

The contribution of fossils to the reconstruction of the higher-level phylogeny of birds

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Abstract

Only a phylogeny based on morphological characters allows the assignment of fossil taxa which so far played a subordinate role in the reconstruction of the phylogenetic relationships within birds. However, although fossils are not compulsory for the reconstruction of the phylogeny between extant taxa, stem lineage representatives can contribute to phylogenetic hypotheses on widely divergent groups of birds, in particular if they exhibit bauplan characteristics which were reduced or transformed in the crown group but are present in its sister taxon. In the present study, the significance of two such "missing links" is exemplified. The †Palaelodidae confirm recent analyses which resulted in sister group relationship between flamingos (Phoenicopteriformes) and the morphologically very different grebes (Podicipediformes) by combining derived skull features of flamingos with leg adaptations for hindlimb propulsion found in grebes. The †Plotopteridae display a mosaic of derived characters of penguins (Spheniscidae) and the Suloidea (boobies, gannets, cormorants, and anhingas), and gave rise to a novel hypothesis concerning the phylogenetic relationships of penguins.

Zusammenfassung

Nur ein auf morphologischen Merkmalen basierender Stammbaum erlaubt die Zuordnung fossiler Taxa, welche bisher eine untergeordnete Rolle in der Rekonstruktion der Verwandtschaftsbeziehungen innerhalb der Vögel spielten. Obgleich Fossilien nicht obligatorisch für die Rekonstruktion der Verwandtschaftsbeziehungen zwischen heutigen Taxa sind, können Stammgruppenvertreter zu phylogenetischen Hypothesen bezüglich morphologisch sehr unterschiedlicher rezenter Taxa beitragen, wenn sie Bauplanmerkmale aufweisen, die in der Kronengruppe reduziert oder transformiert wurden, aber in ihrer Schwestergruppe noch vorhanden sind. Die Bedeutung solcher "missing links" wird anhand von zwei Taxa illustriert. Die †Palaelodidae bestätigen neue Analysen, die in einem Schwestergruppenverhältnis zwischen Flamingos (Phoenicopteridae) und den morphologisch sehr unterschiedlichen Lappentaucher (Podicipedidae) resultierten, indem sie abgeleitete Schädelmerkmale von Flamingos mit Anpassungen kombinieren, welche bei Lappentauchern für einen Antrieb im Wasser mit den Beinen dienen. Die †Plotopteridae zeigen eine mosaikhafte Verteilung von abgeleiteten Merkmalen von Pinguinen (Spheniscidae) und den Suloidea (Tölpel, Kormorane und Schlangenhalsvögel), die eine neue Hypothese zu den Verwandtschaftsbeziehungen der Pinguine anregen.

Introduction

The phylogenetic relationships within Aves are still very controversial, and although there are ongoing efforts to analyze large morphological and molecular data sets (Livezey & Zusi 2001, Cracraft et al. 2004) little consensus has been reached. Even some of the more recent studies proceed from poorly established "orders" (e.g., Cracraft 2001, Cracraft et al. 2004), whose monophyly has not been well supported and which go back to classifications of the 19th century. - New impetus came from the introduction of molecular techniques into avian systematics. However, the often-cited DNA-DNA hybridization studies of Sibley & Ahlquist (1990) have repeatedly been criticized for methodological reasons (e.g., Houde

1987, Lanyon 1992, Harshman 1994), and analyses of gene sequences yield remarkably different results depending on the kind of data evaluated and the way how it is analyzed (e.g., Espinosa de los Monteros 2000, Mindell et al. 1997, Mayr et al. 2003, Cracraft et al. 2004, Fain & Houde 2004). Often these trees seem to reflect the phylogeny of the analyzed gene rather than that of the studied taxa. Results of molecular analyses are particularly convincing if independent analyses of different genes support the same clades, but this is the case for only few avian groups.

In contrast to the situation in mammalian phylogeny, fossils so far played a subordinate role in discussions on avian higher level-phylogeny. Very few fossil members of crown group Aves were found in Cretaceous deposits

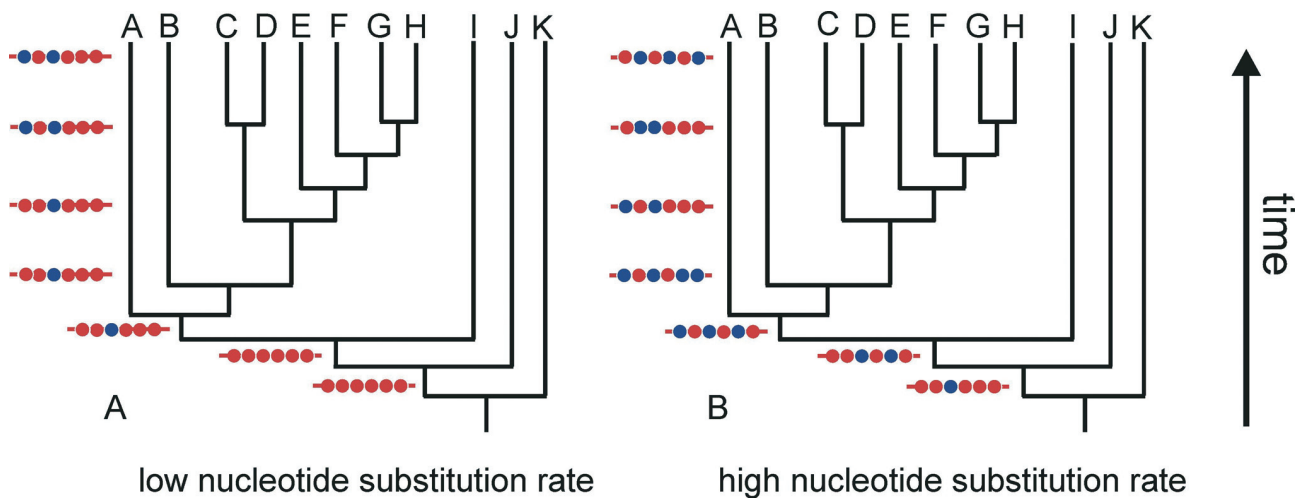


Fig. 1. Hypothetical phylogeny of eleven taxa. The blue dots indicate apomorphic nucleotide substitutions. **A.** A low nucleotide substitution rate is assumed, with little time to accumulate phylogenetically informative nucleotide substitutions on the short basal internodes. **B.** A high nucleotide substitution rate is assumed, and a phylogenetic signal is blurred by random substitutions on the long stem lineages leading to the extant taxa.

(Hope 2002), whereas stem group representatives of most extant avian "orders" are known from the early Eocene (e.g., Mayr 2005a). Taken literally, the fossil record of birds thus indicates that the basal divergences within Aves occurred in a relatively short period in the early Paleogene, in which case the higher-level phylogeny of birds would be characterized by short internodes between the basal divergences and long stem lineages leading to the extant taxa. If true, this poses some problems for phylogenetic analyses based of gene sequences, because in the case of a gene with a low nucleotide substitution rate there would have been little time to accumulate phylogenetically informative nucleotide substitutions on the short basal internodes (Fig. 1A) whereas, if a "fast evolving" gene with a high substitution rate is studied, a phylogenetic signal may be blurred by random nucleotide substitutions on the long stem lineage leading to the extant taxa (Fig. 1B).

Of course, analyses of morphological data face the same problem. However, morphological characters in general are more complex than nucleotide substitutions, and few morphological characters may thus have a greater phylogenetic significance than few nucleotide substitutions (since only few genes are included in most molecular analyses, it is unlikely that these code for any morphological characters). In addition, analysis of morphological characters allows the consideration of stem group representatives which do not yet exhibit all apomorphic bauplan characteristics of the crown group and thus help to overcome the problem of long stem lineages. In the following, two examples of such "missing links" between avian higher-level taxa are presented which bear on the phylogenetic relationships of flamingos and penguins, respectively (the terms used below for the extant taxa refers to the Pan-Monophylum).

Flamingos (Phoenicopteriformes) and grebes

(Podicipediformes)

One of the most surprising findings of recent molecular analyses is sister group relationship between flamingos (Phoenicopteriformes) and grebes (Podicipediformes) (Fig. 2). The flamingo-grebe clade was initially proposed from analyses of DNA sequence and hybridization data (van Tuinen et al. 2001), and subsequently supported by analyses of additional genes (Chubb 2004, Cracraft et al. 2004) and morphological data (Mayr 2004). It is one of the few examples where molecular studies congruently support a novel grouping, which was not suggested before by morphological data.

Flamingos and grebes are very different in their external appearance and way of living. Whereas flamingos are long-legged filter feeders, grebes are diving birds which use their short legs for propulsion (del Hoyo 1992, Llimona & del Hoyo 1992). However, sister group relationship between these two taxa is also well-supported by morphological data, and apomorphies of the clade (Phoenicopteriformes + Podicipediformes) include the presence of fused thoracic vertebrae, an unusually high number of cervical vertebrae, eleven primaries (except for



Fig. 2. **A.** Greater Flamingo (*Phoenicopterus ruber*). **B.** Great grebe (*Podiceps major*). Photos: Johannes Ferdinand.

storks, Ciconiidae, all other birds have nine or ten primaries), a calcium phosphate layer covering the eggshell, and a taxon of Cestodes which is exclusively shared by flamingos and grebes (Mayr 2004).

Because of the great morphological dissimilarity of the two taxa, detailed comparisons in order to evaluate a closer relationship were not made by earlier authors. This is so much the more surprising, as there is a fossil avian taxon which can be considered a "missing link" between flamingos and grebes. This taxon, the †Palaelodidae, is known since more than 150 years from the Paleogene and Neogene of Europe and has an abundant fossil record (e.g., Cheneval 1983). Its assignment to the Phoenicopteriformes has never been doubted and, among other features, is supported by a very deep lower jaw suggesting the existence of a "primitive filter-feeding apparatus" (Cheneval & Escuillié 1992: 209) (Fig. 3). By contrast, being proportionally shorter than that of crown group Phoenicopteridae with a mediolaterally compressed distal end and a plantarly deflected trochlea for the second toe, the foot bones of †palaelodids "show many similarities with those of a foot-propelled diving bird such as *Podiceps* [Podicipedidae]" (Cheneval & Escuillié 1992).

†Palaelodids not only bridge the morphological gap between extant grebes and flamingos, but provide information on the course of evolution not available from study

of the extant taxa. Just looking at the latter and without knowing the sister taxon of the flamingo-grebe clade, it would hardly be possible to make statements on the stem species of (Pan-)Phoenicopteriformes. However since both grebes and †Palaelodidae are aquatic birds which use their hindlimbs for propulsion, it is most parsimonious to assume that the stem species of (Pan-)Phoenicopteriformes also was an aquatic bird which used its hind limbs for propulsion in the water (Mayr 2004). Species on the stem lineage of the Phoenicopteridae then entered a new ecological zone, as filter feeders in shallow waters.

†Plotopteridae and penguins (Spheniscidae)

Penguins (Spheniscidae) exhibit a highly derived morphology which makes it difficult to evaluate their phylogenetic affinities with morphological data (Fig. 4). By many earlier authors they were considered to be most closely related to tubenoses and allies (Procellariiformes) and loons (Gaviiformes) (Cracraft 1985, Sibley & Ahlquist 1990, McKittrick 1991, van Tuinen et al. 2001, Mayr & Clarke 2003), but the evidence for either hypothesis is very weak (Mayr 2005b).

Molecular analyses do not show congruent results concerning the affinities of penguins (see the review in Mayr 2005b), but with regard to the following remarks it is

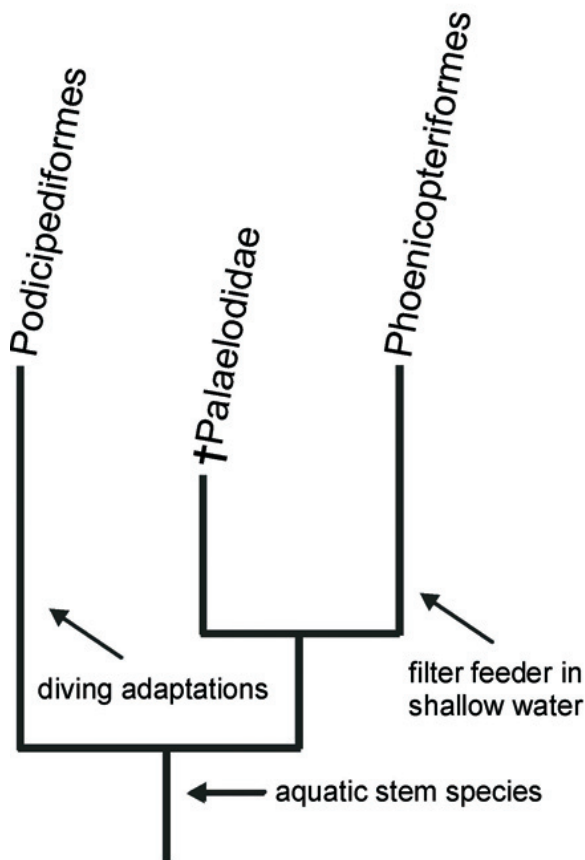


Fig. 3. Phylogenetic relationships between †Podicipediformes, Palaelodidae, and Phoenicopteriformes, with skulls in comparison. **A.** Lesser flamingo (*Phoeniconaias minor*, Phoenicopteridae). **B.** *Palaelodus* sp. (†Palaelodidae; uncatalogued specimen from Alliers in France in the collection of Forschungsinstitut Senckenberg). **C.** Great crested grebe (*Podiceps cristatus*, Podicipedidae). Note that the upper beak and part of the cranium in B are reconstructed. Scale bars equal 10 mm.



Fig. 4. Immature (left) and adult (right) Magellanic Penguin (*Spheniscus magellanicus*), Seno Otway, Chile. Photo: Eun-Joo Shin.

noteworthy that in a recent analysis of the beta-fibrinogen gene by Fain & Houde (2004) penguins were shown to be the sister taxon of a clade including the "pelecaniform" *Fregatidae* (frigatebirds) and *Suloidea* (gannets and boobies [*Sulidae*], cormorants [*Phalacrocoracidae*], and anhingas [*Anhingidae*]) (Fig. 5).

Evidence for this latter hypothesis comes from a fossil taxon of flightless, wing-propelled diving birds, the †*Plotopteridae*, which are known from the late Eocene to early Miocene of Japan and North America. †*Plotopterids* and penguins share a highly derived wing morphology including a thin, sheet-like, and greatly expanded scapula, a peculiar humerus with a strongly flattened and ventrally protruding distal end, as well as a flattened and greatly expanded radius and ulna, the latter bearing a row of marked pits for the attachment of feather quills (Mayr 2005b; Fig. 6). The derived similarities between †*Plotopteridae* and crown group *Spheniscidae* are not restricted

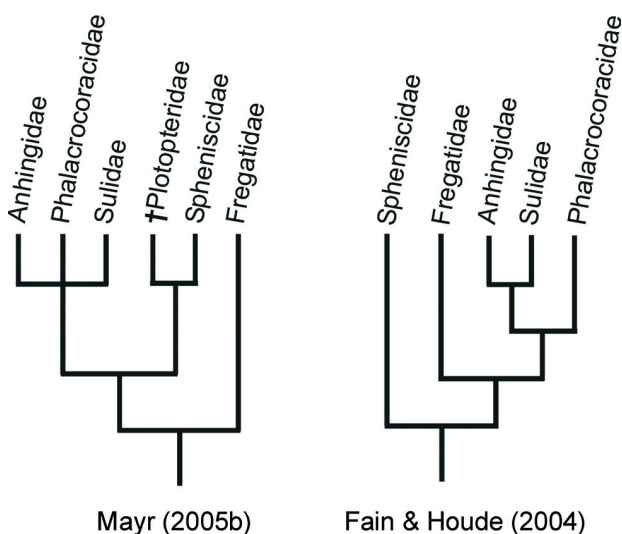


Fig. 5. Two phylogenetic hypotheses on the relationships between penguins and the *Suloidea*. **A.** After Mayr (2005b). **B.** After Fain & Houde (2004). Note that the former study has been submitted before the latter was published and that the results of both studies are thus independently obtained.

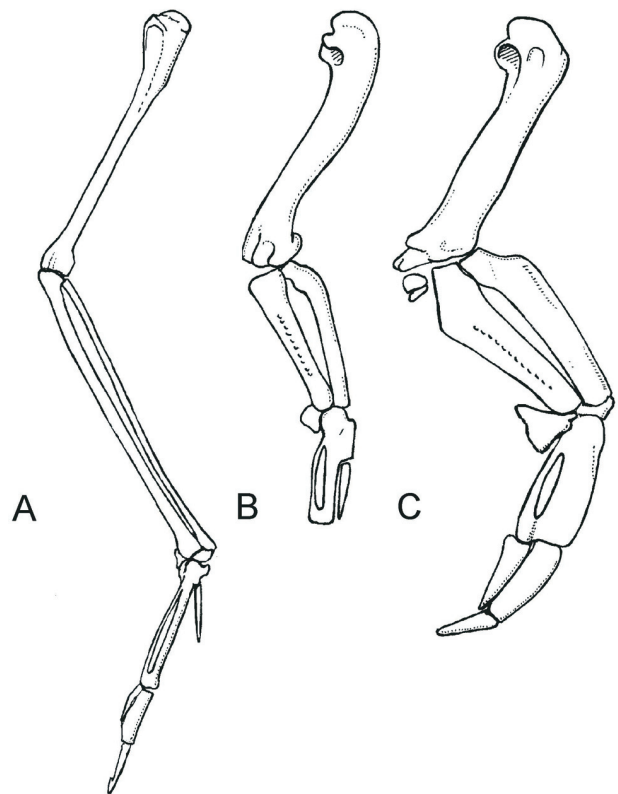


Fig. 6. Right wing in comparison. **A.** *Phalacrocorax carbo* (*Suloidea*, *Phalacrocoracidae*). **B.** *Copepteryx hexeris* (†*Plotopteridae*). **C.** *Eudyptula minor* (*Spheniscidae*). Not to scale and slightly schematic; in B the distal phalanges are not shown; from Mayr (2005b), modified.

to the wing skeleton and both taxa also share, for example, a greatly abbreviated tarsometatarsus in which the distal vascular foramen is distally open or completely absent (Fig. 7).

The similarities between †*plotopterids* and penguins, which are especially evident if †*plotopterids* are compared with stem lineage representatives of the *Spheniscidae* (Fig. 7, Mayr 2005b), were however attributed to convergence, and †*plotopterids* were considered to be most closely related to the pelecaniform anhingas (Olson 1980, Olson & Hasegawa 1979, 1996).

However, assignment of †*plotopterids* to "pelecaniform" birds does not necessarily preclude them from being the sister taxon of penguins, and cladistic analysis of morphological data supports sister group between *Suloidea* and the clade (†*Plotopteridae* + *Spheniscidae*) (Mayr 2005b; Fig. 5). Penguins and members of the *Suloidea* share greatly reduced external narial openings, opisthocoelous thoracic vertebrae, a very large patella which bears a marked furrow/canal for the tendon of the ambiens muscle, a single-lobed glandula nasalis with only a single efferent ductus, and a layer of amorphous calcium carbonate covering the eggshell (Mayr 2005b). The young of penguins and "pelecaniform" birds are further fed down the gullet of the adults, which was considered "a good synapomorphy" for "Pelecaniformes" by Cracraft (1985: 841).

†*Plotopteridae* were not recognized as stem lineage representatives of the *Sphenisciformes* because they share with *Suloidea* several derived characters which are absent

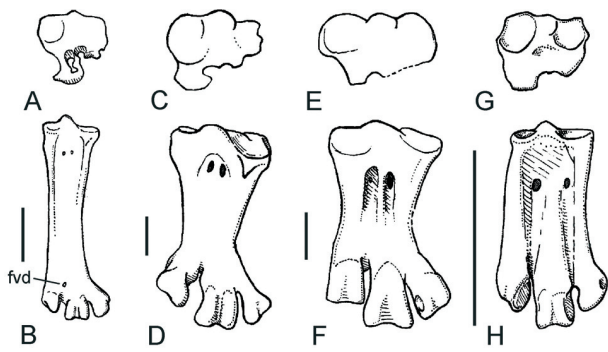


Fig. 7. Dorsal aspect (B, D, F, H) and proximal end in proximal view (A, C, E, G) of right tarsometatarsus in comparison. **A, B.** Miocene giant aninga *Macranhinga paranensis* (Suloidea, Anhingidae). **C, D.** Plotopterid *Copepteryx hexeris* (†Plotopteridae). **E, F.** Late Eocene *Palaeudyptes marplei* (Spheniscidae). **G, H.** Extant *Eudyptula minor* (Spheniscidae). Scale bars equal 2 cm. Abbreviation: fvd - distal vascular foramen. From Mayr (2005b), modified.

in crown group Spheniscidae, including a marked nasofrontal hinge and derived coracoid/furcula and furcula/sternum articulations (see Mayr 2005b). However, several traits of the peculiar penguin morphology are known to be of neotenic origin and neoteny may also account for many differences between crown group penguins and the Suloidea (Mayr 2005b).

Conclusion

Only a phylogeny which is based on morphological characters allows the assignment of fossil taxa, which is important not only because there is an increasing number of well-preserved fossil birds. Stem lineage representatives can also contribute to phylogenetic hypotheses on widely divergent taxa if they exhibit old bauplan characteristics, which were reduced or transformed in the crown group but are present in its sister taxon.

Although fossils are not compulsory for the reconstruction of phylogenetic relationships between extant taxa, they may provide important clues for detection of sister group relationship between morphologically divergent modern groups. One of the most instructive examples therefore is sister group between crocodiles and birds which can be shown by study of crown group Aves and Crocodylia, but would probably not have become universally accepted without fossil taxa such as *Archaeopteryx* and sphenosuchians (stem group representatives of Crocodylia).

Morphological characters further raise questions concerning character transformations and allow plausible assessment of convergence, as correlation with behavioral and ecological traits is often only feasible for morphological characters. For example, grebes and loons share similar derived transformations of the hindlimbs which can be explained with the fact that both taxa use their feet for propulsion in the water. By contrast, given the very different way of living of grebes and flamingos, it is much more difficult to explain by convergence the above-listed derived morphological similarities shared by these taxa.

Unquestionably, molecular analyses are an important tool for the reconstruction of the higher-level phylogeny of birds. However, it is to be hoped that in future phylogenetic analyses the consideration of morphological data and fossils is intensified for a more comprehensive understanding of avian phylogeny and evolution.

Acknowledgements

I thank R. Willmann for inviting me to take part at the Phylogenetisches Symposium in Göttingen and A. Manegold for critical comments on an earlier version of the manuscript.

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