A skull of a new pelecaniform bird from the Middle Eocene of Messel, Germany

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A skull of a new pelecaniform bird is described from the Middle Eocene of Messel (Germany). *Masillastega rectirostris* gen. et sp. nov. is tentatively referred to the Sulidae (boobies and gannets). If this assignment is correct, the new taxon would represent the earliest fossil record of the family, preceding *Sula ronzoni* Milne-Edwards, 1867 from the lowermost Oligocene of France by about 15 million years. *Masillastega rectirostris* most distinctly differs from extant Sulidae in the proportionally longer beak which indicates that the Eocene taxon was not adapted to plunge-diving. Contrary to extant Sulidae, which are exclusively marine birds, *Masillastega rectirostris* was found in a freshwater deposit. It is the first pelecaniform bird known from Messel and one of the few large birds discovered at this site.

Key words: Birds, Pelecaniformes, Sulidae, *Masillastega*, Messel, Eocene.

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Introduction

Pelecaniform birds traditionally comprise six extant families of aquatic birds, the Sulidae (boobies and gannets), Phalacrocoracidae and Anhingidae (cormorants and darters), Pelecanidae (pelicans), Fregatidae (frigatebirds), and Phaethontidae (tropicbirds). Although monophyly of these six families has been questioned by some authors, all recent phylogenetic analyses of pelecaniform birds resulted in monophyly of a taxon including Sulidae, Phalacrocoracidae, and Anhingidae (see Cracraft 1985; Sibley and Ahlquist 1990; Siegel-Causey 1997), which was termed Suloidea by Cracraft (1985). Recent studies further support a sister group relationship between the Pelecanidae and the aberrant Shoe-bill (Balaenicipitidae) (Cottam 1967; Siegel-Causey 1997; Livezey and Zusi 2001).

Whereas most extant pelecaniform families are represented in late Oligocene and Miocene deposits (Olson 1985), reliable records from deposits older than Oligocene only exist from the Fregatidae, of which *Limnofregata azygosternon* was described from the Lower Eocene of North America (Olson 1977). *Eostega lebedinskyi* was described by Lambrecht (1929) based on a mandible from putatively Middle Eocene deposits of Romania, and was considered to be closely related to extant Sulidae and Phalacrocoracidae. The age of this specimen, however, needs further confirmation, since Lambrecht (1929: 1270) listed sirenians ("*Halitherium*") and dolphins ("*Delphinus*") in the accompanying fauna. According to E. Kessler (personal communication) the deposits probably are late Eocene in age and the putative dolphins also belong to the Sirenia.

In addition, a few extinct Paleogene families were assigned to the Pelecaniformes. The Prophaethontidae Harrison and Walker, 1976a are known from Late Paleocene to Middle Eocene deposits of North America and Europe and are morphologically closest to extant Phaethontidae; their exact phylogenetic affinities, however, remain to be investigated (Harrison and Walker 1976a; Olson 1994; Mayr and Smith 2002). The Plotopteridae are large flightless members of the Suloidea that were wing-propelled divers and occur in Early Oligocene to Early Miocene marine deposits of the North Pacific (e.g., Olson and Hasegawa 1996). The Pelagornithidae are also considered to be members of the Pelecaniformes by some authors (see Olson 1985) and include very large pseudo-toothed seabirds, which are known from Early Eocene to Miocene deposits of all continents except South America (e.g., Harrison and Walker 1976b; Olson 1985).

Described in this study is an isolated skull of a new pelecaniform bird from the Middle Eocene of Messel (Hessen, Germany), which might represent the earliest fossil record of the Sulidae. The deposits from Messel originated in a lake of tectonic or volcanic origin, about 49 million years ago (see Schaal and Ziegler 1988 for detailed information on the site). A survey on the rich Messel avifauna was given by Mayr (2000a). The anatomical terminology used in this study follows Baumel and Witmer (1993).

Institutional abbreviations.—IPB, Institut für Paläontologie, Universität Bonn, Germany; SMF, Forschungsinstitut Senckenberg, Frankfurt am Main, Germany.

Systematic paleontology

Order Pelecaniformes (*sensu* Cracraft 1985)
Suborder Steganopodes (*sensu* Cracraft 1985)

Superfamily ?Suloidea (*sensu* Cracraft 1985)
Family ?Sulidae Reichenbach, 1849

Remarks.—The specimen described herein is assigned to the suborder Steganopodes of the Pelecaniformes (*sensu* Cracraft 1985) because of the following characters: (1) beak long, with tip of upper beak hooked; (2) narial openings strongly reduced; (3) dorsal surface of mandibular rami medio-laterally very wide, with a plane dorsal surface; (4) pars symphysialis of mandible very short; (5) presence of distinct fossae temporales.

At least characters (1), (2) and (3) unquestionably are derived within neognathous birds. The hooked rostrum is primitively absent in the extant Phaethontidae and Paleogene Prophaethontidae (see Harrison and Walker 1976a) and justifies assignment of the Messel pelecaniform to the suborder Steganopodes *sensu* Cracraft (1985), i.e., a clade comprising Fregatidae, Pelecanidae, Sulidae, Phalacrocoracidae, and Anhingidae. Characters (3) and (4), as well as the fairly long pterygoids distinguish it from ciconiiform birds (storks, herons and allies), of which especially the Scopidae (hamerkop) have a superficially similar bill shape (see below).

Tentative assignment to the Sulidae is based on the following characters: (1) upper beak and mandibular rami deep and (2) bearing numerous impressions of vessels; (3) presence of a deeply excavated recessus tympanicus dorsalis (Fig. 1, "upper tympanic recess" of Cracraft 1985: 836). I consider these three characters to be derived within neognathous birds, and within the Pelecaniformes their combination only occurs in the Sulidae. However, since characters (1) and (2) are widespread among other neognathous birds, and character (3) is also found in Fregatidae and Phaethontidae, classification of the Messel pelecaniform into the Sulidae is tentative.

Masillastega gen. nov.

Type species: *Masillastega rectirostris* sp. nov.

Etymology: The genus name is derived from *Masilla* (Latin), an old Latin name for Messel and *steganos* (Greek), webbed, in reference to the pelecaniform affinities of the new taxon (all extant pelecaniform birds have webbed feet). The name is feminine in gender.

Diagnosis.—The genus *Masillastega* is characterized by the following features: beak straight and conical, deep in its proximal part and measuring more than 2/3 of entire length of skull; tip of the rostrum slightly hooked; narial openings greatly ossified; dorsal surface of mandibular rami medio-laterally very wide; tip of mandible truncated in lateral view and pars symphysialis short; upper beak and mandible bearing many impressions of vessels; recessus tympanicus dorsalis deep.

Differential diagnosis.—*Masillastega* n. gen. differs from:
- all extant Pelecaniformes in the shape of the long and dorso-ventrally high beak (see description below);
- the Eocene pelecaniform genera *Limnofregata* Olson, 1977 (Fregatidae) and *Prophaethon* Andrews, 1899 (Prophaethontidae) in the strongly ossified narial openings (long and slit-like in the former two genera) and the relatively longer beak which lacks a hooked rostrum in *Prophaethon*;
- *Eostega lebedinskyi* Lambrecht, 1929 in its smaller size (Lambrecht 1929 estimated the total length of the mandible of *Eostega* at about 152 mm, in the Messel pelecaniform it measures 135 mm) and in the straight dorsal margin of the mandibular rami (slightly convex in *Eostega*, see Lambrecht 1929: fig. 13).

Remarks.—The description of two large avian taxa from Messel, i.e. the idiornithid species *Idiornis tuberculata* Peters, 1985 and the putative phorusrhacid *Aenigmavis sapea* Peters, 1987, is based on postcranial material only. However, a possibly idiornithid skull from Messel was identified by Peters (1988: fig. 202), which resembles the skull of extant Cariamidae (seriemas) and bears no resemblance to that of *Masillastega*. Independent thereof, whether it is a true phorusrhacid or a flightless member of the Idiornithidae (see Mayr 2000b), it is also very unlikely that *Aenigmavis sapea* had a "pelecaniform" skull.

Masillastega rectirostris sp. nov.

Fig. 1.

Holotype and only known specimen: Isolated skull on two slabs, IPB 140a+b (Fig. 1; specimen 140a only shows fragmentary remains of the cranium and the mandible).

Type locality: Messel, near Darmstadt (Hessen, Germany).

Type horizon: Lower Middle Eocene.

Etymology: "Straight-billed", from *rectus* (Latin), straight and *rostrum* (Latin), beak.

Diagnosis.—Same as for genus.

Description and comparison.—Measurements (in millimeters): maximum length of skull, 139; length of upper beak from naso-frontal hinge to tip, 99; length of mandible, 135.

In its shape and relative proportions but not in morphological details (see below) the beak of *Masillastega rectirostris* resembles that of the extant hamerkop, *Scopus umbretta* (Ciconiiformes, Scopidae; Fig. 2). Compared to extant pelecaniform birds, it is most similar to the beak of the Sulidae which is, however, relatively shorter (Fig. 2). The bill of the Pelecanidae is much longer and has a completely different shape; that of Fregatidae, Phalacrocoracidae and Anhingidae is not so deep, and the beak of extant Phaethontidae is relatively shorter and lacks a terminal hook. The beaks of the Eocene genera *Limnofregata* (Fregatidae, see Olson 1977) and *Prophaethon* (Prophaethontidae) also are relatively shorter; that of the putatively pelecaniform Pelagornithidae exhibits numerous pseudo-teeth along the cristae tomiales (see Harrison and Walker 1976b).

The upper beak is long, measuring more than 2/3 of the complete length of the skull. It is high in its proximal part and gradually becomes narrower towards the tip. The cristae tomiales are straight, the culmen also is hardly curved. The tip of the rostrum is hooked as in all extant pelecaniform birds except the Phaethontidae and Anhingidae, although this hook is only moderately developed as in extant Sulidae and

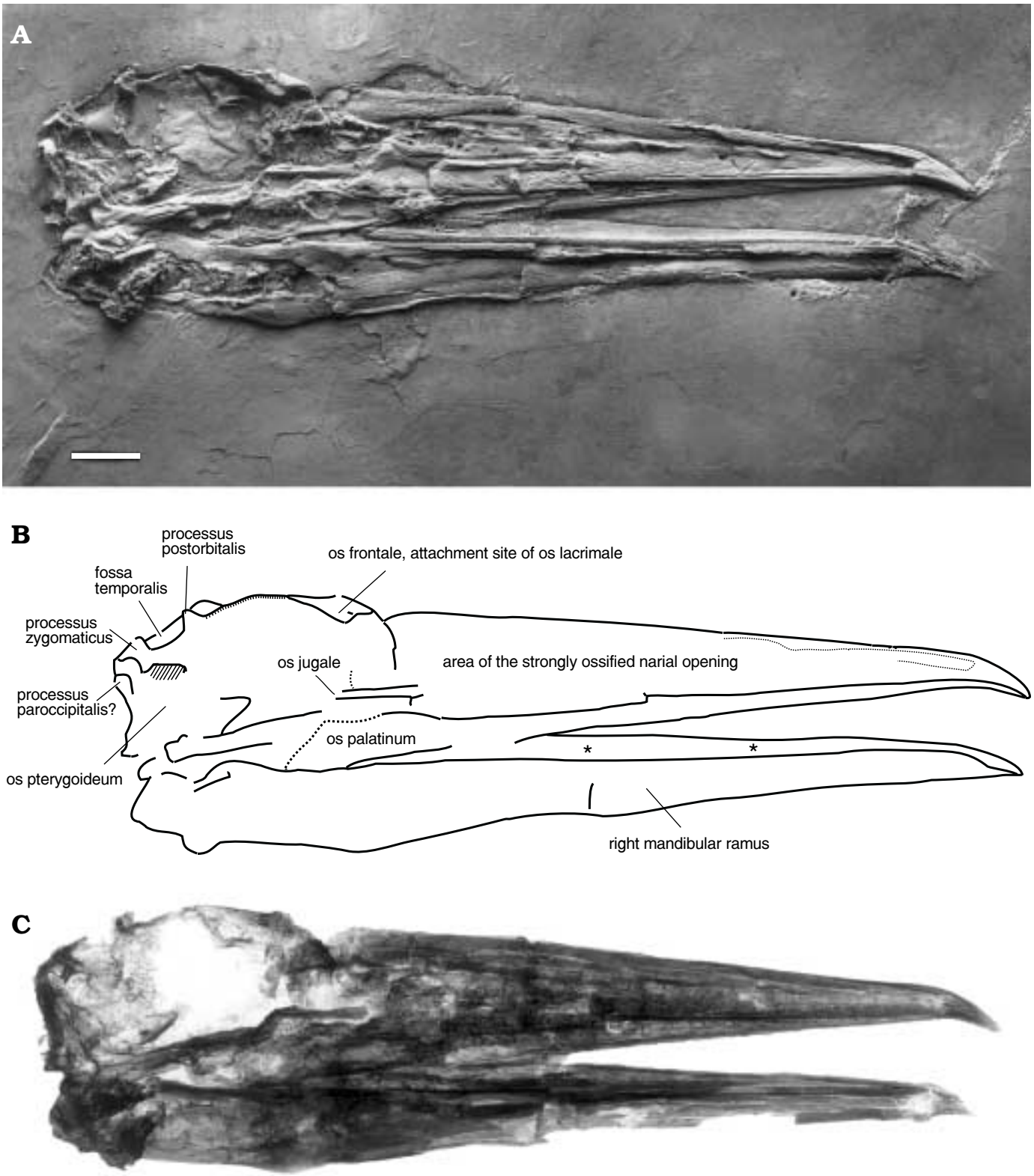

Fig. 1. *Masillastega rectirostris* gen. et sp. nov., holotype (Universität Bonn, Institut für Paläontologie; collection number 140b). **A**. Coated with ammonium chloride to enhance contrast, note the impressions of vessels on the beak; scale bar equals 10 mm. **B**. Interpretative drawing; the hatched area marks the recessus tympanicus dorsalis, the asterisks indicate the wide, plane dorsal surface of the left mandibular ramus. **C**. X-ray photograph.

the Eocene frigatebird *Limnofregata*. The narial openings are greatly reduced as in other extant Pelecaniformes, but whether they are only very small or completely absent as in extant Sulidae remains uncertain; the narial openings are long and narrow in the early Tertiary pelecaniform taxa *Limnofregata* (Fregatidae) and *Prophaethon* (Prophaethon-

Fig. 2. Skulls of extant pelecaniform and ciconiiform birds in comparison. **A**. *Sula bassana* (Pelecaniformes, Sulidae), SMF 1535; note the impressions of vessels on the mandible and the upper beak, the small arrow indicates the deep recessus tympanicus dorsalis. **B**. *Phalacrocorax aristotelis* (Pelecaniformes, Phalacrocoracidae), SMF 2861. **C**. *Scopus umbretta* (Ciconiiformes, Scopidae), SMF 1906. Scale bars 10 mm.

tidae). The ventral surface of the upper beak of *Masillastega* seems to have been greatly ossified as in all extant Pelecaniformes. Due to the crushing of the specimen, a longitudinal furrow along the rostrum, which is characteristic for extant Pelecaniformes, cannot be clearly discerned in *Masillastega*. As in extant Sulidae and Phaethontidae, the surface of both the upper beak and the mandible is covered with many distinct impressions of vessels.

The dorsal margin of the mandible is straight over its entire length. As in other pelecaniform birds, but in contrast to the Scopidae and other ciconiiform birds, the dorsal surface of the mandibular rami is medio-laterally very wide (Fig. 3), measuring about 3.5 mm in the mid-section of the mandible. The mandibular rami are deep as in extant Sulidae, whereas in other extant Pelecaniformes they are lower. A fenestra mandibulae seems to be absent. As in extant Pelecaniformes, but also in contrast to the Ciconiiformes, the pars symphysialis appears to have been very short (although the pars symphysialis itself is not visible, in specimen 140a it can be seen that the mandibular rami are separated over most of their length). A characteristic feature of extant Suloidea is a bipartite processus coronoideus (see Lambrecht 1929) but, owing to preservation of the specimen, this feature cannot be discerned in *Masillastega rectirostris*. The mandible lacks a terminal hook, in lateral view its tip appears truncated as in extant Phalacrocoracidae, whereas it is more pointed in extant Sulidae.

The cranial part of the skull is crushed and only allows the recognition of few details. The os lacrimale is detached from the frontal which opens the view on the articular facet at the

Fig. 3. Mandibles of extant pelecaniform and ciconiiform birds in comparison (dorsal view). **A**. *Sula bassana* (Pelecaniformes, Sulidae), SMF 1535. **B**. *Scopus umbretta* (Ciconiiformes, Scopidae), SMF 1906. Note the medio-laterally wide and plane dorsal surface of the mandibular rami in *Sula bassana*. Scale bars 10 mm.

frontal. The interorbital septum is greatly ossified (visible in specimen 140a), as in all extant Pelecaniformes except the Anhingidae and Phalacrocoracidae. The right os palatinum is visible in specimen 140b, but whether the palatina were fused along their midline as in extant Sulidae cannot be discerned. The pterygoids are fairly long, whereas these bones are much more abbreviated in *Scopus* and other Ciconiiformes (thus in ciconiiform birds the processus mandibularis of the quadrate and the caudal end of the mandible are shifted much more rostrally than in *Masillastega* and other Pelecaniformes). The tip of the short processus postorbitalis projects laterally; it appears not to have been bifurcated as in extant Sulidae (I did not have access to skeletons of *Sula abbotti* which, according to Olson and Warheit (1988), has long, pointed, and ventrally oriented processus postorbitales). As in extant Sulidae, the fossae temporales are well developed and wide (apart from the Pelecanidae, these fossae are well developed in all extant Pelecaniformes). As in extant Sulidae, Fregatidae, and Phaethontidae, there further is a deeply excavated recessus tympanicus dorsalis (this recess is small or absent in extant Pelecanidae, Phalacrocoracidae, and Anhingidae, and most other neognathous birds). The processus zygomaticus has a similar shape to that of extant Sulidae, Phalacrocoracidae, and Fregatidae; its tip also projects laterally. Details of the quadrate cannot be discerned and it is not even certain whether this element is preserved at all. A process which is visible at the caudal end of the cranium in specimen 140b probably represents the deformed right processus paroccipitalis.

Discussion

I consider classification of *Masillastega rectirostris* into Cracraft's (1985) suborder Steganopodes of the Pelecaniformes to be well supported. However, its assignment to the Sulidae is tentative. *M. rectirostris* would be the earliest fossil record of the Sulidae, preceding *Sula ronzoni* Milne-Edwards 1867 from the lowermost Oligocene of France (Mourer-Chauviré 1996: 582) by about 15 million years (see Harrison 1978; Olson 1985; and Darga et al. 1999 for a survey on fossil Sulidae).

The earliest described fossil record of the Phalacrocoracidae is a specimen from the Upper Oligocene of Germany (Mayr 2001), but Mourer-Chauviré (1982) mentioned cormorant remains from the Upper Eocene to Upper Oligocene deposits of the Quercy (France). The earliest certain and well-dated record of the Anhingidae is from the Lower Miocene of North America (Becker 1986). Thus, the Suloidea might well have diverged into the sulid and phalacrocoracid/anhingid lineages by the Early Eocene.

The Messel avifauna is predominated by small arboreal birds (Mayr 2000a), and *Masillastega rectirostris* is the first pelecaniform bird known from this site. Judging from the length of its skull, the new taxon probably had a similar overall size to the extant Shag (*Phalacrocorax aristotelis*) and thus adds to the record of the few larger birds discovered in Messel. According to the morphology of its bill, the Messel

pelecaniform probably was predominantly piscivorous as all extant Pelecaniformes, but might also have fed on various amphibians which, together with small fishes, constitute a significant part of the diet of *Scopus umbretta* (Elliott 1992). Extant Sulidae differ from *Masillastega rectirostris* in the proportionally shorter beak which might, however, be an autapomorphic adaptation to plunge-diving.

Recent Sulidae comprise nine very similar species of exclusively marine birds (Carboneras 1992). If correctly assigned to the Sulidae, *Masillastega* thus paralleled the Eocene frigatebird *Limnofregata* which, unlike its extant relatives, also is known from a limnic paleoenvironment. This supports Olson's (1977: 32) assumption that sulids are among those avian taxa which "may originally have been more diverse ecologically but were subsequently replaced in continental habitats by more advanced groups, with the result that they have been restricted to a purely oceanic environment where they now exist in a sense as relicts".

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References

Baumel, J.J. and Witmer, L.M. 1993. Osteologia. *In*: J.J. Baumel, A.S. King, J.E. Breazile, H.E. Evans, and J.C. Vanden Berge (eds.), Handbook of Avian Anatomy: Nomina Anatomica Avium. *Publications of the Nuttall Ornithological Club* 23: 45–132.

Becker, J.J. 1986. Reidentification of "*Phalacrocorax*" *subvolans* Brodkorb as the earliest record of Anhingidae. *Auk* 103: 804–808.

Carboneras, C. 1992. Family Sulidae (Gannets and Boobies). *In*: J. del Hoyo, A. Elliott, and J. Sargatal (eds.), *Handbook of the Birds of the World 1*, 312–325. Lynx Edicions, Barcelona.

Cracraft, J. 1985. Monophyly and phylogenetic relationships of the Pelecaniformes: a numerical cladistic analysis. *Auk* 102: 834–853.

Darga, R., Böhme, M., Göhlich, U.B., and 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.

Elliott, A. 1992. Family Scopidae (Hamerkop). *In*: J. del Hoyo, A. Elliott, and J. Sargatal (eds.), *Handbook of the Birds of the World* 1, 430–435. Lynx Edicions, Barcelona.

Harrison, C.J.O. 1978. Fossil boobies and gannets. *In*: J.B. Nelson, *The Sulidae—Gannets and Boobies*, 974–977. Oxford University Press, Oxford.

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

Harrison, C.J.O. and Walker, C.A. 1976b. A review of the bony-toothed birds (Odontopterygiformes). *Tertiary Research Special Paper* 2: 1–62.

Lambrecht, K. 1929. Mesozoische und tertiäre Vogelreste aus Siebenbürgen. *In*: E. Csiki (ed.), *X^e Congrés International de Zoologie*, 1262–1275. Stephaneum, Budapest.

Livezey, B.C. and Zusi, R.L. 2001. Higher-order phylogenetics of modern Aves based on comparative anatomy. *Netherlands Journal of Zoology* 51 (2): 179–205.

Mayr, G. 2000a. Die Vögel der Grube Messel – ein Einblick in die Vogelwelt Mitteleuropas vor 49 Millionen Jahren. *Natur und Museum* 130: 365–378.

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

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

Mayr, G. and Smith, R. 2002. 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.

Mourer-Chauviré, C. 1982. Les oiseaux fossiles des Phosphorites du Quercy (Eocène supérieur à Oligocène supérieur): Implications paléobiogéographiques. *In*: E. Buffetaut, P. Janvier, J.-C. Rage, and P. Tassy (eds.), Phylogénie et paléobiogéographie. Livre jubilaire en l'honneur de Robert Hoffstetter. *Geobios, Mémoire Spécial* 6: 413–426.

Mourer-Chauviré, C. 1996. Paleogene Avian Localities of France. *In*: J. Mlíkovský (ed.), Tertiary Avian Localities of Europe. *Acta Universitatis Carolinae, Geologica* 39: 567–598.

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

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

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. and Hasegawa, Y. 1976. A new genus and two new species of gigantic Plotopteridae from Japan (Aves: Pelecaniformes). *Journal of Vertebrate Paleontology* 16: 742–751.

Olson, S.L. and Warheit, K.I. 1988. A new genus for *Sula abbotti*. *Bulletin of the British Ornithologists' Club* 108: 9–12.

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

Schaal, S. and Ziegler, W. 1988. *Messel – Ein Schaufenster in die Geschichte der Erde und des Lebens*. 315 pp. Kramer, Frankfurt a.M.

Sibley, C.G. and Ahlquist, J.E. 1990. *Phylogeny and Classification of Birds: A Study in Molecular Evolution*. Yale University Press, New Haven.

Siegel-Causey, D. 1997. Phylogeny of the Pelecaniformes: Molecular Systematics of a Privative Group. *In*: D.P. Mindell (ed.), *Avian Molecular Evolution and Systematics*, 159–171. Academic Press, San Diego.