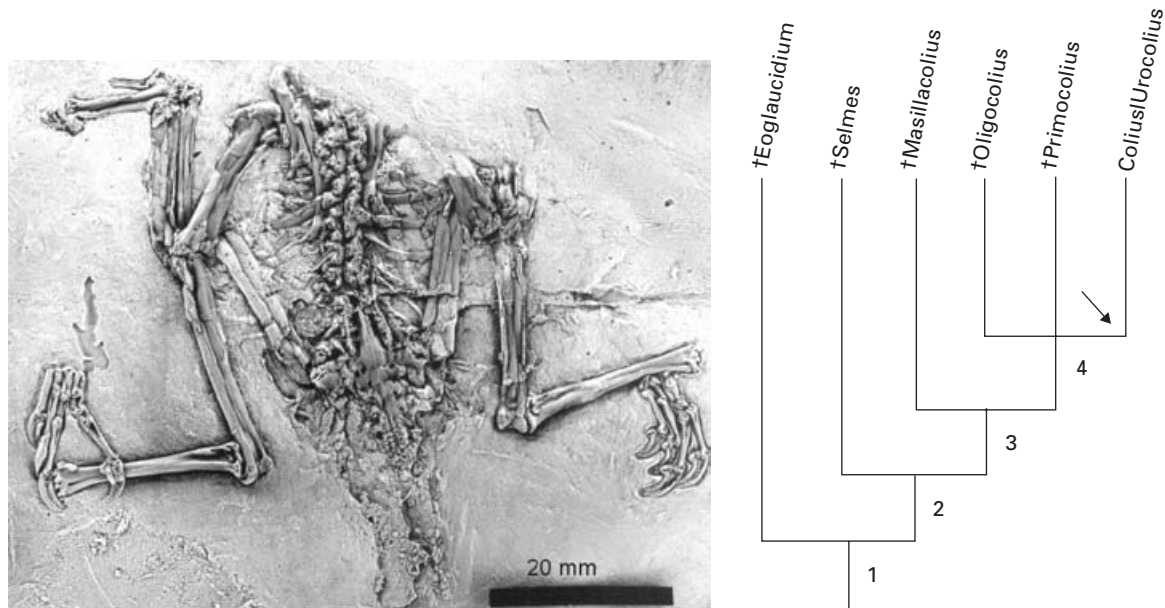
Fig. 4. Phylogenetic relationships between Paleogene and extant taxa of the Coliiformes (after Mayr & Peters, 1998; Mayr & Mourer-Chauviré, 2004), with a figure of *Masillacolius brevidactylus* Mayr & Peters 1998 (Coliidae, holotype specimen) from the Middle Eocene of Messel in Germany. Extinct taxa are indicated by a dagger, the arrow indicates the crown-group. The nodes are supported by the following diagnostic synapomorphies: **1** – ulna, cotyla ventralis very large; femur, distal end thickened with large tuberculum musculi gastrocnemialis lateralis; tibiotarsus, both cristae cnemiales and crista patellaris forming a continuous ridge that circumscribes a groove on the cranial side of the bone, crista cnemialis cranialis continuous with a ridge opposite to crista fibularis; tarsometatarsus, fossa metatarsi I situated on medial side of shaft; proximal phalanges of fourth toe strongly abbreviated. **2** – Discus pygostyli very large; hypotarsus with large canal for tendon of musculus flexor digitorum longus. **3** – Tarsometatarsus, trochleae metatarsorum small, not widely splayed from trochlea metatarsi III. **4** – Humerus with marked, crescent-shaped depression above condylus dorsalis; carpometacarpus with well-developed processus intermetacarpalis.

and Messel and, of the known Paleogene Psittaciformes, appears to be most closely related to modern parrots with which it shares a derived accessory trochlea for the retroverted fourth toe (Mayr & Daniels, 1998). Both Pseudasturidae and *Psittacopes* are, however, clearly shown to be outside crown-group Psittaciformes by the plesiomorphic absence of a parrot-like beak.

The third Paleogene psittaciform taxon, the Quercypsittidae, is known from the Upper Eocene of the Quercy fissure fillings (Mourer-Chauviré, 1992c). The beak of these birds is unknown, but their coracoid exhibits a plesiomorphic, cup-like scapular articulation facet (Mourer-Chauviré, 1992c), which supports their placement outside crown-group Psittaciformes (Mayr, 2002g).

After discovery of more completely preserved remains, the Lower Eocene *Palaeopsittacus*, described as a parrot by Harrison (1982c), turned out to be an anisodactyl bird not related to parrots (Mayr & Daniels, 1998). An articulated postcranial skeleton of this bird was recently described from Messel (Mayr, 2003b) and shows similarities to Podargidae (frogmouths) (see below).

(n) Coliiformes (mousebirds)

Coliiformes today only occur with six very similar species in Africa south of the Sahara, but are fairly abundant and diversified in early Eocene localities. A distinctive taxon are the Sandcoleidae which were originally described from the Paleocene and early Eocene of North America (Houde & Olson, 1992), but are also known from the Middle Eocene of Germany and France (Mayr & Peters, 1998; Mayr, 2001e, 2002f; Mayr & Mourer-Chauviré, 2004). The single named European sandcoleid species is *Eoglaucidium pallas* Fischer 1987, which was originally described as an owl (Fischer, 1987, see Mayr & Peters, 1998) and is very similar to the North American *Sandcoleus* Houde & Olson 1992 and *Anneavis* Houde & Olson 1992 (Mayr & Peters, 1998).

Eocolius walkeri Dyke & Waterhouse 2001 from the London Clay is most similar to *Selmes absurdipes* Peters 1999 from Messel, and may even be a junior synonym of this species. Dyke & Waterhouse (2001) could make their comparisons only with the badly flattened holotype of *S. absurdipes*, but a new specimen of the latter species from Messel (Mayr, 2001e) shows that *E. walkeri* cannot be distinguished from *S. absurdipes* by the characters given by Dyke & Waterhouse (2001, p. 10). An isolated tarsometatarsus of *Selmes* was also reported from the Quercy fissure fillings (Mayr & Mourer-Chauviré, 2004) and provides evidence that *Selmes* is a stem-lineage representative of the Coliidae, not a sandcoleid bird as assumed in the original description (Peters, 1999).

Another record of the Coliidae is *Masillacolius brevidactylus* Mayr & Peters 1998, which is known from two articulated

postcranial skeletons from Messel (Fig. 4), and which apparently had pamprodactyl feet, i.e. the hallux permanently directed forwards as in some modern swifts. The Upper Eocene *Primocolius* Mourer-Chauviré 1988, the Lower Oligocene *Oligocolius* Mayr 2000, and extant mousebirds form a monophyletic taxon that is characterized by the derived presence of a well-developed intermetacarpal process on the carpometacarpus (Mourer-Chauviré, 1988*a*; Mayr, 2000*b*, 2001*e*; Fig. 4). A very fragmentary tarsometatarsus of a mousebird was also reported from the Lowermost Oligocene of Belgium (Mayr & Smith, 2001).

(*o*) *Musophagidae (turacos) and Cuculidae (cuckoos)*

The only European record of Musophagidae is from the late Oligocene of Bavaria in Germany (Ballmann, 1970), as the alleged London Clay musophagid *Promusophaga* Harrison & Walker 1977 was shown to be a member of the Lithornithidae by Houde (1988).

Cuculidae (cuckoos) do not have an unambiguous Paleogene European fossil record. Whether *Dynamopterus* Milne-Edwards 1892, known from two humeri of two species from an unknown horizon of the Quercy fissure fillings, is a member of the Cuculidae (Mourer-Chauviré in Olson, 1985, p. 110), needs to be confirmed by additional skeletal elements. The earliest record of the Cuculidae is from the Lower Oligocene of North America (Weigel, 1963; Chandler, 1999).

(*p*) *Leptosomidae (cuckoo-rollers) and Podargidae (frogmouths)*

Plesiocathartes Gaillard 1908, a taxon known from the Quercy (Mourer-Chauviré, 2002), Messel (Mayr, 2002*b*), and the Geiseltal (Mayr, 2002*f*) was removed from the Cathartidae by Mourer-Chauviré (2002), and the complete skeletons from Messel suggest a sister-group relationship to the Madagascan Leptosomidae (Mayr, 2002*b*). There is no other known fossil member of Leptosomidae.

Podargidae were reported from the Quercy (Mourer-Chauviré, 1989*b*) and from Messel (Mayr, 1999*b*, 2001*d*). The French taxon, *Quercypodargus* Mourer-Chauviré 1989, differs from modern Podargidae in the morphology of the distal tibiotarsus (Mayr, 1999*b*) but is very similar to *Palaeopsittacus* Harrison 1982 from the London Clay (compare Fig. 2 in Mourer-Chauviré, 1989*b* and Fig. 1 in Mayr, 2003*b*). Derived features shared by both taxa include a wide intercondylar incision on the distal tibiotarsus (not present in modern Podargidae) and the presence of two hypotarsal foramina, one of which is however not completely closed in *Quercypodargus*. Contrary to modern Podargidae, the coracoid of *Palaeopsittacus* exhibits a foramen for the supracoracoideus nerve (Fig. 1 in Mayr, 2003*b*; the coracoid of *Quercypodargus* is unknown). Nevertheless, in other features *Quercypodargus* and *Palaeopsittacus* closely resemble modern Podargidae (Mourer-Chauviré, 1989*b*; Mayr, 2003*b*) and may be on the stem-lineage of this taxon. The species from Messel, *Masillapodargus* Mayr 1999, is known from articulated skeletons that preserve the highly derived beak morphology of frogmouths.

(*q*) *Cypselomorphae (aerial insectivores and hummingbirds)*

Most modern non-passeriform aerial insectivores belong to the Cypselomorphae, i.e. a monophyletic (Mayr, 2002*h*; Mayr *et al.*, 2003) taxon including Caprimulgidae (nightjars), Nyctibiidae (potoos), and apodiform birds (swifts and hummingbirds). Today only the Caprimulgidae and the apodiform Apodidae (true swifts) are found in Europe, but aerial insectivores were very diversified in the European Paleogene.

Nyctibiidae, which today only occur in South and Central America, were reported from the Quercy fissure fillings (Mourer-Chauviré, 1989*b*) and from Messel (Mayr, 1999*b*, 2001*d*; Mayr & Manegold, 2002). The taxon from Messel, *Paraprefica* Mayr 1999, shows the highly derived skull and tarsometatarsus morphology of modern Nyctibiidae, but is clearly identified as a stem-lineage representative by its otherwise less derived osteology (Mayr, 1999*b*, 2001*d*; Fig. 5). The French taxon, *Euronyctibius* Mourer-Chauviré 1989, is known from an incomplete but very distinctive humerus. The only Paleogene European record of the Caprimulgidae are two coracoids from the Quercy (Mourer-Chauviré, 1988*a*); identification of these bones needs further confirmation by additional skeletal elements. Lower Eocene Caprimulgidae were reported by Olson (1999*a*, p. 7) from North America.

Two cranial parts of sterna from the Quercy deposits were further tentatively identified as belonging to an oilbird (Steatornithidae) and an owlet nightjar (Aegothelidae) (Mourer-Chauviré, 1982). Certainly, these identifications need to be corroborated by additional skeletal elements, as the sternum of many Paleogene birds still is unknown.

An extinct group of aerial insectivores, the Archaeotrogonidae, are among the most abundant small birds in the Lower Oligocene Quercy fissure fillings (Mourer-Chauviré, 1980), and have also been reported from Messel (Mayr, 1998*c*). Originally considered to be trogons, archaeotrogons were recently recognized as being related to the Cypselomorphae (Mourer-Chauviré, 1995*b*). The alleged swift *Laputavis robusta* (Dyke, 2001*a*, *c*; Mayr, 2001*g*) from the London Clay may also be a representative of the Archaeotrogonidae, most similar to the Messel species *Hassiavis laticauda* Mayr 1998.

The Eocypselidae, which were first described by Harrison (1984*a*) from the London Clay, are outside crown-group Apodiformes (Mayr, 2003*c*; see also Dyke, Waterhouse & Kristoffersen, 2004). The same is true for the Aegialornithidae (Mourer-Chauviré, 1988*b*; Mayr, 2003*c*), which are among the most abundant small birds in the Upper Eocene deposits of the Quercy fissure fillings but disappear towards the Lower Oligocene (Mourer-Chauviré, 1980). The earliest record of the Aegialornithidae is from the Middle Eocene of the Geiseltal (Peters, 1998).

Stem-group Apodidae first occur in the Middle Eocene of Denmark (Harrison, 1984*a*) and in Messel (Mayr & Peters, 1999; Fig. 5), crown-group Apodidae were reported from the late Oligocene of France (Mourer-Chauviré *et al.*, 2004). The putative crown-group swift *Cypseloides mourerchauvireae* (*Cypseloides* is a modern genus), which was described by Mlíkovskỳ (1989) on the basis of an isolated tibiotarsus
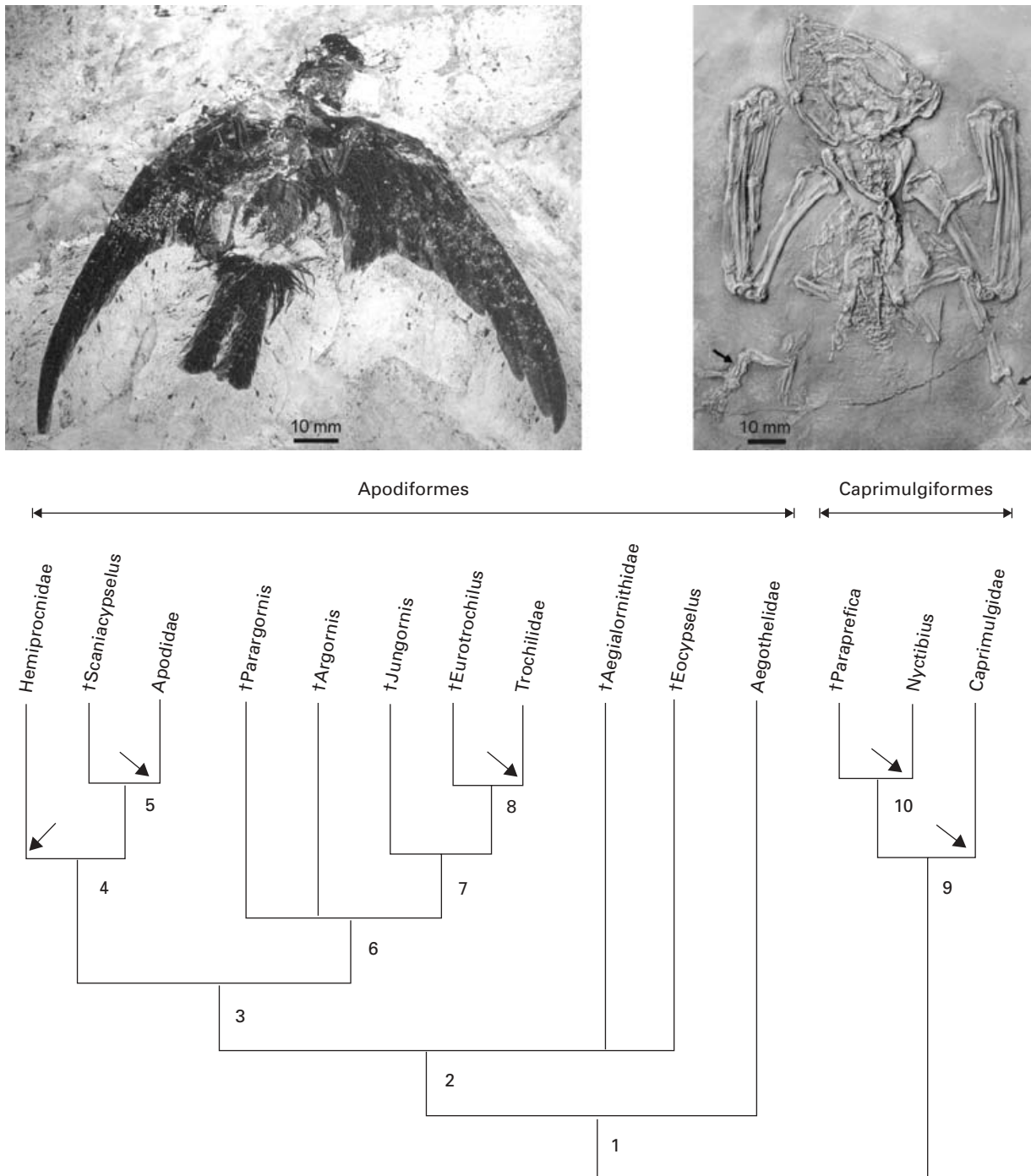
Fig. 5. Phylogenetic relationships between Paleogene and extant taxa of the Cypselomorphae (after Mayr, 2001*d*, 2002*g*, 2003*c*, 2004*d*), with figures of *Scaniacypselus szarskii* (Peters 1985) (Apodidae, left, specimen SMF-ME 3576a in Forschungsinstitut Senckenberg) and *Paraprefica kelleri* Mayr 1999 (Nyctibiidae, right, specimen SMF-ME 3727a in Forschungsinstitut Senckenberg) from the Middle Eocene of Messel in Germany. Extinct taxa are indicated by a dagger, the arrows indicate the crown-groups. The nodes are supported by the following diagnostic synapomorphies: **1** – skull, palatine bone with strongly protruding angulus caudolateralis; processus basipterygoidei reduced; quadratum with pneumatic foramina on caudal surface of processus oticus; coracoid, extremitas omalis hooked and processus lateralis greatly reduced; sternum, incisions in caudal margin closed or completely reduced; musculus splenius capitis with cruciform origin. **2** – Proximo-dorsal part of narial openings covered by an osseous sheet; humerus and ulna strongly abbreviated and hand greatly elongated. **3** – Sternum, facies articularis coracoideus weakly saddle-shaped or convex; humerus, ratio length of bone: width of shaft in midsection less than 7·0. **4** – Humerus, tuberculum supra-condylare ventrale elongated and narrow; humerus, processus musculi extensor metacarpi radialis shifted proximally, situated in proximal two-thirds of the bone; humerus, ratio length of bone: width of shaft in midsection less than 5·0; radius, distal end with

from the Quercy fissure fillings, is, however, a junior synonym of *Aegialornis gallicus* from the same locality (Mayr, 2003a).

Recently, stem-group representatives of hummingbirds (Trochilidae) have also been identified in the Paleogene of Europe, which greatly improves our knowledge on the early evolution of this fascinating group of birds (Mayr, 2003c, d, 2004d). The first specimens were described as an extinct taxon, the Jungornithidae, from the Lower Oligocene of the Caucasus (Karhu, 1988). In addition to the Lower Oligocene *Jungornis* Karhu 1988, Karhu (1999) subsequently reported a second 'jungornithid', *Argornis*, from the Upper Eocene of the Caucasus. Karhu (1988, 1999) noted derived similarities between 'jungornithids' and modern hummingbirds which he attributed to convergence, assigning the 'Jungornithidae' to swifts. However, analysis of the phylogenetic relationships between modern and fossil apodiform birds showed the 'Jungornithidae' *sensu* Karhu (1999) to be paraphyletic, with *Argornis* and *Jungornis* to be successive sister taxa of modern hummingbirds (Mayr, 2003c; Fig. 5). *Argornis* and *Jungornis* are known from wings only, but an *Argornis*-like bird was described from Messel, and in this specimen for the first time the complete skeleton and the feathering of these birds are preserved (Mayr, 2003a). The Messel taxon, *Parargornis* Mayr 2003, still had a swift-like beak and an owlet-nightjar-like feathering, broad wings and a long tail (Mayr & Manegold, 2002; Mayr, 2003a). In the Lower Oligocene, however, even nectarivorous, modern-type hummingbirds occurred in Europe, although these are outside the crown-group of Trochilidae, too (Mayr, 2004d). *Eurotrochilus* Mayr 2004 is nevertheless strikingly similar to modern hummingbirds and leaves no doubt that early hummingbird evolution was not restricted to the New World, with all its implications for the evolution of the ornithophilous Old World flora (see Mayr, 2004d).

Cypselavus gallicus Gaillard 1908 from the Upper Eocene and Lower Oligocene of the Quercy is generally assigned to the Hemiprocnidae (tree swifts, e.g. Harrison, 1984a; Peters, 1985; Mourer-Chauviré, 1988b). However, the coracoid that was assigned to *C. gallicus* by Mourer-Chauviré (1978) was described as a new taxon of the 'Jungornithidae', by Karhu (1988), and its humerus also resembles the corresponding bone of the contemporaneous *Argornis* with which it has not yet been compared (Mayr, 2003a).

(r) Trogoniformes (trogons)

Trogoniformes are well characterized by the unique heterodactyl foot in which the second toe permanently directs backwards. Their earliest fossil records, not only from Europe but in general, are an isolated cranium from the Fur Formation (Kristoffersen, 2002a) and a tarsometatarsus from the London Clay (Mayr, 1999a). The latter specimen clearly shows the tarsometatarsal morphology that is characteristic for the heterodactyl foot. A complete skeleton of an as yet undescribed trogon has also been identified in Messel (Mayr, 2005a). Articulated skeletons of Lower Oligocene trogons were described from Matt in Switzerland (Olson, 1976) and Céreste in France (Mayr, 1999a, 2001c). The Céreste trogon, *Primotrogon wintersteini* Mayr 1999 (Fig. 6), is shown to be outside crown-group Trogoniformes by its plesiomorphic skull morphology and the absence of derived characters of the coracoid (see Mayr, 1999a).

(s) Coraciiformes, Upupiformes, Alcediniformes (rollers, hoopoes, kingfishers, and allies)

The Coraciiformes include the Old World Coraciidae (rollers) and the Madagascan Brachypteraciidae (ground rollers) (Mayr, 1998b). The most basal representatives of this taxon are the Primobucconidae, which were originally described from the Lower Eocene of North America but are meanwhile also known from early Eocene deposits of France, Germany, and England (Mayr, Mourer-Chauviré & Weidig, 2004; M. Daniels, personal communication). Stem-group rollers closely resembling the modern taxa were reported from Messel (Eocoraciidae) and the Upper Eocene Quercy fissure fillings (Geranopteridae) (Mayr & Mourer-Chauviré, 2000). Primobucconidae, Eocoraciidae, and Geranopteridae are successive sister taxa of modern rollers (Mayr & Mourer-Chauviré, 2000; Mayr *et al.*, 2004; Fig. 7). As evidenced by stomach content in some Messel specimens, Paleogene stem-group rollers apparently had a more frugivorous diet than their modern relatives (Mayr *et al.*, 2004). *Cryptornis antiquus* (Gervais, 1848–52) from the Upper Eocene of France was assigned to the Bucerotidae (hornbills) by Milne-Edwards (1867–71), but later transferred to the Coraciidae by Harrison (1979b). It seems to be closely related to, or even conspecific with, *Geranopterus alatus* Milne-Edwards 1892, although the single known specimen is

---

marked tubercle on ventral side of shaft, opposite to tuberculum carpale of ulna; phalanx proximalis digiti majoris, distal part of caudal margin with sulcus for tendon of musculus interosseus ventralis; tarsometatarsus, deep sulcus on dorsal surface, proximal to foramen vasculare distale; outermost primaries greatly elongated, measuring at least 2·5 times the length of the longest secondaries. **5** – Humerus, intumescentia humeri strongly raised with abrupt and steeply sloping dorsal margin; carpometacarpus greatly elongated, about 1·5 times longer than coracoid. **6** – Ulna, cotyla ventralis with weakly pronounced ventro-proximal edge; ulna, olecranon elongated and narrow. **7** – Beak greatly elongated (unknown for *Jungornis* and *Argornis*); humerus, caput humeri bearing a distinct distal protrusion. **8** – Ulna strongly abbreviated, with ratio humerus:ulna greater than 0·7. **9** – Skull, cone-like bony protrusion at caudal margin of foramen nervi optici; ossa palatina extremely widened; processus paroccipitales strongly protruding ventrally; mandible with intraramal joint and caudal half of rami mandibulae greatly widened and dorso-ventrally flattened; caudal end of mandible unusually small, with very short cotyla lateralis and stout processus medialis; ossified cartilago tibialis at intertarsal joint. **10** – Jugal bones markedly bowed; tibiotarsus without ossified pons supratendineus; tarsometatarsus extremely abbreviated.

Fig. 6. *Primotrogon wintersteini* Mayr 1999 (Trogoniformes, specimen SMF Av 432 in Forschungsinstitut Senckenberg) from the Lower Oligocene of Céreste in France.

too poorly preserved for a definitive assignment (Mayr & Mourer-Chauviré, 2000).

The earliest representative of the Alcediniformes (motmots, todies, bee-eaters, and kingfishers) is *Quasisyndactylus* Mayr 1998 from Messel, which is the sister-group of the four modern alcediniform taxa (Mayr, 1998 *b*, 2004 *c*; Fig. 7). There is no published Paleogene record of Meropidae (bee-eaters) and Alcedinidae (kingfishers) but representatives of the New World Momotoidea, i.e. a clade including Momotidae (motmots) and Todidae (todies), were reported from the European Paleogene. *Protornis* Meyer 1844 from the Lower Oligocene of Matt in Switzerland was assigned to the Momotidae by Olson (1976). Cracraft (1980, p. 13) correctly noted, however, that an 'alternative hypothesis to be considered is a sister-group relationship between *Protornis* on the one hand and Todidae + Momotidae on the other' because 'it has not been shown that *Protornis* shares one or more derived characters with the Momotidae'. Todidae were described from the Upper Eocene of the Quercy fissure fillings, in the taxon *Palaeotodus* Olson 1976 (Mourer-Chauviré, 1985), originally described from the Lower Oligocene of North America (Olson, 1976).

Apart from a very similar overall morphology, *Palaeotodus escampsiensis* Mourer-Chauviré 1985 shares with modern Todidae a derived, greatly elongated tarsometatarsus. However, identification of this species, as well as its assignment to *Palaeotodus*, also needs to be further supported with more material.

Fairly abundant small arboreal birds in Messel are the upupiform Messelirrisoridae, which are the sister taxon of modern Upupidae (hoopoes) and Phoeniculidae (woodhoopoes) (Mayr, 1998 *b*, 2000 *h*; Fig. 7). Messelirrisorids were also reported from the London Clay and the Geiseltal in Germany (Mayr, 1998 *b*). Another upupiform taxon are the Laurillardiidae that are known from the Upper Eocene of France (Mayr, 1998 *b*). Whether Laurillardiidae and Messelirrisoridae are synonymous (Mlíkovský 2002, p. 75, *contra* Mayr, 1998 *b*) or whether the Laurillardiidae, which are about 14 million years younger than the Messelirrisoridae, are more closely related to crown-group Upupiformes needs to be evaluated by better preserved specimens of the Laurillardiidae.

(*t*) Piciformes (jacamars, puffbirds, woodpeckers, and allies)

The modern European Piciformes belong to the Pici (woodpeckers and allies), which have a very scanty Paleogene record, the earliest – not only from Europe but in general – being a very fragmentary but diagnostic tarsometatarsus from the Lowermost Oligocene of Belgium (Mayr & Smith, 2001). A more completely preserved tarsometatarsus was further reported from the Upper Oligocene of Germany (Mayr, 2001 *f*).

The tiny, facultatively zygodactyl Middle Eocene to Lower Oligocene Sylphornithidae (Mourer-Chauviré, 1988 *a*; Mayr & Smith, 2002 *b*) were recently shown to be stem-group piciform birds (Mayr, 2004 *f*). Sylphornithids provide a morphological link between the Pici and their sister taxon (Johansson & Ericson, 2003; Mayr *et al.*, 2003), the New World Galbulae (jacamars and puffbirds), and combine a derived, Pici-like carpometacarpus with a plesiomorphic Galbulae-like tarsometatarsus (Mourer-Chauviré, 1988 *a*; Mayr, 2004 *f*). As noted by Mayr (1998 *b*), *Palaegithalus cuvieri* (Gervais, 1848–52) from the Upper Eocene of France may also be a member of the Sylphornithidae. Identification of the Sylphornithidae in Messel (Peters, 1991) turned out to be incorrect, and the specimens belong to the upupiform Messelirrisoridae.

The tiny, long-legged Gracilitarsidae are known from three skeletons of *Gracilitarsus* Mayr 1998 from Messel (Mayr, 1998 *b*, 2001 *b*, 2005 *c*; Fig. 7) and were recently also tentatively identified as stem-group Piciformes (Mayr, 2005 *c*; Fig. 7). Gracilitarsids were also present in the Paleocene of Brazil (*Eutreptodactylus* Baird & Vickers-Rich 1997) and the Lower Eocene of North America (*Neanis schucherti* Feduccia 1973) (Mayr, 2005 *c*) and, in concordance with an intercontinental distribution in the Paleogene, their swallow-like wing bone proportions indicate good flight capabilities. Gracilitarsidae and modern Piciformes exhibit a distinct, derived notch on the medial side of the sternal end of the coracoid that was shown to be a synapomorphy of Piciformes (Mayr *et al.*, 2003).

(u) Primoscenidae (primoscenids) and Passeriformes (passerines or songbirds)

The zygodactyl Primoscenidae are fairly abundant in the Lower Eocene of the Fur Formation, the London Clay, Messel, and the North American Green River Formation (Mayr, 1998 *b*; Kristoffersen, 2002 *b*). The phylogenetic affinities of these birds are uncertain, and they were considered to be most closely related to either Piciformes (Mayr, 1998 *b*) or Passeriformes (Harrison & Walker, 1977; Harrison, 1982 *b*; Mayr, 2004 *f*). Primoscenids unquestionably are closely related to the Lower Miocene Zygodactylidae (Ballmann, 1969; Mayr, 1998 *b*), but whether primoscenids and zygodactylids are sister taxa (Mayr, 2004 *f*) or whether primoscenids are the sister-group of the taxon (Zygodactylidae + Pici) (Mayr, 1998 *b*) is uncertain (Mayr, 2004 *f*).

The earliest fossil record of a passeriform bird comes from the Eocene of Australia (Boles, 1995, 1997), although the described specimens are fragmentary (proximal carpometacarpus and distal tibiotarsus) and need to be substantiated by further remains. There are no Paleogene passerines from Africa and the New World. Passeriformes were not found in Eocene European deposits that yielded numerous small birds, and their earliest European fossil records are from the Lower Oligocene of France (Roux, 2002) and Germany (Mayr & Manegold, 2004). These fossils have not been assigned to any modern passeriform group and at least the specimen from Germany may be outside crown-group Passeriformes (Mayr & Manegold, 2004). However, the earliest European Passeriformes already closely resemble their modern counterparts (Mayr & Manegold, 2004), which supports the hypothesis that evolution of Passeriformes took place outside the Northern Hemisphere (e.g. Olson, 1989; Ericson, Irestedt & Johansson, 2003).

Few remains of passeriform birds were further described from the Upper Oligocene of France (Mourer-Chauviré, Hugueney & Jonet, 1989) and Germany (G. Mayr, unpublished data). The French specimens were assigned to Oscines, the subclade of Passeriformes to which all modern European species belong (Mourer-Chauviré *et al.*, 1989). Most notably, however, even in Miocene deposits of Germany and France there are still fossil passerines that appear to be outside crown-group Eupasseres, i.e. the clade including Suboscines and Oscines (Manegold, Mayr & Mourer-Chauviré, 2004).

III. BIOGEOGRAPHIC AFFINITIES OF PALEOGENE EUROPEAN BIRDS

As recognized by earlier authors (e.g. Houde & Olson, 1989; Peters, 1991; Blondel & Mourer-Chauviré, 1998), the Lower Eocene avifaunas of Europe and North America are very similar, owing to the intermittent presence of land connections by that time (Smith, Smith & Funnell, 1994). Unfortunately, it is not possible to draw generalizing conclusions on the biogeography of birds in the Paleogene, as very little is yet known on Paleogene avifaunas of Asia (e.g. Kurochkin, 1976; Nessov, 1992), and the Southern

continents (e.g. Tonni, 1980; Rasmussen *et al.*, 1987; Vickers-Rich, 1991).

Some Eocene birds are stem-group representatives of avian groups with a worldwide distribution, but the crown-group members of several other taxa have a very different distribution than their stem-lineage representatives that occur in the Paleogene of Europe (e.g. Mourer-Chauviré, 1982, 1999; Olson, 1989; Peters, 1991).

(1) Australia

Australia was widely separated from Asia until the early Neogene (e.g. Smith *et al.*, 1994), and Paleogene European birds do not show close affinities to the modern Australian avifauna. Podargidae today only occur in the Australasian region, and their presence in the Paleogene of Europe shows that they reached Australia *via* Asia as assumed by earlier authors (e.g. E. Mayr, 1972). If the occurrence of Anseranatidae in the Paleogene of Europe (Olson, 1999 *b*; Mourer-Chauviré *et al.*, 2004) can be further supported, magpie geese may be another group of birds that colonized Australia from the North.

The earlier recognition of Megapodiidae in the Eocene of France (Mourer-Chauviré, 1982) was based on plesiomorphic overall resemblance and these birds, the Quercymegapodiidae, are now considered stem-group representatives of Galliformes (Mourer-Chauviré, 1992 *a* and above). The fossil record thus does not support the assumption that megapodes, the earliest fossil record of which is from the late Oligocene of Australia (Boles & Ivison, 1999), reached Australia *via* Asia (*contra* Olson, 1980, 1989; Mourer-Chauviré, 1982), although this may be true for stem-group Galliformes. Because the Quercymegapodiidae are outside crown-group Galliformes, they provide no evidence that the distribution of extant Megapodiidae is relictual (*contra* Mourer-Chauviré, 1992 *a*, p. 90).

As also noted above, the alleged record of Aegothelidae in the Quercy deposits (Mourer-Chauviré, 1982) needs to be confirmed by more skeletal elements.

(2) Africa

The closest extant relatives of comparatively few Paleogene European avian taxa are restricted in their distribution to continental Africa, i.e. the six modern coliiform species, Musophagidae, and the single extant species of the Sagittariidae. If correctly assigned to the Leptosomidae, the closest modern relatives of *Plesiocathartes* live on Madagascar.

Musophagidae are also known from the Lower Oligocene of Egypt (Rasmussen *et al.*, 1987) and thus evidently had a wider distribution in the past. Turacos are frugivorous birds with a poor migration ability (Turner, 1997) and their relictual present distribution may thus be due to climatic cooling towards the Neogene.

(3) South and Central America

Most surprisingly given the isolation of South America during most of the Tertiary (Smith *et al.*, 1994), a fairly large number of Paleogene European taxa have their closest
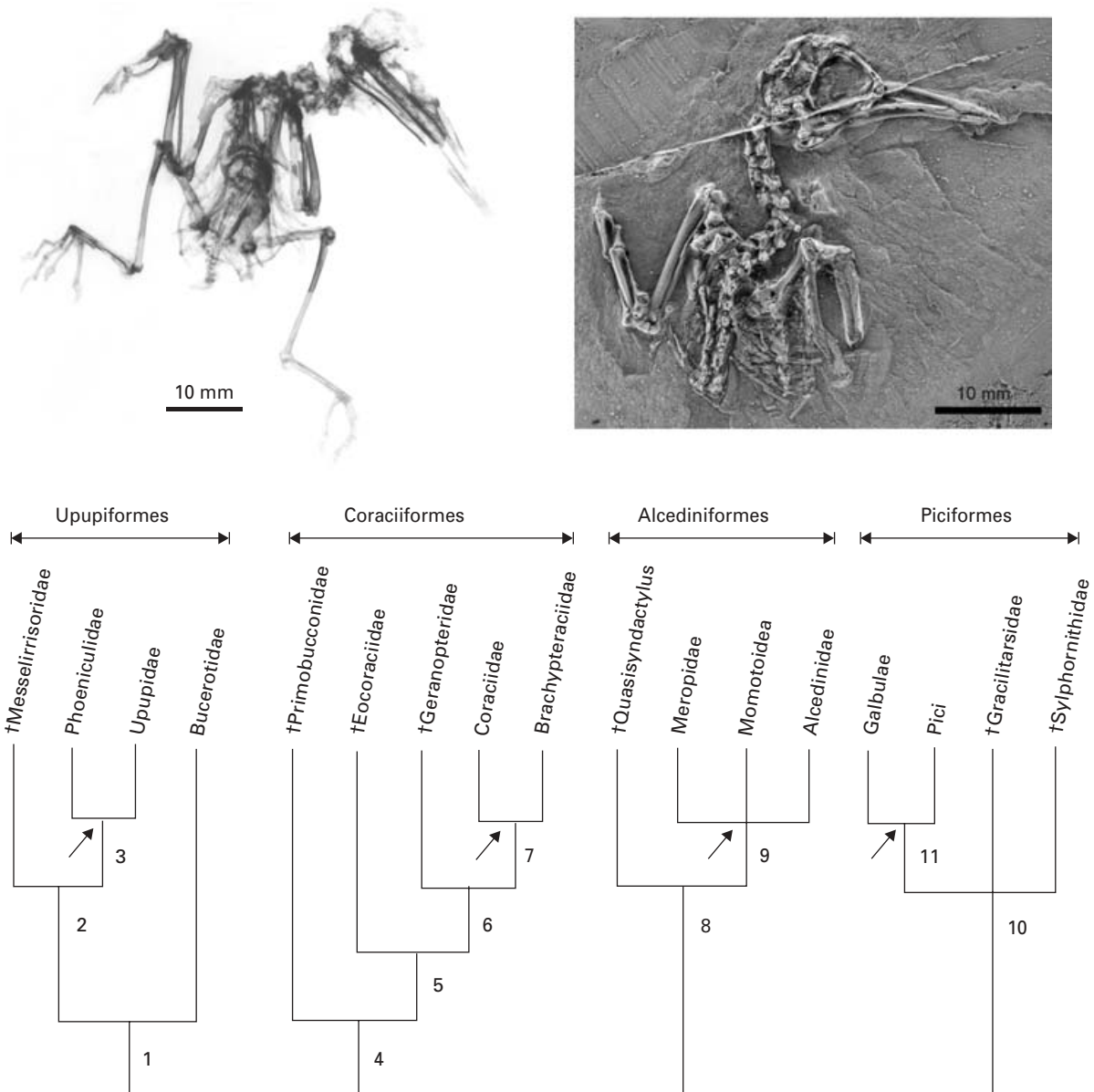
Fig. 7. Phylogenetic relationships between Paleogene and extant taxa of coraciiform, alcediniform, upupiform, and piciform birds (after Mayr, 2000 *h*, 2002 *b*, 2004 *c, f*, 2005 *c*; Mayr & Mourer-Chauviré, 2000; Mayr *et al.*, 2004), with figures of *Messelirrisor halcyrostris* Mayr 1998 (Messelirrisoridae, left, holotype specimen) and *Gracilitarsus mirabilis* Mayr 1998 (Gracilitarsidae, right, specimen SMNK.PAL.3837 in Staatliches Museum für Naturkunde, Karlsruhe) from Messel. Extinct taxa are indicated by a dagger, the arrows indicate the crown-groups. The nodes are supported by the following diagnostic synapomorphies: **1** – mandible with rectangular or trapezoid cross section in proximal area of pars symphysialis and more or less well-developed processus retroarticulares; coracoid with very wide facies articularis sternalis; extremitas omalis of furcula widened and with short processus acromialis; hypotarsus, tendon of musculus flexor hallucis longus enclosed in bony canal. **2** – Ulna, shaft with projection distal to cotyla dorsalis; carpometacarpus, osseous ridge from ventral margin of os metacarpale minus to processus pisiformis and caudal margin of os metacarpale minus undulated. **3** – Coracoid, processus lateralis very irregularly shaped and margo medialis with distinct medially protruding projection; phalanx proximalis digiti majoris hooked; sternum, spina externa et interna fused to form a spina communis. **4** – Carpometacarpus, os metacarpale minus with ventrally protruding projection on ventral side of proximal end; tarsometatarsus, canalis interosseus distalis plantarly not ossified, forming a deep, narrow sulcus on the plantar surface of the bone, between the trochleae metatarsorum III and IV. **5** – Skull, processus postorbitales greatly elongated. **6** – Skull, processus postorbitalis with cranially directed projection, carpometacarpus. **7** – Carpometacarpus, os metacarpale minus with foramen on ventral side of proximal end. **8** – Hallux, first phalanx with proximal end greatly widened; second and third toe coalescent for part of their length. **9** – Columella with large, hollow, bulbous basal and footplate area exhibiting a large fenestra on one side; scapi claviculae of furcula very narrow at extremitas sternalis; carpometacarpus with os metacarpale minus distinctly exceeding os metacarpale majus in length. **10** – Coracoid with distinct notch on medial side of extremitas sternalis; humerus with far ventro-distally extending, large

extant relatives in South or Central America (Mourer-Chauviré, 1982, 1999). Examples therefore are the Idiornithidae, which is the sister taxon of the South American Phorusrhacidae and Cariamidae (e.g. Mourer-Chauviré, 1983*a*; Mayr, 2002*c*), stem-group Nyctibiidae, stem-group Trochilidae (although crown-group hummingbirds today occur in both Americas, they unquestionably originated in South or Central America, e.g. Bleiweiss, 1998*b*), and Momotoidea.

Cathartidae today occur in the entire New World and were reported from the Paleogene of South America (Alvarenga, 1985); their extant distribution can thus be considered relictual. Whether this is also true for the distributions of the other taxa, or whether these shifted in the course of time, remains unknown although I consider a relictual distribution to be more likely.

Restriction of the crown-group of the above taxa to South America is unlikely to be due to climatic cooling in the Tertiary alone, as these birds are also absent from the tropical zones of Africa and Asia. Future research will thus also have to focus on ecological characteristics that distinguish New World biotas, especially in South and Central America, from those in the Old World. Large herbivores, for example, occur in much lower biomass densities in the Neotropics (Cristoffer & Peres, 2003), and in order to explain absence of hummingbirds in the Old World, Cristoffer & Peres (2003, p. 1369) hypothesized that the nectar-rich and highly nutrient understorey flowers that are pollinated by hummingbirds in the Neotropics would be eaten by mammalian herbivores in the Palaeotropics. At present this assumption cannot be tested, as we do not know when exactly hummingbirds disappeared from the Old World and whether this date coincides with the appearance of large herbivores. However, even if this particular hypothesis may turn out to be wrong, it opens a view on complex ecological interactions that may have to be taken into account to explain the present distribution of birds.

IV. DIVERSIFICATION TIME OF MODERN NEORNITHINE LINEAGES

Because few neornithine (crown-group) birds are known from the Mesozoic period and virtually all of these come from the late Cretaceous (Hope, 2002), the fossil record has been considered indicative of an explosive radiation of neornithine birds in the Paleogene (Feduccia, 1995, 2003; Bleiweiss, 1998*a*; Benton, 1999). Molecular clock data, on the other hand, consistently date the divergence time of many modern avian clades far into the Cretaceous

(e.g. Hedges *et al.*, 1996; Cooper & Penny, 1997; Kumar & Hedges, 1998; Waddell *et al.*, 1999; van Tuinen & Hedges, 2001; Paton, Haddrath & Baker, 2002; van Tuinen & Dyke, 2004).

The phylogenetic position of Paleogene neornithine birds only played a subordinate role in this debate. However, as detailed above, no crown-group members of modern 'families' are known from Eocene or older deposits of Europe or anywhere else. This indicates that diversification of the crown-groups within modern avian 'families' did not take place before the Oligocene, irrespective of the relative position of these taxa within Neornithes.

The disagreement between paleontological and molecular data, which also exists for mammals (e.g. Archibald & Deutschmann, 2001), is best exemplified by the fossil record of galliform birds, one of the most basal taxa of neognathous birds (e.g. Sibley & Ahlquist, 1990; Livezey & Zusi, 2001; Mayr & Clarke, 2003). Van Tuinen & Hedges (2001) and van Tuinen & Dyke (2004), for example, found a Middle Cretaceous [about 80 million years ago (mya)] divergence time between Cracidae and Phasianidae, i.e. crown-group Galliformes. However as noted above and also on a world-wide scale, there is no fossil record of crown-group Galliformes before the Oligocene (about 35 mya), thus leaving a gap in the fossil record of about 45 million years. It has been hypothesized that crown-group divergences occurred in the Cretaceous of Gondwana, i.e. on the Southern Hemisphere from where there is a scanty fossil record (e.g. Cooper & Penny, 1997), but this assumption conflicts with the fact that the earliest known South American galliform birds also are outside crown-group Galliformes (Alvarenga, 1995; Mourer-Chauviré, 2000). Assuming a Gondwanan origin of crown-group Galliformes, it is further difficult to imagine a biogeographic scenario that explains their absence in pre-Oligocene deposits of the Northern Hemisphere where galliform taxa outside the crown-group do occur.

To explain the considerable disparity of molecular and paleontological data, Benton (1999) considered it possible that molecular clocks run faster during times of radiation, but van Tuinen & Hedges (2001) noted that molecular calibrations are tested for such deviations. However, Graur & Martin (2004, p. 80) showed that there are also considerable problems with the alleged precision of the molecular clock data in many studies, as the 'illusion of precision was achieved mainly through the conversion of statistical estimates […] into errorless numbers'.

Several calibration points of avian molecular clocks are further based on an incorrect interpretation of the fossil record. Van Tuinen & Dyke (2004), for example, used nine 'internal fossil-based anchorpoints' for their calibration of galliform molecular clocks (see Table 1 in van Tuinen &

---

fossa musculi brachialis which is situated on the far medial side of the bone and has a weakly developed ventral margin; carpometacarpus with well-developed processus intermetacarpalis that is fused with the os metacarpale minus; trochlea metatarsi IV with plantarly projecting wing-like flange; tarsometatarsus, hypotarsus with tendon of musculus flexor hallucis longus situated in a marked sulcus which is medially bordered by a prominent crista lateralis hypotarsi. **11** – Phalanx proximalis digiti majoris, proximal end with large, proximally directing process on ventral side; tarsometatarsus, trochlea metatarsi IV with large trochlea accessoria.

Dyke, 2004). At least six of these were based on incorrectly identified taxa: The Eocene Gallinuloididae and Quercy-megapodiidae (used to calibrate a Phasianinae-Numidinae divergence and 'Crown Megapodiidae', respectively) are stem-group Galliformes, not Phasianidae or Megapodiidae, respectively (see above). *Palaeortyx* (used to calibrate 'Crown Odontophoridae') is not a member of the New World Odontophorinae [Ballmann (1969); van Tuinen & Dyke (2004) curiously referred to Milne-Edwards (1867–71) concerning the phylogenetic affinities of this taxon]. *Schaubortyx* (used to calibrate a *Coturnix-Gallus* divergence) is a junior synonym of *Palaeortyx* (Schaub, 1945; Mlíkovskỳ, 2002). The poorly known Eocene North American taxon *Amitabha* Gulas-Wroblewski & Wroblewski 2003 ('AMNH 30331', see Gulas-Wroblewski & Wroblewski, 2003), used to calibrate 'Crown Phasianidae', is probably not even a galliform bird (Mayr & Weidig, 2004). '*Gallus bravardi*', used to calibrate 'Crown *Gallus*', finally is a peafowl of the genus *Pavo* (*Pavo bravardi*; Mourer-Chauviré, 1989*a*).

Cooper & Penny (1997) incorrectly used the stem-group galliform *Gallinuloides* (see above) as earliest record of the Cracidae to calibrate their molecular clock. *Telecrex*, the taxon used to calibrate an Eocene age of the Numidinae (guineafowl), is known from a single fragmentary bone and is of doubtful affinities (Olson, 1985; van Tuinen & Dyke, 2004). Calibration of the ostrich lineage was based on *Palaeotis*, the struthionid affinities of which also are far from being certain (see above).

Another line of evidence for a Cretaceous origin of modern neornithine taxa was set up by Cracraft (2001), who assumed that the basal divergences of many groups (e.g. Palaeognathae, Galloanseres, 'Gruiformes', 'Caprimulgiformes', Passeriformes) 'demonstrate pervasive trans-Antarctic distribution patterns' and are of vicariant origin owing to the break-up of Gondwana in the Cretaceous. Cracraft's hypothesis is, however, considerably flawed by the presence of stem-group representatives in the Paleogene of the Northern Hemisphere of these modern taxa with a Southern Hemisphere distribution. For example, the assumption that basal divergences within the paraphyletic (Mayr, 2002*h*; Mayr *et al.*, 2003) 'Caprimulgiformes' are due to the break-up of Gondwana in the Cretaceous conflicts with the presence of stem-group Podargidae, Nyctibiidae and Trochilidae in the Paleogene of Europe. Cracraft's (2001, p. 466) explanation that 'numerous neornithine lineages became more cosmopolitan in the late Cretaceous or Early Tertiary' is quite speculative, and 'phylogenetics and biogeography indicate [that] many of these clades had southern origins' only, if considerations are restricted to the modern distribution of these taxa, for which there is no rationale.

The same argumentation was used by Ericson *et al.* (2003) to support a Gondwanan origin of the basal divergences within crown-group Passeriformes, i.e. the clade (Acanthisittidae + (Suboscines + Oscines)). However, although there is convincing evidence that Oscines, to which all modern European passerines belong, originated on the Australian continental plate (e.g. Barker, Barrowclough & Groth, 2002; Ericson *et al.*, 2003), evidence for a Gondwanan origin of the total group is weak, as Suboscines include species with a Northern Hemisphere distribution (the Asian Pittidae) and Acanthisittidae (New Zealand Wrens) occur on New Zealand only.

Moreover, even if it can be shown that certain avian taxa originated in the Southern Hemisphere, this does not automatically imply a Gondwanan origin in the Cretaceous, especially if no Cretaceous fossils of the taxa in question are known.

Dyke (2001*d*) assumed that 'only some of the 'more basal' clades of birds were, most likely, present during the Mesozoic era, and that the radiation of the 'more derived' landbird group occurred in the early Tertiary'. However, the higher-level phylogeny of neornithine birds still is only poorly resolved (e.g. Mayr & Clarke, 2003), making it hardly possible to distinguish 'basal' from 'more derived' clades, and there is still no Cretaceous fossil record of the undisputedly most basal taxa, i.e. palaeognathous birds (Feduccia, 2003; Dyke & van Tuinen, 2004).

V. CONCLUSIONS

(1) In contrast to the modern European avifauna and all other modern continental avifaunas, there was a fair number of large flightless birds in the early Paleogene of Europe, probably owing to the absence of large carnivorous mammals by that time (e.g. van Valkenburgh, 1999).

(2) The pre-Oligocene European avifauna is further characterized by the complete absence of passeriform birds, which today are the most diversified and abundant avian taxon, constituting more than half of all extant avian species. Representatives of small non-passeriform perching birds thus probably had similar ecological niches before the Oligocene to those filled by modern passerines, and it is likely that occurrence of songbirds had a major impact on these birds. This was first discussed by Harrison (1979*a*), who noted that 'non-passerines originally occupied feeding niches available for small birds, and were later excluded from these by the adaptive radiation of the passerines'. However, at the time of Harrison's considerations still very little was known on the composition of the European avifauna, and we now have a much better picture on which taxa exactly may have been affected by the radiation of passerines.

(3) Most modern Passeriformes are insectivorous and/or granivorous perching birds, and a similar way of living can be assumed for their Paleogene representatives. It is thus to be expected that occurrence of passeriform birds in Europe had its greatest effect on small insectivorous and granivorous taxa. Indeed the crown-group representatives of some taxa, the early Tertiary stem-group members of which included insectivorous or omnivorous species, exhibit feeding specializations not found or rare in passeriform birds.

(4) Coliiformes, for example, exhibited a great diversity in the Eocene and, judging from their bill shape, included omnivorous or insectivorous species by that time (Houde & Olson, 1992; Mayr & Peters, 1998; Mayr, 2001*e*), whereas the six modern species of mousebirds are exclusively herbivorous birds. Eocene stem-group Psittaciformes also

appear to have been rather generalized, possibly granivorous feeders (Mayr & Daniels, 1998), whereas many modern parrots are frugivorous birds that exhibit a highly derived bill morphology. As evidenced by their foot structure, the Messelirrisoridae, Eocene Upupiformes, were perching birds (Mayr, 1998 *b*), whereas their modern relatives mainly forage on the ground (Upupidae, hoopoes) or are specialized for trunk climbing (Phoeniculidae, wood-hoopoes). Other arboreal taxa that were diversified in the Eocene are unknown from the Oligocene, for example, the Primoscenidae, one of the most abundant groups of small arboreal birds in the Lower and Middle Eocene with a very songbird-like overall appearance.

(5) There further was a great diversity of aerial insectivores in the Eocene, all of which were members of the Cypselomorphae. By contrast, today only two cypselomorph taxa occur in Europe (Caprimulgidae and Apodidae), and all other insectivores that catch their prey either on the wing or by sallying flights from perches belong to passerines, such as Hirundinidae (swallows), Muscicapidae (flycatchers), and Laniidae (shrikes). Except for swifts that avoid competition with the superficially similar swallows by the use of different nesting sites (e.g. Turner, 1989), all extant insectivorous Cypselomorphae are crepuscular or nocturnal and thereby contrast with the mainly diurnal songbirds.

(6) By the late Oligocene, the European avifauna is already of essentially modern aspect (see also Mourer-Chauviré, 1995 *a*), although some non-passeriform groups that occur in the modern European avifauna still appear to be absent, most notably Podicipedidae, Pelecanidae, Ciconiidae, Otididae (bustards), Falconidae, Strigidae, Columbidae, and Cuculidae. Olson (1989) assumed that Podicipedidae and Columbidae evolved on the Southern Hemisphere and did not arrive in Europe before the Neogene. Likewise, the basal divergences within crown-group Falconidae are in South America where this taxon probably had its origin (Griffiths, 1999), and falcons also may not have dispersed into Europe before the Neogene.

VI. ACKNOWLEDGEMENTS

VII. REFERENCES

ALVARENGA, H. M. F. (1985). Notas sobre os Cathartidae (Aves) e descrição de um novo gênero do Cenozoico brasileiro. *Anais da Academia brasileira de Ciências* **57**, 349–357.

ALVARENGA, H. M. F. (1995). Um primitivo membro da ordem Galliformes (Aves) do Terciário médio da Bacia de Taubaté, estado de São Paulo, Brasil. *Anais da Academia Brasileira de Ciências* **67**, 33–44.

ALVARENGA, H. M. F. & HÖFLING, E. (2003). Systematic revision of the Phorusrhacidae (Aves: Ralliformes). *Papéis Avulsos de Zoologia* **43**, 55–91.

ANDORS, A. (1992). Reappraisal of the Eocene groundbird *Diatryma* (Aves: Anserimorphae). In *Papers in Avian Paleontology honoring Pierce Brodkorb* (ed. K. E. Campbell). *Natural History Museum of Los Angeles County, Science Series* **36**, 109–125.

ARCHIBALD, J. D. & DEUTSCHMANN, D. H. (2001). Quantitative analysis of the timing of the origin and diversification of extant placental orders. *Journal of Mammalian Evolution* **8**, 107–124.

ASLANOVA, S. M. & BURCHAK-ABRAMOVICH, N. I. (1999). A detailed description of *Caspiodontornis kobystanicus* from the Oligocene of the Caspian seashore. *Acta zoologica cracoviensia* **42**, 423–433.

AVERIANOV, A. O., PANTELEYEV, O. R., POTAPOVA, O. R. & NESSOV, L. A. (1997). Bony-toothed birds (Aves: Pelecaniformes: Odontopterygia) of the late Paleocene and Eocene of the western margin of ancient Asia. *Trudy zoologicheskogo Instituta* **252**, 3–12.

BAIRD, R. F. & VICKERS-RICH, P. (1997). *Eutreptodactylus itaboraiensis* gen. et. sp. nov., an early cuckoo (Aves: Cuculiformes) from the Late Paleocene of Brazil. *Alcheringa* **21**, 123–127.

BALLMANN, P. (1969). Die Vögel aus der altburdigalen Spaltenfüllung von Wintershof (West) bei Eichstätt in Bayern. *Zitteliana* **1**, 5–60.

BALLMANN, P. (1970). Ein neuer Vertreter der Musophagidae (Aves) aus dem Chattien von Gaimersheim bei Ingolstadt (Bayern). *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie* **10**, 271–275.

BARKER, F. K., BARROWCLOUGH, G. F. & GROTH, J. G. (2002). A phylogenetic hypothesis for passerine birds: taxonomic and biogeographic implications of an analysis of nuclear DNA sequence. *Proceedings of the Royal Society of London, Series B* **269**, 295–308.

BENTON, M. J. (1999). Early origin of modern birds and mammals: molecules vs. morphology. *BioEssays* **21**, 1043–1051.

BESSONAT, G. & MICHAUT, A. (1973). Découverte d'un squelette complet d'échassier dans le Stampien provençal. *Bulletin du Muséum d'Histoire Naturelle de Marseille* **33**, 143–145.

BLEIWEISS, R. (1998 *a*). Fossil gap analysis supports early Tertiary origin of trophically diverse avian orders. *Geology* **26**, 323–326.

BLEIWEISS, R. (1998 *b*). Origin of hummingbird faunas. *Biological Journal of the Linnean Society* **65**, 77–97.

BLONDEL, J. & MOURER-CHAUVIRÉ, C. (1998). Evolution and history of the western Palaearctic avifauna. *Trends in Ecology and Evolution* **13**, 488–492.

BOCHEŃSKI, Z. (1997). List of European fossil bird species. *Acta zoologica cracoviensia* **40**, 293–333.

BOCK, W. J. & MCEVEY, A. (1969). The radius and relationships of owls. *Wilson Bulletin* **81**, 55–68.

BOLES, W. E. (1995). The world's oldest songbird. *Nature* **374**, 21–22.

BOLES, W. E. (1997). Fossil Songbirds (Passeriformes) from the Early Eocene of Australia. *Emu* **97**, 43–50.

BOLES, W. E. & IVISON, T. J. (1999). A new dwarf megapode (Galliformes: Megapodiidae) from the Late Oligocene of Central Australia. In *Avian Paleontology at the Close of the 20th Century: Proceedings of the 4th International Meeting of the Society of Avian Paleontology and Evolution, Washington, D.C., 4–7 June 1996* (ed. S. L. Olson). *Smithsonian Contributions to Paleobiology* **89**, 199–206.

BRODKORB, P. (1962). The systematic position of two Oligocene birds from Belgium. *Auk* **79**, 706–707.

BRODKORB, P. (1964). Catalogue of fossil birds: Part 2 (Anseriformes through Galliformes). *Bulletin of the Florida State Museum, Biological Sciences* **8**, 195–335.

BRUNET, J. (1970). Oiseaux de l'Éocène supérieur du bassin de Paris. *Annales de Paléontologie* **56**, 3–57.

BUFFETAUT, E. (1997). New remains of the giant bird *Gastornis* from the Upper Paleocene of the eastern Paris Basin and the relationships between *Gastornis* and *Diatryma*. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **1997**, 179–190.

CHANDLER, R. M. (1999). Fossil birds of Florissant, Colorado: with a description of a new genus and species of cuckoo. *Geologic Resource Division Technical Report NPS/NRGRD/GRDTR-***99**, 49–53.

CHENEVAL, J. (1993). L'avifaune Mio-Pliocène de la Formation Pisco (Pérou). Étude préliminaire. *Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon* **125**, 85–95.

CHENEVAL, J. (1995). A fossil shearwater (Aves: Procellariiformes) from the Upper Oligocene of France and the Lower Miocene of Germany. In *Acta palaeornithologica* (ed. D. S. Peters). *Courier Forschungsinstitut Senckenberg* **181**, 187–198.

CHENEVAL, J. & ESCUILLIÉ, F. (1992). New data concerning *Palaelodus ambiguus* (Aves: Phoenicopteriformes: Palaelodidae): ecological and evolutionary interpretations. In *Papers in Avian Paleontology honoring Pierce Brodkorb* (ed. K. E. Campbell). *Natural History Museum of Los Angeles County, Science Series* **36**, 208–224.

CHUBB, A. (2004). New nuclear evidence for the oldest divergence among neognath birds: the phylogenetic utility of ZENK (i). *Molecular Phylogenetics and Evolution* **30**, 140–151.

COOPER, A. & PENNY, D. (1997). Mass survival of birds across the Cretaceous-Tertiary boundary: molecular evidence. *Science* **275**, 1109–1113.

CRACRAFT, J. (1973). Systematics and evolution of the Gruiformes (Class Aves). 3. Phylogeny of the suborder Grues. *Bulletin of the American Museum of Natural History* **151**, 1–127. New York.

CRACRAFT, J. (1980). Phylogenetic theory and methodology in avian paleontology: a critical appraisal. In *Papers in avian paleontology honoring Hildegarde Howard* (ed. K. E. Campbell). *Natural History Museum of Los Angeles County, Contributions to Science* **330**, 9–16.

CRACRAFT, J. (2001). Avian evolution, Gondwana biogeography and the Cretaceous-Tertiary mass extinction event. *Proceedings of the Royal Society of London, Series B* **268**, 459–469.

CRISTOFFER, C. & PERES, C. A. (2003). Elephants versus butterflies: the ecological role of large herbivores in the evolutionary history of two tropical worlds. *Journal of Biogeography* **30**, 1357–1380.

DARGA, R., BÖHME, M., GÖHLICH, U. B. & RÖSSNER, G. (1999). Reste höherer Wirbeltiere aus dem Alttertiär des Alpenvorlandes bei Siegsdorf/Oberbayern. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie* **39**, 91–114.

DYKE, G. J. (2001*a*). A primitive swift from the London Clay and the relationships of fossil apodiform birds. *Journal of Vertebrate Paleontology* **21**, 195–200.

DYKE, G. J. (2001*b*). Fossil pseudasturid birds (Aves, Pseudasturidae) from the London Clay. *Bulletin of the Natural History Museum of London (Geology Series)* **57**, 1–4.

DYKE, G. J. (2001*c*). *Laputavis*, a replacement name for *Laputa* Dyke 2001 (preoccupied name). *Journal of Vertebrate Paleontology* **21**, 401.

DYKE, G. J. (2001*d*). The evolutionary radiation of modern birds: systematics and patterns of diversification. *Geological Journal* **36**, 305–315.

DYKE, G. J. (2001*e*). The fossil waterfowl (Aves: Anseriformes) from the Eocene of England. *American Museum Novitates* **3354**, 1–15.

DYKE, G. J. (2003). The phylogenetic position of *Gallinuloides* Eastman (Aves: Galliformes) from the Tertiary of North America. *Zootaxa* **199**, 1–10.

DYKE, G. J. & COOPER, J. H. (2000). A new psittaciform bird from the London Clay (Lower Eocene) of England. *Palaeontology* **43**, 271–285.

DYKE, G. J. & GULAS, B. E. (2002). The fossil galliform bird *Paraortygoides* from the Lower Eocene of the United Kingdom. *American Museum Novitates* **3360**, 1–14.

DYKE, G. J. & VAN TUINEN, M. (2004). The evolutionary radiation of modern birds (Neornithes): reconciling molecules, morphology and the fossil record. *Zoological Journal of the Linnean Society* **141**, 153–177.

DYKE, G. J., & WATERHOUSE, D. M. (2001). A mousebird (Aves: Coliiformes) from the Eocene of England. *Journal für Ornithologie* **142**, 7–15.

DYKE, G. J., WATERHOUSE, D. M. & KRISTOFFERSEN, A. V. (2004). Three new fossil landbirds from the early Paleogene of Denmark. *Bulletin of the Geological Society of Denmark* **51**, 47–56.

ERICSON, P. G. P. (1999). New material of *Juncitarsus* (Phoenicopteriformes), with a guide for differentiating that genus from the Presbyornithidae (Anseriformes). In *Avian Paleontology at the Close of the 20th Century: Proceedings of the 4th International Meeting of the Society of Avian Paleontology and Evolution, Washington, D.C., 4–7 June 1996* (ed. S. L. Olson). *Smithsonian Contributions to Paleobiology* **89**, 245–251.

ERICSON, P. G. P., IRESTEDT, M. & JOHANSSON, U. S. (2003). Evolution, biogeography, and patterns of diversification in passerine birds. *Journal of Avian Biology* **34**, 3–15.

FAIN, M. G. & HOUDE, P. (2004). Parallel radiations in the primary clades of birds. *Evolution* **58**, 2558–2573.

FEDUCCIA, A. (1973). A new Eocene zygodactyl bird. *Journal of Paleontology* **47**, 501–503.

FEDUCCIA, A. (1995). Explosive evolution in Tertiary birds and mammals. *Science* **267**, 637–638.

FEDUCCIA, A. (1999). *The Origin and Evolution of Birds*, 2nd Edn. Yale University Press, New Haven.

FEDUCCIA, A. (2003). 'Big bang' for Tertiary birds? *Trends in Ecology and Evolution* **18**, 172–176.

FISCHER, K. (1962). Der Riesenlaufvogel *Diatryma* aus der eozänen Braunkohle des Geiseltales. *Hallesches Jahrbuch für mitteldeutsche Erdgeschichte* **4**, 26–33.

FISCHER, K. (1978). Neue Reste des Riesenlaufvogels *Diatryma* aus dem Eozän des Geiseltals bei Halle (DDR). *Mitteilungen aus dem Zoologischen Museum in Berlin* **54**, Supplement: Annalen für Ornithologie **2**, 133–144.

FISCHER, K. (1983). *Oligostrix rupeliensis* n. gen., n. sp., eine neue Ureule (Protostrigidae, Strigiformes, Aves) aus dem marinen Mitteloligozän des Weißelsterbeckens bei Leipzig (DDR). *Zeitschrift für geologische Wissenschaften* **11**, 483–487.

FISCHER, K. (1987). Eulenreste (*Eoglaucidium pallas* nov. gen., nov. sp., Strigiformes, Aves) aus der mitteleozänen Braunkohle des Geiseltals bei Halle (DDR). *Mitteilungen aus dem Zoologischen Museum in Berlin* **63**, Supplement: Annalen für Ornithologie **11**, 137–142.

FISCHER, K. (1990). Der Hühnervogel *Pirortyx major* (Gaillard, 1939) aus dem marinen Mitteloligozän bei Leipzig (DDR). *Mitteilungen aus dem Zoologischen Museum in Berlin* **66**, Supplement: Annalen für Ornithologie **14**, 133–136.

FISCHER, K. (1997). Neue Vogelfunde aus dem mittleren Oligozän des Weißelsterbeckens bei Leipzig (Sachsen). *Mauritiana* **16**, 271–288.

FISCHER, K. (2003). Weitere Vogelknochen von *Diomedeoides* (Diomedeoididae, Procellariiformes) und *Paraortyx* (Paraortygidae, Galliformes) aus dem Unteroligozän des Weißelsterbeckens bei Leipzig (Sachsen). *Mauritiana* **18**, 387–395.

GAILLARD, C. (1939). Contribution à l'étude des oiseaux fossiles. *Nouvelles Archives du Museum de Lyon* **15** (2), 1–100.

GRAUR, D. & MARTIN, W. (2004). Reading the entrails of chickens: molecular timescales of evolution and the illusion of precision. *TRENDS in Genetics* **20**, 80–86.

GRIFFITHS, C. S. (1994). Monophyly of the Falconiformes based on syringeal morphology. *Auk* **111**, 787–805.

GRIFFITHS, C. S. (1999). Phylogeny of the Falconidae inferred from molecular and morphological data. *Auk* **116**, 116–130.

GULAS-WROBLESWKI, B. E. & WROBLEWSKI, A. F.-J. (2003). A crown-group galliform bird from the Middle Eocene Bridger Formation of Wyoming. *Palaeontology* **46**, 1269–1280.

HARRISON, C. J. O. (1979*a*). Small non-passerine birds of the Lower Tertiary as exploiters of ecological niches now occupied by passerines. *Nature* **281**, 562–563.

HARRISON, C. J. O. (1979*b*). The Upper Eocene birds of the Paris basin: a brief re-appraisal. *Tertiary Research* **2**, 105–109.

HARRISON, C. J. O. (1980). A small owl from the Lower Eocene of Britain. *Tertiary Research* **3**, 83–87.

HARRISON, C. J. O. (1982*a*). A new tiny raptor from the Lower Eocene of England. *Ardea* **70**, 77–80.

HARRISON, C. J. O. (1982*b*). Cuculiform, piciform and passeriform birds in the Lower Eocene of England. *Tertiary Research* **4**, 71–81.

HARRISON, C. J. O. (1982*c*). The earliest parrot: a new species from the British Eocene. *Ibis* **124**, 203–210.

HARRISON, C. J. O. (1984*a*). A revision of the fossil swifts (Vertebrata, Aves, suborder Apodi), with descriptions of three new genera and two new species. *Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie* **21**, 157–177.

HARRISON, C. J. O. (1984*b*). Further additions to the fossil birds of Sheppey: A new falconid and three small rails. *Tertiary Research* **5**, 179–187.

HARRISON, C. J. O. (1985). A bony-toothed bird (Odontopterygiformes) from the Palaeocene of England. *Tertiary Research* **7**, 23–25.

HARRISON, C. J. O. & WALKER, C. A. (1976*a*). A reappraisal of *Prophaethon shrubsolei* Andrews (Aves). *Bulletin of the British Museum (Natural History), Geology* **27**, 1–30.

HARRISON, C. J. O. & WALKER, C. A. (1976*b*). A review of the bony-toothed birds (Odontopterygiformes): with descriptions of some new species. Tertiary Research Special Paper **2**, 1–72.

HARRISON, C. J. O. & WALKER, C. A. (1976*c*). Birds of the British Upper Eocene. *Zoological Journal of the Linnean Society* **59**, 323–351.

HARRISON, C. J. O. & WALKER, C. A. (1977). Birds of the British Lower Eocene. Tertiary Research Special Paper **3**, 1–52.

HARRISON, C. J. O. & WALKER, C. A. (1978). *Proherodius oweni* as a species of Presbyornithidae. *Tertiary Research* **2**, 1–3.

HARRISON, C. J. O. & WALKER, C. A. (1979*a*). Birds of the British Lower Oligocene. *Tertiary Research Special Paper* **5**, 29–43.

HARRISON, C. J. O. & WALKER, C. A. (1979*b*). Birds of the British Middle Eocene. *Tertiary Research Special Paper* **5**, 19–27.

HEDGES, S. B., PARKER, P. H., SIBLEY, C. G. & KUMAR, S. (1996). Continental breakup and the ordinal diversification of birds and mammals. *Nature* **381**, 226–229.

HESSE, A. (1990). Die Beschreibung der Messelornithidae (Aves: Gruiformes: Rhynocheti) aus dem Alttertiär Europas und Nordamerikas. *Courier Forschungsinstitut Senckenberg* **128**, 1–176.

HESSE, A. (1992). A new species of *Messelornis* (Aves: Gruiformes: Messelornithidae) from the Middle Eocene Green River Formation. In *Papers in Avian Paleontology honoring Pierce Brodkorb* (ed. K. E. Campbell). *Natural History Museum of Los Angeles County, Science Series* **36**, 171–178.

HOPE, S. (2002). The Mesozoic radiation of Neornithes. In *Mesozoic birds: Above the Heads of Dinosaurs* (eds. L. M. Chiappe and L. M. Witmer), pp. 339–388. University of California Press, Berkeley.

HOU, L. (1980). New form of the Gastornithidae from the Lower Eocene of the Xichuan, Honan. *Vertebrata PalAsiatica* **18**, 111–115[Chinese with English abstract].

HOUDE, P. (1986). Ostrich ancestors found in the Northern Hemisphere suggest new hypothesis of ratite origin. *Nature* **324**, 563–565.

HOUDE, P. (1988). Palaeognathous birds from the early Tertiary of the Northern Hemisphere. *Publications of the Nuttall Ornithological Club* **22**, 1–148.

HOUDE, P. & HAUBOLD, H. (1987). *Palaeotis weigelti* restudied: a small Middle Eocene ostrich (Aves: Struthioniformes). *Palaeovertebrata*, **17** (2), 27–42.

HOUDE, P. & OLSON, S. L. (1989). Small arboreal nonpasserine birds from the Early Tertiary of western North America. In *Acta XIX congressus internationalis ornithologici* (ed. H. Ouellet), pp. 2030–2036. University of Ottawa Press, Ottawa.

HOUDE, P. & OLSON, S. L. (1992). A radiation of coly-like birds from the early Eocene of North America (Aves: Sandcoleiformes new order). In *Papers in Avian Paleontology honoring Pierce Brodkorb* (ed. K. E. Campbell). *Natural History Museum of Los Angeles County, Science Series* **36**, 137–160.

HOWARD, H. (1965). First record of avian fossils from the Eocene of California. *Journal of Paleontology* **39**, 350–354.

HUGUENEY, M., BERTHET, D., BODERGAT, A.-M., ESCUILLIÉ, F., MOURER-CHAUVIRÉ, C. & WATTINNE, A. (2003). La limite Oligocène-Miocène en Limagne: changements fauniques chez les mammifères, oiseaux et ostracodes des différents niveaux de Billy-Créchy (Allier, France). *Geobios* **36**, 719–731.

JOHANSSON, U. S. & ERICSON, P. G. P. (2003). Molecular support for a sister group relationship between Pici and Galbulae (Piciformes *sensu* Wetmore 1960). *Journal of Avian Biology* **34**, 185–197.

KARHU, A. (1988). Novoye semeystvo strizheobraznykh iz paleogena Yevropy [A new family of swift-like birds from the Paleogene of Europe]. *Paleontological Journal* **3**, 78–88 [Russian with English abstract].

KARHU, A. (1999). A new genus and species of the family Jungornithidae (Apodiformes) from the Late Eocene of the Northern Caucasus, with comments on the ancestry of hummingbirds. In *Avian Paleontology at the Close of the 20th Century: Proceedings of the 4th International Meeting of the Society of Avian Paleontology and Evolution, Washington, D.C., 4–7 June 1996* (ed. S. L. Olson). *Smithsonian Contributions to Paleobiology* **89**, 207–216.

KRISTOFFERSEN, A. V. (1999). Lithornithid birds (Aves, Palaeognathae) from the Lower Palaeogene of Denmark. *Geologie en Mijnbouw* **78**, 375–381.

KRISTOFFERSEN, A. V. (2002*a*). An early Paleogene trogon (Aves: Trogoniformes) from the Fur Formation, Denmark. *Journal of Vertebrate Paleontology* **22**, 661–666.

KRISTOFFERSEN, A. V. (2002*b*). *The avian diversity in the latest Paleocene – earliest Eocene Fur Formation, Denmark. A synopsis.* Unpublished Ph.D. thesis, University of Copenhagen, Geological Institute.

KRUMBIEGEL, G., RÜFFLE, L. & HAUBOLD, H. (1983). *Das eozäne Geiseltal. Neue Brehm-Bücherei*, Vol. 237. A. Ziemsen, Wittenberg.

KUMAR, S. & HEDGES, S. B. (1998). A molecular timescale for vertebrate evolution. *Nature* **392**, 917–920.

KUROCHKIN, E. N. (1976). A survey of the paleogene birds of Asia. *Smithsonian Contributions to Paleobiology* **27**, 75–86.

LAMBRECHT, K. (1931). *Cygnopterus* und *Cygnavus*, zwei fossile Schwäne aus dem Tertiär Europas. *Bulletin du Musée royal d'Histoire naturelle de Belgique* **7** (31), 1–6.

LEGENDRE, S. & LÉVÊQUE, F. (1997). Etalonnage de l'échelle biochronologique mammalienne du Paléogène d'Europe occidentale: vers une intégration à l'échelle globale. In *Actes du Congrès BiochroM'97* (eds. J.-P. Aguilar, S. Legendre and J. Michaux). *Mémoires et Travaux de l'Ecole Pratique des Hautes Etudes, Institut de Montpellier* **21**, 461–473.

LIVEZEY, B. C. (1986). A phylogenetic analysis of recent anseriform genera using morphological characters. *Auk* **103**, 737–754.

LIVEZEY, B. C. (1998). A phylogenetic analysis of the Gruiformes (Aves) based on morphological characters, with an emphasis on the rails (Rallidae). *Philosophical Transactions of the Royal Society of London, Series B* **353**, 2077–2151.

LIVEZEY, B. C. & MARTIN, L. D. (1988). The systematic position of the Miocene anatid *Anas*[?] *blanchardi* Milne-Edwards. *Journal of Vertebrate Paleontology* **8**, 196–211.

LIVEZEY, B. C. & ZUSI, R. L. (2001). Higher-order phylogenetics of modern Aves based on comparative anatomy. *Netherlands Journal of Zoology* **51**, 179–205.

MANEGOLD, A., MAYR, G. & MOURER-CHAUVIRÉ, C. (2004). Miocene songbirds and the composition of the European passeriform avifauna. *Auk* **121**, 1155–1160.

MARTIN, L. D. (1992). The status of the Late Paleocene birds *Gastornis* and *Remiornis*. In *Papers in Avian Paleontology honoring Pierce Brodkorb* (ed. K. E. Campbell). *Natural History Museum of Los Angeles County, Science Series* **36**, 97–108.

MARTIN, L. D. & BLACK, C. C. (1972). A new owl from the Eocene of Wyoming. *Auk* **89**, 887–888.

MAYR, E. (1972). Continental drift and the history of the Australian birdfauna. *Emu* **72**, 26–28.

MAYR, G. (1998a). A new family of Eocene zygodactyl birds. *Senckenbergiana lethaea* **78**, 199–209.

MAYR, G. (1998b). „Coraciiforme" und „piciforme" Kleinvögel aus dem Mittel-Eozän der Grube Messel (Hessen, Deutschland). *Courier Forschungsinstitut Senckenberg* **205**, 1–101.

MAYR, G. (1998c). Ein Archaeotrogon (Aves: Archaeotrogonidae) aus dem Mittel-Eozän der Grube Messel (Hessen, Deutschland)? *Journal für Ornithologie* **139**, 121–129.

MAYR, G. (1999a). A new trogon from the Middle Oligocene of Céreste, France. *Auk* **116**, 427–434.

MAYR, G. (1999b). Caprimulgiform birds from the Middle Eocene of Messel (Hessen, Germany). *Journal of Vertebrate Paleontology* **19**, 521–532.

MAYR, G. (1999c). *Pumiliornis tessellatus* n. gen. n. sp., a new enigmatic bird from the Middle Eocene of Grube Messel (Hessen, Germany). *Courier Forschungsinstitut Senckenberg* **216**, 75–83.

MAYR, G. (2000a). A new basal galliform bird from the Middle Eocene of Messel (Hessen, Germany). *Senckenbergiana lethaea* **80**, 45–57.

MAYR, G. (2000b). A new mousebird (Coliiformes: Coliidae) from the Oligocene of Germany. *Journal für Ornithologie* **141**, 85–92.

MAYR, G. (2000c). A new raptor-like bird from the Lower Eocene of North America and Europe. *Senckenbergiana lethaea* **80**, 59–65.

MAYR, G. (2000d). A remarkable new "gruiform" bird from the Middle Eocene of Messel (Hessen, Germany). *Paläontologische Zeitschrift* **74**, 187–194.

MAYR, G. (2000e). Charadriiform birds from the early Oligocene of Céreste (France) and the Middle Eocene of Messel (Hessen, Germany). *Geobios* **33**, 625–636.

MAYR, G. (2000f). Die Vögel der Grube Messel – ein Einblick in die Vogelwelt Mitteleuropas vor 49 Millionen Jahren. *Natur und Museum* **130**, 365–378.

MAYR, G. (2000g). New or previously unrecorded avian taxa from the Middle Eocene of Messel (Hessen, Germany). *Mitteilungen aus dem Museum für Naturkunde in Berlin, Geowissenschaftliche Reihe* **3**, 207–219.

MAYR, G. (2000h). Tiny hoopoe-like birds from the Middle Eocene of Messel (Germany). *Auk* **117**, 968–974.

MAYR, G. (2001a). A cormorant from the late Oligocene of Enspel, Germany (Aves, Pelecaniformes, Phalacrocoracidae). *Senckenbergiana lethaea* **81**, 329–333.

MAYR, G. (2001b). A new specimen of the tiny Middle Eocene bird *Gracilitarsus mirabilis* (new family: Gracilitarsidae). *Condor* **103**, 78–84.

MAYR, G. (2001c). A second skeleton of the early Oligocene trogon *Primotrogon wintersteini* Mayr 1999 (Aves: Trogoniformes: Trogonidae) in an unusual state of preservation. *Senckenbergiana lethaea* **81**: 335–338.

MAYR, G. (2001d). Comments on the osteology of *Masillapodargus longipes* Mayr 1999 and *Paraprefica major* Mayr 1999, caprimulgiform birds from the Middle Eocene of Messel (Hessen, Germany). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **2001**, 65–76.

MAYR, G. (2001e). New specimens of the Middle Eocene fossil mousebird *Selmes absurdipes* Peters 1999. *Ibis* **143**, 427–434.

MAYR, G. (2001f). The earliest fossil record of a modern-type piciform bird from the late Oligocene of Germany. *Journal für Ornithologie* **142**, 2–6.

MAYR, G. (2001g). The relationships of fossil apodiform birds – a comment on Dyke (2001). *Senckenbergiana lethaea* **81**, 1–2.

MAYR, G. (2002a). A contribution to the osteology of the Middle Eocene ibis *Rhynchaeites messelensis* (Aves: Threskiornithidae: Rhynchaeitinae nov. subfam.). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **2002**, 501–512.

MAYR, G. (2002b). A new species of *Plesiocathartes* (Aves: ?Leptosomidae) from the Middle Eocene of Messel, Germany. *PaleoBios* **22**, 10–20.

MAYR, G. (2002c). A new specimen of *Salmila robusta* (Aves: Gruiformes: Salmilidae n. fam.) from the Middle Eocene of Messel. *Paläontologische Zeitschrift* **76**, 305–316.

MAYR, G. (2002d). A skull of a new pelecaniform bird from the Middle Eocene of Messel, Germany. *Acta Palaeontologica Polonica* **47**, 507–512.

MAYR, G. (2002e). An owl from the Paleocene of Walbeck, Germany. *Mitteilungen aus dem Museum für Naturkunde in Berlin, Geowissenschaftliche Reihe* **5**, 283–288.

MAYR, G. (2002f). Avian Remains from the Middle Eocene of the Geiseltal (Sachsen-Anhalt, Germany). In *Proceedings of the 5th Symposium of the Society of Avian Paleontology and Evolution, Beijing, 1–4 June 2000* (eds. Z. Zhou and F. Zhang), pp. 77–96. Science Press, Beijing.

MAYR, G. (2002g). On the osteology and phylogenetic affinities of the Pseudasturidae – Lower Eocene stem-group representatives of parrots (Aves, Psittaciformes). *Zoological Journal of the Linnean Society* **136**, 715–729.

MAYR, G. (2002 h). Osteological evidence for paraphyly of the avian order Caprimulgiformes (nightjars and allies). *Journal für Ornithologie* **143**, 82–97.

MAYR, G. (2003 a). A new Eocene swift-like bird with a peculiar feathering. *Ibis* **145**, 382–391.

MAYR, G. (2003 b). A postcranial skeleton of *Palaeopsittacus* Harrison, 1982 (Aves incertae sedis) from the Middle Eocene of Messel (Germany). *Oryctos* **4**, 75–82.

MAYR, G. (2003 c). Phylogeny of early Tertiary swifts and hummingbirds (Aves: Apodiformes). *Auk* **120**, 145–151.

MAYR, G. (2003 d). The phylogenetic relationships of the shoebill, *Balaeniceps rex. Journal für Ornithologie* **144**, 157–175.

MAYR, G. (2004 a). A partial skeleton of a fossil loon (Aves, Gaviiformes) from the early Oligocene of Germany with preserved stomach content. *Journal of Ornithology* **145**, 281–286.

MAYR, G. (2004 b). Morphological evidence for sister group relationship between flamingos (Aves: Phoenicopteridae) and grebes (Podicipedidae). *Zoological Journal of the Linnean Society* **140**, 157–169.

MAYR, G. (2004 c). New specimens of *Hassiavis laticauda* (Aves: Cypselomorphae) and *Quasisyndactylus longibrachis* (Aves: Alcediniformes) from the Middle Eocene of Messel, Germany. *Courier Forschungsinstitut Senckenberg* **252**, 23–28.

MAYR, G. (2004 d). Old World fossil record of modern-type hummingbirds. *Science* **304** (5672), 861–864.

MAYR, G. (2004 e). Phylogenetic relationships of the early Tertiary Messel rails (Aves, Messelornithidae). *Senckenbergiana lethaea* **84**, 317–322.

MAYR, G. (2004 f). The phylogenetic relationships of the early Tertiary Primoscenidae and Sylphornithidae and the sister taxon of crown group piciform birds. *Journal of Ornithology* **145**, 188–198.

MAYR, G. (2005 a). New trogons from the early Tertiary of Germany. *Ibis.* In press.

MAYR, G. (2005 b). "Old World phorusrhacids" (Aves, Phorusrhacidae) – a new look at *Strigogyps* ("*Aenigmavis*") *sapea* (Peters 1987). *PaleoBios.* In press.

MAYR, G. (2005 c). Phylogenetic affinities and composition of the early Eocene Gracilitarsidae (Aves, ?Piciformes). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **2005**, 1–16.

MAYR, G. (in press). The postcranial osteology and phylogenetic position of the Middle Eocene *Messelastur gratulator* Peters, 1994 – a morphological link between owls (Strigiformes) and 'falconiform' birds? *Journal of Vertebrate Paleontology.*

MAYR, G. & CLARKE, J. (2003). The deep divergences of neornithine birds: a phylogenetic analysis of morphological characters. *Cladistics* **19**, 527–553.

MAYR, G. & DANIELS, M. (1998). Eocene parrots from Messel (Hessen, Germany) and the London Clay of Walton-on-the-Naze (Essex, England). *Senckenbergiana lethaea* **78**, 157–177.

MAYR, G. & DANIELS, M. (2001). A new short-legged landbird from the early Eocene of Wyoming and contemporaneous European sites. *Acta Palaeontologica Polonica* **46**, 393–402.

MAYR, G. & MANEGOLD, A. (2002). Eozäne Stammlinienvertreter von Schwalmvögeln und Seglern aus der Grube Messel bei Darmstadt. *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin* (*N. F.*) **41**, 21–35.

MAYR, G. & MANEGOLD, A. (2004). The oldest European fossil songbird from the early Oligocene of Germany. *Naturwissenschaften* **91**, 173–177.

MAYR, G., MANEGOLD, A. & JOHANSSON, U. (2003). Monophyletic groups within "higher land birds" – comparison of morphological and molecular data. *Journal of Zoological Systematics and Evolutionary Research* **41**, 233–248.

MAYR, G. & MOURER-CHAUVIRÉ, C. (2000). Rollers (Aves: Coraciiformes s.s.) from the Middle Eocene of Messel (Germany) and the Upper Eocene of the Quercy (France). *Journal of Vertebrate Paleontology* **20**, 533–546.

MAYR, G. & MOURER-CHAUVIRÉ, C. (2004). Unusual tarsometatarsus of a mousebird from the Paleogene of France and the relationships of *Selmes* Peters, 1999. *Journal of Vertebrate Paleontology* **24**, 366–372.

MAYR, G., MOURER-CHAUVIRÉ, C. & WEIDIG, I. (2004). Osteology and systematic position of the Eocene Primobucconidae (Aves, Coraciiformes sensu stricto), with first records from Europe. *Journal of Systematic Palaeontology* **2**, 1–12.

MAYR, G. & PETERS, D. S. (1998). The mousebirds (Aves: Coliiformes) from the Middle Eocene of Grube Messel (Hessen, Germany). *Senckenbergiana lethaea* **78**, 179–197.

MAYR, G. & PETERS, D. S. (1999). On the systematic position of the Middle Eocene swift *Aegialornis szarskii* Peters 1985 with description of a new swift-like bird from Messel (Aves, Apodiformes). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **1999**, 312–320.

MAYR, G., PETERS, D. S. & RIETSCHEL, S. (2002). Petrel-like birds with a peculiar foot morphology from the Oligocene of Germany and Belgium (Aves: Procellariiformes). *Journal of Vertebrate Paleontology* **22**, 667–676.

MAYR, G. & SMITH, R. (2001). Ducks, rails, and limicoline waders (Aves: Anseriformes, Gruiformes, Charadriiformes) from the lowermost Oligocene of Belgium. *Geobios* **34**, 547–561.

MAYR, G. & SMITH, R. (2002 a). A new record of the Prophaethontidae (Aves: Pelecaniformes) from the Middle Eocene of Belgium. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* **72**, 135–138.

MAYR, G. & SMITH, R. (2002 b). Avian remains from the lowermost Oligocene of Hoogbutsel (Belgium). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* **72**, 139–150.

MAYR, G. & WEIDIG, I. (2004). The Early Eocene bird *Gallinuloides wyomingensis* – a stem group representative of Galliformes. *Acta Palaeontologica Polonica* **49**, 211–217.

MILLER, E. R., RASMUSSEN, D. T. & SIMONS, E. L. (1997). Fossil storks (Ciconiidae) from the Late Eocene and Early Miocene of Egypt. *Ostrich* **68**, 23–26.

MILNE-EDWARDS, A. (1867–71). *Recherches anatomiques et paléontologiques pour servir à l'histoire des oiseaux fossiles de la France.* Victor Masson et fils, Paris.

MILNE-EDWARDS, A. (1892). Sur les oiseaux fossiles des dépots éocènes de phosphate de chaux du Sud de la France. *Comptes Rendus du Second Congrès Ornithologique International*, 60–80.

MLÍKOVSKÝ, J. (1987). Eine neue Alkenart (Aves: Alcidae) aus dem Ober-Oligozän Österreichs. *Annalen des Naturhistorischen Museums in Wien, Serie A* **88**, 131–147.

MLÍKOVSKÝ, J. (1989). A new swift (Aves: Apodidae) from the late Eocene of France. *Annalen des Naturhistorischen Museums in Wien, Serie A* **90**, 59–62.

MLÍKOVSKÝ, J. (1996 a). Tertiary avian faunas of Europe. In *Tertiary Avian Localities of Europe* (ed. J. Mlíkovský). *Acta Universitatis Carolinae, Geologica* **39**, 777–818.

MLÍKOVSKÝ, J. (1996 b) (ed.). *Tertiary Avian Localities of Europe.* Acta Universitatis Carolinae, *Geologica* **39**, 1–852.

MLÍKOVSKÝ, J. (1998). A new barn owl (Aves: Strigidae) from the early Miocene of Germany, with comments on the

fossil history of the Tytonidae. *Journal für Ornithologie* **139**, 247–261.

MLÍKOVSKÝ, J. (2002). *Cenozoic birds of the world. Part 1: Europe*. Ninox Press, Praha.

MLÍKOVSKÝ, J. & ŠVEC, P. (1989). Review of the Tertiary waterfowl (Aves: Anseridae) of Czechoslovakia. *Časopis pro mineralogii a geologii* **34**, 199–203.

MOURER-CHAUVIRÉ, C. (1978). La poche à phosphate de Ste. Néboule (Lot) et sa faune de vertébrés du Ludien Supérieur. Oiseaux. *Palaeovertebrata* **8**, 217–229.

MOURER-CHAUVIRÉ, C. (1980). The Archaeotrogonidae from the Eocene and Oligocene deposits of "Phosphorites du Quercy", France. In *Papers in avian paleontology honoring Hildegarde Howard* (ed. K. E. Campbell). *Natural History Museum of Los Angeles County, Contributions to Science* **330**, 17–31.

MOURER-CHAUVIRÉ, C. (1981). Première indication de la présence de Phorusracidés [sic], famille d'oiseaux géants d'Amérique du Sud, dans le Tertiaire européen: *Ameghinornis* nov. gen. (Aves, Ralliformes) des Phosphorites du Quercy, France. *Geobios* **14**, 637–647.

MOURER-CHAUVIRÉ, C. (1982). Les oiseaux fossiles des Phosphorites du Quercy (Eocène supérieur à Oligocène supérieur): implications paléobiogéographiques. *Geobios, mémoire special* **6**, 413–426.

MOURER-CHAUVIRÉ, C. (1983a). Les Gruiformes (Aves) des Phosphorites du Quercy (France). 1. Sous-ordre Cariamae (Cariamidae et Phorusrhacidae). Systématique et biostratigraphie. *Palaeovertebrata* **13** (4), 83–143.

MOURER-CHAUVIRÉ, C. (1983b). *Minerva antiqua* (Aves, Strigiformes), an owl mistaken for an edentate mammal. *American Museum Novitates* **2773**, 1–11.

MOURER-CHAUVIRÉ, C. (1985). Les Todidae (Aves, Coraciiformes) des Phosphorites du Quercy (France). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series B* **88**, 407–414.

MOURER-CHAUVIRÉ, C. (1987). Les Strigiformes (Aves) des Phosphorites du Quercy (France): Systématique, biostratigraphie et paléobiogéographie. *Documents des Laboratoires de Géologie de Lyon* **99**, 89–135.

MOURER-CHAUVIRÉ, C. (1988a). Le gisement du Bretou (Phosphorites du Quercy, Tarn-et-Garonne, France) et sa faune de vertébrés de l'Eocène supérieur. II Oiseaux. *Palaeontographica (A)* **205**, 29–50.

MOURER-CHAUVIRÉ, C. (1988b). Les Aegialornithidae (Aves: Apodiformes) des Phosphorites du Quercy. Comparaison avec la forme de Messel. *Courier Forschungsinstitut Senckenberg* **107**, 369–381.

MOURER-CHAUVIRÉ, C. (1989a). A peafowl from the Pliocene of Perpignan, France. *Palaeontology* **32**, 439–446.

MOURER-CHAUVIRÉ, C. (1989b). Les Caprimulgiformes et les Coraciiformes de l'Eocène et de l'Oligocène des Phosphorites du Quercy et description de deux genres nouveaux de Podargidae et Nyctibiidae. In *Acta XIX congressus internationalis ornithologici* (ed. H. Ouellet), pp. 2047–2055. University of Ottawa Press, Ottawa.

MOURER-CHAUVIRÉ, C. (1991). Les Horusornithidae nov. fam., Accipitriformes (Aves) a articulation intertarsienne hyperflexible de l'Eocène du Quercy. *Geobios, mémoire spécial* **13**, 183–192.

MOURER-CHAUVIRÉ, C. (1992a). The Galliformes (Aves) from the Phosphorites du Quercy (France): systematics and biostratigraphy. In *Papers in Avian Paleontology honoring Pierce Brodkorb* (ed. K. E. Campbell). *Natural History Museum of Los Angeles County, Science Series* **36**, 67–95.

MOURER-CHAUVIRÉ, C. (1992b). Un ganga primitif (Aves, Columbiformes, Pteroclidae) de très grande taille de Paléogène des Phosphorites du Quercy (France). *Comptes rendus de l'Académie des Sciences Série II* **214**, 229–235.

MOURER-CHAUVIRÉ, C. (1992c). Une nouvelle famille de Perroquets (Aves, Psittaciformes) dans l'Eocène supérieur des phosphorites du Quercy, France. *Geobios, mémoire spécial* **14**, 169–177.

MOURER-CHAUVIRÉ, C. (1993). Les gangas (Aves, Columbiformes, Pteroclidae) du Paléogène et du Miocène inférieur de France. *Palaeovertebrata* **22**, 73–98.

MOURER-CHAUVIRÉ, C. (1994). A large owl from the Palaeocene of France. *Palaeontology* **37**, 339–348.

MOURER-CHAUVIRÉ, C. (1995a). Dynamics of the avifauna during the Paleogene and the Early Neogene of France. Settling of the recent fauna. *Acta zoologica cracoviensia* **38**, 325–342.

MOURER-CHAUVIRÉ, C. (1995b). Les Garouillas et les sites contemporains (Oligocène, MP 25) des Phosphorites du Quercy (Lot, Tarn-et-Garonne, France) et leurs faunes de Vertébrés. 3. Oiseaux. *Palaeontographica (A)* **236**, 33–38.

MOURER-CHAUVIRÉ, C. (1995c). The Messelornithidae (Aves: Gruiformes) from the Paleogene of France. In *Acta palaeornithologica* (ed. D. S. Peters). *Courier Forschungsinstitut Senckenberg* **181**, 95–105.

MOURER-CHAUVIRÉ, C. (1996). Paleogene avian localities of France. In *Tertiary Avian Localities of Europe* (ed. J. Mlíkovský). *Acta Universitatis Carolinae, Geologica* **39**, 567–598.

MOURER-CHAUVIRÉ, C. (1999). Les relations entre les avifaunas du Tertiaire inférieur d'Europe et d'Amérique du Sud. *Bulletin de la Société Géologique de France* **170**, 85–90.

MOURER-CHAUVIRÉ, C. (2000). A new species of *Ameripodius* (Aves: Galliformes: Quercymegapodiidae) from the Lower Miocene of France. *Palaeontology* **43**, 481–493.

MOURER-CHAUVIRÉ, C. (2002). Revision of the Cathartidae (Aves, Ciconiiformes) from the Middle Eocene to the Upper Oligocene Phosphorites du Quercy, France. In *Proceedings of the 5th Symposium of the Society of Avian Paleontology and Evolution, Beijing, 1–4 June 2000* (eds. Z. Zhou and F. Zhang), pp. 97–111. Science Press, Beijing.

MOURER-CHAUVIRÉ, C. (2004). Review of: Cenozoic Birds of the World, Part 1: Europe. *Auk* **121**, 623–627.

MOURER-CHAUVIRÉ, C., BERTHET, D. & HUGUENEY, M. (2004). The late Oligocene birds of the Créchy quarry (Allier, France), with a description of two new genera (Aves: Pelecaniformes: Phalacrocoracidae, and Anseriformes: Anseranatidae). *Senckenbergiana lethaea* **84**, 303–315.

MOURER-CHAUVIRÉ, C. & CHENEVAL, J. (1983). Les Sagittariidae fossiles (Aves, Accipitriformes) de l'Oligocène des Phosphorites du Quercy et du Miocène inférieur du Saint-Gérand-le-Puy. *Geobios* **16**, 443–459.

MOURER-CHAUVIRÉ, C., HUGUENEY, M. & JONET, P. (1989). Découverte de Passeriformes dans l'Oligocène supérieur de France. *Comptes rendus de l'Académie des Sciences Série II* **309**, 843–849.

NESSOV, L. A. (1992). Mesozoic and Paleogene birds of the USSR and their paleoenvironments. In *Papers in Avian Paleontology honoring Pierce Brodkorb* (ed. K. E. Campbell). *Natural History Museum of Los Angeles County, Science Series* **36**, 465–478.

OLSON, S. L. (1976). Oligocene Fossils Bearing on the Origins of the Todidae and the Momotidae (Aves: Coraciiformes). *Smithsonian Contributions to Paleobiology* **27**, 111–119.

OLSON, S. L. (1977 *a*). A Lower Eocene Frigatebird from the Green River Formation of Wyoming (Pelecaniformes: Fregatidae). *Smithsonian Contributions to Paleobiology* **35**, 1–33.

OLSON, S. L. (1977 *b*). A synopsis of the fossil Rallidae. In *Rails of the World: A monograph of the family Rallidae* (ed. D. S. Ripley), pp. 339–379. Godine, Boston.

OLSON, S. L. (1980). The significance of the distribution of the Megapodiidae. *Emu* **80**, 21–24.

OLSON, S. L. (1981). The generic allocation of *Ibis pagana* Milne-Edwards, with a review of fossil ibises (Aves: Threskiornithidae). *Journal of Vertebrate Paleontology* **1**, 165–170.

OLSON, S. L. (1985). The fossil record of birds. In *Avian Biology*, Vol. 8 (eds. D. S. Farner, J. R. King and K. C. Parkes), pp. 79–238. Academic Press, New York.

OLSON, S. L. (1989). Aspects of global avifaunal dynamics during the Cenozoic. In *Acta XIX Congressus Internationalis Ornithologici* (ed. H. Ouellet), pp. 2023–2029. University of Ottawa Press, Ottawa.

OLSON, S. L. (1994). A giant *Presbyornis* (Aves: Anseriformes) and other birds from the Paleocene Aquia Formation of Maryland and Virginia. *Proceedings of the Biological Society of Washington* **107**, 429–435.

OLSON, S. L. (1999 *a*). Early Eocene birds from eastern North America: A faunule from the Nanjemoy Formation of Virginia. In *Early Eocene Vertebrates and Plants from the Fisher/Sullivan Site (Nanjemoy Formation) Stafford County, Virginia* (eds. R. E. Weems and G. J. Grimsley). Virginia Division of Mineral Resources Publication **152**, 123–132.

OLSON, S. L. (1999 *b*). The anseriform relationships of *Anatalavis* Olson and Parris (Anseranatidae), with a new species from the Lower Eocene London Clay. In *Avian Paleontology at the Close of the 20th Century: Proceedings of the 4th International Meeting of the Society of Avian Paleontology and Evolution, Washington, D.C., 4–7 June 1996* (ed. S. L. Olson). *Smithsonian Contributions to Paleobiology* **89**, 231–243.

OLSON, S. L. & FEDUCCIA, A. (1980 *a*). *Presbyornis* and the origin of the Anseriformes (Aves: Charadriomorphae). *Smithsonian Contributions to Zoology* **323**, 1–24.

OLSON, S. L. & FEDUCCIA, A. (1980 *b*). Relationships and evolution of flamingos (Aves: Phoenicopteridae). *Smithsonian Contributions to Zoology* **316**, 1–73.

OLSON, S. L. & PARRIS, D. C. (1987). The Cretaceous birds of New Jersey. *Smithsonian Contributions to Paleobiology* **63**, 1–22.

ONO, K., HASEGAWA, Y. & KAWAKAMI, T. (1985). First record of the Pliocene bony-toothed bird (Odontopterygiformes) from Japan. *Bulletin of the Iwate Prefectural Museum* **3**, 155–157.

PATON, T., HADDRATH, O. & BAKER, A. J. (2002). Complete mitochondrial DNA genome sequences show that modern birds are not descended from transitional shorebirds. *Proceedings of the Royal Society of London, Series B* **269**, 839–846.

PATON, T. A., BAKER, A. J., GROTH, J. G. & BARROWCLOUGH, G. F. (2003). RAG-21 sequences resolve phylogenetic relationships within charadriiform birds. *Molecular Phylogenetics and Evolution* **29**, 268–278.

PETERS, D. S. (1983). Die „Schnepfenralle" *Rhynchaeites messelensis* Wittich 1898 ist ein Ibis. *Journal für Ornithologie* **124**, 1–27.

PETERS, D. S. (1985). Ein neuer Segler aus der Grube Messel und seine Bedeutung für den Status der Aegialornithidae (Aves: Apodiformes). *Senckenbergiana lethaea* **66**, 143–164.

PETERS, D. S. (1987 *a*). Ein „Phorusrhacide" aus dem Mittel-Eozän von Messel (Aves: Gruiformes: Cariamae). *Documents des Laboratoires de Géologie de Lyon* **99**, 71–87.

PETERS, D. S. (1987 *b*). *Juncitarsus merkeli* n. sp. stützt die Ableitung der Flamingos von Regenpfeifervögeln (Aves: Charadriiformes: Phoenicopteridae). *Courier Forschungsinstitut Senckenberg* **97**, 141–155.

PETERS, D. S. (1988 *a*). Die Messel – Vögel – eine Landvogelfauna. In *Messel – Ein Schaufenster in die Geschichte der Erde und des Lebens* (eds. S. Schaal and W. Ziegler), pp. 135–151. Kramer, Frankfurt a.M.

PETERS, D. S. (1988 *b*). Ein vollständiges Exemplar von *Palaeotis weigelti* (Aves, Palaeognathae). *Courier Forschungsinstitut Senckenberg* **107**, 223–233.

PETERS, D. S. (1991). Zoogeographical relationships of the Eocene avifauna from Messel (Germany). In *Acta XX Congressus Internationalis Ornithologici* (eds. B. D. Bell, R. O. Cossee, J. E. C. Flux, B. D. Heather, R. A. Hitchmough, C. J. R. Robertson and M. J. Williams), pp. 572–577. New Zealand Ornithological Congress Trust Board, Christchurch.

PETERS, D. S. (1992). A new species of owl (Aves: Strigiformes) from the Middle Eocene Messel oil shale. In *Papers in Avian Paleontology honoring Pierce Brodkorb* (ed. K. E. Campbell). *Natural History Museum of Los Angeles County, Science Series* **36**, 161–169.

PETERS, D. S. (1994). *Messelastur gratulator* n. gen. n. spec., ein Greifvogel aus der Grube Messel (Aves: Accipitridae). *Courier Forschungsinstitut Senckenberg* **170**, 3–9.

PETERS, D. S. (1995). *Idiornis tuberculata* n. spec., ein weiterer ungewöhnlicher Vogel aus der Grube Messel (Aves: Gruiformes: Cariamidae: Idiornithinae). In *Acta palaeornithologica* (ed. D. S. Peters). *Courier Forschungsinstitut Senckenberg* **181**, 107–119.

PETERS, D. S. (1998). Erstnachweis eines Seglers aus dem Geiseltal (Aves: Apodiformes). *Senckenbergiana lethaea* **78**, 211–212.

PETERS, D. S. (1999). *Selmes absurdipes*, new genus, new species, a sandcoleiform bird from the oil shale of Messel (Germany, Middle Eocene). In *Avian Paleontology at the Close of the 20th Century: Proceedings of the 4th International Meeting of the Society of Avian Paleontology and Evolution, Washington, D.C., 4–7 June 1996* (ed. S. L. Olson). *Smithsonian Contributions to Paleobiology* **89**, 217–222.

PETERS, D. S. & HAMEDANI, A. (2000). *Frigidafons babaheydariensis* n. sp., ein Sturmvogel aus dem Oligozän des Irans (Aves: Procellariidae). *Senckenbergiana lethaea* **80**, 29–37.

RASMUSSEN, D. T., OLSON, S. L. & SIMONS, E. L. (1987). Fossil Birds from the Oligocene Jebel Qatrani Formation, Fayum Province, Egypt. *Smithsonian Contributions to Paleobiology* **62**, 1–20.

ROUX, T. (2002). Deux fossiles d'oiseaux de l'Oligocène inférieur du Luberon. *Courrier Scientifique du Parc Naturel Régional du Luberon* **6**, 38–57.

SCHAAL, S. & ZIEGLER, W. (1988). *Messel – Ein Schaufenster in die Geschichte der Erde und des Lebens*. Kramer, Frankfurt am Main.

SCHAUB, S. (1940). Ein Ratitenbecken aus dem Bohnerz von Egerkingen. *Eclogae geologicae Helveticae* **33**, 274–284.

SCHAUB, S. (1945). Bemerkungen zum Typus von Taoperdix keltica Eastman. *Eclogae geologicae Helveticae* **38**, 616–621.

SIBLEY, C. G. & AHLQUIST, J. E. (1990). *Phylogeny and Classification of Birds: A Study in Molecular Evolution*. Yale University Press, New Haven.

SMITH, A. G., SMITH, D. G. & FUNNELL, B. M. (1994). *Atlas of Mesozoic and Cenozoic coastlines*. Cambridge University Press, Cambridge.

STEADMAN, D. W. (1981). (Review of Harrison & Walker 1976 *c*, 1977). *Auk* **98**, 205–207.

STORER, R. W. (1956). The fossil loon, *Colymboides minutus*. *Condor* **58**, 413–426.

TONNI, E. P. (1980). The present state of knowledge of the Cenozoic birds of Argentina. In *Papers in avian paleontology honoring Hildegarde Howard* (ed. K. E. Campbell). *Natural History Museum of Los Angeles County, Contributions to Science* **330**, 105–114.

TRUNKÓ, L. & MUNK, W. (1998). Geologische Beobachtungen in drei tertiären Aufschlußkomplexen im Randbereich des Mittleren Rheingrabens. *Carolinea* **56**, 9–28.

TURNER, A. (1989). *A Handbook of the Swallows and Martins of the World*. Helm, London.

TURNER, D. A. (1997). Family Musophagidae (Turacos). In *Handbook of the Birds of the World, volume 4, Sandgrouse to Cuckoos* (eds. J. del Hoyo, A. Elliott and J. Sargatal), pp. 480–506. Lynx Edicions, Barcelona.

VAN TUINEN, M., BUTVILL, D. B., KIRSCH, J. A. W. & HEDGES, S. B. (2001). Convergence and divergence in the evolution of aquatic birds. *Proceedings of the Royal Society of London, Series B* **268**, 1345–1350.

VAN TUINEN, M. & DYKE, G. J. (2004). Calibration of galliform molecular clocks using multiple fossils and genetic partitions. *Molecular Phylogenetics and Evolution* **30**, 74–86.

VAN TUINEN, M. & HEDGES, S. B. (2001). Calibration of avian molecular clocks. *Molecular Biology and Evolution* **18**, 206–213.

VAN VALKENBURGH, B. (1999). Major patterns in the history of carnivorous mammals. *Annual Reviews of Earth and Planetary Sciences* **27**, 463–493.

VICKERS-RICH, P. (1991). The Mesozoic and Tertiary history of birds on the Australian Plate. In *Vertebrate Palaeontology of Australasia* (eds. P. Vickers-Rich, T. M. Monaghan, R. R. Baird and T. H. Rich), pp. 721–808. Pioneer Design Studio and Monash University Publications Committee, Melbourne.

WADDELL, P. J., CAO, Y., HASEGAWA, M. & MINDELL, D. P. (1999). Assessing the Cretaceous superordinal divergence times within birds and placental mammals by using whole mitochondrial protein sequences and an extending statistical framework. *Systematic Biology* **48**, 119–137.

WEIGEL, R. D. (1963). Oligocene birds from Saskatchewan. *Quarterly Journal of the Florida Academy of Sciences* **26**, 257–262.

WETMORE, A. (1933). The status of *Minerva antiqua*, *Aquila ferox* and *Aquila lydekkeri* as fossil birds. *American Museum Novitates* **680**, 1–4.

WETMORE, A. (1960). A classification for the birds of the world. *Smithsonian Miscellaneous Collections* **139**, 1–37.