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Two additional synapomorphies of grebes Podicipedidae and flamingos Phoenicopteridae

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Abstract. Sister group relationship of grebes and flamingos is well supported by both molecular and morphological data. Surprisingly, most of the morphological characters now recognized as synapomorphies of grebes and flamingos have long been known in both taxa, but they were never considered to be homologous. The same is true of two additional synapomorphies discussed here, the presence of nail-like ungual phalanges and prominent caudolateral projections on the ventral side of the cervical vertebrae (processus ventrales).

Key words: Podicipedidae, Phoenicopteridae, †Palaelodidae, morphology, phylogeny

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One of the most surprising findings of recent studies of bird phylogeny was the hypothesis of a sister group relationship between grebes and flamingos. It was first supported by sequence analyses of mitochondrial and nuclear genes combined with DNA-DNA hybridisation (van Tuinen et al. 2001) and then received further support from the analysis of other nuclear genes (Chubb 2004) and detailed comparisons of diverse morphological characters (Mayr 2004). Furthermore, the †Palaelodidae, stem-lineage representatives of the extant flamingos, known as “swimming flamingos” (Feduccia 1996), show derived characters also present in extant grebes, but absent in extant flamingos. This character mosaic is best explained as being due to retention of characters evolved in the common stem-lineage of extant grebes and flamingos but transformed or completely reduced in the ancestral lineage of extant flamingos (Mayr 2005). Sangster (2005) coined a new name for the clade comprising Podicipedidae and Phoenicopteridae (Mirandornithes), and quoted the list of characters introduced

by Mayr (2004) as apomorphies for this monophyletic group. Some of the characters now recognized as synapomorphies, such as the presence of an additional primary on the carpometacarpus in grebes and flamingos (Stresemann 1963, Stresemann & Stresemann 1966, Mayr 2004), have long been known to be present in both grebes and flamingos, but were never before considered to be shared derived characters. Reported here are two additional synapomorphic characters that were not recognized as such before.

Comparisons were made with representatives of all taxa which were once thought to be the closest living relatives of grebes and flamingos, respectively (Mayr 2004). Taxa which were already known to possess similar features were reinvestigated and their supposed close relatives checked. An exhaustive study of the two characters in question is beyond the scope of this note. Study skins, mounted specimens, and defrosted deep-frozen specimens of the following taxa in the collection of Forschungsinstitut

Senckenberg, Frankfurt/Main were studied: *Anhima cornuta*, *Anseranas semipalmata*, *Dendrocygna viduata*, *Cygnus atrata*, *Aptenodytes patagonica*, *Pygoscelis papua*, *Gavia stellata*, *Phoebetria palpebrata*, *Macronectes giganteus*, *Fulmarus glacialis*, *Daption capense*, *Pagodroma nivea*, *Calonectris diomedea*, *Pachyptila vittata*, *Puffinus puffinus*, *Pelecanoides urinatrix*, *Tachybaptus ruficollis*, *Podiceps cristatus*, *Phoenicopterus ruber*, *Ciconia episcopus*, *Leptoptilos crumeniferus*, *Geronticus eremita*, *Ajaia ajaja*, *Botaurus stellaris*, *Ardea cinerea*, *Phaethon rubricauda*, *Fregata aquila*, *Scopus umbretta*, *Balaeniceps rex*, *Pelecanus onocrotalus*, *Morus bassanus*, *Phalacrocorax carbo*, *Anhinga anhinga*, *Rhynochetos jubatus*, *Eurypyga helias*, *Gallirallus australis*, *Aramides ypecaha*, *Porphyrio porphyrio*, *Fulica atra*, *Fulica gigantea*, *Heliornis fulica*, *Haematopus ostralegus*, *Himantopus himantopus*, *Recurvirostra avosetta*, *Limosa limosa*, *Numenius arquata*, *Pluvianus aegyptius*, *Larus canus*, *Sterna hirundo*, *Fratercula arctica*.

Skeletons of the following specimens in the same collection were studied: *Gavia stellata*, *Tachybaptus ruficollis*, *Podiceps cristatus*, †*Palaelodus ambiguus*, *Phoenicopterus ruber*, *Ciconia ciconia*, *Geronticus eremita*, *Ajaia ajaja*, *Botaurus stellaris*, *Ardea cinerea*, *Phaethon lepturus*, *Fregata magnificens*, *Scopus umbretta*, *Balaeniceps rex*, *Pelecanus onocrotalus*, *Morus bassanus*, *Sula sula*, *Phalacrocorax carbo*,

Rhynochetos jubatus, *Eurypyga helias*, *Haematopus ostralegus*, *Himantopus himantopus*, *Recurvirostra avosetta*, *Limosa limosa*, *Numenius arquata*, *Larus canus*, *Sterna hirundo*, *Fratercula arctica*.

Grebes are well-known for their dorso-plantar flattening of unguals and nail-like ungual sheaths (e.g. Hartert 1912–1921:1444). This character was mentioned for flamingos in early handbooks (e.g. Reichenow 1913:235). The unguals of *Phoenicopterus* are relatively smaller, but as flattened as the unguals of grebes (Fig. 1). The only other bird species with flattened unguals I am aware of are the storm-petrels (Oceanitinae, Hydrobatidae) including *Fregetta tropica*, *F. grallaria*, and *Nesofregetta fuliginosa* (Olson 1985, Mayr et al. 2002), and †*Diomedeoides brodkorbi*, a fossil procellariiform bird from the Oligocene of Germany (Mayr et al. 2002). These taxa are certainly closer related to taxa without such nail-like unguals, namely Hydrobatinae (Hydrobatidae) and presumably Procellariidae (see Mayr et al. 2002) than to grebes and flamingos.

All other investigated taxa exhibit laterally compressed and more or less curved ungual phalanges. In particular, this is the case in taxa previously thought to be close relatives of grebes (e.g. Gaviidae) or flamingos (e.g. Anseriformes, Ciconiidae, Recurvirostridae), as well as in taxa

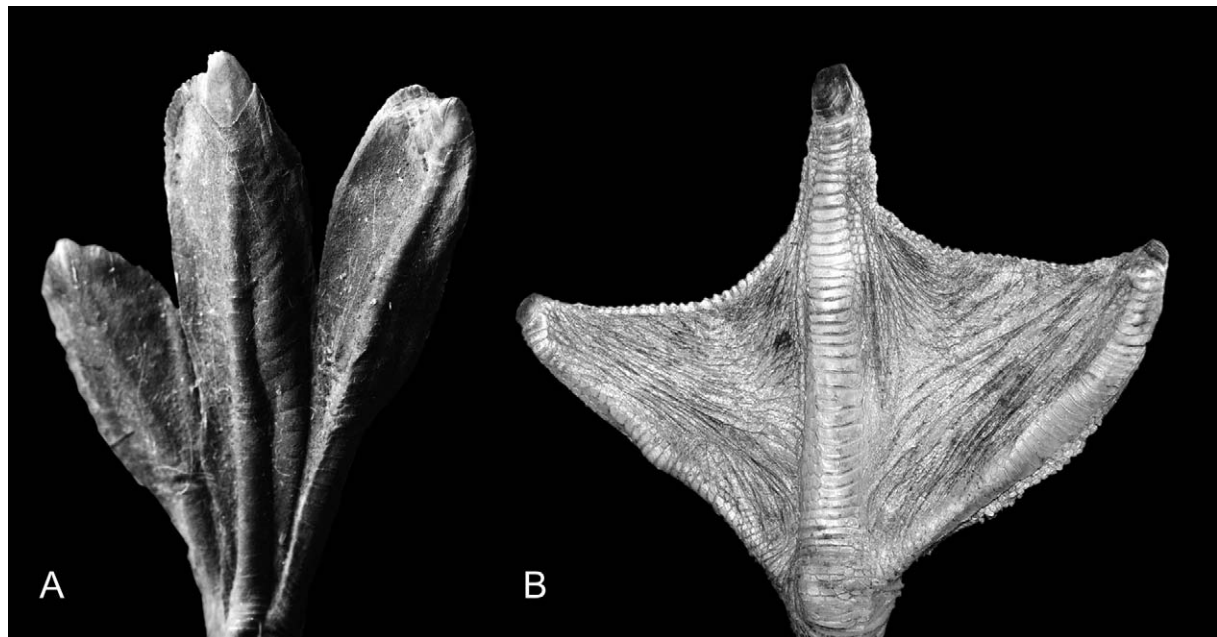


Fig. 1. Foot of (A) Little Grebe *Tachybaptus ruficollis* and (B) Greater Flamingo *Phoenicopterus ruber* in comparison showing dorso-plantar flattened unguals. Not to scale.

resembling them in having lobate (*Fulica* spp., Rallidae and *Heliornis fulica*, Heliornithidae) and semipalmate feet (e.g. *Ajaia ajaja*, Threskiornithidae).

Another synapomorphy of grebes and flamingos can be found on their cervical vertebrae. Zusi & Storer (1969) pointed out that grebes possess prominent caudolateral projections on the ventral side of their cervical vertebrae ("processus postlaterales") which serve as additional attachment sites for *Musculus longus colli ventralis*. Landolt & Zweers (1985) designated this structure as *processus ventrolateralis* which is the only name that is correct both grammatically and anatomically (A. Elżanowski, pers. comm.). Such prominent processes and attachment sites are also known for flamingos (Baumel & Witmer 1993:87, Annot. 121), and prominent *processus ventrolaterales* are present in †*Palaelodus ambiguus* (Fig. 2). Taxa traditionally considered as close relatives of either grebes or flamingos, e.g. loons (Gaviidae), finfoots (Heliornithidae), storks (Ciconiidae), lack prominent *processus ventrolaterales* (Zusi & Storer 1969 and pers. obs.). However, similar processes are present in some other taxa. Baumel & Witmer (1993) mention them for *Morus*, which I can confirm for the Northern Gannet *Morus bassanus* (pers. obs.), and I also found such processes in the Red-footed Boobie *Sula sula*, the Sunbittern *Eurypyga helias*, and the Kagu *Rhynchotus jubatus*. Again, other characters suggest a relationship of these taxa to other groups of birds lacking such processes (see Mayr & Clarke 2003).



Fig. 2. Fourth cervical vertebra of Greater Flamingo *Phoenicopterus ruber* in (A) lateral and (B) in ventral view. Arrows indicate the prominent processus. Scale bar = 5 mm.

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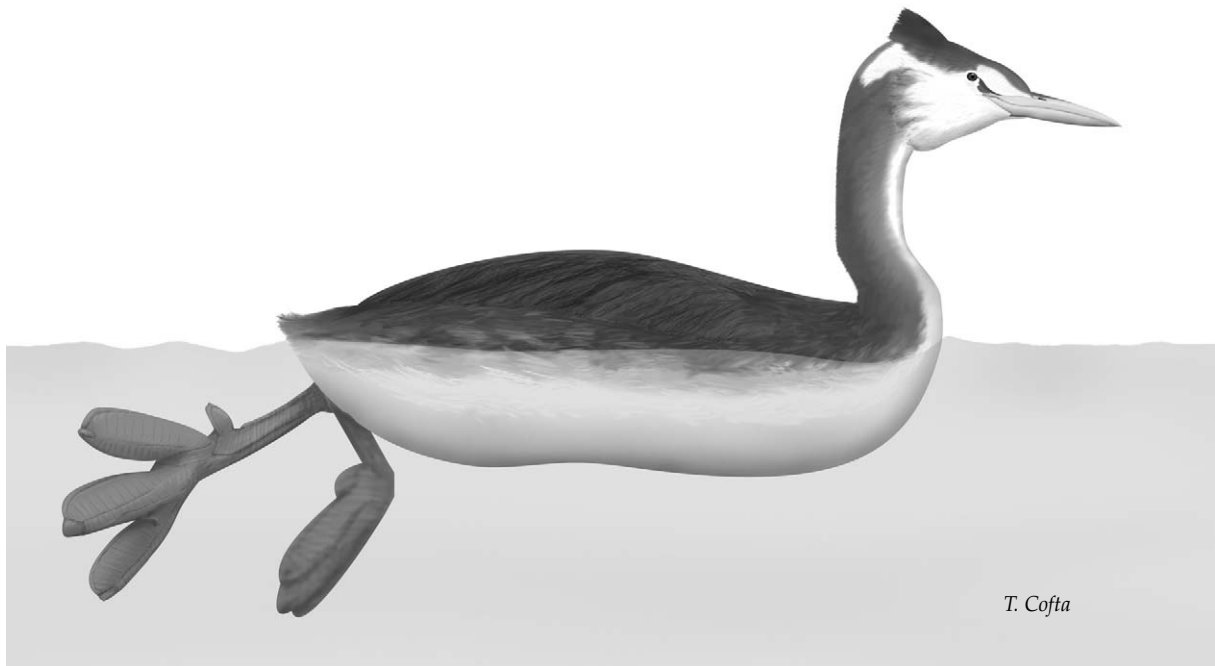
STRESZCZENIE

[Dwie dodatkowe synapomorfie perkozów i flamingów]

Bliższe pokrewieństwo perkozów i flamingów, jedno z nieoczekiwanych odkryć molekularnej

filogenetyki, potwierdzone zostało porównaniami morfologicznymi. Paradoksalnie, cechy uznane ostatnio za synapomorfie perkozów i flamingów w większości znane były od dawna w obydwu grupach, ale nigdy nie były rozpoznane jako cechy homologiczne. Dotyczy to również dwóch

dodatkowych synapomorfii rozpoznanych w tej pracy: paznokciowatych członów pazurowych (phalanges unguales) stopy oraz wydatnych tylnobocznych wyrostków (processus ventrolaterales) kręgów szyjnych.



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