A dwarf species of the Phalacrocoracoidea (cormorants and anhingas) from the early Miocene of Germany

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A tarsometatarsus of a diminutive representative of the Phalacrocoracoidea, the clade including the Phalacrocoracidae (cormorants) and Anhingidae (anhingas), is described from the early Miocene of Germany. The fossil is assigned to a new species *Limicorallus (?) carbunculus*, and closely resembles the tarsometatarsus of extant Phalacrocoracidae in overall morphology. *Limicorallus (?) carbunculus* is the smallest representative of the Phalacrocoracoidea, reaching only two-thirds the size of the extant Pygmy Cormorant *Phalacrocorax pygmeus*. By significantly lowering the minimum size of the Phalacrocoracoidea, this new species adds to our knowledge of the early diversity of this clade.

**Keywords:** evolution, fossil birds, *Limicorallus*, Mainz-Weisenau, paleontology.

Forschungsinstitut Senckenberg holds a collection of avian bones that was assembled in the early 19th century by the renowned paleontologist Hermann von Meyer, the author of *Archaeopteryx lithographica*, but the collection has not been studied to date. Although no locality data are associated with these fossils, they most likely stem from the early Miocene of Mainz-Weisenau (Rheinland-Pfalz, Germany). Abundant avian remains from this locality were mentioned by von Meyer (1839, 1843) and included explicit mention of the ungual phalanges of diurnal birds of prey. The Senckenberg material contains a box with such phalanges, and there are no other early 19th century localities to which von Meyer had access that have yielded significant numbers of avian remains in a similar state of preservation (the specimens are uncrushed with a brownish coloration, and some still shows the remains of a limestone matrix).

The calcareous sediments of Mainz-Weisenau were deposited during a marine transgression, but have yielded bones of both marine (such as the procellariiform Diomedeoididae; Cheneval 1995) and non-marine species. Most remarkable among these fossils is a tarsometatarsus of a representative of the Phalacrocoracoidea (cormorants: Phalacrocoracidae and anhingas: Anhingidae), which is significantly smaller than the corresponding bone of any other species of this taxon, measuring only two-thirds the size of the smallest extant cormorant. The specimen is described in the present study and adds to an understanding of the early diversity of the Phalacrocoracoidea, whose known fossil representatives that fall outside the size range of the extant species are larger (e.g. Noriega 2002, Alvarenga & Guilherme 2003), rather than being dwarf forms like the species described in this study.

**METHODS**

Osteological terminology follows Baumel and Witmer (1993). The fossil specimen is deposited in Forschungsinstitut Senckenberg, Frankfurt am Main (SMF, catalog no. SMF Av 228i).

Skeletons of the following species of extant Phalacrocoracidae were examined in the collection of SMF (taxonomy after Siegel-Causey 1988, in parentheses): *Phalacrocorax* (‘Microcarbo’) *pygmeus*, *Phalacrocorax* (‘Compsohalieus’) *penicillatus*, *Phalacrocorax* (‘Stictocarbo’) *aristotelis*, *Phalacrocorax* (‘S.’) *gaimardi*, *P.* (‘S.’) *magellanicus*, *P.* (‘S.’) *punctatus*, *Phalacrocorax* (‘Notocarbo’) *atriiceps*, *P.* (‘Hypoleuco’)*s auritus*, and *Phalacrocorax carbo*. Comparisons...
with the Anhingidae are based on the *Phalacrocorax* figures in Alvarenga and Guilherme (2003) and Noriega and Alvarenga (2002).

**SYSTEMATICS**

Phalacrocoracoidea *sensu* Livezey and Zusi (2007) cf. Phalacrocoracidae Bonaparte 1854

*Limicorallus (?)* Kurochkin 1968

*Limicorallus (?)* *carbunculus* sp. nov.

**HOLOTYPE**

SMF Av 228i: right tarsometatarsus lacking most of the hypotarsus and the trochlea metatarsi II (Fig. 1 a–d).

**TYPE LOCALITY AND HORIZON**

 Probably Mainz-Weisenau (Rheinland-Pfalz, Germany); early Miocene, biostratigraphic unit MN 1; about 23 million years ago (Mlíkovský & Hesse 1996).

**DIFFERENTIAL DIAGNOSIS**

Distinguished from all other extinct or extant representatives of the Phalacrocoracoidea by its very small size; tarsometatarsus measuring only two-thirds of that of a male of the smallest extant cormorant, the Pygmy Cormorant, *P. pygmeus* (length 27.1 mm vs. 38.0 mm).

Distinguished from *Protoplotus beauforti* Lambrcht 1931 (Protoplotidae) from the Paleocene or Eocene of Sumatra (van Tets et al. 1989) in that the tarsometatarsus is more elongate and smaller (length 27.1 mm vs. 32 mm), with more prominent eminentia intercotylaris, and dorsal ridges of trochlea metatarsi III converging and not nearly parallel.

**MEASUREMENTS**

Maximum length as preserved 27.1 mm; width of trochlea metatarsi III 2.8 mm; minimum width of shaft in midsection 3.3 mm; estimated proximal width c. 6.5 mm.

**ETYMOLOGY**

Diminutive of carbo (Latin for ‘charcoal’), a component of the scientific name of many phalacrocoracid taxa.

**DESCRIPTION AND COMPARISON**

Apart from being much smaller (see diagnosis), the fossil resembles the tarsometatarsus of the extant *P. pygmeus* in its proportions (Fig. 1), but differs in some morphological details. Only the two lateral-most sulci of the hypotarsus are preserved, which, judging from the figures and descriptions in Owre (1967), presumably guided the tendons of musculus flexor hallucis longus and m. flexor perforatus digitii II (Fig. 2a). In *L. (?)* *carbunculus* sp. nov. these two sulci are very shallow and separated by a low crista, whereas in the Anhingidae and all extant Phalacrocoracidae examined except *P. punctatus* and
The fossil tarsometatarsus can be assigned to the Phalacrocoracidae because of the presence of: (1) a marked furrow for the tendon of musculus extensor hallucis longus on the medial surface of the shaft (Fig. 1a); (2) an equally marked sulcus for musculus abductor digitii IV along the lateral surface of the shaft (Fig. 1c); and (3) two far laterally situated hypotarsal sulci (Fig. 2a). In overall morphology, the specimen closely resembles the tarsometatarsus of extant Phalacrocoracidae. It is not as abbreviated as the tarsometatarsus of the Anhingidae and the foramen vasculare distale is much larger. However, as I could not identify derived features that unambiguously support an assignment of *L. (?) carbunculus* sp. nov. to the Phalacrocoracidae, there remains a possibility that the resemblances to extant cormorants are due to the retention of a plesiomorphic morphology. As detailed earlier (Mayr 2007), some late Paleogene/early Neogene taxa with a cormorant-like overall morphology may actually be stem-lineage representatives of the Phalacrocoracoidea.

The Weisenau tarsometatarsus has been tentatively assigned to the taxon *Limicolalus*, which was erected for *Limicolalus saiensis* Kurochkin 1968 from the late Oligocene [*Paraceratherium* (‘Indricotherium’)] Beds] of Kazakhstan. Originally described as a rail, this species was identified as a cormorant by Mlíkovský and Švec (1986). I agree with an assignment of *L. saiensis* to the Phalacrocoracidae, but its assignment to the Phalacrocoracidae still has to be bolstered with derived characters. *Limicolalus saiensis* is based on a distal humerus, whose width is only 8.6 mm (Kurochkin 1968). By comparisons with the ratios of the width of the distal humerus to the length of the tarsometatarsus of other fossil and extant Phalacrocoracoidea (Table 1), and assuming similar limb proportions, this indicates a tarsometatarsus length of about 33–40 mm for *L. saiensis*. This latter species is the smallest of the presently known representatives of the Phalacrocoracoidea, but is still larger than *L. (?) carbunculus*. Although a close relationship between the Weisenau fossil and *L. saiensis* cannot be firmly established owing to the lack of overlap of skeletal elements, I prefer a tentative assignment to the slightly older *Limicolalus* to the erection of a new taxon. All other fossil Phalacrocoracoidea are significantly larger than the Weisenau fossil, and the tarsometatarsus length of...
the next smallest fossil species, *Nectornis miocaenus* (Milne-Edwards 1867) from the early Miocene of France, is 38.9–41.5 mm (Cheneval 1984, see Göhlisch 2003 and Mayr 2007 for a review of early Cenozoic Phalacrocoracidae).

The discovery of a diminutive cormorant-like bird in the early Miocene of Central Europe raises the question why such small representatives of the Phalacrocoracoidea no longer exist in the extant avifauna. A sound evaluation of factors leading to the extinction of these small species depends, however, on the actual paleoenvironment inhabited by *L. (?) carbunculus*, which remains unknown.

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REFERENCES


