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The tarsometatarsus of the Middle Eocene loon *Colymbiculus udovichenkoi*

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Abstract — We describe the previously unknown tarsometatarsus of the earliest unambiguously identified loon, *Colymbiculus udovichenkoi*, from the Middle Eocene of the Ukraine. Except for being more elongate and apart from details of the hypotarsus morphology, the bone resembles the tarsometatarsus of the Early Miocene *Colymboides minutus*. We consider the hypotarsus morphology of *Colymbiculus* to be plesiomorphic for Gaviiformes. *Colymboides* and crown group Gaviiformes are each characterized by an autapomorphic hypotarsus morphology, which precludes the former from being directly ancestral to the latter. The similarities shared by *C. udovichenkoi* and *C. minutus*, including their small size, are likely to be plesiomorphic for Gaviiformes. Although the disappearance of small stem group Gaviiformes may be related to the retreat of loons to cold Northern latitudes, more data are needed to firmly establish this hypothesis. We finally note that early Paleogene stem group Gaviiformes markedly differ from putative Late Cretaceous loons, whose identification needs to be verified by further fossil specimens.

Key words: *Colymbiculus*, *Colymboides*, fossil birds, Gaviiformes, Eocene, Lutetian, Ukraine

Introduction

Loons (Gaviiformes) have a fairly comprehensive Neogene fossil record (OLSON 1985; MAYR 2009a), but the early evolutionary history of these foot-propelled diving birds is still incompletely known. The first fossil loon recognized as such, and also one of the best-represented species, is *Colymboides minutus* MILNE-EDWARDS, 1867 from the Early Miocene of France and the Czech Republic (MILNE-EDWARDS 1867–71, STORER 1956; CHENEVAL 1984; MLÍKOVSKÝ 2002). Other species from the Neogene of Europe were assigned to *Gavia*, the taxon that includes the four extant species, with *Gavia egeriana* ŠVEC,

1982 from the Early Miocene of the Czech Republic (ŠVEC 1982), the earliest stem lineage representative, being distinctly smaller than its modern congeners. Disregarding the poorly known *Gaviella pusilla* (SHUFELDT, 1915), whose exact age is uncertain but possibly Oligocene (WETMORE 1940), loons first appear in North America in the Early Miocene (RASMUSSEN 1998). All Neogene North American species were classified in the taxon *Gavia* (OLSON 1985; OLSON & RASMUSSEN 2001).

Pre-Miocene Gaviiformes are morphologically clearly distinguished from their extant relatives. Most of the fossils were, at least tentatively, assigned to *Colymboides*, and the two

named Paleogene species of this taxon are *Colymboides anglicus* LYDEKKER, 1891 from the Late Eocene of England (HARRISON 1976; HARRISON & WALKER 1976) and ?*Colymboides metzleri* MAYR, 2004 from the Early Oligocene of Germany and Belgium (MAYR 2004, 2009b). Contemporaneous with the latter species there was also a large gaviiform species of undetermined affinities in the Early Oligocene of Belgium (MAYR & SMITH 2002). A *Colymboides*-like loon of uncertain species identity was further reported from the Late Oligocene of Germany (MAYR & POSCHMANN 2009), and undescribed remains of *Colymboides* were also found in the Late Oligocene of Kazakhstan (KUROCHKIN 1976).

Putative Upper Cretaceous records of Gaviiformes were described from Chile (*Neogaeorinis wetzeli* OLSON, 1992) and Antarctica (*Polarornis gregorii* CHATTERJEE, 2002), but these are based on a single bone and a very fragmentary partial skeleton, respectively, and their identification needs to be corroborated with more material (see also below). The earliest well-documented stem group representative of Gaviiformes is *Colymbiculus udovichenkoi* MAYR & ZVONOK, 2011, which occurs in Middle Eocene (about 48 million years ago) marine sediments of the eastern Tethys Sea in Ukraine (MAYR & ZVONOK 2011, 2012). *Colymbiculus udovichenkoi* is quite abundant at the type locality, but up to now the material assigned to this small species consisted only of four skeletal elements, *i.e.*, the humerus, ulna, radius, and tibiotarsus. In light of the fact that loons are highly specialized foot-propelled diving birds, one of the most significant bones of *C. udovichenkoi* – the tarsometatarsus – remained thus unknown. This bone was found in the 2012 excavation campaign at the type locality and is described in the present study.

Material and methods

Osteological terminology follows BAUMEL & WITMER (1993). Measurements are in millimeters. The fossils are deposited in Naturhistorisches Museum Basel, Switzerland (NMB) and Forschungsinstitut Senckenberg, Frankfurt am Main (SMF).

Systematic Paleontology

Gaviiformes WETMORE & MILLER, 1926 Gaviidae ALLEN, 1897

Colymbiculus udovichenkoi MAYR & ZVONOK, 2011

Referred specimen: SMF Av 592 (complete left tarsometatarsus).

Locality and horizon: Ikovo sand quarry, about 1 km west Novoposkov, Luhansk Province, Ukraine (49°31'42"N, 39°3'59.5"E); Middle Eocene (Lower Lutetian).

Measurements: Length, 39.4; proximal width, 7.0; distal width, 6.0; minimum mediolateral width of shaft, 2.9.

Description and comparisons: The tarsometatarsus of *Colymbiculus udovichenkoi* resembles that of *Colymboides minutus*, but is proportionally longer relative to the humerus (the tarsometatarsus of other *Colymboides* species is unknown or too poorly preserved for detailed comparisons): Whereas the lengths of humerus and ulna of *Colymbiculus* correspond with the lower size range of *C. minutus* (~63.3 and 49.1 versus 62.0–66.0 and 49.8–56.0, respectively; STORER 1956, MAYR & ZVONOK 2011, 2012), that of the tarsometatarsus is distinctly larger (39.4 mm versus 30.8–32.8 mm; STORER 1956). Further unlike *C. minutus*, the hypotarsus of *C. udovichenkoi* does not exhibit a canal for the tendon of musculus flexor digitorum longus (Fig. 1E, I). Instead, there are three well-developed sulci for, from medial to lateral, musculus flexor digitorum longus, m. flexor perforatus digiti II, and m. flexor hallucis longus. The lateral surface of the crista medialis hypotarsi bears a shallow furrow for the tendon of musculus flexor perforans et perforatus digiti II. The small foramina vascularia proximalia are closely adjacent. The distal end of the bone corresponds well with *Colymboides minutus*, and as in the latter and modern loons the trochlea metatarsi II is short and planarly deflected. The foramen vasculare distale is situated farther distally than in extant loons. The canalis interosseus distalis is dorsally open. A fossa metatarsi I is absent.

The tarsometatarsus of *Colymbiculus* is less mediolaterally compressed than that of extant

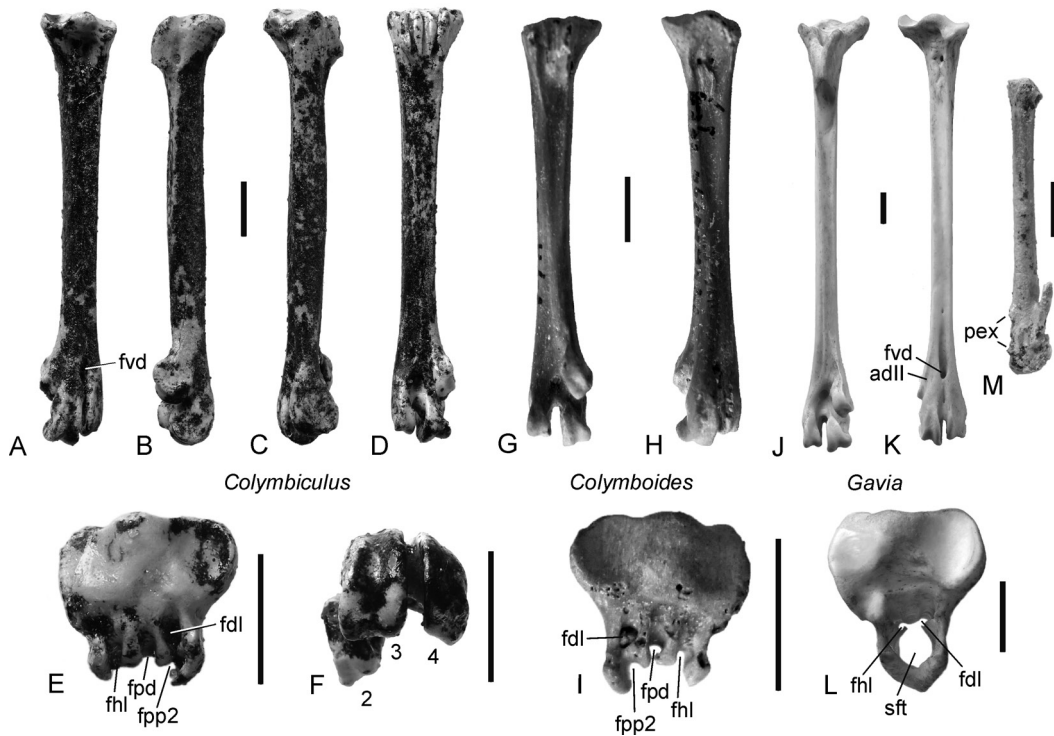


FIGURE 1. Tarsometatarsus of **A–F**, *Colymbiculus udovichenkoi* from the Middle Eocene of Ukraine in comparison with **G–I**, the Early Miocene *Colymboides minutus* and **J–L**, the extant *Gavia stellata*. **A–F**, left tarsometatarsus (SMF Av 592) in dorsal (**A**), medial (**B**), lateral (**C**), plantar (**D**), proximal (**E**), and distal (**F**) view. **G, H**, left tarsometatarsus (NMB MA. 2668) in plantar (**G**) and dorsal (**H**) view. **I**, right tarsometatarsus (NMB S.G. 20829) in proximal view. **J–L**, left tarsometatarsus in plantar (**J**), dorsal (**K**), and proximal (**L**) view. **M**, left carpalometacarpus (SMF Av 593, ventral view) of an unidentified small bird from the Middle Eocene of the Ikovo sand quarry. Abbreviations: adII, sulcus for tendon of musculus abductor digiti II; fdl, canal for tendon of musculus flexor digitorum longus; fhl, canal for tendon of musculus flexor hallucis longus; fpd, canal for tendon of musculus flexor perforatus digiti II; fpp2, canal for tendon of musculus flexor perforans et perforatus digiti II; fvd, foramen vasculare distale; pex, base of broken processus extensorius; sft, canal for superficial flexor tendons. In (**F**) the trochleae are numbered. Scale bars equal 5 mm.

Gaviidae. There is further no marked sulcus for the tendon of musculus abductor digiti II. Proximal of the foramen vasculare distale, on the dorsal surface of the bone, the sulcus extensorius is less marked than in extant loons. In the hypotarsus of modern Gaviidae the cristae mediales et lateralis hypotarsi are much better developed and fuse plantarly, thus enclosing a large canal for the superficial flexor tendons (Fig. 1L; WILCOX 1952). There is a marked sulcus for these tendons on the plantar surface of the tarsometatarsus, which is absent in *Colymbiculus*.

Discussion

Like *C. minutus* (STORER 1956), *C. udovichenkoi*

was less specialized for foot-propelled diving than extant Gaviiformes, in which the tarsometatarsus is much more mediolaterally compressed and in which the tibiotarsus exhibits much better developed cnemial crests (MAYR & ZVONOK 2012). *Colymbiculus udovichenkoi* further distinctly differs from *Colymboides minutus* and extant loons in the much more pronounced crista deltopectoralis of the humerus (MAYR & ZVONOK 2012), and reduction of the deltopectoral crest is here considered a synapomorphy of *Colymboides* and *Gavia*. With *Colymbiculus* thus being the sister taxon of the clade (*Colymboides*+*Gavia*), the similar tarsometatarsus morphology shared by *Colymbiculus* and *Colymboides* is likely to be plesiomorphic for Gaviiformes.

We also regard the hypotarsus morphology

of *Colymbiculus*, with three plantar open sulci, to be plesiomorphic for the clade including *Colymbiculus*, *Colymboides*, and *Gavia*. Absence of hypotarsal canals is certainly primitive for Neornithes, the clade including all modern birds, as such canals are absent in non-neornithine Mesozoic taxa close to the crown group as well as in palaeognathous birds. Aequornithes, the “waterbird clade” to which Gaviiformes belong (ERICSON *et al.* 2006; HACKETT *et al.* 2008; MAYR 2011), includes taxa with and without hypotarsal canals, but in those where canals are present (*i.e.*, Pelecanidae, Scopidae, Balaenicipitidae, Fregatidae, Sulidae, Phalacrocoracidae, Anhingidae) hypotarsus morphology is different from that of loons. Moreover, in the phylogeny of HACKETT *et al.* (2008) these latter taxa form a clade within Aequornithes, whereas the basally branching Spheniscidae, Procellariiformes, and Ciconiidae lack hypotarsal canals. We thus conclude that the hypotarsus morphologies of *Colymboides* (closed canal for tendon of musculus flexor digitorum longus; Fig. 1I) and *Gavia* (cristae medialis et lateralis forming large canal; Fig. 1L) constitute two independently acquired derived states, and that *Colymboides* is not directly ancestral to crown group Gaviiformes.

Stem group Gaviiformes were much smaller than their extant relatives for more than 30 million years, from the Middle Eocene (48 mya [*Colymbiculus udovichenkoi*]; MAYR & ZVONOK 2012) to the Early Miocene (17 mya [*Colymboides minutus*]; MLÍKOVSKÝ 2002). Although species with a size approaching that of extant loons did occur in the Late Eocene and Early Oligocene of Europe (HARRISON & WALKER 1976; MAYR & SMITH 2002), the disappearance of small gaviiform species is notable. In the Paleogene and early Neogene loons still inhabited warm tropical and subtropical environments, which is vividly illustrated by the recent discovery of a loon leg in association with a crocodile tooth (MAYR & POSCHMANN 2009); the remains of *Colymbiculus* were also found in the same horizon as crocodylians (ZVONOK & SKUTSCHAS 2011). It may thus be near at hand to assume that extinction of small stem group Gaviiformes was related to the retreat of loons to cold environments, where larger-bodied animals have a selective advantage (reduced heat loss) owing to a lower body

surface area to volume ratio (Bergmann’s rule; *e.g.*, MEIRI & DAYAN 2003). Still, however, there are many avian species with a small body size, which occur in aquatic habitats of far Northern or Southern latitudes today (*e.g.*, Pelecanoididae, Phalaropidae, and some Alcidae), and more data on the exact correlation between the size, distribution, and extinction dates of stem group Gaviiformes are needed to firmly establish, or refute, this hypothesis.

The two Late Cretaceous putative loons, *Neogaeornis wetzeli* LAMBRECHT, 1929 and *Polarornis gregorii* CHATTERJEE, 2002, are larger than *Colymbiculus udovichenkoi* and *Colymboides minutus*. We note, however, that the tarsometatarsus of *N. wetzeli* is very different from that of *Colymbiculus* (the tarsometatarsus of *P. gregorii* is unknown). Instead of four cristae as in *C. udovichenkoi*, the hypotarsus of *N. wetzeli* only exhibits two widely separated ones with a very indistinct sulcus in between (OLSON 1992). The shaft is much more mediolaterally compressed in *N. wetzeli* and, most unusually and unlike *Colymbiculus*, *Colymboides*, and extant Gaviidae, the trochlea metatarsi IV reaches farther distally than the trochlea metatarsi III (OLSON 1992 considered this to possibly be an artifact of preparation, but this is not evident from the published figures). With regard to the latter feature, the tarsometatarsus of *Neogaeornis* is in fact more similar to the tarsometatarsus of grebes (Podicipedidae) than that of Cenozoic and extant loons. We acknowledge the possibility that there was a derived lineage of gaviiform birds in the Late Cretaceous of the Southern Hemisphere, where Gaviiformes do not occur today. However, we also note that evidence for gaviiform affinities of both, *Neogaeornis* and *Polarornis*, is not yet compelling, and their identification should be regarded tentative until more material becomes available (see also VAN TUINEN & HEDGES 2004).

We finally note that the new material from the Ikovo sand quarry also includes an incomplete carpometacarpus (Fig. 1M). Although the bone resembles the carpometacarpus of *Colymboides minutus* in overall proportions, the (broken) processus extensorius was not proximodistally elongated as in *Colymboides* and extant loons. Moreover, the specimen is significantly short than the tarsometatarsus, whereas carpometacarpus and

tarsometatarsus are of equal length in *C. minutus* (STORER 1956). Another, morphologically distinct, carpometacarpus from the Ikovo sand quarry was reported by MAYR & ZVONOK (2012), who discussed the possibility that it is from *Colymbiculus udovichenkoi*. This latter specimen likewise significantly differs from the carpometacarpus of *Colymboides* and extant Gaviiformes, and despite the relative abundance of other postcranial bones of *C. udovichenkoi* at the type locality, an unambiguous identification of its carpometacarpus has to await further specimens.

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