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Metaves, Mirandornithes, Strisores and other novelties – a critical review of the higher-level phylogeny of neornithine birds

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Abstract

Recent hypotheses on the higher-level phylogeny of modern birds are reviewed, and areas of agreement and major conflict are detailed, with emphasis being put on congruence among independent molecular and morphological data sets. Although molecular data significantly contributed to a better understanding of avian phylogeny, they do not seem to be free of homoplasy and caution is warranted in the interpretation of some results. The recently proposed 'Metaves' clade is likely to be an artefact of the β-fibrinogen gene, and current molecular data do not yield well-supported phylogenies for some groups whose interrelationships can be resolved with morphological evidence. There exists, however, congruent and strong molecular evidence for several novel clades that were not recognized by morphologists before, and to ease future discussions the terms Picocoraciae (non-leptosomid 'Coraciiformes' and Piciformes) and Aequornithes ('waterbird assemblage') are introduced. Molecular studies further congruently recover some clades, which have not yet been adequately appreciated and are outlined in the present review.

Key words: Aves – molecular systematics – morphology – phylogenetic congruence – Picocoraciae – Aequornithes

Introduction

After some 150 years of research, several clades of modern birds (Neornithes) are now strongly supported by multiple lines of evidence, and there exists cautious optimism that the main features of avian higher-level phylogeny will be resolved in the near future (e.g., Harshman 2007). Sibley and Ahlquist's (1990) comprehensive DNA–DNA hybridization studies certainly marked a turning point in avian phylogenetics and boosted subsequent molecular analyses. Their results were, however, criticized for methodological reasons, and many aspects of the Sibley and Ahlquist phylogeny have not been supported by more recent studies (e.g., Cracraft et al. 2004; Harshman 2007).

Current molecular analyses focus on mitochondrial or nuclear gene sequences, and the first study that covered virtually all higher-level taxa was by Fain and Houde (2004), who sequenced an intron of the nuclear β-fibrinogen gene. Ericson et al. (2006) added four additional nuclear loci to the β-fibrinogen sequences, and the to date most comprehensive molecular data set for birds was analysed by Hackett et al. (2008), whose study covered 19 nuclear gene loci. In spite of the different amount of data and the fact that only two of the five gene loci of Ericson et al. (2006) were included in the Hackett et al. (2008) study (i.e., β-fibrinogen intron 7 and myoglobin intron 2), the two analyses resulted in very similar tree topologies (Fig. 1). Comprehensive mitochondrial data sets were further analysed in the past years, which provide independent evidence to test the nuclear phylogenies (e.g., Brown et al. 2008; Morgan-Richards et al. 2008; Pratt et al. 2009).

Surprisingly, the early neornithine divergences are among the best resolved ones in molecular analyses (Fain and Houde 2007; Harshman 2007), and it is now generally assumed that Neornithes fall into two clades, Palaeognathae and Neognathae (see, however, Brinkmann 2010 who considered the palaeognathous Apterygidae to be the sister taxon of all other Neornithes). Neognathous birds can be divided into the sister taxa Galloanseres and Neoaves, with reduction in the phallus being a neoavian apomorphy (Montgomerie and Briskie 2007; Brennan et al. 2008; Mayr 2008a). An unexpected major result of some of the new molecular studies is recognition of two neoavian clades, termed 'Coronaves' and 'Metaves', with the latter including morphologically widely divergent taxa, such as Phaethontidae, Phoenicopteriformes and Apodiformes (Fain and Houde 2004; Ericson et al. 2006; Hackett et al. 2008). The 'metavian' taxon is, however, only obtained in analyses including the β-fibrinogen gene, and for reasons detailed in the discussion, it does probably not constitute a monophyletic group.

Attempts were also made to tackle neornithine phylogeny through analyses of large morphological data sets (e.g., McKitrick 1991; Mayr and Clarke 2003). The by far most comprehensive of these was gathered by Livezey and Zusi (2006, 2007), whose matrix included nearly 3000 morphological characters and representatives of most extant non-passeriform family-level taxa. Except for the early divergences (Palaeognathae and Galloanseres), the Livezey and Zusi phylogeny resembles the tree depicted by Fürbringer (1888), which actually constitutes the first explicit phylogenetic hypothesis of birds and formed the basis for most traditional classifications (Fig. 2). In some aspects, and because of questionable character scorings and inherent problems of numerical cladistic analyses of large morphological character matrices, Livezey and Zusi's cladogram is, however, at odds with both, traditional hypotheses and new molecular evidence (Mayr 2008a).

In the case of competing phylogenies, it is often difficult, if possible at all, to decide which hypothesis more closely reflects the true interrelationships of the taxa in question. However, there exist a number of clades that are supported by many independent lines of evidence, such as mitochondrial and nuclear DNA sequences or gene loci on different chromosomes, and for which no equally supported alternative hypotheses exist. Seeking for congruence among independent

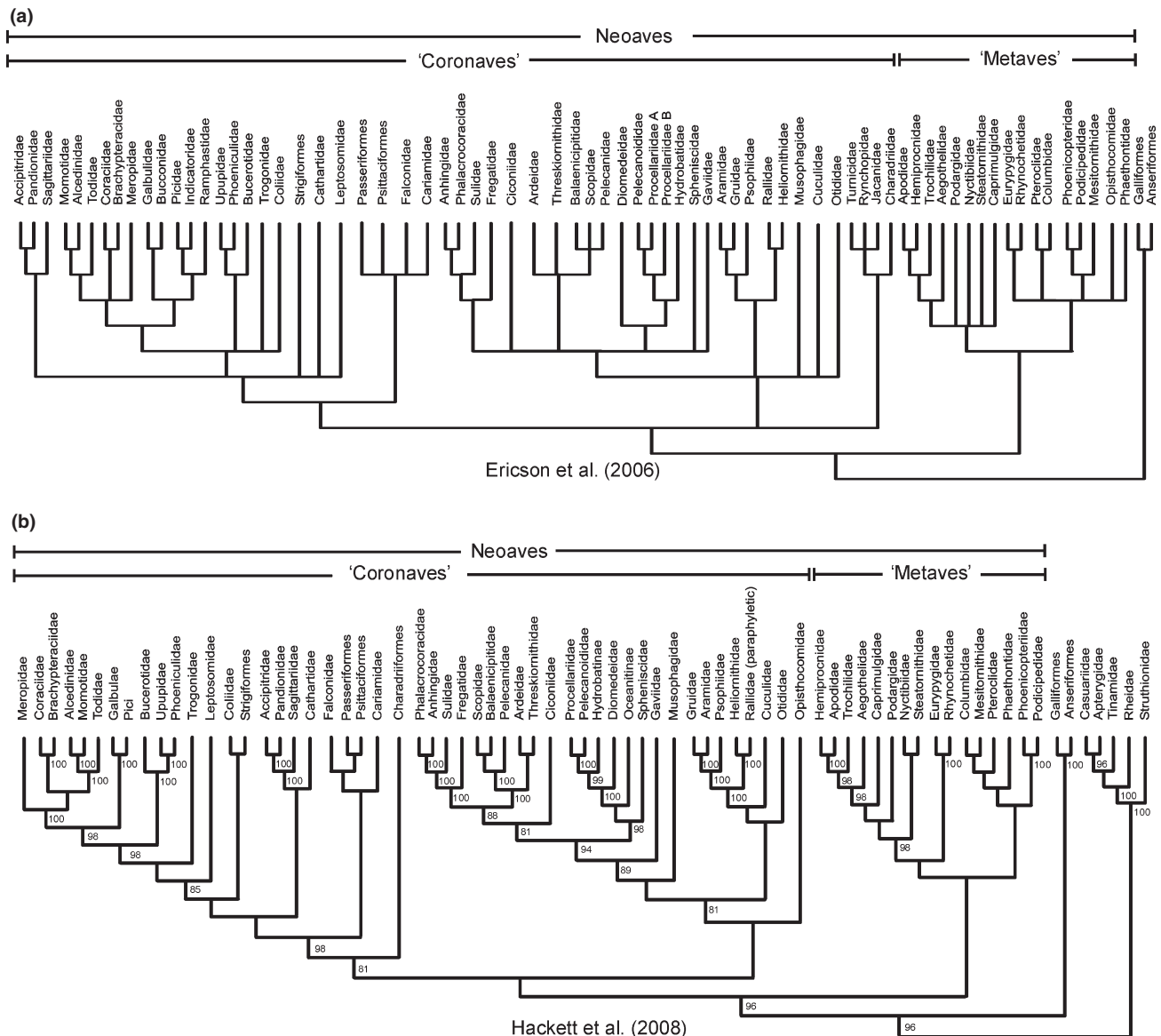*Corresponding author*: Gerald Mayr (e-mail: Gerald.Mayr@senckenberg.de)

Fig. 1. Two recent phylogenies based on nuclear gene sequences and a comprehensive taxon sampling. (a) Tree resulting from Bayesian analysis of five nuclear genes by Ericson et al. (2006); nodes that received are posterior probability below 95% are collapsed. (b) Tree resulting from a maximum likelihood analysis of 19 nuclear gene loci by Hackett et al. (2008); maximum likelihood bootstrap values above 80% from the original publication are indicated next to the nodes

data sets is thus a promising approach to detect previously unrecognized clades, and the present review gives a brief overview of areas of agreement and major conflict in neornithine higher-level phylogeny. I focused on extant or recently extinct taxa, and fossil Neornithes are only mentioned if they contribute to an understanding of the interrelationships of modern groups (see Mayr 2009 for a review of the phylogenetic affinities of Palaeogene Neornithes).

Palaeognathae (tinamous and ratites)

Extant Palaeognathae include the volant Tinamidae, and the flightless Rheidae, Struthionidae, Casuariidae and Apterygidae. A clade including these five taxa is supported by a number of morphological characters, most of which pertain to the skull (Bock 1963; Parkes and Clark 1966; Cracraft 1974; Mayr and

Clarke 2003), and was strongly supported by Hackett et al's. (2008) analysis, which used crocodilian outgroups.

The interrelationships of palaeognathous birds are among the most controversial issues of avian systematics, with the only uncontested hypothesis being sister group relationship between the morphologically very similar emus and cassowaries, i.e., a monophyletic Casuariidae. Most authors united the flightless taxa as 'ratites' and considered Tinamidae to be their sister taxon. Cladistic analyses of morphological data usually further supported sister group relationship between Apterygidae and all other extant ratites, as well as sister group relationship between Struthionidae and Rheidae (e.g., Cracraft 1974; Lee et al. 1997; Livezey and Zusi 2007). A recent morphology-based analysis, however, found Rheidae and Casuariidae to be sister taxa, with Struthionidae branching next (Bourdon et al. 2009).
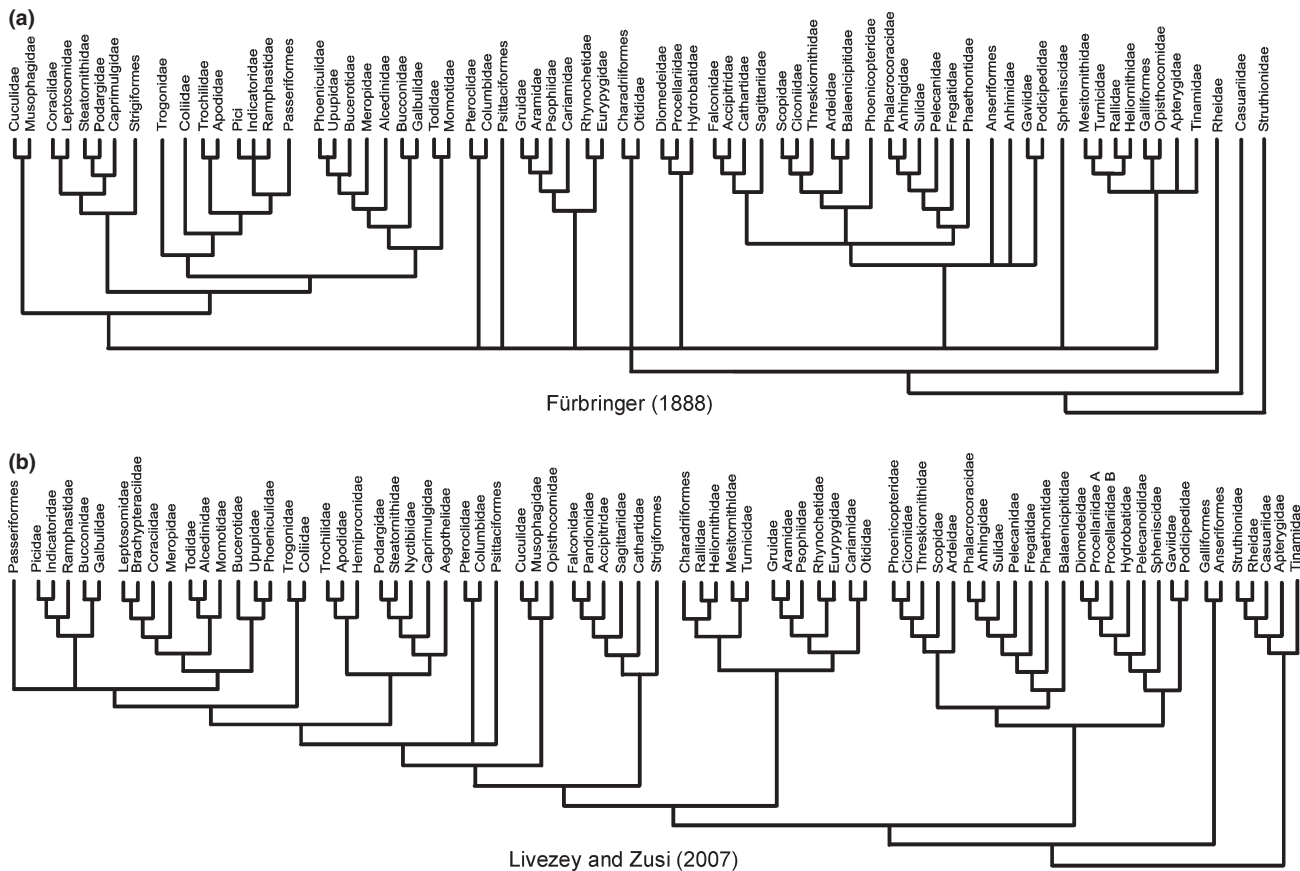
Fig. 2. Two morphology-based hypotheses on neornithine interrelationships. (a) Phylogeny of Fürbringer (1888: pls. 27–30). (b) Tree resulting from an analysis of 2954 morphological characters by Livezey and Zusi (2007)

Earlier analyses of molecular data also resulted in sister group relationship between Tinamidae and all other palaeognathous birds, but congruently supported a clade formed by Apterygidae and Casuariidae (e.g., Cooper et al. 1992; Lee et al. 1997; van Tuinen et al. 1998; Haddrath and Baker 2001; Paton et al. 2002). The Apterygidae/Casuariidae clade was also recovered in recent analyses of large molecular data sets, which added a further twist to the phylogeny of palaeognathous birds in that they showed Struthionidae to be the sister taxon of all other Palaeognathae, i.e., placed Tinamidae within the flight-less ratites. This new tree topology was congruently obtained from analyses of nuclear and mitochondrial sequences, and is also supported by insertion/deletion events (Hackett et al. 2008; Harshman et al. 2008; Phillips et al. 2010). In the Harshman et al. (2008) study, placement of Tinamidae was variable depending on the model applied to the analyses, with maximum likelihood and Bayesian analyses recovering sister group relationship between Tinamidae and the Apterygidae/Casuariidae clade, but maximum parsimony and purine/pyrimidine-coded analyses resulting in sister group relationship between Tinamidae and Rheidae, which in turn were shown to be the sister taxon of Apterygidae and Casuariidae. Because both tinamous and rheas occur in the New World, the latter hypothesis is more likely from a biogeographical point of view (Harshman et al. 2008), but mitochondrial data supported the maximum likelihood topology (Phillips et al. 2010).

To explain the discrepancy between molecular and morphological data regarding the position of Apterygidae, Lee et al.

(1997) assumed that rooting problems because of short internodes and long terminal branches lead to incorrect molecular tree topologies. Harshman et al. (2008), however, detailed that the known phylogenetic artefacts, such as long-branch attraction, convergence in base composition, stochastic lineage sorting, or ambiguous alignment, are unlikely to explain ratite polyphyly, and Phillips et al. (2010) noted that earlier analyses of mitochondrial genomes either did not account for rates-across-sites heterogeneity or were actually constrained to retain ratite monophyly.

Ratites are characterized by a number of derived character-istics, and the large-sized Struthionidae, Rheidae and Casu-ariidae share further features that are absent in Tinamidae and Apterygidae (e.g., Cracraft 1974; Bourdon et al. 2009). How-ever, none of the putative synapomorphies presented so far constitutes irrefutable evidence. Apart from features related to flightlessness, such as the loss of a sternal keel and presence of a scapulocoracoid, many shared characters pertain to either the pelvis or the hindlimbs and may thus have evolved convergently in these large cursorial birds. The skull of Struthionidae, Rheidae and Casuariidae exhibits large supra-orbital processes, but this feature evolved convergently in other neornithine birds and shows unambiguous homoplasy in core-Gruiformes. The results of Bourdon et al.'s (2009) anal-ysis are further challenged by the fact that ratites were a priori considered monophyletic and Tinamidae only included as outgroup taxon.

Although no morphological apomorphies in support of a position of tinamous within ratites have been published, it is

notably that a [(Tinamidae + Rheidae) + (Apterygidae + Casuariidae)] clade corresponds with the classification of palaeognathous birds by Bock and Bühler (1990), which was based on tongue morphology but has only been outlined in an extended congress abstract. In contrast to most other morphological studies, an analysis of postcranial characters by Bledsoe (1988) also supported an Apterygidae/Casuariidae clade, but the character evidence, which mainly pertains to the reduced forelimbs, was considered ambiguous by subsequent authors (Lee et al. 1997; Bourdon et al. 2009).

The extant distribution of ratites is restricted to the Southern Hemisphere. With most species being flightless, palaeognathous birds would thus be the prime example for vicariance biogeography among birds, and possible dispersal routes across Gondwana were suggested in numerous studies (e.g., Cracraft 1974; van Tuinen et al. 1998; Cooper et al. 2001; Haddrath and Baker 2001). A vicariance origin of ratite taxa conflicts, however, with the occurrence of flightless, ratite-like palaeognathous birds in the early Paleogene of the Northern Hemisphere (Houde 1986; Mayr 2009). If the results of the new molecular analyses reflect the true interrelationships of palaeognathous birds, they suggest an at least threefold loss of flight capability in extant palaeognathous birds and would render obsolete vicariance-based hypotheses to explain their modern distribution (Harshman et al. 2008).

Knowledge of the exact interrelationships of extant Palaeognathae is also of significance for the placement of two extinct taxa, the Madagascan Aepyornithidae and the Dinornithidae of New Zealand. Morphological data suggest sister group relationship between Dinornithidae and Apterygidae, which, among others, share large caudal nasal conchae that at least in kiwis are associated with a well-developed olfactory sense (e.g., Fürbringer 1888; Cracraft 1974; Lee et al. 1997; Bourdon et al. 2009). Analyses of short 12S rRNA sequences, however, resulted in sister group relationship between Dinornithidae and the clade [Struthionidae + (Apterygidae + Casuariidae)]. The same tree topology was obtained from complete mitochondrial genomes (Cooper et al. 2001), whereas another analysis of mitochondrial data suggested sister group relationship between Dinornithidae and all extant ratites (Haddrath and Baker 2001). Analysis of complete mitochondrial genomes by Phillips et al. (2010) showed Dinornithidae to be the sister group of Tinamidae, and the clade including these two taxa in turn resulted as the sister group of the Apterygidae/Casuariidae clade. Although Dinornithidae and Tinamidae are the only palaeognathous birds, which exhibit a supratendinal bridge on the tibiotarsus, I do not know of any morphological features that convincingly support sister group relationship between moas and tinamous. Moreover, molecular analyses, which evaluated the phylogenetic affinities of Dinornithidae, so far only used mitochondrial sequences, and it remains to be seen whether future analyses of nuclear genes (e.g., Huynen et al. 2003) produce similar results.

Morphology-based analyses suggest sister group relationship between Aepyornithidae and a clade including Struthionidae, Rheidae and Casuariidae (Cracraft 1974; Bourdon et al. 2009). If, however, the latter clade does not constitute a natural group because of ratite polyphyly, aepyornithid affinities are unresolved and open to debate; DNA sequences of elephantbird bones have not yet been isolated (see, however, Oskam et al. 2010).

Galloanseres[1] (land- and waterfowl)

Sister group relationship between Galliformes and Anseriformes was already suggested by Beddard (1898: 304) and Simonetta (1963), but has only been universally accepted after unequivocal molecular evidence was available (e.g., Cracraft 1981, 1985; Sibley and Ahlquist 1990; Groth and Barrowclough 1999; van Tuinen et al. 2000; Cracraft et al. 2004; Poe and Chubb 2004; Ericson et al. 2006; Hackett et al. 2008).
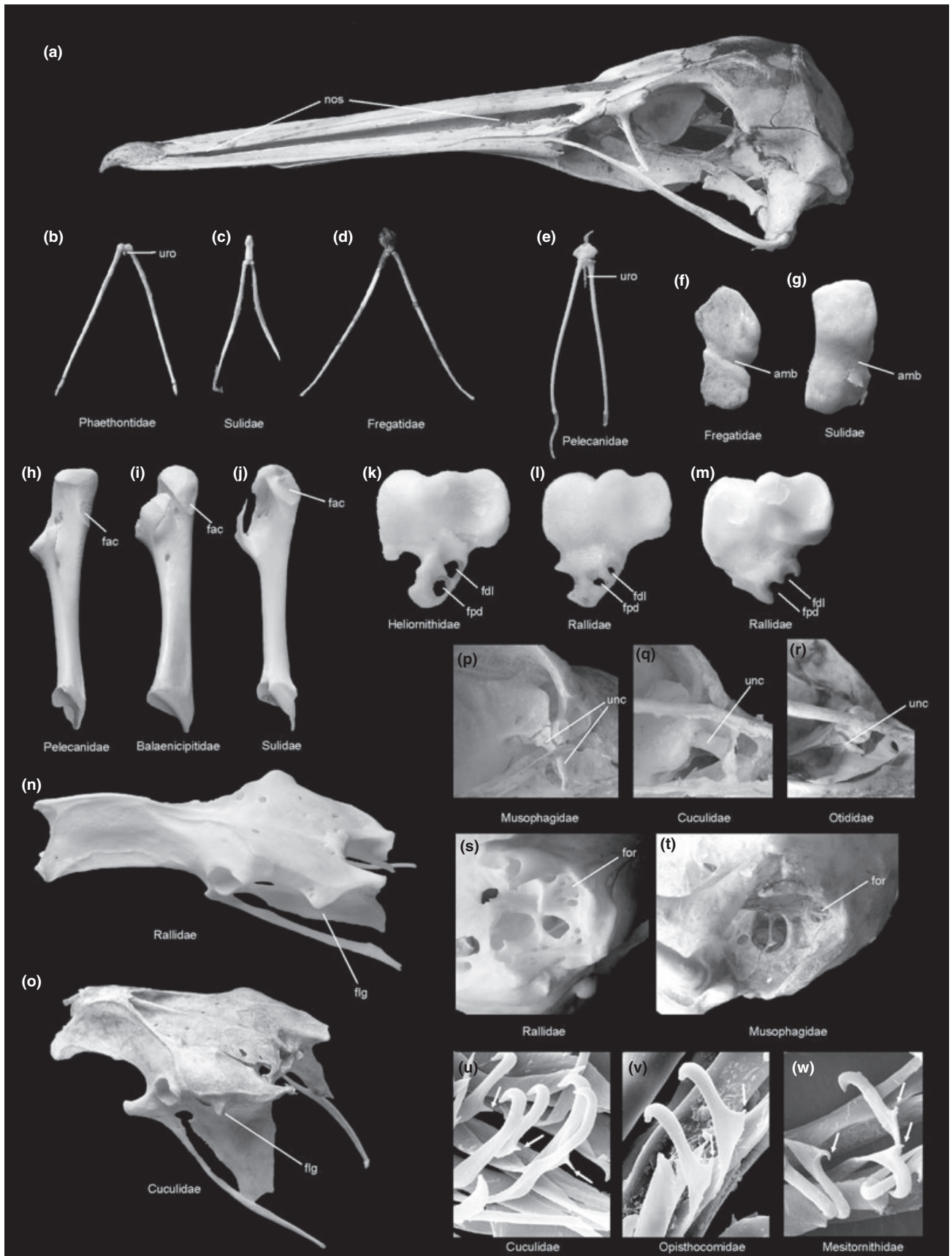
As in the case of palaeognathous birds, the known morphological apomorphies of Galloanseres are restricted to cranial features (Dzerzhinsky 1992; Cracraft and Clarke 2001; see also Ericson 1996). Extant land- and waterfowl are clearly distinguished in postcranial osteology, but some of the differences are because of the formation of a large crop in Galliformes and are bridged by the morphology of Paleogene stem group Galliformes (Mayr 2005b).

Within Galliformes, Megapodiidae are the sister taxon of a clade including Cracidae and Phasianidae. Numidinae are the sister taxon of all other Phasianidae, with Odontophorinae branching next; Meleagridinae and Tetraoninae are sister taxa and nested within Phasianidae (e.g., Kriegs et al. 2007). The anseriform Anhimidae are the sister taxon of a clade including Anseranatidae and Anatidae; Dendrocygninae are generally considered the sister taxon of all other Anatidae (Donne-Goussé et al. 2002; see, however, Worthy and Lee 2008). Despite this general agreement concerning the interrelationships of the major groups of extant Galloanseres, however, the evolutionary history of the taxon is far from being well understood. Mainly because of the presence of derived skull features, such as basipterygoid processes of the derived Galloanseres-type and a galloanserine quadrate morphology, a number of morphologically very disparate fossil taxa have been assigned to Galloanseres, including the long-legged anseriform Presbyornithidae, the giant graviportal Gastornithidae and Dromornithidae, and the 'bony-toothed' Pelagornithidae, which reached wing spans above five metres (e.g., Mayr 2009). If all of these taxa are correctly referred to Galloanseres, the clade must have undergone a dramatic radiation in the late Mesozoic/early Paleogene.

The 'waterbird assemblage'

The studies of Ericson et al. (2006) and Hackett et al. (2008) congruently support a clade including Gaviiformes, Sphenisciformes, Procellariiformes, 'Ciconiiformes' and 'Pelecaniformes' except Phaethontidae. This clade, which was termed 'water bird clade' by Hackett et al. (2008), is recovered in analyses of concatenated sequences of c-myc, RAG-1, myoglobin, and ornithine decarboxylase (Fig. 3b; Ericson et al. 2006) and an alpha A-crystallin locus (Hackett et al. 2008: fig. 1) and received fairly high support in Hackett et al's (2008) analysis (Fig. 1b). A similar clade, albeit interspersed with Musophagiformes and some apodiform and 'caprimulgiform' taxa, is also obtained from mitochondrial sequences

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[1]I consider the often-used alternative term Galloanserae inappropriate. This name was introduced by Sibley et al. (1988), who falsely assumed that Galloanseres are the sister taxon of Palaeognathae, hence their subdivision of Neornithes into Palaeognathae, Galloanserae, and Neognathae. These three taxa do, however, not have the same rank, and because sister group relationship between Galloanseres and Neoaves is now universally accepted, the ending –es is to be preferred against –ae.

Fig. 3. Comparison of two phylogenies resulting from Bayesian analysis of nuclear genes. (a) Tree derived from β-fibrinogen intron 7 sequences (Ericson et al. 2006: fig. ESM-4). (b) Tree based on combined sequences of *c-myc* exon 3, RAG-1 exon, myoglobin intron 2, and ornithine decarboxylase introns 6 and 7 with intercepting exon 7 (Ericson et al. 2006: fig. ESM-6). Nodes with a posterior probability of 95% or more are labelled, those that received a posterior probability below 50% are collapsed

(Brown et al. 2008; see also Gibb et al. 2007; Morgan-Richards et al. 2008; Pratt et al. 2009).

Livezey and Zusi's (2007) analysis of morphological data recovered a similar clade, which received, however, low bootstrap support and also included Phaethontidae, Phoenicopteriformes and Podicipediformes. The authors could not identify apomorphies of this clade (Livezey and Zusi 2007: table 2), but in a comparative study of rhamphotheca morphology, Hieronymus and Witmer (2010: 599) noted that the 'separate, heavily cornified naricorns that have led to the name "tube-noses" for procellariiform seabirds are an apomorphy of the [Gaviiformes + (Pelecaniformes + Ciconiiformes) + (Sphenisciformes + Procellariiformes)] clade'. Most 'ciconiiform', 'pelecaniform', procellariiform and sphenisciform birds are further characterized by marked furrows along the sides of the beak, which were termed nasolabial grooves by Hieronymus and Witmer (2010), and which are only absent in Ciconiidae and

Phaethontidae (weakly developed in Ardeidae). The functional significance of these furrows is unknown, by they may be correlated with the ontogenetic occurrence of long, slit-like nostrils, which I could verify in juvenile Ardeidae, Pelecanidae and Phalacrocoracidae (Fig. 4a; juvenile skulls of other taxa were not available to me). Notably, early Eocene stem group Phaethontidae, Fregatidae and Sphenisciformes (Olson 1977; Clarke et al. 2007; Mayr 2009) also have very long nostrils, which may be a plesiomorphic trait of the taxa of the 'waterbird assemblage', or a subclade thereof.

Comprising the highly aerial frigatebirds, the flightless penguins, and the long-legged storks and herons, this 'waterbird assemblage' is one of the morphologically most diversified groups of birds, and knowledge of the exact interrelationships of its component taxa is essential for an understanding of the morphological, ecological and behavioural diversification of these birds.

Molecular analyses indicate that the 'waterbird assemblage' is closely related to core-Gruiformes, Otididae, Musophagiformes and Cuculiformes. These taxa were placed in a polytomy in the analysis by Ericson et al. (2006), and a clade including the 'waterbird assemblage', core-Gruiformes, Otididae, Musophagiformes and Cuculiformes received a bootstrap

Fig. 4. (a) Skull of a juvenile *Pelecanus occidentalis* (Pelecanidae) with long, slit-like nostrils. (b)–(e) Hyoid apparatus of (b) *Phaethon rubricauda* (Phaethontidae), (c) *Sula nebouxii* (Sulidae), (d) *Fregata magnificens* (Fregatidae), and (e) *Pelecanus onocrotalus* (Pelecanidae). (f)–(g) Patella of (f) *F. magnificens*, and (g) *Sula leucogaster* (Sulidae). (h)–(j) Coracoid (medial view) of (h) *P. onocrotalus*, (i) *Balaeniceps rex* (Balaenicipitidae), and (j) *S. leucogaster*. (k)–(m) Left hypotarsus of (k) *Heliornis fulica* (Heliornithidae), (l) *Sarothrura pulchra* (Rallidae), and (m) *Crex crex* (Rallidae). (n)–(o) Pelvis of (n) *Aramides saracura* (Rallidae) and (o) *Tauraco erythrolophus* (Musophagiformes). (p)–(r) Uncinate bone of (p) *T. erythrolophus*, (q) *Carpococcyx renauldi* (Cuculiformes), and (r) *Eupodotis melanogaster* (Otididae). (s), (t) Otic region of (s) *T. erythrolophus* and (t) *A. saracura*. (u)–(w) 'Prong'-like projections (arrows) on the hamuli of the wing feathers of (u) *Coua cristata* (Cuculiformes); (v) *Opisthocomus hoazin* (Opisthocomidae); and (w) *Mesitornis unicolor* (Mesitornithidae). Figures are not to scale. amb, furrow for ambiens muscle; fac, furcula articulation facet (facies articularis clavicularis); fdl, hypotarsus canal for tendon of flexor digitorum longus muscle; flg, laterally protruding flange in midsection of dorsolateral iliac crest; for, foramina in pila otica; fpd, hypotarsus canal for tendon of flexor perforatus digiti II muscle; nos, nostril; unc, uncinate bone; uro, urohyal bone

support of 81% in the analysis by Hackett et al. (2008). In the latter study, the grouping was only supported by β-fibrinogen sequences (Hackett et al. 2008 fig. 1; see also Fain and Houde 2004). However, a similar clade, which, besides, included Charadriiformes and the 'metavian' Phoenicopteriformes, Podicipediformes, Mesitornithidae, and Phaethontidae, was also retained in an analysis of four nuclear genes exclusive of β-fibrinogen (Fig. 3b; Ericson et al. 2006). Equivalent clades further resulted from analysis of clathrin heavy chain genes, which were not included in the Ericson et al. (2006) study (Chojnowski et al. 2008; minus Charadriiformes and Spheniscidae, plus Columbidae), and from mitochondrial data (Brown et al. 2008; plus Apodidae and Steatornithidae).

'Ciconiiformes' (storks and allies) and 'Pelecaniformes' (pelicans and allies)

Analyses of nuclear and mitochondrial sequences congruently indicate non-monophyly of the traditional 'Ciconiiformes' and 'Pelecaniformes', and provide a well-supported framework for the interrelationships of some taxa of these groups, which conflicts with previous hypotheses based on morphological data. In particular, there now exists strong molecular evidence that Fregatidae are the sister taxon of the Suloidea, i.e., a clade including Sulidae, Phalacrocoracidae and Anhingidae, and that Pelecanidae are within a clade including the 'ciconiiform' Scopidae and Balaenicipitidae (Fig. 1; van Tuinen et al. 2001; Cracraft et al. 2004: fig. 27.4; Fain and Houde 2004; Ericson et al. 2006; Brown et al. 2008; Hackett et al. 2008; Mayr 2008a). Non-monophyly of the traditional 'Pelecaniformes' also resulted from DNA–DNA hybridization studies (Sibley and Ahlquist 1990) and suggests a convergent origin of the characteristic derived traits shared by pelicans, frigatebirds and suloids, such as totipalmate feet, a gular pouch and features of the pectoral girdle.

Based on morphological studies, Cottam (1957) already assumed that *Balaeniceps* is more closely related to the 'Pelecaniformes', but her hypothesis did not get widely accepted, and the first morphology-based cladistic analysis of 'pelecaniform' interrelationships resulted in monophyly of the traditional 'Pelecaniformes' (Cracraft 1985). Livezey and Zusi's (2007) study also showed 'Pelecaniformes' to be monophyletic, with Balaenicipitidae as the sister taxon of this clade and Scopidae within the 'Ciconiiformes'. Mayr (2003a) hypothesized that Scopidae and Balaenicipitidae are successive sister taxa of a clade including all other 'pelecaniform' birds except Phaethontidae. All of the above morphology-based studies recovered sister group relationship between Fregatidae and a clade including Pelecanidae and Suloidea, which is not in concordance with the results of the molecular analyses.

However, Fregatidae and Suloidea do indeed share a number of derived features, which are absent in Pelecanidae

and support the results of the molecular studies. For example, in both taxa the patella bears a marked sulcus/canal for the tendon of the ambiens muscle (Fig. 4f,g), the tarsometatarsus is short and stocky, with the trochlea for the second toe being distinctly longer than that for the fourth toe, and the claw of the third toe is pectinate (this character also occurs in Scopidae, Ardeidae and the threskiornithid *Plegadis*, but its absence in Pelecanidae is notable because of the otherwise very similar totipalmate foot). Another previously unrecognized derived similarity shared by Fregatidae and Suloidea is the loss of the urohyal bone of the hyobranchial apparatus, which is well developed in Pelecanidae, Balaenicipitidae and most other birds (Fig. 4b–e). The latter feature is of particular significance, because all 'pelecaniform' birds share a greatly reduced tongue. Hieronymus and Witmer (2010) further noted that Fregatidae and Suloidea share a derived morphology of the rhamphotheca, which exhibits a separate beak plate, the jugal operculum, that is correlated with the occurrence of an accessory ossification, the suprajugal ossiculum (the latter was erroneously considered an apomorphy of all 'pelecaniform' birds by Livezey and Zusi 2007: table 2, character 720). Because the name 'Pelecaniformes' is attached to the Pelecanidae, Christidis and Boles (2008) proposed the term Phalacrocoraciformes for the clade including Fregatidae and Suloidea.

It is more difficult to characterize a clade including Pelecanidae, Balaenicipitidae and Scopidae with morphological apomorphies. Mayr (2008a) listed the very short pterygoid and the loss of the ambiens muscle as possible synapomorphies; other derived characters shared by these taxa, such as fusion of the caudal portions of the palatina, also occur in the Suloidea. The interrelationships between Pelecanidae, Balaenicipitidae and Scopidae are also not yet well established. Hackett et al.'s (2008) study weakly supported sister group relationship between Balaenicipitidae and Scopidae (Fig. 1b), whereas β-fibrinogen sequences resulted in a Balaenicipitidae/Pelecanidae clade (Fain and Houde 2004; Fig. 3a). The three taxa resulted in a polytomy in the primary analysis by Ericson et al. (2006) (Fig. 1a), but after exclusion of the β-fibrinogen sequences, Scopidae and Balaenicipitidae were recovered as sister taxa (Fig. 3b; Ericson et al. 2006). Balaenicipitidae and Pelecanidae share derived features that are absent in Scopidae, but none of these are unique to the two taxa, and some clearly evolved convergently. For example, in Balaenicipitidae and Pelecanidae, the neck is retracted in flight and rests on the back (also in Ardeidae), the tracheolateralis muscle of the syrinx is either absent or reduced to a narrow ligament (also in Ciconiidae; Beddard 1898), and the furcula is fused with the tip of the sternal carina (this feature clearly evolved convergently as it is absent in early Miocene Pelecanidae; Milne-Edwards 1867–71: pl. 38).

The analysis by Hackett et al. (2008) strongly supports a clade including Ardeidae, Threskiornithidae, Scopidae,

Balaenicipitidae and Pelecanidae (Fig. 1b), which was also recovered by Ericson et al. (2006). This clade has, however, not been established with independent data and is poorly characterized from a morphological point of view. Although most of its component taxa share greatly enlarged and inflated maxillopalatine processes of the maxillaries as well as a very deep choanal part of the palatine, both features are absent in Ardeidae. In Ardeidae, Threskiornithidae, Balaenicipitidae and Pelecanidae, the carotic processes of the 8th–11th cervical vertebrae are further ankylozed along the midline and form a canal, but this feature is absent in Scopidae and also present in Sulidae and Anhingidae.

If the tree topology resulting from the Hackett et al. (2008) analysis correctly reflects the phylogenetic affinities, Pelecanidae are separated from other 'pelecaniform' birds by a number of 'ciconiiform' taxa, and the characters listed by Mayr (2003a, 2005a) to support a clade including Scopidae, Balaenicipitidae, Pelecanidae, Fregatidae and Suloidea evolved at least two times convergently. One of these features is the presence of a solid articulation between coracoid and furcula, which is accompanied by strongly developed articulation facets on both bones. Coracoid and furcula are fused in extant Fregatidae, but in stem group frigatebirds they are not, and articulation facets are likewise absent (Olson 1977). A convergent origin of this articulation in Pelecanidae and Suloidea is further suggested by the fact that the coracoidal articulation facet occupies the entire medial surface of the acrocoracoid process in the Suloidea, but is smaller and situated farther in sternal direction in Scopidae, Balaenicipitidae and Pelecanidae (Fig. 4h–j).

Pelecanidae, Fregatidae and Suloidea share a totipalmate foot, i.e., the hallux is directed medially and included in the foot webbing. This foot type does not occur in any non-'pelecaniform' taxon. In other birds with webbed feet the hindtoe is, however, very short, and there may exist ontogenetic or functional constraints, which enforce inclusion of a long hallux in the foot web (note that in early ontogenetic stages of Anatidae the hallux is also included in the webbing, whereas in adult birds only the three anterior toes are connected; Romanoff 1960: fig. 373).

Phaethontidae are widely separated from other 'pelecaniform' birds in the molecular analyses of Fain and Houde (2004), Ericson et al. (2006), and Hackett et al. (2008), in which they resulted in the 'metavian' taxon. After exclusion of the β-fibrinogen locus, nuclear sequences recovered a Phaethontidae/Musophagiformes clade, but this grouping did not receive significant support (Fig. 3b; Ericson et al. 2006). Analysis of mitochondrial sequences by Brown et al. (2008) supported sister group relationship between the clades (Phaethontidae + Sphenisciformes) and (Fregatidae + Suloidea), but another analysis of mitochondrial data resulted in sister group relationship between Phaethontidae and Accipitridae, with the clade including these two taxa being widely separated from Fregatidae (Morgan-Richards et al. 2008). In tropicbirds, the urohyal bone is vestigial, and Phaethontidae share other morphological features with Fregatidae and Suloidea, such as a greatly enlarged dorsal tympanic recess that is situated rostrally to the articular facets of the quadrate, and an articulation between the furcula and the sternal keel. Because molecular data do not yield a strongly based placement of tropicbirds, their position in the 'waterbird assemblage' has not been refused (see also Mayr and Clarke 2003; Livezey and Zusi 2007). I assume that it more correctly reflects the true phylogenetic affinities of these birds, and that their separation in the 'metavian' taxon is an artefact of the β-fibrinogen sequences.

Sphenisciformes (penguins), Gaviiformes (loons), and Procellariiformes (tubenoses and allies)

The exact affinities of penguins within the 'waterbird assemblage' are controversial, but most often Procellariiformes were considered to be their closest relatives (e.g., Livezey and Zusi 2007). However, the seven characters listed as diagnostic apomorphies of a Sphenisciformes/Procellariiformes clade by Livezey and Zusi (2007: table 2) do not constitute compelling evidence, as some are poorly defined or incomprehensible (e.g., derived similarities in the lacrimo-ectethmoidal region and a straight shaft of the humerus) and others, such as the alleged occurrence of tubular nostrils in the early ontogeny of penguins need to be verified in studies with a broader taxon sampling (see also Hieronymus and Witmer 2010: 599). It has also been assumed that Sphenisciformes and Gaviidae form a clade (Olson 1985), but this hypothesis was not evaluated in a cladistic context and is not supported by molecular data.

A morphology-based analysis that included the extinct Plotopteridae, penguin-like birds of the Northern Pacific (Mayr 2005a), resulted in a sister group relationship between Sphenisciformes and the Suloidea, with Fregatidae, Pelecanidae, Balaenicipitidae and Scopidae as successive sister taxa of the Plotopteridae/Sphenisciformes/Suloidea clade. To account for the molecular results, which strongly support a Fregatidae/Suloidea clade to the exclusion of Sphenisciformes, a modified hypothesis was presented by Mayr (2009), who considered the (Plotopteridae + Sphenisciformes) clade to be the sister taxon of the clade (Fregatidae + Suloidea). Derived characters shared by Sphenisciformes, Fregatidae and Suloidea that are absent in procellariiform birds include, among others (Mayr 2005a), an abbreviated and stocky tarsometatarsus, a single-lobed nasal gland that has only a single efferent duct, coating of the eggshell with a layer of amorphous calcium carbonate, and feeding of the young down the gullet of the adults. Penguins do, however, not exhibit the derived morphology of the hyoid apparatus, which is characteristic for Fregatidae and Suloidea and also occurs in Phaethontidae.

Sphenisciformes indeed resulted as sister taxon of the Fregatidae/Suloidea clade in the analysis by Fain and Houde (2004), and as noted earlier, mitochondrial data recovered sister group relationship between the clades (Phaethontidae + Sphenisciformes) and (Fregatidae + Suloidea) (Brown et al. 2008). In most analyses of Ericson et al. (2006), both of the concatenated and the individual sequences, the position of Sphenisciformes within the 'waterbirds assemblage' was not resolved, the sole exception being an analysis that was rooted with Galloanseres instead of palaeognathous birds (Ericson et al. 2006: fig. ESM-7), which resulted in a polytomy including Sphenisciformes, Ciconiidae and the clade (Fregatidae + Suloidea). Hackett et al. (2008), however, recovered sister group relationship between Sphenisciformes and Procellariiformes, and this result received a high bootstrap support; unfortunately, the authors did not indicate whether the clade was also retained in analyses of individual gene partitions. Analysis of mitochondrial and nuclear genes by van Tuinen et al. (2001) also supported sister group relationship between tubenoses and penguins. Other analyses of nuclear data did not conclusively resolve the affinities of penguins, but did not

recover sister group relationship to either procellariiform birds or the clade (Fregatidae + Suloidea) (Cracraft et al. 2004: fig. 27.4; Chubb 2004; Simon et al. 2004; Watanabe et al. 2006a; Slack et al. 2006).

Much new data on early Paleogene Sphenisciformes has become available in the past years (see Mayr 2009). Most notable among the recent discoveries are the earliest known penguins, from the Paleocene of New Zealand (Slack et al. 2006), whose osteology is different from that of plotopterids in several aspects (contrary to plotopterids, for example, the furcula lacks a well-developed articulation facet for the acrocoracoid, and unlike in plotopterids and crown group, Sphenisciformes the corpus of the scapula is not greatly widened). New material was also described for plotopterids (Sakurai et al. 2008), and a detailed description of a putative plotopterid skull figured by Hasegawa et al. (1979) is still pending. It is to be hoped that once these new data are brought together and analysed, they will shed more light on the affinities of penguins.

Sister group relationship between Gaviiformes and Sphenisciformes is not supported by any of the above molecular analyses. Gaviiformes resulted as sister taxon of a strongly supported clade including Procellariiformes, Sphenisciformes, 'Ciconiiformes' and 'Pelecaniformes' in the Hackett et al. (2008) study. Retroposon data also indicate a position of Gaviiformes outside a clade including Procellariiformes, Ciconiidae and Sphenisciformes (Watanabe et al. 2006b; this study did not include Fregatidae or representatives of the Suloidea). Morphological characters in support of a sister group relationship between Gaviiformes and all other taxa of the 'waterbird assemblage' have not yet been identified, but the beak of loons lacks the above-mentioned furrow distal of the nasal openings, that is characteristic for Procellariiformes, Sphenisciformes, and most 'Ciconiiformes' and 'Pelecaniformes'.

'Gruiformes' (cranes, rails, and allies)

All molecular analyses with a sufficiently broad taxon sampling do not recover monophyly of the traditional 'Gruiformes', which is likewise not well supported on morphological grounds. Turnicidae are part of Charadriiformes, and Cariamidae appear to be more closely related to 'falconiform' birds and the 'higher landbird assemblage'.

Molecular studies congruently resulted in sister group relationship between Ralloidea and Gruoidea, i.e., between the clades (Rallidae + Heliornithidae) and [Psophiidae + (Aramidae + Gruidae)] (Cracraft et al. 2004: fig. 27.7; Fain and Houde 2004; Ericson et al. 2006; Fain et al. 2007; Hackett et al. 2008; Yang et al. 2010). A clade including these taxa is strongly supported by individual analyses of multiple gene loci (Ericson et al. 2006: figs. ESM 1-5; Hackett et al. 2008: fig. 1) and may be referred to as core-Gruiformes (Fain et al. 2007). So far, few morphological apomorphies of these birds were identified, which is mainly because of the fact that Heliornithidae exhibit a highly apomorphic morphology. Most core-Gruiformes share, however, a narrow, dorsally projecting hook-like projection on the caudal end of mandible (except Psophiidae, very weakly developed in Heliornithidae), well-developed supraorbital processes (except Psophiidae), a widened rostral end of the pterygoid; an elongate and narrow sternum (except Heliornithidae), intratendinous ossifications along the leg bones, and a pelvis with a completely closed

iliosynsacral canal (except Heliornithidae and Fulicinae [Rallidae]) and a deeply excavated caudal recess (Mayr 2008a).

Monophyly of Heliornithidae, Psophiidae, Aramidae and Gruidae is uncontested, but it is notable that the analysis by Hackett et al. (2008) resulted in paraphyly of Rallidae with respect to Heliornithidae, which were recovered as sister taxon of the rallid Sarothrura. This finding, which was not further discussed by the authors, was strongly supported with a bootstrap support of 100%, and a sister group relationship between Heliornithidae and Sarothrura was also noted by Fain et al. (2007). In most osteological features, Sarothrura resembles other Rallidae, but the taxon shares a previously unrecognized derived hypotarsus morphology with Heliornis (tarsometatarsi of the two other sungrebe taxa were not available to me), with the tendon of the flexor perforatus digiti II muscle being enclosed in a bony canal (Fig. 4k–m). This feature alone does not provide strong evidence for paraphyly of Rallidae, but most of the osteological differences between rails and sungrebes pertain to the highly apomorphic morphology of the sternum, pelvis and hindlimbs of the latter. Certainly, position of sungrebes within rails is no less likely than that of the likewise morphologically aberrant Turnicidae within Charadriiformes, and the hypothesis of rallid paraphyly needs to be scrutinized in future studies with a more comprehensive taxon sampling. Usually, the morphologically distinct Himantornis is considered the sister taxon of other Rallidae (e.g., Olson 1973; Livezey 1998), and if the molecular phylogenies correctly nest Himantornis within Rallidae, there must have been a high degree of homoplasy in the evolution of rails.

Earlier authors most often considered Otididae to be closely related to either 'gruiform' or charadriiform birds (e.g., Fürbringer 1888; Gadow 1893), but analyses of morphological data did not yield convincing and well-supported tree topologies concerning the affinities of bustards (Mayr and Clarke 2003; Livezey and Zusi 2007). Otididae were recovered as sister taxon of a clade including Cuculiformes and core-Gruiformes in the analysis by Hackett et al. (2008), but this grouping received low bootstrap support. In the primary analysis by Ericson et al. (2006), bustards were placed in a polytomy with Cuculiformes, Musophagiformes, core-Gruiformes and the taxa of the 'waterbird assemblage'; after exclusion of β-fibrinogen sequences, they resulted as sister taxon of a clade including Mesitornithidae, Phoenicopteriformes/Podicipediformes, Charadriiformes and core-Gruiformes (Fig. 3b; Ericson et al. 2006). Analysis of mitochondrial data by Brown et al. (2008) supported sister group relationship between Otididae and core-Gruiformes, whereas an analysis of complete mitochondrial genomes with a less dense taxon sampling (Yang et al. 2010) placed Otididae in a polytomy, together with core-Gruiformes, Mesitornithidae and Charadriiformes. In concordance with earlier hypotheses, most molecular analyses thus support close affinities between Otididae and either core-Gruiformes or Charadriiformes, with Cuculidae and Musophagidae being potential further candidates as closest extant relatives.

Sister group relationship between the South American Eurypygidae and the New Caledonian Rhynochetidae, which contain a single species each, was already assumed by 19th-century authors (e.g., Fürbringer 1888) and is supported by virtually all analyses of molecular and morphological data (e.g., Houde et al. 1997; Mayr and Ericson 2004; Ericson et al. 2006; Livezey and Zusi 2007; Hackett et al. 2008;

Chojnowski et al. 2008). Both taxa share a suite of derived morphological characters including schizorhinal nostrils, a notarium, a deep incision between ilium and ischium in the caudal margin of pelvis, and powder down patches. The Eurypygidae/Rhynochetidae clade was placed into 'Metaves' in the analyses of Fain and Houde (2004), Ericson et al. (2006), and Hackett et al. (2008); after exclusion of β fibrinogen sequences, it resulted as sister taxon of Cuculiformes in the analysis by Ericson et al. (2006) (Fig. 3b). Analysis of clathrin heavy chain genes supported sister group relationship between (Eurypygidae + Rhynochetidae) and Falconidae (Chojnowski et al. 2008), whereas c-myc sequences recovered sister group relationship to Ciconiidae (Cracraft et al. 2004: fig. 27.4). None of these groupings received appreciable bootstrap/jackknife support, and current molecular data therefore do not shed light on the affinities of sunbittern and kagu.

The Madagascan Mesitornithidae are among the few avian taxa not studied by Fürbringer (1888) and Sibley and Ahlquist (1990). Although these birds were traditionally placed in the 'Gruiformes', few anatomical studies actually exist, and only recently mesites were included in analyses with a comprehensive taxon sampling. Mayr and Ericson (2004) hypothesized that Mesitornithidae are the sister taxon of Cuculiformes, whereas they resulted as sister taxon of Turnicidae in Livezey and Zusi's (2007) study. Mesitornithidae are part of 'Metaves' (Fain and Houde 2004; Ericson et al. 2006; Hackett et al. 2008). In the Ericson et al. (2006) study, they resulted as sister taxon of Phoenicopteriformes and Podicipediformes, and the clade including these taxa was in turn placed in a polytomy together with Charadriiformes and core-Gruiformes. The (Mesitornithidae + [Phoenicopteriformes + Podicipediformes]) clade was recovered in an analysis of concatenated sequences of four nuclear genes excluding β-fibrinogen (Fig. 3b; Ericson et al. 2006) and was also retained with parsimony jack-knifing (Ericson et al. 2006: fig. ESM-8); analysis of β-fibrinogen sequences supported a clade (Phoenicopteriformes + Mesitornithidae) (Fig. 3a; Ericson et al. 2006), whereas analyses of c-myc sequences resulted in a clade (Podicipediformes + [Megapodiidae + Mesitornithidae]) (Ericson et al. 2006: fig. ESM-1). In Hackett et al.'s (2008) analysis, the Phoenicopteriformes/Podicipediformes clade resulted as sister taxon of a clade including Phaethontidae, Pteroclidae, Mesitornithidae and Columbidae, but this grouping received no significant support (Fig. 1b). Analysis of clathrin heavy chain genes (Chojnowski et al. 2008) recovered a clade {(Phoenicopteriformes + Ciconiidae) + [Mesitornithidae + (Psophiidae + Rallidae)]}; taxon sampling was, however, limited and only the (Psophiidae + Rallidae) clade was strongly supported. Complete mitochondrial genomes indicated sister group relationship between Mesitornithidae and Charadriiformes, and the clade including these two taxa was in turn recovered as sister taxon of core-Gruiformes (Yang et al. 2010; Phoenicopteriformes and Podicipediformes were not included in the analysis). In summary, molecular analyses including Mesitornithidae, Phoenicopteriformes and Podicipediformes support a close relationship between these three taxa, and there is evidence from different gene loci that they form a clade (although such was only obtained in analyses of concatenated sequences of different gene loci, two individual gene loci recovered close affinities between Mesitornithidae and either Phoenicopteriformes or Podicipediformes; see also Mayr 2008a).

Musophagiformes (turacos), Cuculiformes (cuckoos), and Opisthocomiformes (hoatzin)

Analyses of morphological data support sister group relationship between the zygodactyl Cuculiformes and the semizygodactyl Musophagiformes (Mayr and Clarke 2003; Livezey and Zusi 2007), which was also assumed by most earlier authors (see, however, Berger 1960; Mayr and Ericson 2004). Molecular analyses, by contrast, do not recover a Cuculiformes/Musophagiformes clade.

As detailed earlier, sequence data place cuckoos and turacos in a clade together with Otididae, core-Gruiformes and the taxa of the 'waterbird assemblage'. Whereas this clade is adequately established for serious consideration, there exists no congruent evidence from independent gene loci for the position of cuckoos and turacos within it. Hackett et al.'s (2008) study recovered sister group relationship between Musophagiformes and the 'waterbird assemblage' as well as a clade (Cuculiformes + core-Gruiformes), but both groupings were weakly supported and are because of the influence of the β-fibrinogen gene sequences (Fain and Houde 2004; Hackett et al. 2008: fig. 1). Musophagiformes even resulted within the 'waterbird assemblage' in an analysis of mitochondrial sequences (Brown et al. 2008), but Cuculiformes were recovered as sister taxon of Trogoniformes in this study.

Morphological evidence for a clade including Cuculiformes, Musophagiformes, core-Gruiformes and taxa of the 'waterbird assemblage' has not been put forward, but as in the case of grebes and flamingos, detailed morphological comparisons between these birds were not performed. The skull of Musophagiformes and many Cuculiformes exhibits an uncinate bone (Fig. 4p–r), which within neognathous birds otherwise only occurs in Fregatidae, many Procellariiformes, some Threskiornithidae (Plegadis) and Charadriiformes, Otididae and Steatornithidae. The midsection of the dorsolateral iliac crest of the pelvis of Cuculiformes, Musophagiformes, Mesitornithidae, Heliornithidae and Rallidae also bears a prominent, laterally protruding flange or tubercle (Fig. 4n,o; see also Mayr and Ericson 2004). Cuckoos and turacos further share with core-Gruiformes and Otididae a deeply excavated caudal recess of the pelvis, and foramina in the pila otica (skull; Fig. 4s,t), which were considered a derived characteristic of 'gruiform' birds (e.g., Cracraft 1988; Mayr and Clarke 2003). Certainly, these derived similarities cannot be considered convincing morphological evidence for close affinities, but they may represent underlying apomorphies and illustrate that the molecular results are not in total conflict with morphological data.

Opisthocomiformes were traditionally considered to be most closely related to either Galliformes, Cuculiformes or Musophagiformes (see the review in Sibley and Ahlquist 1990). Galliform affinities are now clearly disproved, as the hoatzin was shown to be within Neoaves in all analyses. Analyses of morphological data supported sister group relationship between Opisthocomiformes and the clade (Cuculiformes + Musophagiformes) (Livezey and Zusi 2007), or sister group relationship between the clades (Cariamidae + Opisthocomiformes) and (Musophagiformes + Cuculiformes) (Mayr and Clarke 2003). Combined mitochondrial and nuclear sequences showed Opisthocomiformes and Musophagiformes to be sister taxa (Hughes and Baker 1999), but a study with a more comprehensive taxon sampling by Sorenson et al. (2003) did not support such a clade, and instead resulted in a weakly supported sister group relationship between Opisthocomiformes

and Columbidae, which was also recovered with the larger mitochondrial data set of Brown et al. (2008). The analyses by Fain and Houde (2004) and Ericson et al. (2006) placed Opisthocomiformes in the 'Metaves' taxon; after exclusion of β-fibrinogen sequences from the latter study, they resulted in a polytomy together with Musophagiformes, Phaethontidae, and a clade including core-Gruiformes, Charadriiformes, Mesitornithidae, Phoenicopteriformes and Podicipediformes (Fig. 3b; Ericson et al. 2006). The analysis by Hackett et al. (2008) also supported sister group relationship between Opisthocomiformes and a clade including the 'waterbird assemblage', core-Gruiformes, Cuculiformes, Musophagiformes and Otididae, but this grouping received no significant bootstrap support. Although molecular data thus do not conclusively resolve the position of Opisthocomiformes, they likewise do not strongly reject closer affinities to Cuculiformes and Musophagiformes, which remain to be considered in future analyses.

As noted by Mayr and Ericson (2004), Cuculidae and Musophagidae share unusual 'prong'-like projections on the hamuli of the distal barbulae of the wing feathers (Fig. 4u–w). These structures are also present in Opisthocomidae, Mesitornithidae and some Columbiformes, but comparative studies across comprehensive taxon samplings are needed before their phylogenetic value can be appreciated.

Phoenicopteriformes (flamingos) and Podicipediformes (grebes)

The affinities of the Phoenicopteriformes, which were among the long-standing problems in avian systematics, are now firmly established. Based on a molecular analysis, van Tuinen et al. (2001) first proposed that their closest extant relatives are not Anseriformes, Ciconiidae or Charadriiformes (e.g., Olson and Feduccia 1980), but the morphologically very dissimilar Podicipediformes. The flamingo-grebe clade, which was termed Mirandornithes by Sangster (2005), was subsequently supported by most molecular analyses including these two taxa, both of nuclear and mitochondrial sequences (e.g., Chubb 2004; Cracraft et al. 2004; Ericson et al. 2006; Hackett et al. 2008; Morgan-Richards et al. 2008). Mayr (2004) and Manegold (2006) identified morphological apomorphies that support this grouping, including the presence of fused thoracic vertebrae, an unusually high number of cervical vertebrae, nail-like ungual phalanges, eleven primaries (except for 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.

Storer (2006) and most recently, Livezey (in press a) harshly criticized the hypothesis of a sister group relationship between flamingos and grebes. However, although Livezey (in press a) correctly noted that many of the proposed synapomorphies shared by the two taxa exhibit homoplasy, this is also true for the characters supporting alternative placements of flamingos. Contrary to Livezey's (in press a) statement, molecular evidence for a Phoenicopteriformes/Podicipediformes clade is not contradictory but among the strongest for all avian higher-level clades, and to the best of my knowledge, there exists not a single molecular study, which supports his proposed alternative phylogeny, i.e., the traditional hypothesis of Podicipedidae/Gaviidae and Phoenicopteriformes/Ciconiidae clades (see also Mayr 2007).

Flamingos and grebes distinctly differ in both their external appearance and ecology, with the former being long-legged filter feeders, and the latter short-legged divers. The osteological differences are, however, bridged by the extinct Palaelodidae which, for example, exhibit the deep lower jaw of phoenicopteriform birds and a mediolaterally compressed tarsometatarsus as in Podicipediformes (Mayr 2004, 2009).

As detailed earlier, molecular studies indicate that Mesitornithidae may be the sister group of the flamingo/grebe clade. Phoenicopteriformes, Podicipediformes and Mesitornithidae are placed in the 'Metaves' taxon in the analyses by Fain and Houde (2004), Ericson et al. (2006) and Hackett et al. (2008). After exclusion of the β-fibrinogen gene, they resulted in a polytomy with Charadriiformes and core-Gruiformes (Fig. 3b; Ericson et al. 2006). Mitochondrial data supported sister group relationship between the Phoenicopteriformes/Podicipediformes clade and Charadriiformes (Brown et al. 2008; Morgan-Richards et al. 2008), but representatives of Mesitornithidae were not included in these studies.

A close relationship between Charadriiformes and Phoenicopteriformes was already assumed by Feduccia (1976) and Olson and Feduccia (1980), who did, however, not present unequivocal-derived character evidence in support of this hypothesis. Zusi and Storer (1969) mentioned that grebes share a derived morphology of the cervical longus colli ventralis muscle with Eurypygidae and Rhynochetidae, which is otherwise only known from Rheidae. Manegold (2006) noted that Phoenicopteriformes and Podicipediformes further share a derived morphology of the cervical vertebrae with sunbittern and kagu. Podicipediformes, Phoenicopteriformes, Mesitornithidae, Eurypygidae and Rhynochetidae also exhibit a notarium, and as part of 'Metaves', share derived properties of the β-fibrinogen gene.

In summary, the Phoenicopteriformes/Podicipediformes clade most likely is the sister taxon of Mesitornithidae, and the clade including these three taxa may be closest to either Charadriiformes, core-Gruiformes or Rhynochetidae and Eurypygidae. More research is, however, needed for a strongly based phylogeny.

Charadriiformes (shorebirds and allies)

Molecular data provide a congruent and robust phylogeny of charadriiform birds, and show that Turnicidae, which were traditionally classified into 'Gruiformes', are also nested within Charadriiformes (Ericson et al. 2003a; Paton et al. 2003; Paton and Baker 2006; Baker et al. 2007; Fain and Houde 2007). These studies further support three charadriiform clades, which were termed Scolopaci (Jacanidae, Rostratulidae, Pedionomidae, Thinocoridae, and Scolopacidae), Lari (Turnicidae, Dromadidae, Glareolidae except the Egyptian Plover *Pluvianus aegyptius*, Alcidae, Stercorariidae, Laridae, Sternidae [possibly paraphyletic; Baker et al. 2007], and Rhynchopidae), and Charadrii (Burhinidae, *P. aegyptius*, Chionidae, Pluvianellidae, 'Charadriidae' [paraphyletic], Ibidorhynchidae, Haematopodidae and Recurvirostridae).

Nuclear and mitochondrial sequence data congruently recovered a clade [Charadrii + (Scolopaci + Lari)] and sister group relationship between Stercorariidae and Alcidae, and all analyses in which the Turnicidae were included resulted in sister group relationship between buttonquails and the Lari (Ericson et al. 2003a; Paton et al. 2003; Baker et al. 2007; Fain and Houde 2007). Although several clades were already identified by earlier morphologists, the molecular tree topology is clearly distinguished from previous classifications based

on morphological data, which, for example, assumed a closer relationship between Scolopaci and Charadrii, and which set the Alcidae apart from all other charadriiform birds (Strauch 1978; Chu 1995). Livezey and Zusi's (2007) analysis did not support monophyly of either Scolopaci, Charadrii or Lari. The same is true for a reanalysis of an emended data set for Charadriiformes by Livezey (2009, in press b), which yielded a phylogeny that in most aspect is similar to that of Livezey and Zusi (2007). Neither Livezey and Zusi (2007) nor Livezey (in press b) listed the character evidence for their trees, and the character matrix of the latter study was not available at the time this review was submitted.

Of the three major charadriiform clades, only Scolopaci and Charadrii can be characterized with morphological apomorphies (Mayr in press), but because highly congruent tree topologies resulted from analyses of different gene loci, the molecular data are likely to reflect the true phylogenetic affinities of charadriiform birds.

Despite the fact that sequence data yielded strongly supported and congruent hypotheses for charadriiform interrelationships, they did not provide unambiguous evidence for the sister taxon of shorebirds so far. Hackett et al.'s (2008) analysis resulted in sister group relationship between Charadriiformes and a clade including 'Falconiformes' and the 'higher landbirds'. This weakly supported placement is, however, essentially because of the influence of the β-fibrinogen gene and was also obtained in analyses of this gene alone (Fig. 3a; Fain and Houde 2004; Ericson et al. 2006: ESM-4; Hackett et al. 2008: fig. 1). After exclusion of β-fibrinogen sequences, nuclear genes supported a position of Charadriiformes in a clade including core-Gruiformes, Mesitornithidae, Phoenicopteriformes and Podicipediformes (Fig. 3b; Ericson et al. 2006). As noted in the preceding section, mitochondrial data also supported close affinities between Charadriiformes and the Phoenicopteriformes/Podicipediformes clade.

Charadriiformes are morphologically diversified birds, and even if the highly aberrant Turnicidae are disregarded, it is difficult to diagnose the group with morphological characters. The single apomorphic feature that may be present in all representatives of the taxon is an unusually low electrophoretic motility of the malate dehydrogenase (Kitto and Wilson 1966; the properties of this enzyme are unknown for Turnicidae). Unfortunately, this feature appears to autapomorphic for Charadriiformes and does not provide clues about their sister taxon. As detailed by Mayr (in press), the stem species of Charadriiformes most likely had schizorhinal nostrils, which also occur in several of the core-Gruiformes (Aramidae, Gruidae, and many Rallidae) and in columbiform birds (see also sections on these taxa).

Columbiformes (doves and sandgrouse)

Whether Columbidae and Pteroclidae are each others closest relatives has been subjected to much debate. As noted by earlier authors (e.g., Fürbringer 1888; Gadow 1893; Stegmann 1968), the osteology of Columbidae and Pteroclidae is very similar, and both taxa agree in many derived features, such as the inflated pterygoids, the morphology of the ectethmoid/lacrimal complex, the presence of a notarium, the morphology of coracoid and sternum, the shape of the stocky humerus, the presence of a large internal index process on the proximal phalange of the major wing digit, and the shape of the wide pelvis. Morphological data thus clearly indicate that Columbidae and Pteroclidae are sister groups, and a clade including these two taxa was also obtained in the analyses by Mayr and Clarke (2003) and Livezey and Zusi (2007).

Analysis of nuclear gene sequences by Ericson et al. (2006) also supported a Columbidae/Pteroclidae clade, which was, however, not obtained in analyses of individual gene partitions. Hackett et al. (2008) recovered a clade [Pteroclidae + (Mesitornithidae + Columbidae)], which received no significant support. Mitochondrial data did not provide clear evidence for the affinities of columbiform birds, and whereas Columbidae and Pteroclidae were widely separated in the analysis by Brown et al. (2008), the study by Gibb and Penny (2010) resulted in a clade [Pteroclidae + (Columbidae + Falconidae)]. Molecular evidence for a Pteroclidae/Columbidae clade is thus not unambiguous, but in the light of the morphological data in support of it, and given the fact that there exists no strong evidence for an alternative placement, this clade can be considered reasonably well established.

The higher-level affinities of columbiform birds, however, are unresolved. Columbidae and Pteroclidae are placed in the 'metavian' taxon in analyses including β-fibrinogen sequences (Fain and Houde 2004; Ericson et al. 2006; Hackett et al. 2008). After exclusion of this gene, Ericson et al.'s (2006) analysis resulted in sister group relationship between Columbiformes and all other Neoaves. Clathrin heavy chain sequences, by contrast, supported affinities of Columbidae to the 'waterbird assemblage' and core-Gruiformes (Chojnowski et al. 2008). Earlier authors most often considered columbiform birds to be closely related to either Psittaciformes of Charadriiformes (Sibley and Ahlquist 1990). Morphological evidence for either hypothesis is, however, weak, and the derived similarities in the wing skeleton of parrots and doves are probably because of the presence of a large crop in these birds (Stegmann 1964). Likewise, no morphological apomorphies were described that are present in all charadriiform and columbiform birds, and the hypothesis of closer affinities is mainly based on derived similarities between Pteroclidae and some shorebird taxa (e.g., Fjeldså 1976). Columbiformes also share some derived characters with individual taxa of the Strisores ('caprimulgiform' and apodiform birds), such as an intertarsal sesamoid bone (present in Caprimulgidae and Nyctibiidae) and loss of one phalange of the fourth toe (Pteroclidae, Caprimulgidae, and some Apodidae), with whom they further share derived 'metavian' properties of the β-fibrinogen gene.

Strisores (nightjars and allies, swifts, and hummingbirds)

Paraphyly of the crepuscular or nocturnal 'Caprimulgiformes' with respect to Apodiformes is now well established, and in particular sister group relationship between the 'caprimulgiform' Aegothelidae and Apodiformes, which was first suggested in a study of morphological data, is strongly supported by many lines of independent morphological and molecular evidence (Mayr 2002, 2010; Mayr et al. 2003; Cracraft et al. 2004; Barrowclough et al. 2006; Ericson et al. 2006; Hackett et al. 2008; Pratt et al. 2009).

Mayr (2010) introduced the name Strisores for a clade including all 'Caprimulgiformes' and Apodiformes. This clade was obtained in analyses of multiple individual gene loci (Fig. 3; Ericson et al. 2006; Mayr 2008a, 2010; Hackett et al. 2008) and received high support in Hackett et al's (2008) study

(Fig. 1b); equal molecular evidence does not exist for alternative phylogenies. From a morphological point of view, however, Strisores are still ill-defined, and the only apomorphy recognized so far, an elongated crus longum of the ulnar carpal bone, also occurs in other avian groups (Mayr 2010).

'Caprimulgiform' birds distinctly differ in anatomical features, and analysis of morphological data resulted in a well-supported tree topology (Mayr 2010) that, except for the position of the Nyctibiidae, agrees with the results of the Hackett et al. (2008) study. Steatornithidae are the sister taxon of all other Strisores, which share a strongly protruding caudolateral angle of the palatine and a low number of less than 19 free praesacral vertebrae (Mayr 2010). Another apomorphy of a clade including all Strisores except Steatornithidae may be the capability of torpor, i.e., facultative hypothermic responses to environmental conditions, which was reported for Podargidae, Caprimulgidae, Aegothelidae, Apodidae and Trochilidae (Mayr 2010).

Caprimulgidae, Nyctibiidae, Aegothelidae and Apodiformes form a clade termed Cypselomorphae by Mayr (2002). These birds exhibit a short beak that is very wide at its base and with narial openings extending into its tip, a quadrate with a greatly reduced orbital process and caudal condyle, a very narrow distal portion of the mandibular rami, and a cerebellum with a reduced anterior lobe and particularly small folia II and III (Iwaniuk et al. 2006).

Sister group relationship between Caprimulgidae and Nyctibiidae is, among others, supported by an extremely wide lateral part of the palatine, a cone-like bony protrusion at the foramen for the optic nerve, a mandible with an intraramal joint and a greatly widened and flattened caudal section, and presence of an intertarsal sesamoid bone. Molecular data, by contrast, indicate sister group relationship between Nyctibiidae and Steatornithidae (Hackett et al. 2008), which would imply homoplasy of at least 13 morphological features, some of which are unparalleled within Aves (Mayr 2010). However, molecular evidence for a Steatornithidae/Nyctibiidae clade is weak, as this clade received only low support in Hackett et al's. (2008) analysis and did not result from other analyses of sequence data (Mariaux and Braun 1996; Barrowclough et al. 2006; Ericson et al. 2006; Brown et al. 2008). Sister group relationship between Nyctibiidae and Caprimulgidae thus more likely reflects the true phylogenetic affinities of these birds, and Strisores are among those avian taxa where morphological data do contribute to a better understanding of the phylogenetic relationships (Mayr 2010).

Analyses of nuclear gene sequences placed Strisores in the 'Metaves' taxon (Fain and Houde 2004; Ericson et al. 2006; Hackett et al. 2008). After exclusion of the β-fibrinogen gene, they resulted as sister taxon of a clade including Falconiformes and the 'higher landbirds' (Fig. 3b; Ericson et al. 2006; see also Cracraft et al. 2004: fig. 27.4). Mitochondrial evidence is inconclusive and either indicated sister group relationship between Strisores and a clade including Falconiformes, Strigiformes, and taxa of the 'waterbird assemblage' (Pratt et al. 2009), or supported a polyphyletic Strisores, whose component taxa are widely scattered over the tree (Brown et al. 2008).

Morphological data likewise do not provide conclusive clues on the sister taxon of Strisores. In part this is because of the anatomical diversity of these birds and the difficulties in reconstruction the ancestral states of critical features (it is, for example, equally parsimonious to assume that the stem species had basipterygoid processes and that these were lost in the

lineages leading to Podargidae and the Aegothelidae/Apodiformes clade, or that these processes evolved in the lineages leading to Steatornithidae and the Caprimulgidae/Nyctibiidae clade). The analysis by Livezey and Zusi (2007) resulted in sister group relationship between the 'Caprimulgiformes'/Apodiformes clade and the 'higher landbird' clade (Fig. 2b), but this grouping received low bootstrap support, and apomorphies were not listed.

The 'landbird assemblage'

The analyses by Ericson et al. (2006) and Hackett et al. (2008) supported a clade including the 'gruiform' Cariamidae, as well as Falconiformes, Psittaciformes and the taxa of the traditional Anomalogonatae, i.e., the 'higher landbirds' and Strigiformes. This grouping, was termed 'land bird clade' by Hackett et al. (2008) and received high bootstrap support in their analysis (Fig. 1b). It was congruently recovered in separate analyses of β-fibrinogen sequences and, further involving Strisores, four other nuclear genes (Fig. 3; Ericson et al. 2006). 'Anomalogonatous' birds, which are characterized by the loss of the ambiens muscle (e.g., Mayr et al. 2003), did not form a clade in the above studies.

Derived morphological characters shared by all taxa of the 'landbird assemblage' are unknown, and especially position of the South American Cariamidae within this group is unexpected, although affinities between seriemas and diurnal birds of prey were previously suggested (see Sibley and Ahlquist's 1990 review). The two extant species of Cariamidae are but relics of a group that underwent a radiation in the early Cenozoic and has a substantial fossil record in the Old World (Mayr 2009). Seriemas were traditionally assigned to the 'Gruiformes', but morphological evidence for this classification has always been weak. Concerning possible affinities with Falconidae (Ericson et al. 2006; Hackett et al. 2008), it is notable that some stem group representatives of the Cariamidae, i.e., the South American Phorusrhacidae, were predatory birds with a raptor-like skull (Mayr 2009).

Falconiformes (diurnal birds of prey) and Strigiformes (owls)

In their traditional composition, 'Falconiformes' include Cathartidae, Sagittariidae, Accipitridae, and Falconidae. Many 19th century ornithologists considered these diurnal birds of prey to be closely related to the nocturnal Strigiformes. Mainly owing to the work by Fürbringer (1888) and Gadow (1893), both taxa were separated and Strigiformes classified next to 'caprimulgiform' birds, although some cladistic analyses of osteological characters indeed result in a clade including 'falconiform' and strigiform birds (Mayr and Clarke 2003; Livezey and Zusi 2007).

Within 'Falconiformes', the affinities of the Cathartidae were controversially discussed by earlier authors, some of whom considered New World vultures to be more closely related to 'ciconiiform' birds (e.g., Ligon 1967). A close relationship between Accipitridae and Falconidae has been questioned by only few authors (e.g., Starck 1959; Olson 1985), but analyses of nuclear gene sequences congruently and strongly support a clade (Sagittariidae + Accipitridae) to the exclusion of the Falconidae (Cracraft et al. 2004; Fain and Houde 2004; Ericson et al. 2006; Hackett et al. 2008; note that the analysis by Brown et al. 2008 was constrained to retain this clade). There exists little morphological evidence in support of this

clade, but Sagittariidae and Accipitridae share a derived syrinx morphology (Griffiths 1994) and also differ from other 'Falconiformes' in that they lack the plantaris muscle, which is present in Falconidae, Cathartidae, and most other birds (George and Berger 1966: 442; see also Mayr 2008a).

Cathartidae resulted as sister group of the Accipitridae/Sagittariidae clade in the analyses by Ericson et al. (2006) and Hackett et al. (2008). Although bootstrap support for a [Cathartidae + (Accipitridae + Sagittariidae)] clade was low in the latter study, it was recovered in four individual gene partitions (Hackett et al. 2008: fig. 1) and was also obtained in an analysis of ornithine decarboxylase sequences (Ericson et al. 2006: fig. ESM-5), which were not included in Hackett et al.'s (2008) study. Molecular data therefore confirm close affinities between New World vultures and non-falconid diurnal birds of prey.

Falconidae resulted as sister taxon of a clade (Psittaciformes + Passeriformes) in Hackett et al's. (2008) analysis. This grouping received only moderate bootstrap support, but a clade including these three taxa was recovered in separate analyses of two loci, i.e., introns of the eukaryotic translation elongation factor and somatotropin introns (Hackett et al. 2008: fig. 1). Notably, a clade including Cariamidae, Falconidae, Psittaciformes and Passeriformes also resulted from Ericson et al's (2006) analysis, which did not include sequences of the latter two genes. This clade was not supported by any of the individual gene sequences included in Ericson et al.'s (2006) analysis, but resulted from concatenated data of four genes (Fig. 3b), of which only the myoglobin intron was also analysed by Hackett et al. (2008). Mitochondrial data do not conclusively resolve the affinities of diurnal birds of prey, and either support sister group relationship between Falconidae and Accipitridae (Slack et al. 2006, 2007), a clade including Falconidae, Coliidae and Podargidae (Brown et al. 2008), or a clade [Falconidae + (Strigiformes + Accipitridae)] (Pratt et al. 2009).

Sequence data do not conclusively resolve affinities of Strigiformes, which were placed in a polytomy with various 'falconiform' and 'higher landbird' taxa in the Ericson et al. (2006) study. The analysis by Hackett et al. (2008) resulted in sister group relationship between Strigiformes and Coliidae, but this grouping received no significant support. Falconidae and Strigiformes share derived features of the cranial muscles that are innervated by the trigeminus nerve (e.g., Starck 1959). In their study of the avian egg white proteins, Sibley and Ahlquist (1972: 105) found that the 'patterns of the falcons are unlike those of the hawks and match almost exactly those of the owls, especially *Tyto* […]. There is less overall resemblance between accipitrids and *Falco* patterns than between *Falco*, *Tyto* and the strigid owls'. Based on the DNA–DNA hybridization studies, however, Sibley and Ahlquist (1990) concluded that Strigiformes and 'Caprimulgiformes' form a clade, although in several of the melting curves underlying their analysis owls are next to the Falconidae (their Figs. 89, 98, 139, 142).

Passeriformes (passerines), Psittaciformes (parrots), and Coliiformes (mousebirds)

Passeriformes constitute the vast majority of extant bird species, and because few comprehensive morphological studies were undertaken, molecular data significantly contributed to a better understanding of passeriform phylogeny. A major novel finding of sequence-based analyses is the recognition of sister group relationship between the New Zealand Acanthisittidae and all other extant passeriform birds, the Eupasseres, which fall into two clades, the predominantly New World Suboscines and the Oscines (Barker et al. 2002, 2004; Ericson et al. 2002, 2003b). The interrelationships of suboscine and oscine passerines are addressed in numerous recent studies, and the reader is referred to, e.g., Chesser (2004), Harshman (2007), Johansson et al. (2008), Treplin et al. (2008), and Claramunt (2010) for current reviews.

The sister taxon of Passeriformes is still controversial. Most earlier authors considered them closest to either piciform or 'coraciiform' birds (e.g., Cracraft 1988), and Livezey and Zusi's (2007) analysis indeed placed passerines in a polytomy with Piciformes and 'Coraciiformes' (see also Manegold 2005). Fain and Houde's (2004) study of β-fibrinogen sequences also resulted in sister group relationship between Passeriformes and a clade including Piciformes and 'Coraciiformes' except Bucerotes, but the grouping was not robust to bootstrapping. Mitochondrial data recovered sister group relationship between Passeriformes and all other neoavian taxa (e.g., Brown et al. 2008; Morgan-Richards et al. 2008). The analyses by Ericson et al. (2006) and Hackett et al. (2008) supported inclusion of Passeriformes in a clade together with Cariamidae, Falconidae and Psittaciformes. Whereas this clade as a whole, as well as sister group relationship between Passeriformes and the zygodactyl Psittaciformes, received bootstrap support values below 80% (Fig. 1b; Hackett et al. 2008), the Passeriformes/Psittaciformes clade was recovered by independent analyses of three nuclear genes, i.e., the eukaryotic translation elongation factor (Hackett et al. 2008: fig. 1B), the PEPCK gene (Sorenson et al. 2003: fig. 3), and c-*myc* (Cracraft et al. 2004: fig. 27.4; see also Ericson et al. 2006: fig. ESM-1). No morphological characters are known that convincingly support a Passeriformes/Psittaciformes clade, but it is notable that Passeriformes have a zygodactyl sister taxon, the extinct Zygodactylidae (Mayr 2008b, 2009).

Berman and Raikow (1982) recognized that Psittaciformes and Coliiformes share a unique derived morphology of the deep flexor tendons. Concerning molecular data, however, sister group relationship between Psittaciformes and Coliiformes is only supported by the analyses of nuclear ZENK gene sequences (Chubb 2004). The study by Hackett et al. (2008) showed Coliidae and Strigiformes to be sister taxa, but the grouping received low bootstrap support. Other analyses of molecular data also did not conclusively resolve the affinities of mousebirds (Poe and Chubb 2004; Ericson et al. 2006; Brown et al. 2008).

'Coraciiformes' (rollers and allies), Piciformes (woodpeckers and allies), and Trogoniformes (trogons)

All current analyses of morphological and molecular data support monophyly of Piciformes, i.e., sister group relationship between Pici and the Neotropic Galbulae (Johansson and Ericson 2003; Mayr et al. 2003; Manegold 2005; Ericson et al. 2006; Livezey and Zusi 2007; Hackett et al. 2008). The traditional 'Coraciiformes', however, have always been an ill-defined taxon, and molecular analyses show the taxon to be paraphyletic with respect to Piciformes (Mayr et al. 2003; Cracraft et al. 2004; Fain and Houde 2004; Ericson et al. 2006; Hackett et al. 2008). In the following, the 'coraciiform' taxa are referred to as Coraciiformes *sensu stricto* (Brachypteraciidae and Coraciidae), Alcediniformes (Meropidae,

Alcedinidae, Todidae, and Momotidae) and Bucerotes (Upup-iformes and Bucerotiformes).

A clade including Coraciiformes *sensu stricto*, Alcediniformes, Piciformes and Bucerotes received strong support in the Ericson et al. (2006) and Hackett et al. (2008) studies and was recovered in separate analyses of three gene loci (Hackett et al. 2008: fig. 1). From a morphological point of view, this clade may be supported by the fact that the mandible of the hatchling projects distinctly beyond the upper beak, which, however, is also the case in some passerines and few other Neoaves (Manegold 2005). Bucerotes were recovered as sister taxon of Coraciiformes *sensu stricto*, Alcediniformes, and Piciformes in the study of Hackett et al. (2008) and a four-gene analysis by Ericson et al. (2006) (Fig. 3b; the complete data set placed Bucerotes in a polytomy). Morphological data, by contrast, support sister group relationship between Bucerotes and Piciformes (Manegold 2005; Mayr 2005c), or a clade including Bucerotes and all other 'coraciiform' birds (Livezey and Zusi 2007).

Molecular data congruently indicate a clade including Coraciiformes *sensu stricto* and Alcediniformes (Mayr et al. 2003; Ericson et al. 2006; Hackett et al. 2008), which is also recovered in some analyses of morphological data (Manegold 2005). Alcediniform birds share a number of features, including a derived morphology of the columella (also in Trogoniformes and the passeriform Suboscines), an unusually wide proximal end of the basal phalange of the hallux, a unique derived arrangement of the deep flexor tendons, and a syndactyl foot in which the three fore-toes are extensively fused (George and Berger 1966: 448; Feduccia 1977; Mayr 1998; Manegold 2005). Alcediniform birds show, however, a great morphological variety, and their monophyly is not supported by Livezey and Zusi's (2007) study. Likewise, an alcediniform clade was not recovered in the analysis by Hackett et al. (2008), in which Meropidae resulted as sister taxon of a weakly supported clade including Coraciidae/Brachypteraciidae, Todidae, Alcedinidae and Momotidae (the same tree topology resulted from an analysis of mitochondrial sequences by Brown et al. 2008; in which, however, constraints were enforced to recover a non-monophyletic Alcediniformes). The primary analysis by Ericson et al. (2006) placed Meropidae in a polytomy with Coraciiformes *sensu stricto* and the remaining Alcediniformes, but an alcediniform clade was obtained in an analysis of four nuclear genes (Fig. 3b; Ericson et al. 2006). In the absence of strongly supported alternative phylogenies, I therefore consider Alcediniformes monophyletic. Traditional ideas about the interrelationships of alcediniform birds, however, are likely to be incorrect. Whereas most earlier authors assumed that the New World Todidae and Momotidae are sister groups, molecular data support a clade [Todidae + (Momotidae + Alcedinidae)], which is congruently obtained in analysis of β-fibrinogen sequences and those excluding this gene (Fig. 3; Ericson et al. 2006), and which received strong support in the study of Hackett et al. (2008).

The Madagascan Leptosomidae, which include a single extant species, are usually considered to be most closely related to Coraciidae and Brachypteraciidae. On morphological grounds, 'coraciiform' affinities of the cuckoo-roller were, however, already questioned by Mayr (1998), and these are also not supported by molecular analyses (Mayr et al. 2003; Ericson et al. 2006; Hackett et al. 2008; Mayr 2008c; contra Sibley and Ahlquist 1990; Cracraft et al. 2004; Livezey and Zusi 2007). Although molecular analyses indicate a position of

Leptosomidae within the 'landbird assemblage', their exact affinities remain unresolved, and in different studies the courol resulted as sister taxon of Falconidae (Mayr et al. 2003: fig. 5), Strigidae (Ericson et al. 2006: fig. ESM-3), Trogoniformes (Ericson et al. 2006: fig. ESM-5), or a clade including all other 'Coraciiformes', Piciformes, and Trogoniformes (Hackett et al. 2008).

Trogoniformes were often considered to be most closely related to 'coraciiform birds', with whom they share syndactyl feet. Trogons further exhibit the derived 'alcediniform' morphology of the columella (Feduccia 1977; Maurer and Raikow 1981). Mayr (2003b) assumed sister group relationship between Trogoniformes and the 'caprimulgiform' Steatornithidae. Although this hypothesis is now conclusively disproved, it is notable that an analysis of c-*myc* sequences supports a clade including Trogoniformes and part of Strisores (Cracraft et al. 2004: fig. 27.4). Analysis of mitochondrial and ribosomal sequences by Espinosa de los Monteros (2000) supported sister group relationship between Trogoniformes and Coliiformes, which also resulted from Livezey and Zusi's (2007) analysis, whereas another analysis of mitochondrial data resulted in sister group relationship between Trogoniformes and Cuculiformes (Brown et al. 2008). Nuclear gene sequences, by contrast, recovered a sister group relationship between Trogoniformes and a clade including non-leptosomid 'Coraciiformes' and Piciformes (Mayr et al. 2003: fig. 6; Hackett et al. 2008). There exists, however, no congruent molecular evidence for this grouping, and the affinities of trogons are therefore not yet well established.

Conclusion

It is a widely held belief among molecular systematists that 'molecular data are not as influenced by the ecology and habits of organisms and thus are more appropriate for phylogeny estimation' (van Tuinen 2002: 5; see also Bennu 2004; Harshman 2007). Regarding the analysis of very large data sets, molecular data may indeed be superior to morphological ones, which are prone to unfavourable signal-to-noise ratios because of variable character complexity (Mayr 2008a). Disparate morphological evolution and convergence further conceal the true affinities of closely related taxa, and molecular analyses recovered several well-supported clades, which would probably not have been identified on the basis of morphological data alone.

On the other hand and as detailed earlier, current molecular data do not conclusively resolve the position of some taxa, whose affinities are well supported by morphological evidence, such as Nyctibiidae or Pteroclidae. The 'metavian' taxon most likely is another example where analyses of gene sequences lead to questionable phylogenies and demonstrates that molecular data are not free of homoplasy. 'Metaves' are only retained in studies including one locus (intron 7) of the β-fibrinogen gene, and no more than 22 nucleotide sites of that locus are responsible for the grouping (Morgan-Richards et al. 2008). Metaves and Coronaves are each characterized by two indels of the β fibrinogen intron, but three of these four indels exhibit homoplasy and also occur in neornithine taxa outside the respective clades (Fain and Houde 2004: 2562); homoplasy is further indicated by the fact that the 'metavian' Opisthocomiformes resulted within 'Coronaves' in Hackett et al's (2008) analysis. For some 'metavian' taxa, there exists alternative molecular evidence, which is in better concordance with morphological data (see above concerning, e.g.,
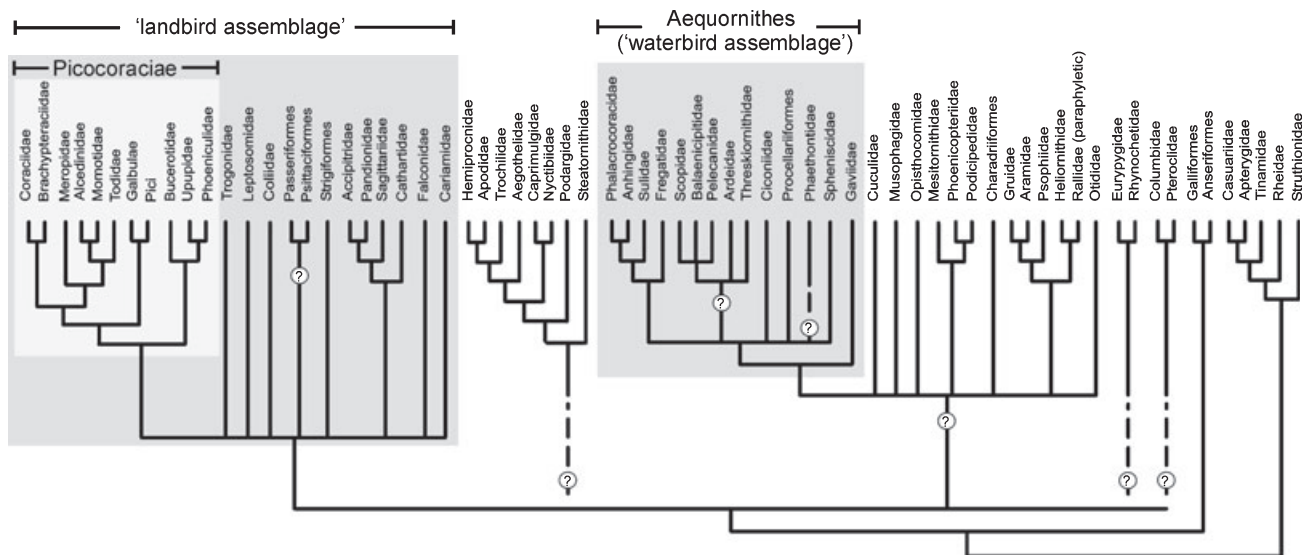
Fig. 5. Summary phylogenetic hypothesis as discussed in the present review. Question marks on dashed lines indicate that the position of a clade is uncertain, whereas question marks on continuous lines demark weakly supported clades. The shaded fields outline composition of the 'land bird assemblage' and the newly introduced terms Picocoraciae and Aequornithes ('waterbird assemblage')

Phaethontidae). Most likely, thus, 'Metaves' do not constitute a monophyletic group, and recovering the true phylogenetic affinities of some of its component taxa is among the major challenges of avian higher-level phylogeny.

Figure 5 depicts a hypothesis on the interrelationships of extant Neornithes, which summarizes the considerations in the preceding sections of this review. Clades based on equivocal evidence are denoted by question marks, the dotted lines leading to Strisores, Columbiformes and Eurypygidae/Rhynochetidae indicate the uncertain position of these taxa, which may be within one of the larger clades. To ease future discussions, I propose the following names for two as yet unnamed well-supported clades, which emerged from recent analyses:

(1) Picocoraciae: for the clade including Coraciiformes *sensu stricto*, Alcediniformes, Piciformes and Bucerotes.

(2) Aequornithes (from Lat. aequor, expanse of water): for the taxa of the 'waterbird assemblage', i.e., the least inclusive clade containing Gaviidae and Phalacrocoracidae.

I do not suggest a new name for the 'landbird assemblage', because the exact composition of this group, which may include Strisores (Fig. 3), has not yet been settled.

Future studies of retroposon data (e.g., Kriegs et al. 2007) may resolve some of the critical nodes, but the potential of morphological analyses likewise has not yet been exhausted. Many osteological character complexes, like those pertaining to the ear region, cranial nerve foramina and vertebral column, were not studied in a sufficiently broad comparative context. The myology of some of the more common groups, such as Charadriiformes, is poorly known, and modern comparative studies on, e.g., the nerve and cardiovascular systems are almost completely lacking. As even analysis of the relatively well-known osteology of birds led to the recognition of some new and well-supported clades (e.g., Mayr 2002, 2010), it is to be expected that thorough studies of unexplored anatomical data will further deepen our understanding of neornithine interrelationships.

The present review draws attention to some of the critical taxa and nodes that need to be further investigated and better characterized. Although the phylogeny proposed in Fig. 5 is

still quite comb-like, several clades are better characterized than in the tree I proposed only three years ago (Mayr 2008a). If the numbers of new analyses continue to be as high as during the past years, we can indeed be confident that a robust phylogenetic framework will be available in the near future. Even if so, however, knowledge of the correct tree topology is only the first step towards understanding neornithine evolution. Without further characterization of nodes with morphological apomorphies, phylogenies are of limited evolutionary significance beyond divergence dating and the reconstruction of biogeographical scenarios, and understanding character evolution is also prerequisite for placement of the numerous fossil taxa with controversial affinities.

Acknowledgements

Zusammenfassung

Metaves, Mirandornithes, Strisores und andere Neuheiten – ein kritischer Überblick über die Phylogenie neornithiner Vögel

Es wird ein Überblick über neuere Hypothesen zur Großgruppensystematik der modernen Vögel gegeben. Dargelegt werden Bereiche in denen Übereinstimmung herrscht und solche mit größeren Kontroversen, wobei der Schwerpunkt auf Übereinstimmung zwischen unabhängigen molekularen und morphologischen Daten liegt. Obgleich molekulare Daten erheblich zu einem besseren Verständnis der Vogelsystematik beitrugen, scheinen sie nicht frei von Homoplasie zu sein, und bei der Deutung einiger Resultate ist Vorsicht angebracht. So ist etwa das vor kurzem vorgeschlagene Taxon „Metaves" wahrscheinlich ein Artefakt des β-fibrinogen-Gens, und gegenwärtige molekulare Daten liefern keine gut gestützten Phylogenien für einige Gruppen, deren Verwandtschaftsbeziehungen mit morphologischen Daten

aufgelöst werden können. Es existiert jedoch ein übereinstimmender und überzeugender molekularer Hinweis auf einige Monophyla, welche von Morphologen bisher nicht erkannt wurden, und um zukünftige Diskussionen zu erleichtern werden die Termini Picocoraciae („Coraciformes" ohne Leptosomidae und Piciformes) und Aequornithes („Wasservogel-Gruppe") eingeführt. Molekulare Studien stützen zudem übereinstimmend einige bisher noch nicht ausreichend gewürdigte Monophyla, welche im vorliegenden Review-Artikel umrissen werden.

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