

A small loon and a new species of large owl from the Rupelian of Belgium (Aves: Gaviiformes, Strigiformes)

Gerald Mayr

Received: 12 February 2009 / Accepted: 1 April 2009 / Published online: 5 May 2009
© Springer-Verlag 2009

Abstract The early Oligocene Boom Formation in Belgium yielded many avian remains from the Rupelian unit-stratotype, most of which have remained unstudied so far. Here, I describe a small loon (Gaviiformes) and a new species of large owl (Strigiformes) that are represented by associated bones of a single individual each. The loon, of which wing and pectoral girdle bones are preserved, is assigned to *Colymboides (?) metzleri*, a species previously known from a partial skeleton from the Rupelian of Germany. The owl is based on a tarsometatarsus and distal tibiotarsus and described as a new species, *Selenornis steendorpensis*. It constitutes the most substantial fossil record of the taxon *Selenornis*, which was before known from a distal tibiotarsus from an unknown horizon of the Quercy fissure fillings in southwestern France. It is detailed that there are differences in the higher level taxonomic composition of the known early Oligocene avifaunas of northern and southern Europe, which may reflect true zoogeographic facts owing to a different climate and vegetation.

Keywords Fossil birds · Rupelian · North Sea basin · *Colymboides (?) metzleri* · *Selenornis steendorpensis* n. sp.

Kurzfassung Die unteroligozäne Boom Formation in Belgien lieferte zahlreiche Vogelüberreste aus dem Stratotyp der Rupel-Stufe, von denen die meisten allerdings bis jetzt unbearbeitet blieben. Hier beschreibe ich einen kleinen Seetaucher (Gaviiformes) und eine neue Art einer großen Eule (Strigiformes), die jeweils durch mehrere Knochen eines einzelnen Individuums repräsentiert sind.

Der Seetaucher, von dem Flügel- und Schultergürtel-elemente erhalten sind, wird zu *Colymboides (?) metzleri* gestellt, einer Art, die bisher nur von einem Teilskelett aus dem Rupelton Deutschlands bekannt war. Die Eule basiert auf einem Tarsometatarsus und einem distalen Tibiotarsus und wird als neue Art, *Selenornis steendorpensis*, beschrieben. Sie stellt den umfangreichsten Fossilnachweis des Taxons *Selenornis* dar, welches bisher nur von einem distalen Tibiotarsus von einem unbekanntem Horizont der Spaltfüllungen des Quercy im südwestlichen Frankreich bekannt war. Es wird ausgeführt, dass es Unterschiede bezüglich der taxonomischen Zusammensetzung der unteroligozänen Avifaunen von Nord- und Südeuropa gibt, welche möglicherweise tatsächliche tiergeographische Tatsachen infolge eines unterschiedlichen Klimas und einer unterschiedlichen Vegetation widerspiegeln.

Introduction

The Institut Royal des Sciences Naturelles de Belgique holds a substantial collection of avian remains from the early Oligocene (Rupelian) of Belgium, which was assembled in the late nineteenth/early twentieth centuries. The fossils stem from marine deposits around the villages Rupelmonde, Boom, and Steendorp that originated in the southern North Sea basin (e.g., van Simaey and Vandenberghe 2006). The fact notwithstanding that many represent multiple three-dimensionally preserved bones of single individuals and come from the Rupelian unit stratotype, most have not been studied so far (Cheneval 1996). Except for a putative anseriform species described by Lambrecht (1931), all of the currently recognized taxa from the deposits of the Rupelmonde area were erected by

G. Mayr (✉)
Forschungsinstitut Senckenberg, Sektion Ornithologie,
Senckenberganlage 25, 60325 Frankfurt am Main, Germany
e-mail: Gerald.Mayr@senckenberg.de

van Beneden (1871), whose identifications are poorly established and, at least concerning that latter study, probably erroneous throughout (Brodkorb 1962; Olson 1985; Mayr 2009).

The avifauna of the Boom Formation is dominated by the procellariiform Diomedoididae, which are represented by postcranial bones of numerous individuals. Judging from the published illustrations, many of the avian remains described by van Beneden (1871) also belong to this group of birds (Mayr et al. 2002; Mayr 2009). Such seems to be true for the holotypic distal tibiotarsus of *Rupelornis definitus* van Beneden 1871, whose affinities were considered uncertain in the original description, the holotypic distal humerus of *Vanellus selysii* van Beneden 1871, which was identified as a lapwing (Charadriidae), and a fragmentary humerus referred to the Anseriformes (waterfowl; van Beneden 1871: fig. 4). For a definitive assessment of the affinities of these specimens and settling of the nomenclatural issues arising from such a revision, rediscovery of the type material, which is not in the collection of the Brussels museum (pers. obs.), would be desirable.

Cheneval (1996, p. 538) pointed out that the “main problem with the avifaunas from Belgium is the lack of recent studies,” and as a first step towards a better knowledge of the Rupelian avifauna of the North Sea basin, a small loon and a new species of large owl are reported in the present study.

Materials and methods

Osteological terminology follows Baumel and Witmer (1993); measurements are in millimeters. The fossils are deposited in the Institut Royal des Sciences Naturelles des Belgique, Brussels, Belgium (IRSNB).

The fossil owl was compared with bones of the following extant Strigiformes (all in the collection of Forschungsinstitut Senckenberg): Tytonidae: *Tyto alba*, *T. novaehollandiae*; Strigidae: *Aegolius acadicus*, *Ae. funereus*, *Asio (Rhinoptynx) clamator*, *A. flammeus*, *A. otus*, *Athene noctua*, *Bubo africanus*, *B. bubo*, *B. magellanicus*, *B. virginianus*, *Glaucidium passerinum*, *Ninox boobook*, *N. scutulata*, *Otus asio*, *O. choliba*, *O. scops*, *Ptilopsis leucotis*, *Speotyto cunicularia*, *Surnia ulula*, *Strix aluco*, *S. nebulosa*, *S. perspicillata*, and *S. uralensis*.

Systematic paleontology

- Gaviiformes Wetmore and Miller 1926.
- Gaviidae Allen 1897.
- ?*Colymboides* Milne-Edwards 1867.
- *Colymboides* (?) *metzleri* Mayr 2004.

Referred specimen

IRSNB Av 85a-j; pectoral girdle and forelimb elements of a single individual (both coracoids and scapulae, right humerus, shaft of left humerus, left and right ulnae lacking the proximal ends, proximal end of left carpometacarpus, and right carpometacarpus lacking os metacarpale minus; Fig. 1).

Locality and horizon

Boom, south of Antwerp, Belgium; early Oligocene, Rupelian, Boom Formation (MP ?23–24; Cheneval 1996); collected in 1896.

Measurements [dimensions of the holotype of *C. (?) metzleri* in brackets; after Mayr 2004]

Coracoid, length from processus acrocoracoideus to angulus medialis, 27.9 (left), 27.7 (right). Right humerus, length, ~62.0 [60.5]. Right ulna, length as preserved, 42.8; estimated total length, ~46–47 [~46.6]. Right carpometacarpus, length, 35.5 [33.4].

Remarks

IRSNB Av 85a–j can be assigned to the Gaviiformes (loons) because of, e.g., the strongly mediolaterally bowed scapula whose facies articularis humeralis is greatly elongated, the dorsoventrally flattened distal end and protruding tuberculum carpale of the ulna, and the proximodistally elongated and low os metacarpale alulare of the carpometacarpus.

The four extant species of loons are aquatic birds with a Northern Hemispheric distribution. The Paleogene fossil record of these birds increased in the past years, but is still quite sketchy (Mayr 2009). All of the named species have been assigned to the taxon *Colymboides*, which was originally established for *Colymboides minutus* Milne-Edwards 1867 from the early Miocene of France. *Colymboides anglicus* Lydekker 1891 is known from the late Eocene of England, *C. belgicus* Mayr and Smith 2002 occurs in the lowermost Oligocene of Belgium, and *C. (?) metzleri* Mayr 2004 is based on a dissociated partial skeleton from the Rupelian of Germany (this species was only tentatively referred to *Colymboides* in the original description). From the late Oligocene of Germany, Mayr and Poschmann (in press) further described an isolated foot of a *Colymboides*-like loon.

In size, the new Belgian loon corresponds well with *Colymboides* (?) *metzleri* and *C. minutus*, whereas *C. anglicus* and *C. belgicus* are distinctly larger. Its coracoid, humerus, ulna, and carpometacarpus closely match the corresponding elements of *C. minutus*, which were described in detail by Milne-Edwards (1867–1871) and Storer (1956), and the new fossils do not show morphological features of



Fig. 1 a–j *Colymboides (?) metzleri* Mayr 2004 from the Rupelian of Boom (IRSNB Av 85a–j), with **k** the carpometacarpus of the extant Red-throated Diver, *Gavia stellata*, for size comparison. **a** right coracoid in dorsal view; **b** left coracoid in ventral view; **c** right scapula in dorsomedial view; **d** left scapula in lateral view; right humerus in cranial (**e**) and caudal (**f**) view; **g** right ulna in ventral

view; **h** left ulna in ventral view; **i** right carpometacarpus in ventral view; **j** proximal left carpometacarpus in dorsal view; **k** right carpometacarpus in ventral view. Note that the ventrodistal portion of the distal end of the right humerus exploded owing to the decay of marcasite inside the bone; as a consequence, its shape is distorted and has unnatural proportions. All figures to scale

taxonomic or phylogenetic interest that were not already described by these authors.

C. (?) metzleri and *C. minutus* are mainly distinguished by features of the hindlimbs (Mayr 2004). However, as in the holotype of *C. (?) metzleri* the carpometacarpus of the new Belgian loon is slightly longer than that of *C. minutus* [35.5 mm vs. 29.9–34.1 in *C. minutus* (measurements from Cheneval 1984)] and, also as in the holotype of *C. (?) metzleri*, the ulna appears to have been somewhat shorter (~46–47 vs. 48.7–56.0 in *C. minutus* [Cheneval 1984]).

- Strigiformes Wagler 1830.
- Selenornithidae Mourer-Chauviré 1987.
- *Selenornis* Mourer-Chauviré 1987.
- *Selenornis steendorpensis* n. sp.

Holotype

IRSNB Av 84a + b; distal end of right tibiotarsus and right tarsometatarsus of the same individual (Fig. 2).

Differential diagnosis

Larger than any other Paleogene owl known from Europe except the species of the taxa *Berruornis*, *Sophiornis*, and *Palaeobyas* (Table 1). Tibiotarsus with narrow condyles and symmetric distal end. Distinguished in the following features from the species of:

- *Berruornis* and *Sophiornis*: much deeper fossa infracotylaris dorsalis and sulcus flexorius of tarsometatarsus.
- *Palaeobyas*: tarsometatarsus more slender, trochlea metatarsi II more strongly plantarly deflected.
- *Necrobyas*: distal end of tibiotarsus not slanting medially; tarsometatarsus with trochlea metatarsi II less plantarly deflected, not exceeding trochlea metatarsi III in length, and with dorsomedial edge more protruding; trochlea metatarsi IV with more medially inflected plantarly directing flange (Fig. 3).
- *Palaeoglaux*: canalis interosseus distalis of tarsometatarsus dorsally open.

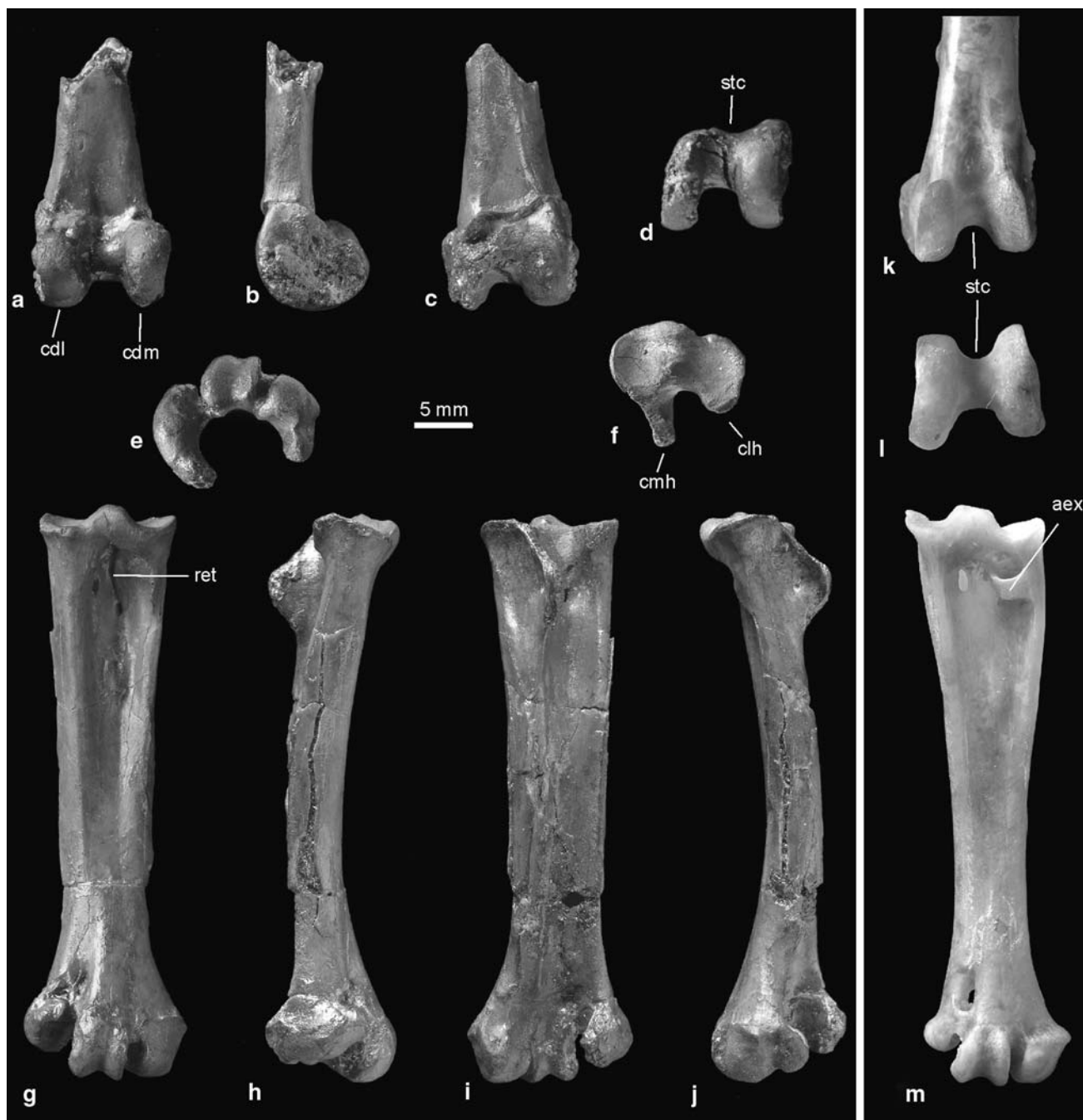


Fig. 2 Distal end of **a–d** right tibiotarsus and **e–j** right tarsometatarsus of *Selenornis steendorpensis* n. sp. from the Rupelian of Steendorp (IRSNB Av 84 a+b) in comparison to **k, l** the distal tibiotarsus and **m** the tarsometatarsus of the extant Ural Owl, *Strix uralensis*. Tibiotarsus in **a** cranial, **b** lateral, **c, k** caudal, and **d, l** distal view; tarsometatarsus in **e** distal, **f** proximal, **g, m** dorsal, **h** lateral,

i plantar, and **j** medial view. Abbreviations: *aex* arcus extensorius, *cdl* condylus lateralis, *cdm* condylus medialis, *clh* crista lateralis hypotarsi, *cmh* crista medialis hypotarsi, *ret* attachment scar for the retinaculum extensorium tarsometatarsi, *stc* sulcus of trochlea cartilaginosa tibialis. All figures to scale

- *Prosybris*: tarsometatarsus less elongated and stouter.
- *Oligostrix* and other Protostrigidae: condylus medialis of tibiotarsus not greatly widened.
- all Strigidae (except three species, Ford 1967, p. 67): tarsometatarsus without ossified arcus extensorius.

Comparisons with *Palaeotyto* and *Nocturnavis* are not possible owing to the fact that tibiotarsi and tarsometatarsi of these taxa are unknown; at least the single species recognized in the former taxon is, however, larger than the new owl from Belgium.

Table 1 Measurements of *Selenornis steendorpensis* n. sp. in comparison to other Paleogene Strigiformes

	Tarsometatarsus, length	Tarsometatarsus, width of distal end	Tarsometatarsus, width of proximal end	Tibiotarsus, distal width
<i>Selenornis steendorpensis</i> n. sp.	48.8	14.2	11.9	11.0
<i>S. henrici</i> ^a	–	–	–	8.2
<i>Palaeoglaux perrierensis</i> ^a	–	11.5	–	–
<i>P. artophoron</i> ^b	30.5	–	–	–
<i>Necrobys arvernensis</i> ^a	43.5	11.6	9.7–9.8	9.9
<i>N. edwardsi</i> ^a	39.4–42.5	10.4–11.9	8.8–10.3	8.8–10.0
<i>N. harpax</i> ^a	35.3–38.0	9.6–10.8	8.8–10.2	8.5–8.9
<i>N. rossignoli</i> ^a	32.3–34.6	8.7–9.5	8.0–8.7	7.9
<i>N. medius</i> ^a	–	7.8	–	–
<i>Prosybris antiqua</i> ^c	34	6.6	–	–
<i>Palaeobys cracrafti</i> ^a	~53.6	~17.9	~16.5	–
<i>Sophiornis quercyni</i> ^a	74.0 ^f	23.7	19.9	–
<i>Berruornis orbisantiqum</i> ^d	68.5–69.8 ^f	24.1	19.9	~14.2
<i>B. halbedelti</i> ^e	~57	~16–17	~15	–

^a After Mourer-Chauviré (1987: Tables 3 and 5)

^b After Peters (1992)

^c After Mlíkovský (1998)

^d After Mourer-Chauviré (1994)

^e After Mayr (2002)

^f Proximal end to tip of trochlea metatarsi II

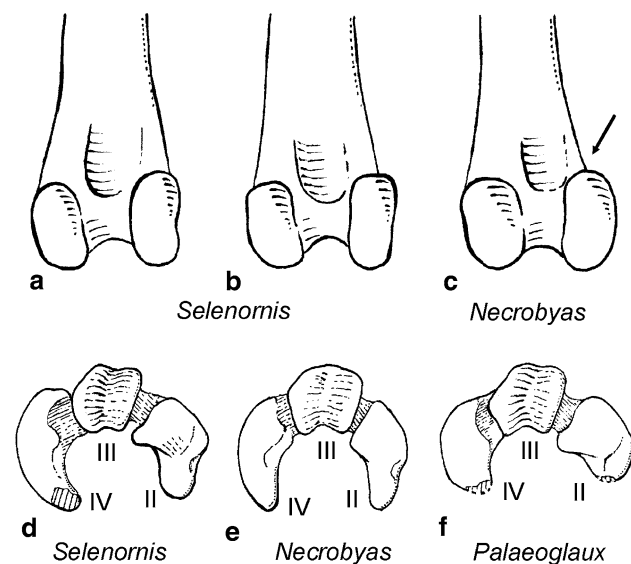


Fig. 3 Distal tibiotarsi (a–c; cranial view) and tarsometatarsi (d–f; distal view) in comparison. **a, d** *Selenornis steendorpensis* n. sp.; **b** *S. henrici* (Milne-Edwards 1892) (after Mourer-Chauviré 1987: pl. 3, fig. 5; reversed to facilitate comparisons); **c** *Necrobys harpax* Milne-Edwards 1892 (after Mourer-Chauviré 1987: pl. 1, fig. 13; reversed to facilitate comparisons); **e** *N. harpax* (after Mourer-Chauviré 1987: pl. 1, fig. 4; reversed to facilitate comparisons); **f** *Palaeoglaux perrierensis* Mourer-Chauviré 1987 (after Mourer-Chauviré 1994: fig. 17). The arrow in **c** indicates the medial slant of the distal tibiotarsus of *Necrobys*; the trochleae in **d–f** are numbered. All figures are slightly schematic and not to scale (see Table 1 for measurements)

Type locality and horizon

Steendorp, Belgium; early Oligocene, Rupelian, Boom Formation (MP ?23–24; Cheneval 1996).

Measurements

See Table 1.

Etymology

The species name refers to the type locality.

Remarks

The Paleogene fossil record of owls has been reviewed by Mourer-Chauviré (1987, 1999), Mlíkovský (1998, 2002) and Mayr (2009). Most Eocene and Oligocene European fossils come from the Quercy fissure fillings in France and were assigned to the taxon *Necrobys*, which includes five species from late Eocene to early Miocene deposits. As detailed in the differential diagnosis, the tibiotarsus and tarsometatarsus of IRSNB Av 84a+b are clearly distinguished from the corresponding bones of *Necrobys*. The tarsometatarsus is also very different from that of *Palaeobys cracrafti* from an unknown horizon of the Quercy fissure, and from that of the Sophiornithidae (*Sophiornis*

and *Berruornis*). Both tibiotarsus and tarsometatarsus of the new species can further easily be told apart from the corresponding bones of the Protostrigidae, a highly distinctive strigiform taxon to which all owls from the Eocene of North America belong, and which is represented in Europe by *Oligostrix* from the early Oligocene of Germany (Fischer 1983).

The new species is assigned to the taxon *Selenornis*, as its distal tibiotarsus closely resembles the distinctive tibiotarsus of the smaller *Selenornis henrici* (Milne-Edwards 1892) (Fig. 3). *S. henrici* is the only species so far recognized within *Selenornis* and based on a distal tibiotarsus from an unknown horizon of the middle Eocene to late Oligocene Quercy fissure fillings (Mourer-Chauviré 1987: pl. 3, figs 5, 6).

The distal tarsometatarsus of *Selenornis steendorpensis* n. sp. resembles that of *Palaeoglaux perrierensis* Mourer-Chauviré 1987 from late Eocene deposits of the Quercy fissure fillings (Fig. 3). The proximal tarsometatarsus and the tibiotarsus of this latter species are unknown, but taking into account size differences owing to sexual dimorphism, the dimensions of the holotypic tibiotarsus of *S. henrici* would be compatible with the tarsometatarsus of *P. perrierensis* (the ratio distal width of tarsometatarsus: distal width of tibiotarsus is 1.4 for *Palaeoglaux/Selenornis* and 1.3 for *S. steendorpensis*). Because of this match in size and the morphological similarities to the new Belgian owl, there remains a possibility that *S. henrici* and *P. perrierensis* are congeners or even conspecific. As long as, however, the exact stratigraphic occurrence of *S. henrici* is unknown and without overlapping skeletal elements of both species, such a hypothesis can neither be conclusively established nor refused.

Description and comparison

Selenornis steendorpensis n. sp. had the size of a male of the extant Ural Owl, *Strix uralensis*. The distal tibiotarsus closely resembles that of *S. henrici*, and as in that species the shaft is wide above the mediolaterally narrow and widely spaced condyles, and there is no deep fossa proximal of the incisura intercondylaris (this fossa is more marked in *Necrobyas*). The condylus medialis is slightly taller than the condylus lateralis. On the cranial surface of the bone there is a small depression proximal to the condylus lateralis; such a depression has also been noted for *Selenornis* by Mourer-Chauviré (1987: 112). The shallow trochlea cartilaginosa tibialis distinguishes the bone from the tibiotarsus of all extant Strigiformes examined (Fig. 2; note that the caudal portion of this trochlea is damaged in the fossil).

The tarsometatarsus has similar overall proportions to that of the *Necrobyas* species, although the distal end

differs in several details (see differential diagnosis and below). As in most other strigiform birds, the shaft of the bone is markedly curved in lateral view. The proximal margin of the crista medialis of the hypotarsus is damaged; the crista lateralis is low and broadly rounded. The fossa infracotylaris dorsalis is very deep; within this fossa a marked attachment scar for the retinaculum extensorium tarsometatarsi runs parallel to the longitudinal axis of the bone. In contrast to most extant Strigidae, there is no ossified arcus extensorius; absence of this bony bridge is a plesiomorphic feature found in all Paleogene Strigiformes. The lateral foramen vasculare proximale is larger than the medial one and situated farther proximally; on the plantar surface of the bone there is a small depression proximal of it. The tuberositas musculi tibialis cranialis is bipartite, with a smaller proximal portion. On the distal end of the bone, the fossa metatarsi I is marked. The canalis interosseus distalis is dorsally open as in some large extant owls (e.g., the Eurasian Eagle-owl, *Bubo bubo*); the foramen vasculare distale is of average size. As in *Palaeoglaux perrierensis*, the trochlea metatarsi II reaches as far distally as the trochlea metatarsi III, whereas it slightly exceeds this trochlea in the species of *Necrobyas* (Mourer-Chauviré 1987: 115). Unlike many extant owls but as in most other Paleogene taxa, the lateral rim of the trochlea metatarsi III is not strongly plantarly protruding. The plantarly directed wing-like projection of the trochlea metatarsi IV is more medially inflected than in *Necrobyas harpax*.

Discussion

Although our knowledge of early Oligocene avifaunas of Europe has significantly increased in the past decades, the majority of the fossils stems from a few localities. The most important and best studied of these outside Belgium are the Quercy fissure fillings and Céreste in southern France, and Wiesloch-Frauenweiler in southern Germany (Mayr 2009).

During marine transgressions, the southern North Sea basin was intermittently connected with a seaway along the Rhine Graben in the early Oligocene (e.g., Berger et al. 2005; van Simaey and Vandenberghe 2006). Concerning the association of small *Colymboides* loons with diomedid Procellariiformes, the marine avifauna of the Boom Formation thus closely resembles that of the Rupelian deposits of Wiesloch-Frauenweiler, the type locality of *Colymboides* (?) *metzleri* (Mayr et al. 2002; Mayr 2004; Micklich and Hildebrandt 2005).

Whereas the Rhine Graben locality Wiesloch-Frauenweiler yielded remains of several small land birds (Mayr 2009), little is known about the non-aquatic avifaunas of the Boom Formation. A taxonomically diverse

avifauna was, however, reported from the slightly older, early Rupelian (MP 21, i.e., about 33 million years ago), fluvio-lacustrine deposits of Boutersem and Hoogbutsel in Belgium (Mayr and Smith 2001, 2002). The birds from these localities include representatives of the Anseriformes (waterfowl), Gaviiformes, Phoenicopteriformes (flamingos), Charadriiformes (shorebirds and allies), Rallidae (rails), Accipitridae (hawks), Strigiformes, Coliiformes (mousebirds), Piciformes (woodpeckers and allies), the extinct taxon Sylphornithidae, as well as a tentative record of the Idiornithidae [stem group representatives of the Cariamidae (seriemas); Mayr and Smith 2001, 2002].

Most of the non-aquatic taxa from the above list also occur in the comprehensive and well-studied late Eocene/early Oligocene avifaunas of the Quercy fissure fillings (Mourer-Chauviré 1996, 2006). A notable absence in the Quercy deposits, however, concerns piciform birds, which are also unknown from the early Oligocene of Céreste, but have been reported in Wiesloch-Frauenweiler (Mayr 2009). The Idiornithidae on the other hand are abundant in the Quercy localities, but very rare, if present at all (see above), in the early Oligocene of Belgium. Also unknown from the Rupelian of Belgium and Germany are the Archaeotrogonidae, small aerial insectivores, which are very common in the early Oligocene of southwestern France.

Northern and southern Europe were distinguished by floristic and climatic features in the early Oligocene, with the more sclerophyllous floras of southern Europe indicating a slightly drier climate (e.g., Collinson and Hooker 2003). It is thus well possible that some of the avifaunal differences reflect zoogeographic realities rather than artifacts of an incomplete fossil record, although certainly more data are needed to establish such hypotheses convincingly.

Acknowledgments I thank Thierry Smith and Annelise Folie (both IRSNB) for the loan of the fossil specimens, Sven Tränkner (Forschungsinstitut Senckenberg) for taking the photographs, and J. Noriega (CONICET, Argentina) and U. Göhlich (Naturhistorisches Museum Wien) for reviewing the manuscript.

References

- Baumel, J.J., and L.M. Witmer. 1993. Osteologia. In *Handbook of avian anatomy: Nomina Anatomica Avium*, eds. J.J. Baumel, A.S. King, J.E. Breazile, H.E. Evans., and J.C. Vanden Berge, *Publications of the Nuttall Ornithological Club* 23: 45–132.
- Berger, J.-P., B. Reichenbacher, D. Becker, M. Grimm, K. Grimm, L. Picot, A. Storni, C. Pirkenseer, C. Derer, and A. Schaefer. 2005. Paleogeography of the Upper Rhine Graben (URG) and the Swiss Molasse Basin (SMB) from Eocene to Pliocene. *International Journal of Earth Sciences* 94: 697–710. doi:10.1007/s00531-005-0475-2.
- Brodkorb, P. 1962. The systematic position of two Oligocene birds from Belgium. *Auk* 79: 706–707.
- Cheneval, J. 1984. Les oiseaux aquatiques (Gaviiformes à Ansériiformes) du gisement aquitain de Saint-Gérard-le-Puy (Allier, France): Révision systématique. *Palaeovertebrata* 14: 33–115.
- Cheneval, J. 1996. Tertiary avian localities of Belgium. In *Tertiary avian localities of Europe*, ed. J. Mlíkovský, *Acta Universitatis Carolinae, Geologica* 39: 535–540.
- Collinson, M.E., and J.J. Hooker. 2003. Paleogene vegetation of Eurasia: Framework for mammalian faunas. *Deinsea* 10: 41–84.
- Fischer, K. 1983. *Oligostrix rupelensis* 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.
- Ford, N.L. 1967. *A systematic study of the owls based on comparative osteology*. Unpublished PhD, Ann Arbor: University of Michigan.
- 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.
- Lydekker, R. 1891. *Catalogue of the Fossil Birds in the British Museum (Natural History)*. London: British Museum (Natural History).
- Mayr, G. 2002. An owl from the Paleocene of Walbeck, Germany. *Mitteilungen aus dem Museum für Naturkunde in Berlin. Geowissenschaftliche Reihe* 5: 283–288.
- Mayr, G. 2004. A partial skeleton of a new fossil loon (Aves, Gaviiformes) from the early Oligocene of Germany with preserved stomach content. *Journal of Ornithology* 145: 281–286. doi:10.1007/s10336-004-0050-9.
- Mayr, G. 2009. *Paleogene fossil birds*. Heidelberg: Springer.
- Mayr, G., D.S. Peters, and S. Rietschel. 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. doi:10.1671/0272-4634(2002)022[0667:PLBWP]2.0.CO;2.
- Mayr, G., and M. Poschmann. A loon leg (Aves, Gaviidae) with crocodylian tooth from the late Oligocene of Germany. *Waterbirds* (in press).
- Mayr, G., and R. Smith. 2001. Ducks, rails, and limicoline waders (Aves: Anseriformes, Gruiformes, Charadriiformes) from the lowermost Oligocene of Belgium. *Geobios* 34: 547–561. doi:10.1016/S0016-6995(01)80069-3.
- Mayr, G., and R. Smith. 2002. Avian remains from the lowermost Oligocene of Hoogbutsel (Belgium). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* 72: 139–150.
- Micklich, N., and L. Hildebrandt. 2005. The Frauenweiler clay pit (“Grube Unterfeld”). *Kaupia, Darmstaedter Beitrage zur Naturkunde* 14: 113–118.
- Milne-Edwards, A. 1867–1871. *Recherches anatomiques et paléontologiques pour servir à l'histoire des oiseaux fossiles de la France*. Paris: Victor Masson et fils.
- Milne-Edwards, A. 1892. Sur les oiseaux fossiles des dépôts éocènes de phosphate de chaux du Sud de la France. *Comptes Rendus du Second Congrès Ornithologique International*: 60–80.
- Mlíkovský, J. 1998. A new barn owl (Aves: Strigidae) from the early Miocene of Germany, with comments on the fossil history of the Tytoninae. *Journal für Ornithologie* 139: 247–261. doi:10.1007/BF01653335.
- Mlíkovský, J. 2002. *Cenozoic birds of the world. Part 1: Europe*. Praha: Ninox Press.
- Mourer-Chauviré, C. 1987. Les Strigiformes (Aves) des phosphorites du Quercy (France): Systematique, biostratigraphie et paleobiogeographie. *Documents des Laboratoires de Géologie de Lyon* 99: 89–135.
- Mourer-Chauviré, C. 1994. A large owl from the Palaeocene of France. *Palaeontology* 37: 339–348.

- 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. Comments on tertiary barn owls of Europe. *Journal of Ornithology* 140: 363–364. doi:[10.1007/BF01651033](https://doi.org/10.1007/BF01651033).
- Mourer-Chauviré, C. 2006. The avifauna of the Eocene and Oligocene Phosphorites du Quercy (France): An updated list. *Strata, séries 1*, 13: 135–149.
- Olson, S.L. 1985. The fossil record of birds. In *Avian biology* 8, ed. D.S. Farner, J.R. King, and K.C. Parkes, 79–238. New York: Academic Press.
- 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.
- Storer, R.W. 1956. The fossil loon, *Colymboides minutus*. *Condor* 58: 413–426. doi:[10.2307/1365096](https://doi.org/10.2307/1365096).
- van Beneden, P.J. 1871. Les oiseaux de l'argile rupélienne. *Bulletins de l'Académie Royale des sciences, des lettres et des beaux-arts de Belgique, série 2*, 32: 256–261.
- van Simaëys, S., and N. Vandenberghe. 2006. Rupelian. *Geologica Belgica* 9: 95–101.