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ORIGINAL ARTICLE

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A partial skeleton of a new fossil loon (Aves, Gaviiformes) from the early Oligocene of Germany with preserved stomach content

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Abstract A partial skeleton of a new fossil loon (Aves, Gaviiformes), ?*Colymboides metzleri* n.sp., is described from the early Oligocene (Rupelian) of Frauenweiler in Germany. The new species resembles the early Miocene species *Colymboides minutus* in size and overall morphology, but differs in several osteological details. The specimen represents the first associated remains of an early Tertiary loon. Preserved stomach content further provides the first direct evidence that early Tertiary loons were already specialized towards a piscivorous diet, hunting fishes in a marine environment.

Keywords Aves · Gaviiformes · *Colymboides metzleri* n. sp. · Oligocene · Diet

Introduction

The four extant species of loons (Gaviiformes, Gaviidae) are foot-propelled diving birds that only occur in the Northern Hemisphere, breeding at northern freshwater sites, but wintering along sea costs in temperate areas (Carboneras 1992). Loons were considered to be closely related to grebes (Podicipediformes) by most earlier authors, but the similarities are now generally attributed to convergence (see Sibley and Ahlquist 1990 for a review of the history of avian classification). There is both morphological and molecular evidence that grebes are the sister taxon of flamingos (Phoenicopteriformes) (van Tuinen et al. 2001; Mayr 2004a), but the relationships of loons are uncertain.

The earliest fossil gaviiform is *Neogaeornis wetzeli* from the Cretaceous of Chile (Olson 1992), known from a single tarsometatarsus that resembles the highly derived bone of modern loons. Chatterjee (2002) reported another supposed loon, *Polarornis gregorii*, from the Cretaceous of Antarctica, of which were found the proximal part of the bill and the adjacent distal part of the cranium, parts of the otic region, four vertebrae, a small sternum fragment, a femur, and a proximal tibiotarsus. Despite this very fragmentary preservation, Chatterjee (2002) presented a detailed "reconstruction" of the entire skeleton and a complete skull in which most parts were "constructed by pressing (...) paper pulp into a mold that was sculpted first in clay" (Chatterjee 2002, pp. 128); it is difficult to understand why Chatterjee (1997, pp. 117) described the skull of *Polarornis* as being "fairly intact, beautifully preserved" and figured a drawing of a complete skull with no indication that substantial parts were reconstructed and are not preserved in the specimen.

Among the most completely known Tertiary fossil loons is the early Miocene species *Colymboides minutus* that was first described from Saint-Gérand-le-Puy in France by Milne-Edwards (1867–1871), and studied in greater detail by Storer (1956) and Cheneval (1984). Storer (1956, p. 423) considered *C. minutus* to be "a small loon" with hind limbs "not as highly adapted for swimming rapidly and powerfully under water as are those of living loons", and noted (p. 425) that the "morphological differences between *Colymboides* and *Gavia* are many and rather great, but they are largely one of size and degree of specialization". *C. minutus* was also reported from the early Miocene of the Czech Republic (Švec 1980, 1982). However, although all major limb elements of this species are known, no associated remains have yet been discovered.

Two other species were assigned to *Colymboides*: *Colymboides anglicus* from the Upper Eocene of England which is known from a coracoid, a referred humerus and a referred frontal part of the skull (Lydekker 1891; Harrison and Walker 1976), and *Colymboides belgicus* from the lowermost Oligocene of Belgium which is based on a proximal carpometacarpus and a

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distal ulna (Mayr and Smith 2002). Olson and Rasmussen (2001) further tentatively assigned to *Colymboides* an incomplete humerus and carpometacarpus from the Miocene of North America.

Gaviella pusilla (Shufeldt 1915), another Tertiary loon, is known from a proximal carpometacarpus from Wyoming (USA) and is considered to be of Oligocene age (Wetmore 1940).

A number of fossil loons from the Miocene and Pliocene of Europe and North America were further assigned to the modern genus *Gavia* (Švec 1982; Olson and Rasmussen 2001; Mlíkovský 2002). Some of these are clearly stem group representatives of the Gaviidae, others may be within the crown group and on the stem lineage of modern species (Olson and Rasmussen 2001, p. 246).

Here I describe the first associated remains of an early Tertiary loon, from early Oligocene (Rupelian) marine deposits of Frauenweiler in Southern Germany (Trunko and Munk 1998). Apart from a rich fish fauna (Micklich and Parin 1996), this site has yielded a diverse avifauna, and the hitherto reported taxa include the procellariiform *Diomedeoides* (Mayr et al. 2002), the mousebird *Oligocolius* (Coliidae, Mayr 2000), the earliest European record of a songbird (Passeriformes, Mayr and Manegold 2004), and the stem group hummingbird *Eurotrochilus* (Trochilidae, Mayr 2004b).

Methods

Osteological terminology follows Baumel and Witmer (1993). Measurements are in millimeters and represent the maximum length of the bone along its longitudinal axis. The fossil specimen is deposited in Staatliches Museum für Naturkunde Stuttgart, Germany (SMNS).

Results

Systematic paleontology

– Gaviiformes Wetmore and Miller, 1926
– Gaviidae Allen, 1897
– ?*Colymboides* (Milne-Edwards, 1867–71)
– ?*Colymboides metzleri* n. sp.(Figs. 1, 2, 3)

Holotype

SMNS 80739/2a + b (dissociated partial skeleton on two slabs, including several praesacral vertebrae, the left

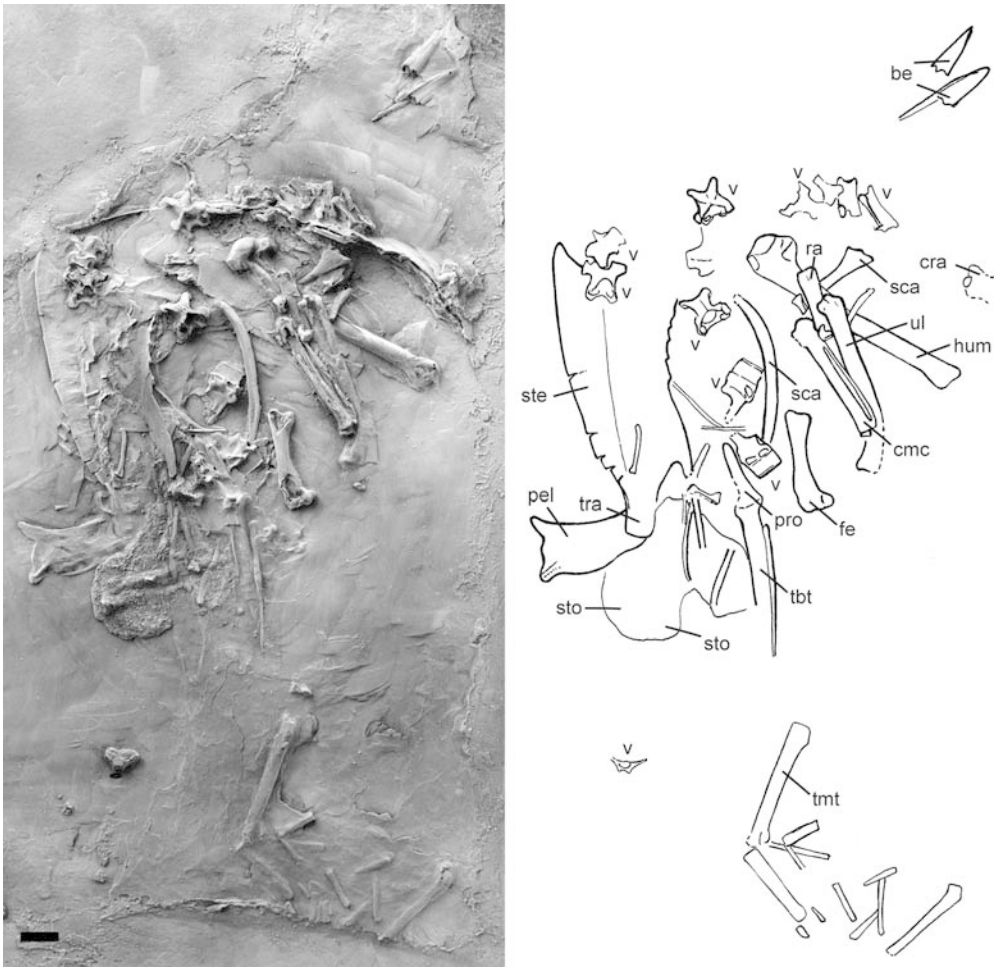

Fig. 1 *Colymboides metzleri* n.sp. from the early Oligocene (Rupelian) of Frauenweiler, specimen SMNS 80739/2a and interpretative drawing. *be* Tip of beak; *cmc* left carpometacarpus; *cra* fragment of cranium; *fe* left femur; *hum* – left humerus; *pel* caudal part of pelvis; *pro* process formed by cnemial crests of tibiotarsus; *ra* left radius; *sca* scapula; *ste* sternum; *sto* stomach content; *tbt* left tibiotarsus; *tmt* left tarsometatarsus; *tra* trabecula mediana of sternum; *ul* left ulna; *v* vertebra. Specimen coated with ammonium chloride to enhance contrast. *Scale bar* equals 10 mm

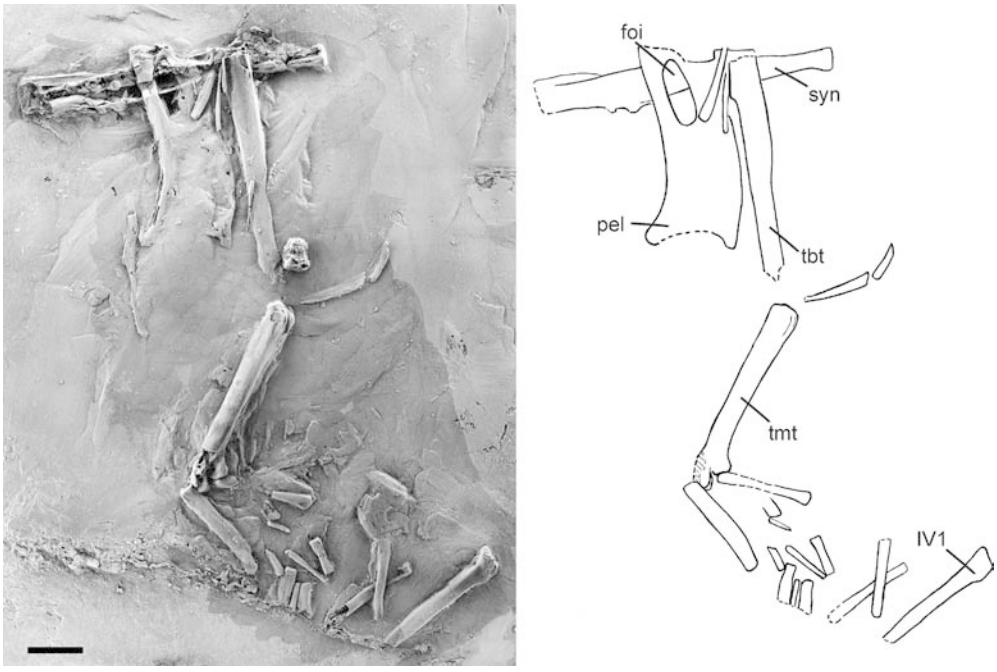

Fig. 2 *Colymboides metzleri* n.sp. from the early Oligocene (Rupelian) of Frauenweiler, specimen SMNS 80739/2b and interpretative drawing. *foi* Foramen ilioischiadicum; *pel* pelvis; *syn* synsacrum; *tbt* tibiotarsus; *tmt* tarsometatarsus; *IV1* first phalanx of fourth toe. Specimen coated with ammonium chloride to enhance contrast.; *Scale bar* equals 10 mm

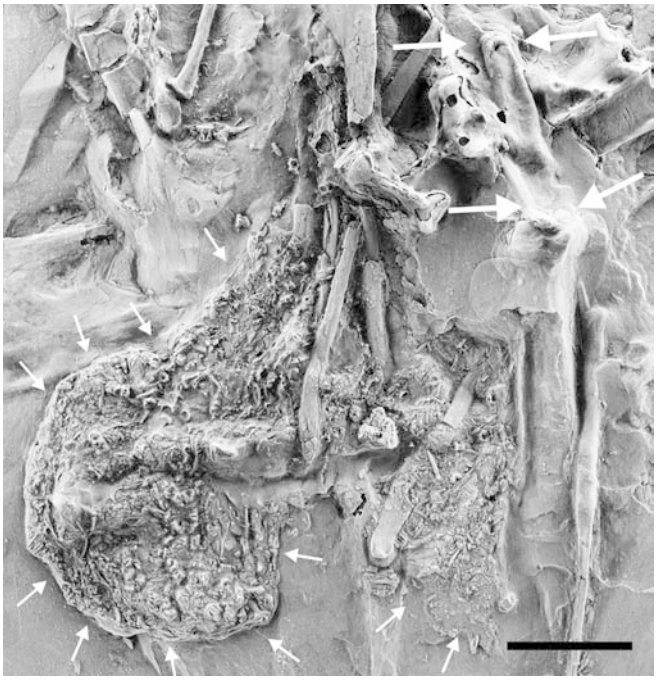

Fig. 3 *Colymboides metzleri* n.sp. from the early Oligocene (Rupelian) of Frauenweiler. Detail of specimen SMNS 80739/2a, showing stomach content (*small arrows*) and process formed by cnemial crests of tibiotarsus (*large arrows*). Specimen coated with ammonium chloride to enhance contrast. *Scale bar* equals 10 mm

wing and left foot, the sternum, and the pelvis), deposited in the collection of the Staatliches Museum für Naturkunde, Stuttgart, Germany (Figs. 1, 2, 3).

Type locality and horizon

Frauenweiler south of Wiesloch (Baden-Württemberg, Germany), clay pit of the Bott-Eder GmbH (''Grube Unterfeld''); Rupelian, early Oligocene.

Differential diagnosis

?*Colymboides metzleri* is decidedly smaller than the Upper Cretaceous loons, *Colymboides anglicus*, *C. belgicus*, and species of the modern genus *Gavia*, measuring about half of the size of the smallest extant species, *Gavia stellata*. The new species is of similar size to *Colymboides minutus* from which it is distinguished in a more protruding and narrower process formed by the cristae cnemiales (length 16 mm vs 11 mm in the slightly larger *C. minutus*), and in a proportionally shorter femur and longer tarsometatarsus (femur 25.9 mm vs 30.6–33.0 mm in *C. minutus*, tarsometatarsus 34.5 mm vs. 30.7–33.0 mm in *C. minutus*). Meaningful comparisons with *Gaviella pusilla* are not possible.

Measurements

Dimensions of *Colymboides minutus* are in parentheses (after Cheneval 1984)

Left humerus, 60.5 (59.4–67.1); left ulna, ~46.6 (48.7–55.9); left radius, 45.5 (48.1–52.8); left carpometacarpus, 33.4 (29.9–34.0); left femur, 25.9 (30.6–33.0); left tarsometatarsus, 34.5 (30.7–33.0); pedal phalanges: II1, 16.5; III1, 18.7.

Etymology

The species has been named after the finder of the holotype, Mr. Rudolf Metzler.

Description and comparison

Only two fragments of the tip of the beak, probably from both the lower and upper jaw, are preserved, as well as a small fragment of the cranium that allows recognition of the condylus occipitalis.

The vertebrae of early Tertiary loons have been unknown so far. In the Frauenweiler specimen, 13 or 14 praesacral vertebrae and a caudal vertebra are scattered over the slab that exhibit a similar morphology to the vertebrae of modern Gaviidae. As in modern loons, the thoracic vertebrae bear very long processus ventrales.

Likewise, the scapula of an early Tertiary loon is preserved in the Frauenweiler specimen for the first time. The left scapula lies next to the femur, and the extremitas omalis of the right scapula is situated next to the mid section of the humerus. The bone is similar to the scapula of modern loons in that its cranial section is markedly bowed medio-laterally and has an ovoid cross section (flattened in most other birds). However, it differs from modern loons in the more pointed acromion.

Although Lydekker (1891) referred a cranial portion of a sternum to *Colymboides anglicus*, this was shown by Harrison and Walker (1976) to be from a duck (Anatidae). In specimen SMNS 80739/2a, the sternum is seen in right lateral view. Only five processus costales can be counted in the fossil, whereas there are eight in modern loons. As in modern loons, the caudal margin exhibits a single pair of incisions and the trabecula mediana is strongly caudally elongated. The apex carinae protrudes cranially.

As far as comparable owing to preservation, humerus, ulna, and carpometacarpus closely resemble the corresponding bones of *Colymboides minutus*, as figured and described by Storer (1956) and Cheneval (1984). As in modern loons, the ulna is much shorter than the humerus.

The radius lies between the ulna and the carpometacarpus. As preserved, its distal end exhibits an unusual morphology in being much more flattened than in modern loons. Whether this reflects the true condition or is of diagenetic origin is, however, uncertain.

The os carpi ulnare is small as in modern *Gavia*. The os carpi radiale differs from that of modern loons in that it does not bear a marked tendinal furrow.

Apart from a synsacrum of *Colymboides minutus* figured by Storer (1956), details of the pelvis of early Tertiary loons were hitherto unknown. The pelvis of specimen SMNS 80739/2 is dissociated and apparently the ilium was not fused to the narrow synsacrum, a condition found in few modern birds including loons, penguins (Sphenisciformes) and tubenoses (Procellariiformes). Apart from being less elongated, the caudal end of the postacetabular ilium exhibits the highly derived morphology of modern loons in that the elongated spina dorsolateralis ilii bears a marked ridge along its lateral surface and there is notch in the caudal margin, between ischium and ilium (Fig. 4).

The femur is not as abbreviated and stout as that of modern Gaviidae, but appears to be proportionally shorter and somewhat stouter than in *Colymboides minutus* (see Measurements).

The tibiotarsus bears strongly elongated, proximally protruding cristae cnemiales (Figs. 1, 3). The process formed by the cnemial crests is proportionally longer and narrower than in *Polarornis* and *Colymboides minutus*, though less elongated than in modern loons: in ?*Colymboides metzleri* it measures about 16 mm, whereas it has a length of only 11 mm in the similar-sized *Colymboides minutus* (tibiotarsus length 69 mm), and 48 mm in *Gavia stellata* (tibiotarsus length 163 mm). Unfortunately, the distal end of the tibiotarsus is not preserved in the specimen, so the complete length of this bone in ?*C. metzleri* is unknown.

The tarsometatarsus of SMNS 80739/2 resembles the corresponding bone of *Colymboides minutus*. The second trochlea is strongly turned plantad. As in *C. minutus* but contrary to modern loons, the hypotarsus apparently lacks a bony bridge and exhibits plantarly open sulci.

The toes of early Tertiary loons have been so far unknown. The Frauenweiler specimen shows that those of *Colymboides* were similar to the toes of modern loons. The proximal phalanx of the fourth toe exhibits the derived morphology of loons in that the proximal end is widened and dorsally projecting. The hallux, which is very small in modern loons, appears not to be preserved in the specimen. The ungual phalanges are of similar shape to those of modern loons and differ from the

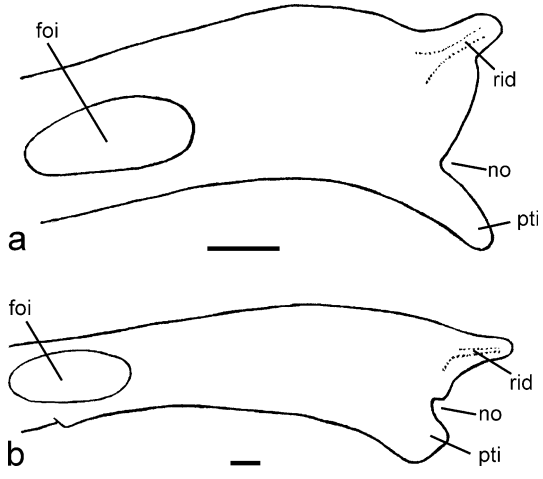

Fig. 4a,b Ilium and postacetabular part of ischium in comparison, left lateral view. **a** ?*Colymboides metzleri* n.sp, **b** modern *Gavia stellata*. *foi* Foramen ilioischiadicum; *no* notch (see text); *pti* processus terminalis ischii; *rid* ridge along lateral surface of spina dorsolateralis ilii. *Scale bars* equal 5 mm

broad, flattened ungual phalanges of grebes (Podicipediformes).

In the specimen a dense package of remains of small fishes (diameter of vertebrae from 0.4–1.0 mm) is preserved that unquestionably represents the former stomach content of the bird (Fig. 3).

Discussion

The new Frauenweiler fossil is assigned to the Gaviiformes because of, e.g., the caudally elongated trabecula mediana of the sternum, the highly derived morphology of the postacetabular part of the pelvis (Fig. 4), the strongly elongated, proximally protruding cristae cnemiales on the tibiotarsus, and the medio-laterally compressed tarsometatarsus.

Whereas the genus *Gavia* is well-characterized by derived characters that are absent in *Colymboides* (e.g., a more elongated processus extensorius of the carpometacarpus and a more derived structure of the hypotarsus), no derived characters are known that support monophyly of the taxa assigned to *Colymboides*, which may turn out to be a paraphyletic genus. Although very similar in size and overall morphology to *Colymboides minutus*, the new species shares with modern Gaviidae a more strongly protruding and narrower process formed by the cristae cnemiales of the tibiotarsus and a proportionally shorter and slightly stouter femur (which is, however, not as short and stout as in *Gavia*). However, whether ?*Colymboides metzleri* indeed is more closely related to *Gavia* spp. than to *Colymboides minutus* needs to be further evaluated by future better preserved specimens of the Frauenweiler loon, showing additional osteological details. At present, I prefer a tentative assignment to *Colymboides*.

The phylogenetic position of *Colymboides minutus* relative to *Neogaeornis* and *Polarornis* is uncertain, owing to the incomplete preservation of the Cretaceous taxa. *Polarornis* significantly differs from modern loons in several characters (Chatterjee 2002, p. 133) and, if correctly assigned to the Gaviiformes, may be a synonym of *Neogaeornis* - a possibility already raised by Olson (1992) but not discussed by Chatterjee (2002).

The Rupelian deposits of Frauenweiler have an age of about 30–33 million years (Legendre and Lévêque 1997), and the fossil loon described in this study is about 4–8 million years younger than *Colymboides anglicus* from England, the type horizon of which dates back 37–38 million years (Mlíkovský 1996; Legendre and Lévêque 1997). There is thus still a gap of more than 25 million years in the fossil record of the Gaviiformes, between *C. anglicus* and the Upper Cretaceous taxa *Neogaeornis* and *Polarornis*.

Apart from representing the first associated remains of an early Tertiary loon, specimen SMNS 80739/2 provides the first direct evidence that early Tertiary loons were already specialized towards a piscivorous diet, hunting fishes in a marine environment.

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References

Baumel JJ, Witmer LM (1993) Osteologia. In: Baumel JJ, King AS, Breazile JE, Evans HE, Vanden Berge JC (eds) Handbook of avian anatomy: Nomina anatomica avium. Publ Nuttall Ornithol Club 23:45–132

Carboneras C (1992) Family Gaviidae (Divers). In: del Hoyo J, Elliott A, Sargatal J (eds) Handbook of the birds of the world, vol 1Lynx Edicions, Barcelona, pp 162–172

Chatterjee S (1997) The rise of birds. John Hopkins University Press, Baltimore

Chatterjee S (2002) The morphology and systematics of *Polarornis*, a Cretaceous Loon (Aves: Gaviidae) from Antarctica. In: Zhou Z, Zhang F (eds) Proceedings of the 5th Symposium of the Society of Avian Paleontology and Evolution, Beijing, 1–4 June 2000. Science Press, Beijing,.pp 125–155

Cheneval J (1984) Les oiseaux aquatiques (Gaviiformes à Ansériformes) du gisement aquitanien de Saint-Gérand-le-Puy (Allier, France): Révision systématique. Palaeovertebrata 14:33–115

Harrison CJO, Walker CA (1976) Birds of the British Upper Eocene. Zool J Linn Soc 59:323–351

Legendre S, Lévêque F (1997) Etalonnage de l'échelle biochronologique mammalienne du Paléogène d'Europe occidentale: vers une intégration à l'échelle globale. In: Aguilar J-P, Legendre S, Michaux J (eds) Actes du Congrès BiochroM'97. Mém Trav EPHE Inst Montpellier 21:461–473

Lydekker R (1891) Catalogue of the fossil birds in the British Museum (Natural History). British Museum (Natural History), London

Mayr G (2000) A new mousebird (Coliiformes: Coliidae) from the Oligocene of Germany. J Ornithol 141:85–92

Mayr G (2004a) Morphological evidence for sister group relationship between flamingos (Aves: Phoenicopteridae) and grebes (Podicipedidae). Zool J Linn Soc 140:157–169

Mayr G (2004b) Old World fossil record of modern-type hummingbirds. Science 304:861–864

Mayr G, Manegold A (2004) The oldest European fossil songbird from the early Oligocene of Germany. Naturwissenschaften 91:173–177

Mayr G, Smith R (2002) Avian remains from the lowermost Oligocene of Hoogbutsel (Belgium). Bull Inst R Sci Nat Belg 72:139–150

Mayr G, Peters DS, Rietschel, S (2002) Petrel-like birds with a peculiar foot morphology from the Oligocene of Germany and Belgium (Aves: Procellariiformes). J Vert Paleontol 22:667–676

Micklich N, Parin N (1996) The fishfauna of Frauenweiler (Middle Oligocene, Rupelian; Germany): First results of a review. Publ Espec Inst Esp Oceanogr 21:129–148

Milne-Edwards A (1867–1871) Recherches anatomiques et paléontologiques pour servir à l'histoire des oiseaux fossiles de la France. Masson, Paris

Mlíkovský J (1996) Tertiary avian localities of the United Kingdom. In: Mlíkovský J (ed) Tertiary avian localities of Europe. Acta Univ Carol 39:759–771

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

Olson SL (1992) *Neogaeornis wetzeli* Lambrecht, a Cretaceous loon from Chile (Aves: Gaviidae). J Vert Paleontol 12:122–124

Olson SL, Rasmussen PC (2001) Miocene and Pliocene birds from the Lee Creek Mine, North Carolina. In: Ray CE, Bohaska DJ (eds) Geology and paleontology of the Lee Creek Mine, North Carolina, III. Smithson Contrib Paleobiol 90:233–365

Shufeldt RW (1915) Fossil birds in the Marsh Collection of Yale University. Yale University Press, New Haven

Sibley CG, Ahlquist JE (1990) Phylogeny and classification of birds: a study in molecular evolution. Yale University Press, New Haven

Storer RW (1956) The fossil loon, *Colymboides minutus*. Condor 58:413–426

Švec P (1980) Lower Miocene birds from Dolnice (Cheb basin), western Bohemia. Cas Mineral Geol 25:377–387

Švec P (1982) Two new species of diving birds from the Lower Miocene of Czechoslovakia. Cas Mineral Geol 27:243–260

Trunkó L, Munk W (1998) Geologische Beobachtungen in drei tertiären Aufschlußkomplexen im Randbereich des Mittleren Rheingrabens. Carolinea 56:9–28

Tuinen M van, Butvill DB, Kirsch JAW, Hedges SB (2001) Convergence and divergence in the evolution of aquatic birds. Proc R Soc Lond B 268:1345–1350

Wetmore A (1940) Fossil bird remains from Tertiary deposits in the United States. J Morphol 66:25–37