A Loon Leg (Aves, Gaviidae) with Crocodilian Tooth from the Late Oligocene of Germany

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Abstract.—The first late Oligocene fossil record of a loon (Gaviiformes) is described from the lacustrine deposits of the German locality Enspel. The specimen is an isolated foot, which is associated with a crocodilian tooth. The fossil belongs to a species about half the size of the smallest extant loon, and is morphologically most similar to the Paleogene taxon *Colymboides*. In all probability it constitutes the prey remains of a crocodilian, which is of particular significance because the distribution ranges of loons and crocodilians hardly overlap today. The Enspel palaeoclimate was warm-temperate and subtropical, and the Enspel specimen and other Paleogene fossils of gaviiform birds raise the, as yet, unanswered question of why loons largely disappeared from inland habitats of the warmer regions.
Received 22 July 2008, accepted 30 December 2008.

Key words.—*Colymboides*, crocodilian tooth, fossil waterbirds, Gaviiformes, palaeoecology.

Waterbirds 32(3): 468-471, 2009

In recent years, the Enspel fossil site (Westerwald, Germany) has yielded several birds of late Oligocene age (MP 28, i.e. 24.7 million years ago; Mertz *et al.* 2007). The fossiliferous sediments originated in a small maar lake, and the avian remains described so far belong to a cormorant-like and a galliform bird (Mayr 2001, 2007; Mayr *et al.* 2006). Here we report a new bird fossil from this locality, which can be assigned to the Gaviiformes (loons).

The four extant species of loons breed on northern freshwater lakes in the subantarctic and boreal zones, but winter along sea coasts or on large lakes in temperate areas (Carboneras 1992). Putative loons are known from late Cretaceous marine localities of Chile and Antarctica, but their identification needs to be bolstered with additional material (Olson 1992; Chatterjee 2002). Paleogene, i.e. early Cenozoic, loons were found in fossil sites of both marine and limnic origin, but the fossils are still scarce (Mayr 2009). With the exception of the North American species *Gaviella pusilla* (Shufeldt 1915), whose holotype is a proximal carpometacarpus of unknown, possibly Oligocene (Wetmore 1940), age, all remains stem from European deposits. *Colymboides anglicus* Lydekker, 1891 from late Eocene lacustrine deposits of England is represented by a coracoid (the holotype), and a referred humerus and frontal portion of the skull (Harrison and Walker 1976). The material assigned to *C. belgicus* Mayr and Smith, 2002, from an early Oligocene lacustrine fossil site in Belgium, consists of a proximal carpometacarpus and a distal ulna (Mayr and Smith 2002). Only *Colymboides metzleri* Mayr, 2004, which has been found in an early Oligocene marine locality in southern Germany, is known by a partial, albeit strongly dissociated skeleton (Mayr 2004).

Most early Neogene loons were assigned to *Colymboides minutus* Milne-Edwards, 1867, which has been reported from the early Miocene of France and the Czech Republic (Mlíkovsky 2002). From the early Miocene of the Czech Republic, a putative representative of the extant taxon *Gavia* was described as *G. egeriana* by Švec (1982).

DESCRIPTION

The specimen described in the present note (Fig. 1) is a right foot with the collection number PW 2007/5157-LS, which is deposited in the Generaldirektion Kulturelles

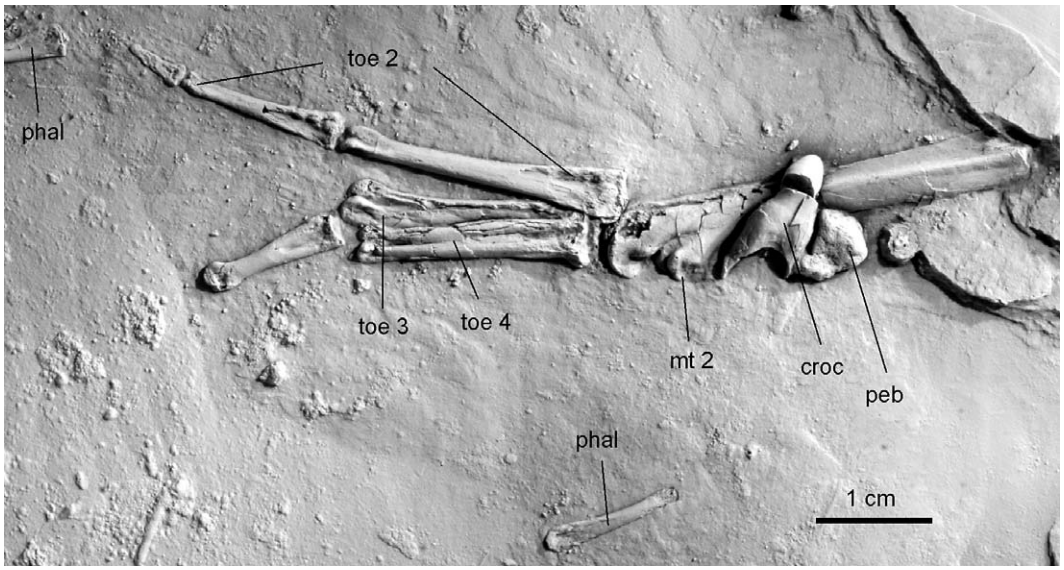

Figure 1. Right foot of a loon from the late Oligocene of Enspel in Germany (Generaldirektion Kulturelles Erbe RLP, Mainz, Germany, PW 2007/5157-LS). Abbreviations: croc – crocodilian tooth; mt 2 – tarsometatarsal trochlea for second toe; peb – pebble; phal – isolated pedal phalange. Specimen coated with magnesium oxide.

Erbe RLP, Direktion Landesarchäologie, Referat Erdgeschichte, Mainz, Germany, and will later be transferred to the Landessammlung für Naturkunde Rheinland-Pfalz, Mainz. The fossil stems from a short-legged diving bird with a mediolaterally compressed tarsometatarsus and a plantarly deflected trochlea for the second toe. In these features and in overall morphology, the tarsometatarsus corresponds to that of the Gaviiformes and Podicipediformes (grebes). In contrast to grebes, which have no Paleogene fossil record in Europe (Mayr 2005), the distal articulation surfaces of the trochleae for the second and third toes bear distinct sulci. The tarsometatarsi of some procellariiform birds are also mediolaterally compressed with a plantarly deflected trochlea for the second toe, but are less stout and proportionally more elongated.

The preserved length of the tarsometatarsus is 37.7 mm. The proximal end is broken, and the total length is estimated at 41.6 mm. The bone is thus larger than the tarsometatarsus of *C. metzleri*, which has a length of 34.5 mm (Mayr 2004), and that of *C. minutus*, which measures 30.7-33.0 mm (Cheneval 1984). Morphologically, however, it corresponds to the tarsometatarsus of these two species, whereas that of the extant taxon *Gavia* is proportionally more elongated and more mediolaterally compressed. Even the smallest extant loon, the Red-throated Diver (*Gavia stellata*) is almost twice as large as the fossil species, with the mean tarsometatarsus length, based on measurements of ten individuals, being 72.6 ± 3.3 mm. As in other Gaviiformes, there is a bulge on the medial surface of the trochlea for the third toe.

In the new specimen, pedal phalanges of a fossil loon are for the first time preserved in articulation (note, the tarsometatarsus is rotated from its life position, so that the fourth toe lies next to the tarsometatarsal trochlea for the second toe). Morphologically, they match the corresponding phalanges of extant loons. The second toe is completely preserved, and as in extant loons its proximal phalanx is the longest of all phalanges, whereas in most other birds it is the proximal phalanx of the third toe, which exceeds the others in length. The ungual phalanx of the second toe also resembles that of extant Gaviiformes and is not greatly widened as in grebes and their sister taxon, the Phoenicopteriformes (flamingos) (Manegold 2006).

DISCUSSION

The Enspel loon is the first late Oligocene fossil record of the Gaviiformes and fills a temporal gap between the known Paleogene and early Neogene specimens of this taxon. The preservation of the fossil does not allow an unambiguous taxonomic identification beyond the "family"-level, but in overall morphology it is clearly more similar to the Paleogene taxon *Colymboides* than to extant loons.

The new specimen is of particular interest, because it is preserved together with a small crocodilian tooth, probably of the alligatorid *Diplocynodon*. Both isolated crocodilian teeth and bird remains are rare in the Enspel fossil site, and it is very unlikely that placement of the tooth right above or below the loon leg is coincidental. A random association caused by bottom currents is considered unlikely as well, because in this case the fossils are expected to rather show a lateral accretion. Furthermore, insect taphonomy studies suggest that there were hardly any water movements at the bottom of Enspel Lake (Wedmann 1998). In crocodilians the roots of the teeth are reduced before they are shed (Njau and Blumenschine 2006). Because the tooth associated with the Enspel loon has a reduced root, we assume that it fell out during feeding shortly before it would have been naturally lost, which is not an unusual event (Hertner 2006). Dismemberment of the carcass into pieces that could be swallowed is often achieved by vigorous shaking of the prey item (Franzen and Frey 1993; Njau and Blumenschine 2006). In the course of this action, the loon leg may have become detached and sunk to the inhospitable lake bottom, where it was embedded in the sediment together with the tooth sticking in the tough skin which covered the tarsometatarsus, or in adherent parts of the shank musculature. This find draws attention to the possibility that other fragmented or otherwise damaged skeletons of tetrapods from Enspel may also be the result of attacks from crocodilians.

Birds contribute to the food spectrum of many crocodilian species (e.g., Pérez-Higareda *et al.* 1989; Tucker *et al.* 1996; Schweizer *et al.* 2006). The association of a crocodilian tooth with a loon leg is, however, remarkable, because the extant distribution ranges of loons and crocodilians only overlap in the southern parts of North America and China. In these areas loons are usually found on the sea, whereas crocodilians are restricted to freshwater sites. The chance that an extant loon is attacked by a crocodilian is thus minimal at best, and the fossil is a vivid example for the profound differences between late Oligocene and extant ecosystems in Central Europe. The specimen further places a caveat on ecological interpretations based on comparisons with the closest extant relatives of fossil taxa, because, taken separately, the crocodilian, an indicator of a warm climate, and the loon, whose extant relatives are denizens of the subantarctic zones, would have led to very different conclusions concerning the paleoenvironment of the fossil locality. Clearly, the Enspel palaeoclimate was warm-temperate and subtropical based on analyses of both plant (Köhler 1997; Herrmann 2007) and insect (Wedmann 2000) taphocoenoses, and future studies will have to identify the factors which led to the retreat of loons from extant inland habitats of the warmer regions.

ACKNOWLEDGMENTS

We thank M. Wuttke (GDKE RLP, Mainz) for allowing access to material in his care, and R. W. Elner and two anonymous referees for comments on the manuscript.

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