

The higher-level phylogeny of birds - when morphology, molecules, and fossils coincide

Gerald Mayr

Forschungsinstitut Senckenberg, Ornithological Section, Senckenberganlage 25, D-60325 Frankfurt/M., Germany; e-mail: Gerald.Mayr@senckenberg.de

ABSTRACT - Although the higher-level relationships of modern birds are still poorly resolved, some clades result from cladistic analyses of both morphological and molecular data, and are in further agreement with the mosaic character distribution in Paleogene fossil taxa. Examples are sister group relationships between Galliformes (landfowl) and Anseriformes (waterfowl), Phoenicopteriformes (flamingos) and Podicipediformes (grebes), Aegothelidae (owlet-nightjars) and Apodiformes, and jacamars/puffbirds (Galbulae) and Pici (woodpeckers and allies). Recent molecular studies further support a position of Turnicidae (buttonquails) within Charadriiformes (shorebirds), which is in concordance with the mosaic distribution of turnicid and charadriiform characters in the early Oligocene taxon *Turnipax*. Most of the above clades have initially been suggested from studies of morphological data, and, despite recent progress in molecular analyses, phylogenies based on morphological characters are still needed to set fossil taxa into a phylogenetic context.

La phylogénie des grands groupes d'oiseaux – lorsque morphologie, molécules et fossils coïncident – Bien que les relations phylogénétiques entre les groupes d'oiseaux modernes ne soient pas encore complètement élucidées, certains clades résultent d'analyses fondées à la fois sur les données morphologiques et les données moléculaires, et en outre sont en accord avec la distribution en mosaïque des caractères de taxons fossiles du Paléogène. On peut citer comme exemples les relations entre les Galliformes et les Anseriformes, les Phoenicopteriformes et les Podicipediformes, les Aegothelidae et les Apodiformes, les Galbulae et les Pici. Des études moléculaires récentes placent en outre les Turniciidae, ce qui est en accord avec la distribution en mosaïque de caractères de turnicidés et de Charadriiformes chez le taxon oligocène *Turnipax*. La plupart des clades ci-dessus ont été suggérés à l'origine par des études morphologiques, et en dépit des progrès récents des analyses moléculaires, les phylogénies fondées sur les caractères morphologiques sont toujours nécessaires pour placer les taxons fossiles dans leur contexte phylogénétique.

INTRODUCTION

Most avian classifications in the 19th and 20th century go back to the system of Fürbringer (1888), that was established long before modern phylogenetic methods were introduced (Hennig, 1950). Even some of the more recent studies proceed from poorly established “orders”, such as “Gruiformes” (e.g., Cracraft, 1988, 2001; Cracraft et al., 2004), whose monophyly has not been well supported. Although new impetus came from the introduction of molecular techniques into avian systematics, these often 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; Cracraft et al., 2004; Fain & Houde, 2004; Ericson et al., 2006). Nevertheless, a number of avian clades received strong support from analyses of different kind of molecular data, and some of these have not been considered by morphologists before.

Contrary to even a few decades ago, there mean-

while is further an extensive Paleogene fossil record of birds, and many Paleogene fossils lack derived features that obscure the phylogenetic affinities of their extant relatives. Here, I give a brief overview over some neornithine clades that are supported by cladistic analyses of both morphological and molecular data and that are in further agreement with the mosaic character distribution in fossil taxa. General surveys on earlier and recently proposed phylogenies can be found in Sibley & Ahlquist (1990), Livezey & Zusi (2001), and Cracraft et al. (2004).

GALLIFORMES + ANSERIFORMES

Sister group relationship between Galliformes (landfowl) and Anseriformes (waterfowl), i.e. monophyly of Galloanseres, was first suggested from morphological studies (e.g., Simonetta, 1963), and is supported by virtually all molecular analyses of DNA-DNA hybridization data, mitochondrial, and nuclear genes (Sibley & Ahlquist, 1990;

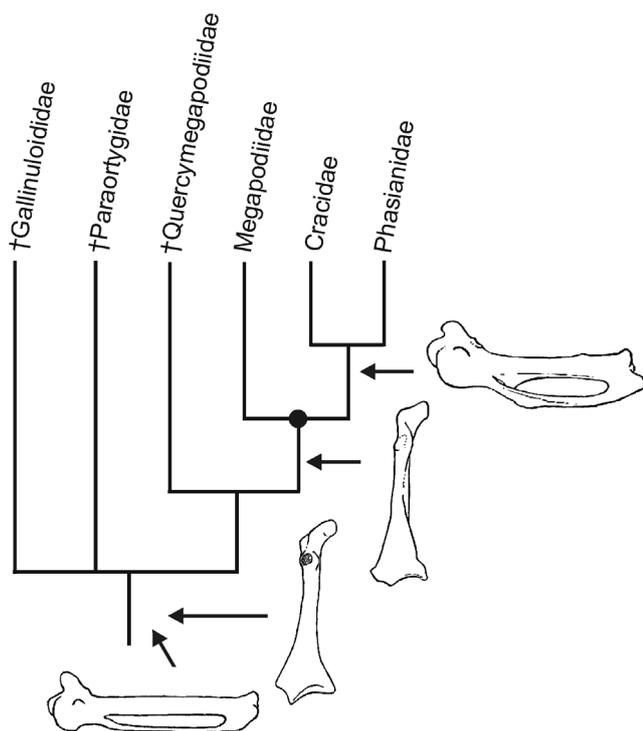


Figure 1 - Cladogram depicting the relationship between fossil (dagger) and extant Galliformes. The black point indicates the crown group. Plesiomorphic (stem group Galliformes) and apomorphic (crown group Galliformes) carpometacarpus and coracoid morphologies are mapped on the tree, see text for details (after Mayr & Weidig, 2004). Note the cup-like facies articularis scapularis in stem group Galliformes.

Groth & Barrowclough, 1999; van Tuinen et al., 2000; Sorenson et al., 2003; Chubb, 2004; Simon et al., 2004; Cracraft et al., 2004; Fain & Houde, 2004; Ericson et al., 2006). Morphological apomorphies of this clade are largely restricted to skull features and include an inflated basiparasphenoid plate, a derived modification of the basiptyergoid processes and the quadrate, as well as greatly elongated retroarticular processes on the mandible (Dzerzhinsky, 1992; Cracraft & Clarke, 2001; see also Ericson, 1996 concerning variation of some of these features within Galloanseres).

The postcranial anatomy of modern land- and waterfowl, however, is quite different. This morphological gap is bridged by the morphology of Paleogene stem group Galliformes, most notably the early Eocene Gallinuloididae which are the earliest known galliform birds (Mayr, 2000a; Mayr & Weidig, 2004). In particular, gallinuloidids exhibit a strikingly “anseriform” morphology of the coracoid that exhibits a cup-like articular facet for the scapula (Fig. 1). Also the

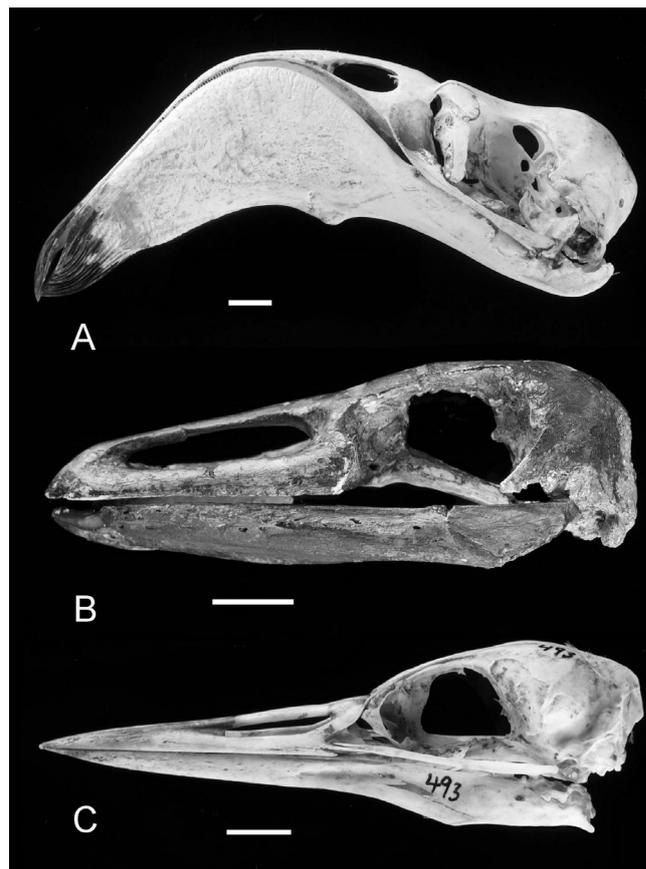


Figure 2 - Skulls in comparison. A: Lesser flamingo (*Phoeniconaias minor*, Phoenicopteridae); B: *Palaelodus* sp. (Palaelodidae; uncatalogued specimen from Alliers in France in the collection of the Forschungsinstitut Senckenberg); C: Great crested grebe (*Podiceps cristatus*, Podicipedidae). Note that the upper beak and part of the cranium in B are reconstructed; an actual specimen is figured by Cheneval & Escuillié (1992) and slightly differs in proportions. Scale bars equal 10 mm.

very long scapula and the long and slender carpometacarpus are more similar to the corresponding bones of anseriform birds than to those of crown group Galliformes (Fig. 1; Mayr, 2000a; Mayr & Weidig, 2004). A cup-like scapular articulation facet on the coracoid and an elongated carpometacarpus are also present in other Paleogene stem group Galliformes, such as the Quercymegapodiidae (Mourer-Chauviré, 1992), and both characters occur in Mesozoic non-neornithine birds. Their modification in extant Galliformes, which exhibit a shallow articulation facet for the scapula and a shorter and wider carpometacarpus, is thus derived within Neornithes.

PODICIPEDIFORMES + PHOENICOPTERIFORMES

The phylogenetic affinities of the Phoenicopteriformes (flamingos) were among the long standing problems in ornithology, and earlier authors assumed that their closest modern relatives are either Anseriformes, Ciconiidae

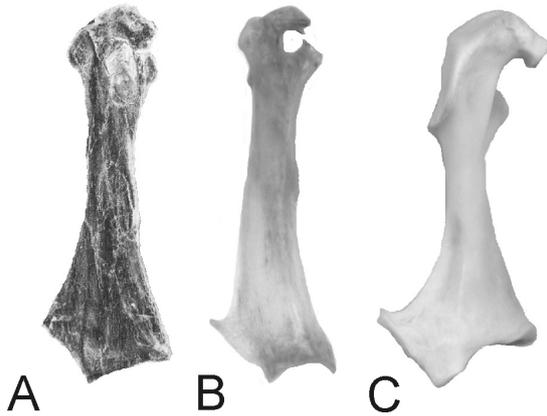


Figure 3 - Coracoids in comparison. A: *Turnipax dissipata* Mayr 2000 (holotype, specimen SMF Av 427 in the collection of Forschungsinstitut Senckenberg, Frankfurt, Germany); B: *Turnix tanki* (Charadriiformes, Turnicidae); C: *Haematopus ostralegus* (Charadriiformes, Haematopodidae). Not to scale.

(storks), or the charadriiform *Recurvirostridae* (stilts and avocets) (see Sibley & Ahlquist, 1990). None of these hypotheses is, however, supported by molecular studies, which instead recovered sister group relationship between *Phoenicopteridae* and *Podicipediformes* (grebes). The flamingo/grebe clade has not been suggested by any earlier author and was first found by van Tuinen et al. (2001), who analyzed mitochondrial and nuclear DNA sequences as well as DNA-DNA hybridization data. Meanwhile it also resulted from analyses of the nuclear ZENK gene (Chubb 2004), the RAG-2 exon (Cracraft et al., 2004), as well as the RAG-1 exon (Ericson et al., 2006: fig. ESM-2) and myoglobin intron 2 (Ericson et al., 2006: fig. ESM-3).

Apomorphies of the clade (*Phoenicopteriformes* + *Podicipediformes*) include the presence of a notarium (fused thoracic vertebrae), an unusually high number of cervical vertebrae, 11 primaries (except for storks, all other birds have 9 or 10 primaries), a layer of calcium phosphate that covers the eggshell and that is found otherwise only in the galliform *Megapodiidae*, and nail-like unguis phalanges (Mayr, 2004a, Manegold, 2006).

Fossil support for this novel hypothesis comes from the fossil phoenicopteriform taxon *Palaelodidae* that provides a morphological link between the highly derived morphology of modern grebes and flamingos (Mayr, 2004a). *Palaelodids* are known since a long time from the Paleogene and Neogene of Europe and have an abundant fossil record (e.g., Cheneval, 1983). Their assignment to the *Phoenicopteriformes* has never been doubted and, among other features, is supported by the very deep lower jaw (Fig. 2). However, contrary to their modern relatives, *palaelodids* have very short hindlimbs and especially the tarsometatarsus strikingly resembles the corresponding bone of modern grebes (Cheneval & Escuillié, 1992). *Palaelodids* have been considered to be specialized swimming or diving flamingos by earlier authors (e.g., Cheneval, 1983), but in the light of the new hypothesis it is more likely that the swimming adaptations of these birds are plesiomorphic traits of *Phoenicopteriformes* (Mayr, 2004a, 2007).

TURNICIDAE AND CHARADRIIFORMES

Turnicidae (buttonquails) are also among those groups that have puzzled avian systematists for decades. Although relationships to palaeognathous birds, *Galliformes*, and *Gruiformes* (cranes and allies) were assumed, they were most often classified in their own “order” by earlier authors, together with the Australian *Pedionomidae* (plains wanderer) (Sibley & Ahlquist, 1990; Rotthowe & Starck, 1998).

Olson & Steadman (1981) presented convincing evidence that the *Pedionomidae* are in fact part of the *Charadriiformes* (sandpipers, gulls, auks, and allies) but considered the position of the *Turnicidae* to be uncertain. Recent analyses of both nuclear and mitochondrial sequences, however, provide strong evidence that buttonquails also are aberrant members of the *Charadriiformes* (Paton et al., 2003; Cracraft et al., 2004; Fain & Houde, 2004; Paton & Baker, 2006; Ericson et al., 2006).

These findings put into a new light a fossil taxon from the early Oligocene of France and Germany which exhibits a striking mosaic of charadriiform and turnicid characters (Mayr, 2000b; Mayr & Knopf, in press). *Turnipax* shares a derived morphology of the coracoid (Fig. 3) with crown group *Turnicidae*, and the new molecular hypothesis on the phylogenetic affinities of buttonquails suggest that the fossil taxon is a stem group representatives of the *Turnicidae*, which exhibits plesiomorphic charadriiform characteristics (see also Mayr & Knopf, 2007).

AEGOTHELIDAE + APODIFORMES

Sister group relationship between *Apodidae* and *Hemiprocnidae* (true swifts and tree swifts) and *Trochilidae* (hummingbirds), i.e. monophyly of the traditional *Apodiformes*, has been assumed by most earlier authors, and results from all cladistic analyses of morphological and molecular data (Sibley & Ahlquist, 1990; Johansson et al., 2001; Livezey & Zusi, 2001; Mayr, 2002; Mayr et al., 2003; Cracraft et al., 2004; Ericson et al., 2006).



Figure 4 - Holotype of the stem group hummingbird *Parargornis messelensis* from the Middle Eocene of Messel (specimen HLMD Be 163 in the collection of the Hessisches Landesmuseum in Darmstadt). The feathering of this species strongly departs from modern Trochilidae and is here considered to be plesiomorphic for hummingbirds.

However, although most authors considered a close relationship to the “Caprimulgiformes” (nightjars and allies), the sister taxon of apodiform birds remained uncertain (see Sibley & Ahlquist, 1990). In 2002, I detailed that the traditional “Caprimulgiformes” (e.g., sensu Wetmore, 1960) are not monophyletic and that the Aegothelidae (owlet-nightjars) are the sister group of Apodiformes (Mayr, 2002). Morphological apomorphies of the clade (Aegothelidae + Apodiformes) include a derived morphology of the quadrate, a foramen for the supracoracoideus nerve on the coracoid, as well as a derived morphology of the splenius capitis muscle (Mayr 2002). Owlet-nightjars, swifts, and hummingbirds further share an indel in the *c-myc* gene (Mayr et al., 2003) and a “15 base synapomorphy” in the RAG-1 gene (Barrowclough et al. 2006: 240), and a clade including these taxa is supported by all recent molecular analyses (Cracraft et al., 2004; Barrowclough et al, 2006; Ericson et al., 2006).

Fossil support for sister group relationship between Aegothelidae and Apodiformes comes from the earliest known, Middle Eocene, stem group hummingbird *Parargornis* (Mayr, 2003a). Among other features, this taxon shares with modern Trochilidae a derived modification of the elbow joint (Mayr, 2003a, b), but still exhibits an owlet-nightjar- or swift-like beak. Most notably, however, the feathering of *Parargornis* trenchantly differs from that of modern hummingbirds and swifts in that the wings are short and rounded and the tail very long (Fig. 4). A similar feathering occurs in modern Aegothelidae and most likely is plesiomorphic for the Trochilidae (Mayr & Manegold, 2002; Mayr, 2005).

GALBULAE + PICI

Several authors questioned sister group relationship between Galbulae (jacamars and puffbirds) and Pici

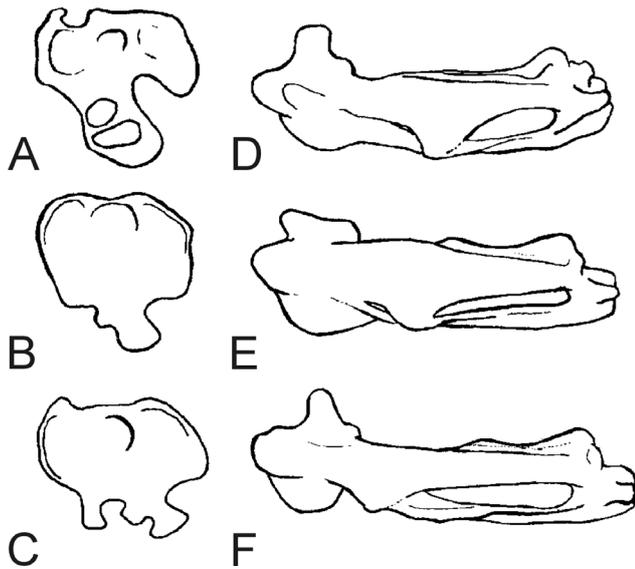


Figure 5 - Hypotarsus (A-C) and carpometacarpus (D-F) of pici-form birds in comparison. A: *Eubucco bourcierii* (Pici, Ramphastidae); D: *Trachyphonus margaritatus* (Pici, Ramphastidae); B, E: *Sylphornis bretoensis* (Sylphornithidae); E: *Chelidoptera tenebrosa* (Galbulae, Bucconidae); F: *Galbula ruficauda* (Galbulae, Galbulidae). Not to scale, after Mayr (2004).

(woodpeckers and allies), i.e. monophyly of the traditional Piciformes, and assumed that the Galbulae are more closely related to coraciiform birds (rollers and allies) (e.g., Olson, 1983; Burton, 1984; Höfling & Alvarenga, 1997).

All morphological apomorphies of the traditional Piciformes recognized by earlier ornithologists concern the hindlimbs (Simpson & Cracraft, 1981; Swierczewski & Raikow, 1981). Recently, however, additional apomorphies were identified which are not related to the foot morphology, including a proximally protruding process on the proximal phalanx of the major digit of the wing, the secondary loss of an intrapterygoid joint, and a shield-like disc on the pygostyle (Mayr et al., 2003; Manegold, 2005). Monophyly of the traditional Piciformes is also strongly supported by analyses of nuclear sequence data (Johansson & Ericson, 2003; Mayr et al., 2003; Cracraft et al., 2004; Ericson et al. 2006; contra Sibley & Ahlquist, 1990).

The Paleogene pici-form (Mayr, 2004b) Sylphornithidae, which are known from the Upper Eocene of France and the early Oligocene of Belgium (Mourer-Chauviré, 1988; Mayr & Smith, 2002), combine a derived, Pici-like morphology of the carpometacarpus (shorter and stouter than in Galbulae, with a larger intermetacarpal process) with a plesiomorphic, Galbulae-like morphology of the tarsometatarsus (hypotarsus with open sulcus for tendon of flexor digitorum longus muscle, distal end with small accessory trochlea) (Fig. 5; Mayr, 2004b).

CONCLUSION

Although the higher-level relationships of birds are often regarded as poorly resolved, there are some clades that are supported by morphological, molecular, and fossil data. The increasing number of molecular studies and the discovery of new Paleogene fossils in particular led to a renaissance of avian systematics and stimulated new phylogenetic

hypotheses, although it has to be noted that most clades discussed above were initially suggested from morphological studies of the extant taxa. Only Galloanseres were recovered in the often cited DNA-DNA hybridization studies of Sibley & Ahlquist (1990) which are a comparison of overall similarity, and have also been criticized for other methodological reasons (Houde, 1987; Lanyon, 1992; Fain & Houde, 2004). Morphological data thus has the potential to resolve the higher-level phylogeny of birds and phylogenies based on morphological characters are especially needed if fossil taxa have to be set into a phylogenetic context (see also, e.g., Wiens, 2004).

As more and more Paleogene fossil taxa are described and molecular techniques are continuously improved, there is good reason to believe that the next years will see further well-supported hypotheses on the relationships of additional taxa. An important requirement for success in this direction is, however, that systematists continue to critically evaluate monophyly of the traditional higher-level taxa, either by comparison of mutually independent molecular evidence (e.g., gene loci on different chromosomes or mitochondrial and nuclear sequence data) or by discussion of morphological apomorphies, and, if necessary, break with long-established traditional views (e.g., Fain & Houde, 2004; Ericson et al., 2006).

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