

The deep divergences of neornithine birds: a phylogenetic analysis of morphological characters

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Abstract

Consensus is elusive regarding the phylogenetic relationships among neornithine (crown clade) birds. The ongoing debate over their deep divergences is despite recent increases in available molecular sequence data and the publication of several larger morphological data sets. In the present study, the phylogenetic relationships among 43 neornithine higher taxa are addressed using a data set of 148 osteological and soft tissue characters, which is one of the largest to date. The Mesozoic non-neornithine birds *Apsaravis*, *Hesperornis*, and *Ichthyornis* are used as outgroup taxa for this analysis. Thus, for the first time, a broad array of morphological characters (including both cranial and postcranial characters) are analyzed for an ingroup densely sampling Neornithes, with crown clade outgroups used to polarize these characters. The strict consensus cladogram of two most parsimonious trees resultant from 1000 replicate heuristic searches (random stepwise addition, tree-bisection-reconnection) recovered several previously identified clades; the at-one-time contentious clades Galloanseres (waterfowl, fowl, and allies) and Palaeognathae were supported. Most notably, our analysis recovered monophyly of Neoaves, i.e., all neognathous birds to the exclusion of the Galloanseres, although this clade was weakly supported. The recently proposed sister taxon relationship between Steatornithidae (oilbird) and Trogonidae (trogons) was recovered. The traditional taxon “Falconiformes” (Cathartidae, Sagittariidae, Accipitridae, and Falconidae) was not found to be monophyletic, as Strigiformes (owls) are placed as the sister taxon of (Falconidae + Accipitridae). Monophyly of the traditional “Gruiformes” (cranes and allies) and “Ciconiiformes” (storks and allies) was also not recovered. The primary analysis resulted in support for a sister group relationship between Gaviidae (loons) and Podicipedidae (grebes)—foot-propelled diving birds that share many features of the pelvis and hind limb. Exclusion of Gaviidae and reanalysis of the data set, however, recovered the sister group relationship between Phoenicopteridae (flamingos) and grebes recently proposed from molecular sequence data.

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While consensus mounts concerning the relationships among fossil outgroups of all extant birds (e.g., Chiappe and Witmer, 2002; Clarke, 2002), those among crown clade lineages (Neornithes sensu Cracraft, 1988 and Sibley and Ahlquist, 1990; Aves sensu Gauthier, 1986), for which comparatively abundant anatomical and molecular data is available, are still largely unresolved and, in many cases, openly contested (e.g., Cracraft and Clarke, 2001; Ericson et al., 2001; Livezey and Zusi, 2001; Sibley and Ahlquist, 1990). Only a handful of phylogenetic analyses to date have densely sampled neornithine higher taxa, and nearly all of these have

evaluated molecular data sets. Further, the large-scale DNA–DNA hybridization study of Sibley and Ahlquist (1990) has been repeatedly criticized for methodological reasons (e.g., Harshman, 1994; Houde, 1987; Lanyon, 1992) and more recent analyses of mitochondrial or nuclear sequence data have yielded strikingly different phylogenetic hypotheses (e.g., Cooper and Penny, 1997; Groth and Barrowclough, 1999; Johnson, 2001; Mindell et al., 1997; van Tuinen et al., 2000, 2001).

Morphology-based cladistic data sets addressing comparatively large neornithine ingroups are comprised of three recent analyses, i.e., of 68 myological characters from the pelvic limb (McKittrick, 1991), of 71 osteological characters focused on the position and intrarelationships of Anseriformes (Ericson, 1997), and of 359 as yet unpublished cranial and vertebral osteological

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characters (Livezey and Zusi, 2001). Cracraft (1988), in an earlier landmark paper, also surveyed a large set of neornithine taxa listing osteological synapomorphies that support 20 crown subclades. We attempted to address some limitations of these previous analyses with the present study. For example, an array of taxa that have been repeatedly considered some of the deepest divergences in Neognathae, such as Opisthocomidae (hoatzin), Musophagidae (turacos), Cuculidae (cuckoos), Psittaciformes (parrots), or mousebirds (Coliidae) were omitted from Cracraft (1988). Inclusion of these taxa is important to test strongly the proposed monophyly of all non-galloanserine neognathous taxa because of their proposed basal positions and, in some cases, proposed affinities with Galliformes (reviewed in Sibley and Ahlquist (1990)). In addition, choice of “ordinal-level” terminal taxa in Cracraft (1988) also left the monophyly of Wetmore’s (1960) major neognath taxonomic groups untested. Monophyly of a number of these traditional orders such as “Gruiformes” (cranes and allies) and “Ciconiiformes” (storks and allies) has been oft-questioned (e.g., Cracraft, 1981; Mayr, 2003a; Olson, 1979; Sibley and Ahlquist, 1990). While addressing these sampling issues, more recent analyses have reported computational limitations; the analyses of McKittrick (1991) and Livezey and Zusi (2001) had to be terminated before the most parsimonious tree was found due to the duration of the analyses (the latter study being specified as preliminary by the authors; Livezey and Zusi, 2001). The results from an analysis of Ericson’s data set (1997) were virtually unresolved.

The history of neornithine classification was reviewed at length by Sibley and Ahlquist (1990). Livezey and Zusi (2001) further contrasted previously proposed phylogenetic hypotheses for Neornithes. Although it may appear as if more data has only produced more markedly incongruent phylogenetic hypotheses, there are several points about which there is growing consensus. These include a basal-most neornithine split between a monophyletic Palaeognathae (tinamous and ratites) and Neognathae (all other birds; e.g., Cracraft, 1988; Groth and Barrowclough, 1999; Livezey and Zusi, 2001; Pycraft, 1900; van Tuinen et al., 2000), as well as the monophyly of Galloanseres (i.e., a clade comprised of galliform and anseriform birds) and placement of this taxon as the sister taxon of all other neognathous birds (e.g., Caspers et al., 1997; Cracraft, 1988; Cracraft and Clarke, 2001; Groth and Barrowclough, 1999; Livezey and Zusi, 2001; Sibley and Ahlquist, 1990; van Tuinen et al., 2000; but see also Ericson, 1996, 1997; Ericson et al., 2001).

Open questions in Neornithine systematics include the basal-most neognath splits. A clade of all neognathous birds other than Galloanseres was proposed and named “Neoaves” by Sibley et al. (1988; “Plethornithes” of Groth and Barrowclough (1999); but see also

Sibley and Ahlquist (1990: fig. 353)). Monophyly of Neoaves has been almost exclusively supported by molecular data and so far no morphological synapomorphy of this taxon has been reported (Cracraft and Clarke, 2001). A cladogram published by Livezey and Zusi (2001) indicated support for neoavian monophyly but this character support has not yet been described. A non-monophyletic Neoaves has also been proposed (Ericson, 1996, 1997; Ericson et al., 2001).

Other analyses of morphological data identified Opisthocomidae, Cuculidae, and Columbidae (pigeons) as basal within neognathous birds (McKittrick, 1991). By contrast, molecular analyses of mitochondrial cytochrome *b* sequence identified Passeriformes (songbirds) as among these earliest divergences of Neornithes (thus making Neognathae paraphyletic; H  r  lid et al., 1998; Haring et al., 2001; Johnson, 2001; Mindell et al., 1997). Elzanowski (1991, p. 18) considered procellariiform birds (tubenoses and allies), Phaethontidae (tropicbirds) and Fregatidae (frigatebirds) the “oldest branches of living neognaths”. Cariamidae (seriemas) were identified as the most basal divergence within a monophyletic Neoaves by Livezey and Zusi (2001). The authors considered these results preliminary, however, and the placement of Cariamidae likely to change with the inclusion of additional characters (Livezey and Zusi, 2001).

In the present study, the phylogenetic relationships of a large sample of neornithine taxa are evaluated with fossil taxa placed closest to Neornithes used as outgroups. Information from these close outgroups to Neornithes as well as fossil taxa placed in the stem lineages of major subclades are for the first time incorporated into analysis of crown clade deep divergences. The comparatively large data set of myological and osteological characters brings together extensive data from prior, significantly less inclusive, analyses with a smaller set of new characters. As such, it offers a synthetic view of the interaction between these previously proposed and new characters and offers the first view of how they are polarized by outgroup morphologies. Combining this data set with other morphological data sets, many of which are not published, constitutes necessary future work.

Materials and methods

Examined taxa

Outgroup taxa included in the analysis comprise three Mesozoic non-neornithines (e.g., Clarke and Norell, 2002) *Apsaravis ukhaana* (Clarke and Norell, 2002; Norell and Clarke, 2001), *Hesperornis regalis* (Elzanowski, 1991; Marsh, 1880; Witmer and Martin, 1987; Witmer, 1990), and *Ichthyornis dispar* (Marsh, 1880;

Clarke, 2002). These terminal taxa were scored from the holotype and only known specimen of *Apsaravis ukhariana* (Norell and Clarke, 2001) as well as from the holotype and referred specimens of *Hesperornis regalis* and *Ichthyornis dispar* listed in Clarke (2002).

The 43 ingroup terminal taxa were scored from skeletons of the following extant taxa (sequence of taxa as in Appendix B): Rheidae: *Rhea*. Apterygidae: *Apteryx*. Tinamidae: *Crypturellus*, *Nothura*, *Rhynchotus*, *Tinamus*. Galliformes: Megapodiidae: *Megapodius* (postcranial skeleton); Cracidae: *Crax*, *Penelope*, *Pipile*; Phasianidae: *Acryllium*, *Lagopus*, *Lyrurus*, *Tetrao*, *Tetrastes*, *Chrysolophus*, *Gallus*, *Meleagris*, *Numida*, *Pavo*, *Phasianus*. Anseriformes: Anhimidae: *Anhima*, *Chauna*; Anatidae: *Aix*, *Anas*, *Anser*, *Aythya*, *Cygnus*, *Dendrocygna*, *Melanitta*, *Oxyura*, *Somateria*, *Tadorna*. Opisthocomidae: *Opisthocomus*. Phoenicopteridae: *Phoenicopiterus*, *Phoeniconaias*. Podicipedidae: *Podiceps*, *Tachybaptus*, *Aechmophorus*. Threskiornithidae: *Eudocimus*, *Geronticus*, *Lophotibis*, *Platalea*, *Plegadis*, *Threskiornis*. Cariamidae: *Cariama*. Strigiformes: *Tyto*, *Athene*, *Strix*, *Aegolius*, *Asio*, *Surnia*, *Bubo*, *Otus*, *Glaucidium*. Recurvirostridae: *Himantopus*, *Recurvirostra*. Burhinidae: *Burhinus*. Accipitridae: *Pandion*, *Pernis*, *Elanus*, *Circus*, *Accipiter*, *Buteo*, *Haliaeetus*, *Aquila*, *Spizaetus*, *Gyps*, *Aegypius*, *Gypaetus*. Falconidae: *Milvago*, *Polyborus*, *Falco*. Sagittariidae: *Sagittarius*. Cuculidae: *Carpococcyx*, *Centropus*, *Ceuthmochares*, *Chrysococcyx*, *Clamator*, *Coua*, *Crotophaga*, *Cuculus*, *Geococcyx*, *Guira*. Musophagidae: *Corythaixoides*, *Crinifer*, *Musophaga*, *Tauraco*. Cathartidae: *Coragyps*, *Cathartes*, *Sarcoramphus*, *Vultur*. Gaviidae: *Gavia*. Spheniscidae: *Spheniscus*, *Pygoscelis*. Phaethontidae: *Phaethon*. Fregatidae: *Fregata*. Phalacrocoracidae: *Phalacrocorax*. Balaenicipitidae: *Balaeniceps*. Eurypyidae: *Eurypyga*. Ardeidae: *Agamia*, *Ardea*, *Ardeola*, *Botaurus*, *Cochlearius*, *Egretta*, *Ixobrychus*, *Nycticorax*. Ciconiidae: *Anastomus*, *Ciconia*, *Leptoptilus*, *Mycteria*. Procellariidae: *Bulweria*, *Calonectris*, *Daption*, *Fulmarus*, *Procellaria*, *Pterodroma*, *Puffinus*. Otidae: *Choriotis*, *Otis*. Pteroclididae: *Syrnhaptis*, *Pterocles*. Columbidae: *Caloenas*, *Columba*, *Ducula*, *Gallicolumba*, *Goura*, *Ptilinopus*, *Streptopelia*, *Treron*, *Trugon*, *Turtur*, *Zenaida*. Rallidae: *Amaurornis*, *Aramides*, *Fulica*, *Gallinula*, *Gallirallus*, *Himantornis* (few postcranial elements), *Laterallus*, *Limnocorax*, *Porphyro*, *Porzana*, *Rallus*. Psophiidae: *Psophia*. Gruidae: *Anthropoides*, *Balearica*, *Bugeranus*, *Grus*. Steatornithidae: *Steatornis*. Psittacidae: *Agapornis*, *Amazona*, *Ara*, *Aratinga*, *Cacatua*, *Coracopsis*, *Melopsittacus*, *Myiopsitta*, *Neophema*, *Nestor*, *Nymphicus*, *Platycercus*, *Poicephalus*, *Polytelis*, *Probosciger*, *Psittacus*, *Psittarchas*, *Trichoglossus*. Coliidae: *Urocolius*, *Colius*. Trogonidae: *Harpactes*, *Pharomachrus*, *Trogon*. Aegothelidae: *Aegotheles*. Coraciidae: *Coracias*, *Eurostomus*. Passeriformes: Eurylaimidae: *Cymbirhynchus*; Furnariidae: *Furnarius*; Formicariidae: *Thamnophilus*; Tyrannidae: *Pitangus*; Cotingidae: *Rupicola*; Alaudidae:

Alauda; Corvidae: *Corvus*. All skeletons evaluated were from Forschungsinstitut Senckenberg, Frankfurt.

Our 43 terminals more densely sample parts of “ordinal” (Wetmore, 1960) taxa that have been suggested to be basal within Neornithes (given the focus of the analysis) and/or non-monophyletic. For higher taxa that have been repeatedly supported as monophyletic in prior analyses (i.e., Charadriiformes and Procellariiformes; Chu, 1995; Ericson, 1997; Livezey and Zusi, 2001; Mayr, 2003a; Sibley and Ahlquist, 1990), only the subclades indicated above (i.e., Recurvirostridae, Burhinidae, and Procellariidae) were included to represent these taxa.

Although supraspecific terminals are not ideal (Prendini, 2001), issues with this approach were minimized as polymorphism affects a comparatively small part of our data set (Appendix B), and we are explicit about the exemplar taxa scored for these terminals (e.g., Prendini, 2001; Simmons, 2001). Evaluated exemplar taxa include basal divergences, as well as deeply nested taxa within these clades based on previous phylogenetic hypotheses (e.g., Kemp and Crowe (1990); Krajewski and Fetzner (1994); Livezey (1986, 1998)).

Phylogenetic analysis

Of the 148 total characters (Appendices A and B), only three vertebral and sternal characters (i.e., 55, 71, and 91) were ordered. The number of such characters was minimized following the recommendations of Slowinski (1993) and limited to instances of apparent “natural” ordination; i.e., (55) number of presacral vertebrae, (71) number of costal processes of the sternum, and (91) number of fused sacral vertebrae. However, the analysis was also run with these characters unordered and the results are reported.

The character matrix (Appendix B) was analyzed using PAUP* 4.0b8 (Swofford, 2001) with a maximum parsimony optimality criterion. Because of the number of taxa included (46), performing a branch and bound search (such as guarantees recovery of all shortest trees) was not computationally feasible (Hillis, 1996), thus, heuristic searches were performed. Because preliminary analysis of our data set (all characters unordered) revealed more than 70 distinct “tree islands” (Maddison, 1991) or local parsimony optima, heuristic search strategies shown to search more complex tree spaces more efficiently (Goloboff, 1999) were implemented. One thousand replicates of random stepwise addition (branch swapping: tree-bisection-reconnection) were performed holding only one tree at each step. No more than 10 trees one step longer than the shortest were retained in each replicate.

Branches were collapsed to create soft polytomies if the minimum branch length was equal to zero. Five hundred bootstrap replicates (Felsenstein, 1985) with 10 random stepwise addition heuristic searches per

replicate were also performed with the same settings as in the primary analysis.

Results

Analysis of the character matrix with three characters ordered (55, 71, and 91) yielded two most parsimonious

trees (Length = 820, CI = 0.32, RI = 0.48, RC = 0.16). The strict consensus cladogram of these trees is shown in Fig. 1. One character was recognized by PAUP* as parsimony uninformative (character 41) because, although supporting ingroup monophyly relative to *Ichthyornis*, it is missing data for the other included outgroup taxa.

When the analysis was repeated with all characters unordered, it yielded 73 most parsimonious trees

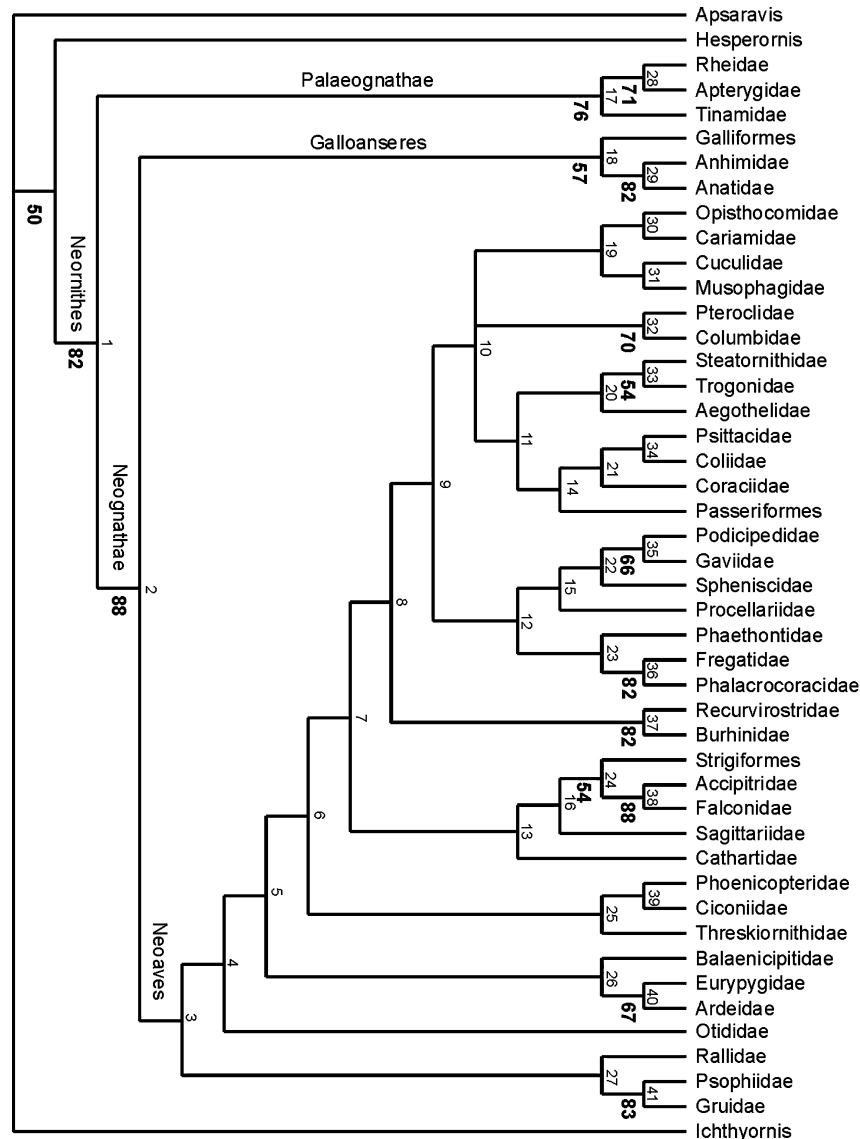


Fig. 1. The strict consensus cladogram of two most parsimonious trees resulting from analysis of the character matrix in Appendix B with three characters (55, 71, and 91) ordered (Length = 820, CI = 0.32, RI = 0.48, RC = 0.16). Bootstrap support values of more than 50% are indicated in boldface next to the corresponding node. Unambiguously optimized synapomorphies of the recovered nodes 1–41 in both most parsimonious trees (numbers reference characters and states listed in Appendix A; asterisked characters have a CI = 1.0): **1**—1*:1, 91:3, 100:1, 107:0. **2**—20:1, 21:1, 22*:1, 29*:1, 32:1, 61:1, 79*:1, 81:1, 94*:1, 103:1. **3**—15:1, 16:1, 23:1, 93:1. **4**—108:1, 120:1. **5**—59:1, 82:1. **6**—31:0, 49:1, 52:1, 61:0. **7**—48:0, 91:2, 135:5. **8**—92:0. **9**—15:0, 120:0. **10**—65:1, 105:1. **11**—60:1, 91:1, 121:1, 125:1, 137:1. **12**—30:1, 33:1, 46:1, 111:1. **13**—2:1, 18:1, 23:0, 45:1, 98:1, 122:1, 136:1, 143:1. **14**—136:1. **15**—25:1, 52:0, 77:0, 82:0, 99:1, 110:1, 126:1, 135:4, 138:1. **16**—8:1, 13:1, 37:0, 133:1, 135:3. **17**—4:1, 10*:1, 40*:1, 43*:1, 71:0, 110:1. **18**—12:1, 19:1, 24*:1, 26*:1, 35:1, 38*:1, 44:1, 45:1, 52:1. **19**—82:0, 86:1, 95:1, 124*:1, 132:1, 140:1. **20**—33:1, 52:0, 71:0. **21**—8:1, 11:1, 53:1, 130:1. **22**—21:1, 73:1, 74:1, 134:1. **23**—19:1, 63:1, 73:2, 112*:1, 121:1. **24**—113*:1, 118:1, 119:1, 120:0, 131:1. **25**—11:1, 19:1, 30:1, 102:1, 104:1, 129*:1. **26**—97:0, 121:1, 125:1, 132:1. **27**—95:1. **28**—68*:1, 108:1, 134:1, 144:1. **29**—11:1, 17:1, 33:1, 59:1. **30**—19:1, 36:1, 48:1, 73:1, 92:1. **31**—8:1, 87*:1, 123*:1, 126:1. **32**—14:1, 18:1, 56:1, 75*:1, 76:1, 97:1, 131:0. **33**—5:1, 8:1, 16:0, 17:1, 39*:1, 80:1. **34**—18:1, 33:1, 46:1, 116:0, 128*:1, 133:1, 144:0. **35**—33:0, 61:1, 70:0, 90:1, 91:4, 96:1, 104:1, 105:1, 127*:1, 130:1. **36**—2:1, 7:1, 9*:1, 65:1, 70:0, 89:1, 105:1, 114:1, 142*:1, 147:1. **37**—57:0, 58:1, 61:1, 64*:1, 77:0, 88:1, 102:1, 110:1, 146*:1. **38**—18:0, 23:1, 73:1, 84:1, 117:1. **39**—72:1, 96:1, 98:1, 101:1, 115:1, 141:1. **40**—33:1, 55:2, 65:1, 91:2, 144:1. **41**—36:1, 56:1, 71:2, 72:1, 73:2, 102:1.

(Length = 817, CI = 0.33, RI = 0.48, RC = 0.16); the strict consensus cladogram of which is shown in Fig. 2. Although the strict consensus of these 73 trees is less resolved, the recovered clades are the same as, but a subset of, those resultant from the ordered analysis. Except for the clade (Podicipedidae + Gaviidae), all clades that were robust to bootstrapping in the analysis with three characters ordered were also recovered in the analysis with all characters unordered.

In a subset (47/73) of the most parsimonious trees from the unordered analysis and both most parsimonious trees from the ordered analysis, *Hesperornis* is placed as more closely related to Neornithes than *Ichthyornis* (Fig. 1), a placement not supported in most recent analyses of avian (avian sensu Gauthier, 1986) interrelationships in which *Ichthyornis* is placed as more

closely related to Neornithes (e.g., Chiappe, 1995; Clarke, 2002; Clarke and Norell, 2002). Comparatively few taxa and characters informative of Neornithes' outgroup interrelationships, however, were included given the focus of the analysis.

If a constraint tree is specified in PAUP* requiring *Ichthyornis* to be placed as more closely related to Neornithes than *Hesperornis* and the ordered analysis is rerun, 13 most parsimonious trees three steps longer than those from the primary analysis result (Length = 823, CI = 0.32, RI = 0.48, RC = 0.15). The strict consensus of the 47 most parsimonious trees from the unordered analysis that recovered *Ichthyornis* as the sister taxon of Neornithes is identical to the strict consensus cladogram of all 73 trees. In the strict consensus of the 13 trees from the ordered analysis nodes 3, 5–10, 12, 23, and 27 (see Fig. 1) from the

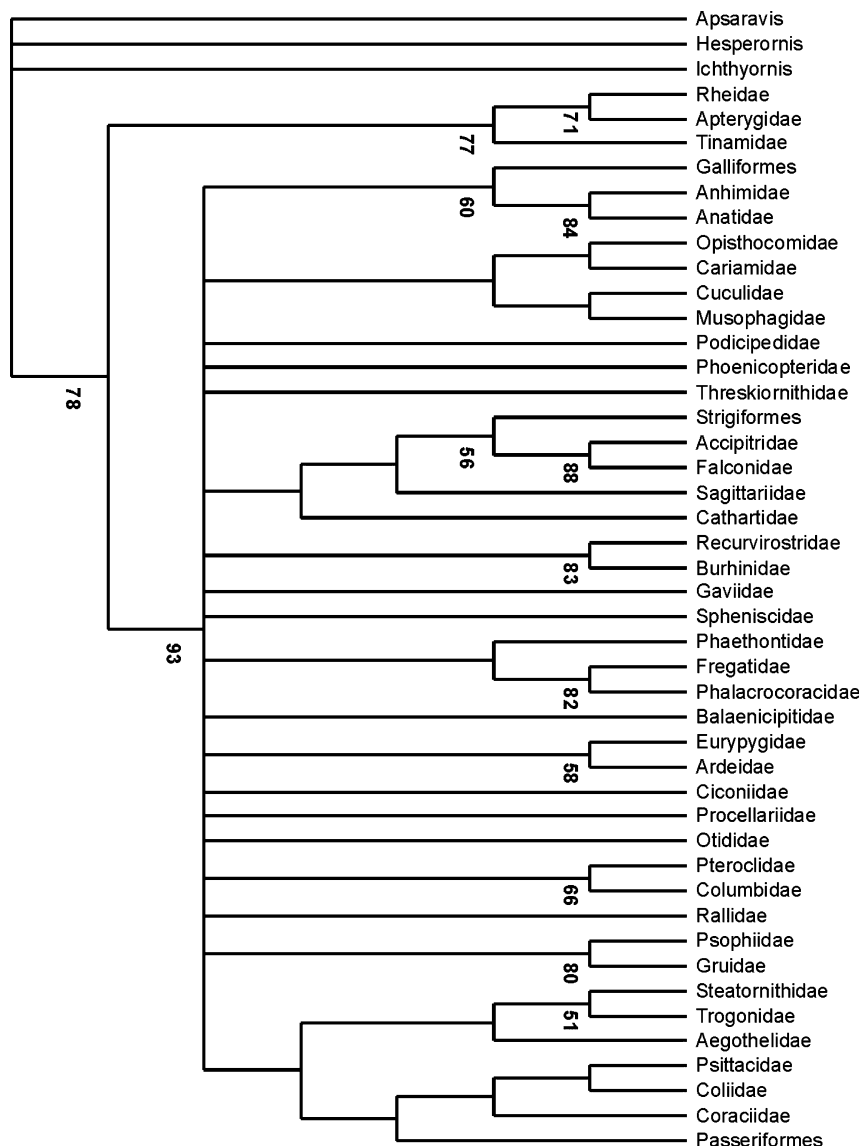


Fig. 2. The strict consensus cladogram of 73 most parsimonious trees resulting from analysis of the character matrix in Appendix B with all characters unordered (Length = 817, CI = 0.33, RI = 0.48, RC = 0.16). Bootstrap support values of more than 50% are indicated next to the corresponding node.

primary analysis collapse. None of these nodes was recovered in greater than 50% of the bootstrap replicates in the primary analysis and all are not considered strongly supported. Only one of these nodes is discussed, node 3 or Neoaves, because it is historically contentious (see Introduction).

Unambiguously optimized synapomorphies of clades resulting from the primary analysis (with the three ordered characters) are discussed below. The focus of this discussion is on those clades that were robust to bootstrapping, which were those also robust to swapping outgroup relationships (see above) and recovered in the unordered analyses.

Monophyly of Neornithes (Fig. 1, node 1) had a bootstrap support of 82% and the following unambiguously optimized synapomorphies of this taxon were recovered (the characters in Appendix A are referenced by the numbers given in parentheses): (1) maxilla without teeth; (91) pelvis with 15–16 vertebrae ankylosed in synsacrum; (100) distal end of tibiotarsus with ossified pons supratendineus; and (107) tarsometatarsus with canalis interosseus distalis. Two of these characters (1, 100) were listed as synapomorphies of Neornithes by Cracraft (1988, p. 344).

Monophyly of palaeognathous birds (Fig. 1, node 17) received bootstrap support of 76% and was supported by the following unambiguously optimized synapomorphies: (4) upper beak with marked furrow rostral of nasal opening; (10) os mesethmoidale reaching rostrally markedly beyond naso-frontal hinge; (40) mandible with two strong grooves on ventral surface of symphysis; (43) mandible with essentially flat dorsal surface of symphysis; (71) sternum with 3–4 processus costales; and (110) hallux greatly reduced.

The clade (Rheidae + Apterygidae) (Fig. 1, node 28), of the sampled ratite birds, was recovered in 71% of the bootstrap replicates and supported by the following unambiguously optimized synapomorphies: (68) coracoid fused with scapula; (108) tarsometatarsus, trochlea metatarsi II not plantarly deflected and distal end not reaching much less far distally than distal end of trochlea metatarsi IV; (134) musculus flexor hallucis longus, tendon to hallux weak or absent; and (144) oil gland minutely tufted/naked.

Neognathae (Fig. 1, node 2), recovered in 88% of the bootstrap replicates, was supported by the following unambiguously optimized synapomorphies: (20) vomers mediolaterally narrow; (21) vomers forming a midline, narrow, and dorsoventrally high lamella; (22) os palatinum and os pterygoideum separated; (29) tubae auditivae paired and close to/adjacent on cranial midline or single anterior opening; (32) fronto-parietal suture closed; (61) pygostyle, corpus not perforated at caudoventral end; (79) humerus with distinct fossa musculi brachialis; (81) humerus with well-developed sulcus scapulotricipitalis; (94) pelvis with foramen ilioischadicum caudally closed;

and (103) tarsometatarsus, hypotarsus with well-developed cristae/sulci. Characters (22) and (94) were also listed as synapomorphies of Neognathae by Cracraft (1988, p. 344f).

Monophyly of the Galloanseres (Fig. 1, node 18) was supported by a rather low bootstrap value of 57% and the following unambiguously optimized synapomorphies: (12) os lacrimale without well developed descending process which touches or nearly touches the jugal bar; (19) vomers, caudal end fused; (24) basipterygoid processes with facet for articulation with pterygoid large and ovoid; (26) cranium with basiparasphenoid plate inflated, rounded, broad, and meeting the parasphenoid rostrum at a very acute angle; ostia canalis carotici et ophthalmici externi situated in a well marked depression; (35) quadratum, processus oticus with eminentia articularis; (38) quadratum with condylus lateralis large and with greatest extension in medio-lateral direction; articular surface of mandible, with single rostrocaudal ridge and lacking caudomedial and lateral walls; (44) mandible with long and strongly mediolaterally compressed processus retroarticularis; (45) mandible with long, narrow, and dorsally oriented processus medialis; and (52) third cervical vertebra with osseous bridge from processus transversus to processus articularis caudalis.

Monophyly of the included Anseriformes, the clade (Anhimidae + Anatidae) (Fig. 1, node 29), was recovered in 82% of the bootstrap replicates and supported by the following unambiguously optimized synapomorphies: (11) palate, processus maxillopalatini of ossa maxillaria fused along their midline; (17) ossa palatina completely fused along their midline; (33) processus zygomaticus absent or vestigial; and (59) posterior caudal vertebrae with well-developed processus haemales.

The strict consensus cladogram recovered a monophyletic Neoaves (Fig. 1, node 3) which was, however, not robust to bootstrapping. The following unambiguously optimized synapomorphies were optimized as supporting neoavian monophyly: (15) os palatinum with well developed crista ventralis; (16) os palatinum, pars lateralis present and well developed; (23) basipterygoid articulation absent in adulthood; and (93) pelvis, tubercula praeacetabularia absent or vestigial. In the analysis with all characters unordered a monophyletic Neoaves was recovered in 11 of 73 trees (15%).

The clade (Podicipedidae + Gaviidae) (Fig. 1, node 35) was recovered in 66% of the bootstrap replicates and supported by the following unambiguously optimized synapomorphies: (33) presence of processus zygomaticus; (61) pygostyle, corpus perforated at caudoventral end; (70) sternum without well-developed, blade-like spina externa rostri; (90) pelvis greatly elongated and strongly compressed mediolaterally, midsection of dorsal part of cristae iliacae dorsales reduced; (91) pelvis with 17–18 vertebrae ankylosed in synsacrum;

(96) femur, short and stout, ratio length to diameter in midsection less than 9.0; (104) tarsometatarsus, hypotarsus with cristae medialis et lateralis hypotarsi strongly protruding and surrounding a canal through which all flexor tendons pass; (105) tarsometatarsus, hypotarsus, tendon of musculus flexor digitorum longus enclosed in bony canal; (127) musculus gastrocnemius with two heads; and (130) musculus fibularis longus without branch to flexor perforatus digiti III. At least character (33) is a reversal into the primitive condition and the last seven characters are related to the greatly modified hindlimb in these foot-propelled diving birds.

Exclusion of the Gaviidae from the analysis resulted in a single most parsimonious tree with the same tree topology as in Fig. 1, except that Podicipedidae were shown to be the sister taxon of Phoenicopteridae (Fig. 3).

In this tree, sister group relationship between Podicipedidae and Phoenicopteridae is supported by a bootstrap value of 79% and the following unambiguously optimized synapomorphies: (33) processus zygomaticus present; (54) fourth to seventh cervical vertebrae strongly elongate and processus spinosus forming a marked ridge; (55) 23 or more praesacral vertebrae; (56) several thoracic vertebrae fused to a notarium; (78) humerus with marked oval depression at attachment site of musculus scapulohumeralis cranialis; (84) ulna, distal end with marked depressio radialis; (96) femur, short and stout, ratio length to diameter in midsection less than 9.0; (104) tarsometatarsus, hypotarsus with cristae medialis et lateralis hypotarsi strongly protruding and delimiting a marked sulcus through which all flexor tendons pass; (115) musculus iliotibialis lateralis without

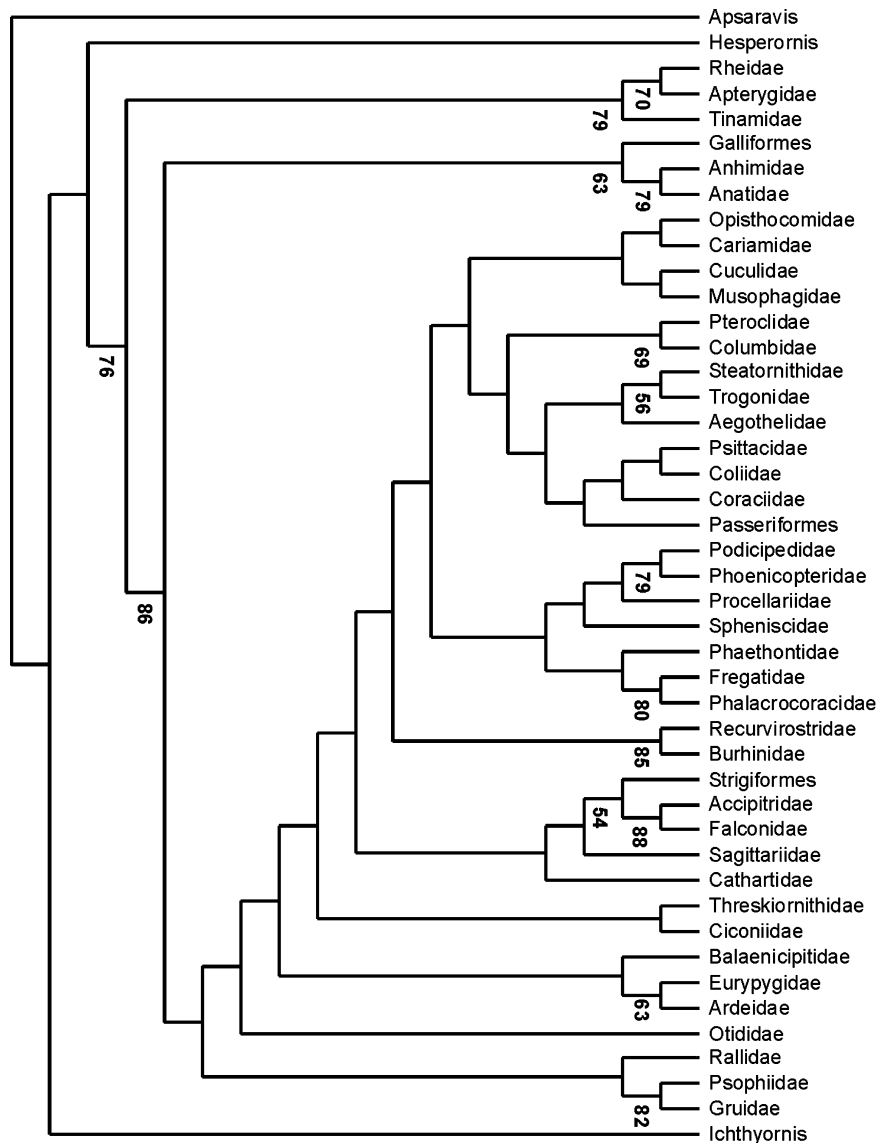


Fig. 3. The single most parsimonious trees resulting from analysis of the character matrix in Appendix B with the same settings as in the primary ordered analysis (Fig. 1) but with the Gaviidae excluded (Length = 807, CI = 0.33, RI = 0.48, RC = 0.16). Bootstrap support values of more than 50% are indicated next to the corresponding node.

pars acetabularis; (120) musculus caudofemoralis, pars caudalis absent; (141) wing with 11 primaries; and (148) eggs covered with a chalky layer of amorphous calcium phosphate. Character (33) is a reversal; most other characters (54, 55, 56, 78, 84, 141, and 148) are listed and discussed as synapomorphies of the clade (Phoenicopteridae + Podicipedidae) by Mayr (2004).

Unambiguously optimized synapomorphies of the clade (Strigiformes + Falconidae + Accipitridae) (Fig. 1, node 24, bootstrap support of 54%): (113) osseous claws, pair of canals lateral and medial to tuberculum extensorium; (118) musculus flexor cruris lateralis, pars accessoria absent; (119) musculus flexor cruris lateralis, pars pelvica absent; (120) musculus caudofemoralis, pars caudalis present; and (131) musculus flexor perforans et perforatus digiti III, vinculum absent. Except for (113), all of these characters show a great degree of homoplasy within Neornithes. Character (120) is a reversal.

The clade (Falconidae + Accipitridae) (Fig. 1, node 38) received a bootstrap value of 88% and was supported by the following unambiguously optimized synapomorphies: (18) vomers vestigial or absent; (23) basiptyergoid articulation absent in adulthood; (73) sternum, caudal margin with two notches/fenestrae; (84) ulna, distal end with marked depressio radialis; and (117) musculus femorotibialis externus without distal head.

Monophyly of the clade (Burhinidae + Recurvirostridae) (Fig. 1, node 37) received a bootstrap support of 82%; the following characters are unambiguously optimized synapomorphies of this clade: (57) thoracic vertebrae: at least part of series with subround, central articular surfaces that lack the dorsoventral compression and saddle-shaped articular surface seen in heterocoelous vertebrae; (58) caudalmost praesacral vertebrae with deep lateral excavations; (61) pygostyle, corpus not perforated at caudoventral end; (64) coracoid, facies articularis clavicularis dorso-ventrally wide and roofing the sulcus supracoracoideus, tuberculum brachiale well developed and strongly ventromedially protruding; (77) humerus without foramina pneumatica at bottom of fossa pneumotricipitalis; (88) os carpi ulnare, tuberculum at area of insertion of ligamentum humerocarpale; (102) tibiotarsus, distal rim of condylus medialis distinctly notched; (110) hallux greatly reduced; and (146) enzyme malate dehydrogenase with unusually slow motility. The last listed character is unique to charadriiform birds (Kitto and Wilson, 1966).

Sister group relationship between Pteroclididae and Columbidae (Fig. 1, node 32) received bootstrap support of 70%, and doves and sandgrouse share the following unambiguously optimized synapomorphies: (14) os ectethmoidale, greatly expanded and more or less inflated, plate-like, with dorsal margin largely fused with

os frontale; (18) vomers vestigial or absent; (56) several thoracic vertebrae fused to a notarium; (75) humerus short and stocky with crista deltopectoralis strongly protruding and triangular; (76) humerus, tuberculum dorsale greatly elongated; (97) femur, crista trochanteris markedly projected cranially; and (131) musculus flexor perforans et perforatus digiti III, vinculum present. Character (131) is a reversal.

A sister group relationship between Steatornithidae and Trogonidae (Fig. 1, node 33, bootstrap support of 54%) is supported by the following unambiguously optimized synapomorphies: (5) skull with distinct naso-frontal hinge; (8) septum internasale largely ossified; (16) os palatinum, pars lateralis absent or very small; (17) ossa palatina fused along their midline; (39) columella with large, hollow, bulbous basal, and footplate area which exhibits a large fenestra on one side; and (80) humerus with very deep and sharply delimited fossa musculi brachialis.

Monophyly of the clade (Fregatidae + Phalacrocoracidae) (Fig. 1, node 36, bootstrap support of 82%) was supported by the following unambiguously optimized synapomorphies: (2) upper beak, praemaxilla with sharply hooked tip; (7) external narial openings greatly reduced or completely absent; (9) conchae nasales greatly reduced or completely absent; (65) coracoid without foramen nervi supracoracoidei; (70) sternum, without well-developed, blade-like spina externa rostri; (89) phalanx proximalis digiti majoris elongate and craniocaudally narrow; (105) tarsometatarsus, hypotarsus, tendon of musculus flexor digitorum longus enclosed in bony canal; (114) claw of third toe distinctly pectinate on its medial side; (142) presence of large and naked gular pouch; and (147) eggshell covered with layer of microglobular material of amorphous calcium carbonate. Character (70) is a reversal.

The clade (Eurypygidae + Ardeidae) (Fig. 1, node 40) was recovered in 67% of the bootstrap replicates and supported by the following unambiguously optimized synapomorphies: (33) processus zygomaticus absent or vestigial; (55) 23 or more praesacral vertebrae; (65) coracoid without foramen nervi supracoracoidei; (91) pelvis, 13–14 vertebrae ankylosed in synsacrum; and (144) oil gland: minutely/naked.

Of parts of the traditional “Gruiformes,” the clade (Psophiidae + Gruidae) (Fig. 1, node 41) was recovered in 83% of the bootstrap replicates and was supported by the following unambiguously optimized synapomorphies: (36) quadratum, processus oticus with pneumatic foramina on dorsal end of caudal surface; (56) several thoracic vertebrae fused to a notarium; (71) sternum with 7–8 processus costales; (72) sternum, facies visceralis with numerous pneumatic foramina along midline and lateral margins; (73) sternum, caudal margin without notches/fenestrae; and (102) tibiotarsus, distal rim of condylus medialis distinctly notched.

Discussion

In concordance with traditional classifications (e.g., Wetmore, 1960), analyses of other morphological data (reviewed in Cracraft and Clarke, 2001), nuclear gene sequence data (e.g., Groth and Barrowclough, 1999; Mayr et al., 2003) or combined nuclear and mitochondrial data (e.g., van Tuinen et al., 2000), our analysis did not support a basal-most position for Passeriformes within Neornithes, but for Paleognathae and Galloanseres (see Introduction).

Of previous analyses of morphological data, monophyly of Neoaves was only recovered by Livezey and Zusi (2001) although the character support for this node has not been reported. Support for neoavian monophyly recovered in our study is independent from the as yet unpublished data of these authors. Those analyses that have hypothesized neoavian non-monophyly based on morphological data got this result with either non-monophyly of Galloanseres (e.g., Ericson, 1997; Ericson et al., 2001) or with both non-monophyly of Galloanseres and a lack of a basal position for either Galliformes or Anseriformes (i.e., McKittrick, 1991). By contrast, we recover both a monophyletic Galloanseres and a monophyletic Neoaves. Support for neoavian monophyly is quite limited, however. It is not robust to bootstrapping, switching the position of the outgroup *Ichthyornis*, or unordering three characters. The characters supporting monophyly of Neoaves show a considerable degree of homoplasy within this clade.

Most recovered nodes within Neognathae with bootstrap support are consistent with previous phylogenetic hypotheses. This is true for sister taxon relationship between Pteroclididae (sandgrouse) and Columbidae (e.g., Cracraft, 1981; Livezey and Zusi, 2001; contra Sibley and Ahlquist, 1990; Mindell et al., 1997), Fregatidae and Phalacrocoracidae as two representatives of the traditional (sensu Wetmore, 1960) Pelecaniformes (e.g., Livezey and Zusi, 2001; Mayr, 2003a; contra Sibley and Ahlquist, 1990; van Tuinen et al., 2001), that of Burhinidae (thicknees) and Recurvirostridae (stilts and avocets) as two representatives of the traditional (sensu Wetmore, 1960) Charadriiformes (e.g., Ericson, 1997; Sibley and Ahlquist, 1990; contra Livezey and Zusi, 2001), and Falconidae and Accipitridae (e.g., Cracraft, 1981; contra McKittrick, 1991; Mindell et al., 1997; Sibley and Ahlquist, 1990).

The sister group relationship between Podicipedidae (grebes) and Gaviidae (loons) recovered here is in concordance with traditional classifications (e.g., Cracraft, 1981, 1982a, 1988) but conflicts with recent phylogenetic analyses (Livezey and Zusi, 2001; Mayr, 2004; Sibley and Ahlquist, 1990; van Tuinen et al., 2001). Van Tuinen et al. (2001) reported strong molecular support for sister group relationship between Podicipedidae and Phoenicopteridae (flamingos), and Mayr (2004)

identified previously overlooked derived morphological characters that supported this hypothesis. Although all of these characters were included in the present study, the analysis did not recover sister group relationship between flamingos and grebes. However, exclusion of the Gaviidae from the analysis resulted in sister group relationship between grebes and flamingos (Fig. 3). Grebes and loons are both foot-propelled diving birds and, as noted above, most of the shared derived similarities of these birds are found in the pelvis and hind limb (see Results). By contrast, the morphological characters shared by flamingos and grebes (see Mayr, 2004 for further discussion) occur in taxa that have a completely different way of living (e.g., style of locomotion, ecology including feeding behavior). We consider it likely that the characters supporting a (loon + grebe) clade be discovered to be due to convergence in further analyses of large morphological data sets and/or combined molecular and morphological analyses. In the analysis of van Tuinen et al. (2001) and Livezey and Zusi (2001), loons are shown to be the sister taxon of Procellariiformes and Spheniscidae (penguins).

A sister taxon relationship between trogons (Trogonidae) and the oilbird (Steatornithidae) was recently proposed by Mayr (2003b). Since the characters from that study were included here, this result is not surprising although it indicates that the results of Mayr (2003b) are robust to evaluation over an increased taxon sample. In traditional classifications (e.g., Wetmore, 1960; reviewed in Sibley and Ahlquist, 1990), Steatornithidae were included in the paraphyletic (Mayr, 2002a) “Caprimulgiformes” (represented by the Aegothelidae in this study). Trogonidae have been considered to be most closely related to coraciiform birds (represented by the Coraciidae in this study; reviewed in Sibley and Ahlquist (1990) and Espinosa de los Monteros (2000)). A critique of the morphological data used to support these previously proposed placements is presented in Mayr (2003b). A recent analysis of complete cytochrome *b* and ribosomal RNA sequence data (Espinosa de los Monteros, 2000) also did not recover a Trogonidae–Coraciiformes relationship and trogons were placed as the sister taxon of Coliidae (mousebirds); unfortunately, Steatornithidae was not sampled. An analysis of nuclear gene sequence data by Johansson et al. (2001) resulted in a sister group relationship between trogons and a clade including some coraciiform and piciform birds, with the Steatornithidae being the sister taxon of this clade.

The traditional “Falconiformes” (sensu Wetmore, 1960; Cathartidae, Sagittariidae, Accipitridae, and Falconidae) were not found to be monophyletic (contra, e.g., Griffiths, 1994; Livezey and Zusi, 2001). Strigiformes (owls) were placed as the sister group of the clade (Falconidae + Accipitridae (including the osprey, *Pandion haliaetus*, see Kemp and Crowe, 1990; Griffiths, 1994; Mindell et al., 1997; Seibold and Helbig, 1995)),

although this result is weakly supported. A clade including these taxa (i.e., owls, hawks, and falcons) was also recovered and discussed by Mayr et al. (2003) who did not, however, include Cathartidae (New World vultures) and Sagittariidae (secretary bird) in their analysis.

Monophyly of the clade (Strigiformes + Falconidae + Accipitridae) was further proposed by Cracraft (1981, 1988) and resulted from McKittrick's (1991) analysis but has not been supported in other cladistic analyses of morphological or molecular data (e.g., Griffiths, 1994; Livezey and Zusi, 2001; Sibley and Ahlquist, 1990; van Tuinen et al., 2000). Doubts concerning the falconiform affinities of New World vultures and the secretary bird have been repeatedly raised (e.g., Avise et al., 1994; Jollie, 1977; Ligon, 1967; Sibley and Ahlquist, 1990; Wink, 1995). In our analysis, Cathartidae and Sagittariidae were shown to be successive sister taxa of the clade including Falconidae, Accipitridae, and Strigiformes, but this grouping was not robust to bootstrapping.

The recovered polyphyly of the traditional "Gruiformes" (sensu Wetmore, 1960; i.e., Rallidae (rails), Psophiidae (trumpeters), Gruidae (cranes), Otididae (bustards), Cariamidae, and Eurypygidae (sunbittern)) and "Ciconiiformes" (i.e., Threskiornithidae (ibises), Ardeidae (herons), Balaenicipitidae (shoebill), and Ciconiidae (storks)), included in our analyses is consistent with the results of several recent phylogenetic analyses including a larger subset of Neornithes (e.g., Livezey and Zusi, 2001; McKittrick, 1991; Sibley and Ahlquist, 1990). Gruiform monophyly was supported in analysis of one large data set (including all taxa of Wetmore's (1960) Gruiformes) for gruiform interrelationships (Livezey, 1998) but only by seven character changes (of trees 967 steps in length) relative to the charadriiform outgroups used. Further, the latter also constitute an extremely limited sample of potential gruiform outgroups and thus a notably weak test to monophyly.

A sister taxon relationship between the "gruiform" Eurypygidae and the "ciconiiform" Ardeidae (herons) has not been found in previous analyses that included both taxa (Livezey and Zusi, 2001; Sibley and Ahlquist, 1990), although a close relationship between these two taxa has been suggested (Olson, 1979). Eurypygidae are considered by many authors to be the sister taxon of the Rhynochetidae (kagu; e.g., Cracraft, 1982b; Houde et al., 1997; Livezey, 1998; contra Livezey and Zusi, 2001; Sibley and Ahlquist, 1990) which were not included in this study.

Sister group relationship between the "ciconiiform" Balaenicipitidae and the clade (Eurypygidae + Ardeidae) conflicts with recent analyses of molecular and morphological data supporting pelecaniform affinities of the Balaenicipitidae (e.g., Hedges and Sibley, 1994; Livezey

and Zusi, 2001; Mayr, 2003a,b; Sibley and Ahlquist, 1990; van Tuinen et al., 2001). However, as our study includes only exemplar taxa of the traditional (e.g., Wetmore, 1960) Pelecaniformes, the phylogenetic affinities of the Balaenicipitidae are not considered strongly tested by our taxon sampling.

Sister group relationship between Psophiidae and Gruidae is in concordance with many traditional classifications (e.g., Gadow, 1893) and a cladistic analysis of the interrelationships between "gruiform" birds by Livezey (1998), which showed monophyly of the clade (Psophiidae + (Gruidae + Aramididae)) (contra Mayr, 2002c; Sibley and Ahlquist, 1990).

There are several interesting and in part novel groupings which received, however, no bootstrap support. Monophyly of the clade (Cariamidae + Opisthocomidae), for example, is noteworthy given morphological similarities that have been noted previously (Olson, 1985, p. 143) and several early Tertiary fossil taxa have been argued to show a putative "mosaic" of characters of Cariamidae and Opisthocomidae (Mourer-Chauviré, 1983; Olson, 1992). Sister group relationship between Musophagidae and Cuculidae is in concordance with most traditional classifications of these taxa (see Sibley and Ahlquist, 1990) but is not supported by more recent analyses (e.g., Livezey and Zusi, 2001; Mayr et al., 2003). Sister group relationship between Psittacidae and Coliidae, which share a unique modification of the tendon of musculus extensor digitorum longus (character 128 in the Appendix A), was proposed by Berman and Raikow (1982) and also resulted from the analysis of McKittrick (1991).

Conclusions

Data sets with dense taxonomic sampling of Neornithes and large numbers of morphological characters are essential to addressing the currently contentious timing and pattern of the emergence of extant lineages (e.g., Bleiweiss, 1998; Chiappe, 1995; Cooper and Penny, 1997; Cracraft, 2001; Dyke and Mayr, 1999; Feduccia, 1995; Feduccia, 2003; Stidham, 1998). Such data sets are further needed to evaluate the phylogenetic affinities of an increasing number of early Tertiary fossil neornithine taxa (e.g., Mayr, 1999, 2000a, 2001; Olson, 1992). Unfortunately, as well illustrated by the comparison of the results of our analysis with those of previous studies, only a few nodes within Neornithes are supported by multiple analyses of molecular and/or morphological data (e.g., Palaeognathae, Galloanseres, Charadriiformes, Podicipedidae, and Phoenicopteridae).

Thus, we must caution that any of the existing phylogenies may be an insecure basis for drawing far-reaching conclusions on patterns of Neornithine character evolution (e.g., Bostwick and Brady, 2002) or

biogeography (e.g., Cracraft, 2001). Recently, for example, published phylogenies of the “Gruiformes” and “Caprimulgiformes” (nightjars and allies) were used to demonstrate that members of these groups show transantarctic geographic patterns and diversified in the late Cretaceous in Gondwana (Cracraft, 2001). However, a primary assumption necessary to this conclusion, that these taxa represent monophyletic groups, has not been supported by the current study or many others, which have not recovered one, or both, of these clades (Livezey and Zusi, 2001; Mayr, 2002a; Mayr et al., 2003; McKittrick, 1991; Sibley and Ahlquist, 1990).

It is to be hoped that future studies of larger taxonomic samples and anatomical data sets will also be combined with large molecular data sets. The strongest hypotheses of Neornithine relationships will come from initiatives that combine distinct individual data sets, such as that presented here, towards a still larger sample of morphological characters and then negotiate the adaptation of this data for combined analyses with the rapidly increasing available sequence data (e.g., scoring of exemplar species as terminal taxa).

Acknowledgments

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Appendix A. Character descriptions. Anatomical terminology follows Baumel and Witmer (1993) and Vanden Berge and Zweers (1993)

1. Teeth on maxilla: present (0), absent (1).
2. Upper beak, praemaxilla with sharply hooked tip: no (0), yes (1). This character was proposed as a synapomorphy of Pelecaniformes and Procellariiformes by Cracraft (1988, p. 349); see also Mayr (2003a).
3. Upper beak, lamellae for filter feeding: absent (0), vestigial (1), well developed (2) (see Olson and Feduccia, 1980b: fig. 6 concerning the presence of vestigial lamellae in the Anhimidae).
4. Upper beak, marked furrow rostral of nasal opening (Fig. 4B; “nasal groove” of Cottam, 1957): absent (0), present (1). This character was proposed as a synapomorphy of Pelecaniformes and Procellariiformes by Cracraft (1988, p. 349); see also Mayr (2003a). Its absence in *Rhynchotus rufescens* (Tinamidae) is here considered autapomorphic for this taxon.
5. Skull, distinct naso-frontal hinge, i.e., caudal part of beak markedly set off by a furrow against rostral part of cranium: absent (0), present (1). This character was proposed as a synapomorphy of the taxon (Trogonidae + Steatornithidae) by Mayr (2003b).

6. Nostrils: schizorhinal, i.e., caudal margin slit-like and extending caudally to naso-frontal hinge; cranial kinesis rhynchokinetic: no (0), yes (1); see Zusi (1984) for a discussion of the various types of kinesis in birds.

7. External narial openings greatly reduced or completely absent: no (0), yes (1), (see Cracraft, 1988; Mayr, 2003a).

8. Septum internasale largely ossified: absent (0), present (1). In the fossil outgroup taxa the absence of this character has been inferred from the morphology of the praemaxilla.

9. Conchae nasales greatly reduced or completely absent: no (0), yes (1); (after Technau, 1936).

10. Os mesethmoidale reaching rostrally markedly beyond naso-frontal hinge (Clarke, 2002, character 26): no (0), yes (1).

11. Palate, processus maxillopalatini of ossa maxillaria fused along their midline (i.e., palate directly desmognathous, Fig. 5B): no (0), yes (1).

12. Os lacrimale, well developed descending process which touches or nearly touches the jugal bar (Fig. 4B): yes (0), no (1). This character was coded as unknown for the Aegothelidae in which the lacrimalia are reduced.

13. Os lacrimale, caudally projecting processus supraorbitales: absent (0), present (1). This character was coded as unknown for the Aegothelidae in which the lacrimalia are reduced. See Mayr et al. (2003) concerning the presence of supraorbital processes in the Strigiformes and Mayr (2002b) concerning their presence in fossil stem group representatives of the Psittaciformes.

14. Os ectethmoidale, greatly expanded and more or less inflated, plate-like, with dorsal margin largely fused with os frontale (Fig. 4C): no (0), yes (1). This character was coded as unknown in taxa in which the ectethmoid is reduced.

15. Os palatinum, well developed crista ventralis (Fig. 5A): absent (0), present (1).

16. Os palatinum, pars lateralis (Fig. 5B): absent or very small (0), present and well developed (1). Cracraft (1988, p. 347) listed a palatinum which is “poorly developed posteriorly” as a synapomorphy of Galloanseres.

17. Ossa palatina completely fused along midline: no (0), yes (1) (Ericson, 1997, character 8). We consider the presence of this character in some Strigidae (e.g., *Aegolius*) to be derived within the taxon.

18. Vomers (Fig. 5): present, variably developed (0), vestigial or absent (1). See Mayr et al. (2003) concerning the presence of vomers in the Musophagidae.

19. Vomers, caudal ends not fused, more or less deeply cleft (Fig. 5C): yes (0), no (1). This character was coded as unknown in taxa in which vomers are reduced/absent.

20. Vomers mediolaterally wide (Fig. 5A): yes (0), no (1). This character was coded as unknown in taxa in which vomers are reduced/absent.

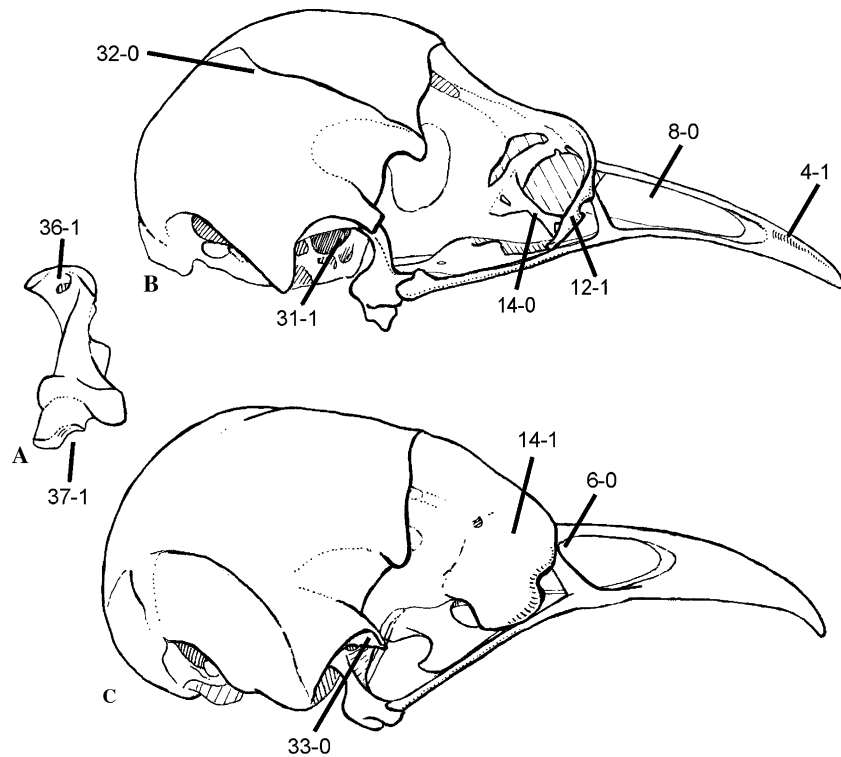


Fig. 4. Caudal view of quadrate (A) and caudolateral view of skull (B, C) to illustrate some cranial characters and character states used in this study (numbers refer to Appendix A). (A) *Psophia crepitans* (Psophiidae, "Gruiformes"); (B) *Crypturellus cinnamomeus* (Tinamidae, Tinamiformes); and (C) *Turdus merula* (Turdidae, Passeriformes). Not to scale.

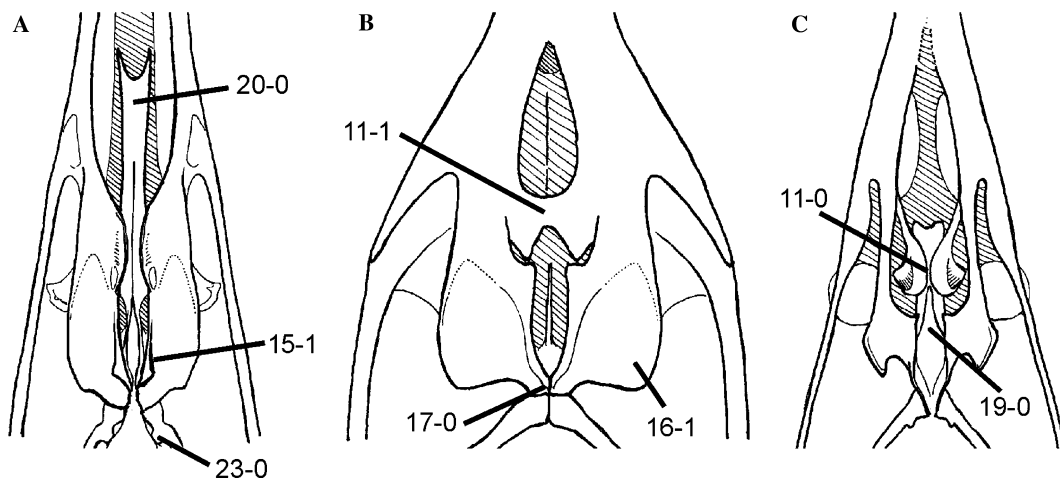


Fig. 5. Ventral view of the palatal region of the skull to illustrate some cranial characters and character states used in this study (numbers refer to Appendix A). (A) *Recurvirostra avosetta* (Recurvirostridae, Charadriiformes); (B) *Eurystomus glaucurus* (Coraciidae, Coraciiformes); and (C) *Turdus merula* (Turdidae, Passeriformes). Not to scale.

21. Vomers forming a midline, narrow, and dorso-ventrally high lamella: no (0), yes (1). This character was coded as unknown in taxa in which vomers are reduced/absent.

22. Os palatinum and os pterygoideum fused: yes (0), no (1). Cracraft (1988) listed separated palatines and pterygoids as a synapomorphy of neognathous birds.

23. Basipterygoid articulation in adulthood (Fig. 5A): present (0), absent (1). Although homology of the basipterygoid articulation of Galloanseres with that of other neornithine birds has been considered uncertain (Weber, 1993; see below), they are considered topologically equivalent potential homologues in this analysis (see Clarke, 2002).

24. Basipterygoid process, facet for articulation with pterygoid large and ovoid: no (0), yes (1). Weber (1993) found developmental differences between the basipterygoid articulation of Galloanseres and that of other neornithine birds, distinguishing the basipterygoid articulation of Galloanseres as rostrompterygoid articulation. However, as he did not include the Anhimidae in his study, we only coded the morphological differences between the basipterygoid processes of Galloanseres and those of other birds.

25. Os frontale, dorsal surface with marked depressions for supraorbital salt glands: absent (0), present (1). Based on the phylogeny of Livezey (1986), we consider the presence of this character in some marine Anatidae to be apomorphic for these taxa and accordingly coded the character.

26. Cranium, basiparasphenoid plate inflated, rounded, broad, and meeting the parasphenoid rostrum at a very acute angle; ostia canalis carotici et ophthalmici externi situated in a well marked depression: no (0), yes (1). This character was coded as two separate characters by Cracraft (1988), and Cracraft and Clarke (2001) but we agree with Ericson (1996) that it represents a single character complex.

27. Cranium, fonticuli occipitales in adult birds (Ericson, 1997, character 1): absent (0), present (1).

28. Tubae auditivae (eustachian tubes) completely ossified ventrally: yes (0), no (lateral osseous wall lacking) (1).

29. Tubae auditivae: paired and lateral (0), paired and close to/adjacent on cranial midline or single anterior opening (tuba auditiva communis) (1); (see Cracraft, 1988, 344f; Clarke, 2002, character 27).

30. Marked processus parasphenoidales mediales: absent (0), present (1).

31. Os opisthoticum/prooticum, pila otica with cluster of small pneumatic openings (Fig. 4B): no (0), yes (1). This character was first noted by Lowe (1925, 1926) and corresponds to the “large fenestra/foramen [...] immediately posterior to the facet for the medial head of the quadrate” of Cracraft (1988, p. 351). It was listed as a synapomorphy of gruiform birds by the latter author and noted present in palaeognathous birds and some Gruiformes by Witmer (1990).

32. Fronto-parietal suture (Fig. 4B): open (0), closed (1).

33. Processus zygomaticus: present, variably developed (0), absent or vestigial (1). See Zusi and Livezey (2000) concerning the processus zygomaticus of galliform and anseriform birds.

34. Quadratum, processus oticus, two well-separated heads for articulation with os squamosum and os prooticum: absent (0), present (1). The presence of a double-headed quadrate was proposed as a synapomorphy of Neognathae by Cracraft (1988, 345); see comments in Witmer (1990).

35. Quadratum, processus oticus, eminentia articularis (see Clarke and Norell, 2002, p. 33; Cracraft and Clarke, 2001, character 37; Weber and Hesse, 1995): absent (0), present (1).

36. Quadratum, processus oticus, pneumatic foramina on dorsal end of caudal surface (Fig. 4A): absent (0), present (1).

37. Quadratum, condylus medialis, marked, rostrally projecting, concave articular surface (Fig. 4A; Strauch, 1978, character 11): absent (0), present (1).

38. Quadratum, condylus lateralis (“external mandibular condyle” of Cracraft, 1988, p. 347) large and with greatest extension in mediolateral direction; articular surface of mandible, “with single antero-posterior [= rostrocaudal] ridge” and “lacking posteromedial [= caudomedial] and lateral walls” (Cracraft and Clarke, 2001, characters 39 and 40): no (0), yes (1). In concordance with Ericson (1996) but contrary to Cracraft (1988), we consider these features to be part of a single character complex. Usually, the condylus lateralis has its greatest extension in rostro-caudal direction.

39. Columella with large, hollow, bulbous basal, and footplate area which exhibits a large fenestra on one side: no (0), yes (1). This character was proposed as a synapomorphy of the taxon (Trogonidae + Steatorniithidae) by Mayr (2003b).

40. Mandible, two strong grooves on ventral surface of the mandibular symphysis: absent (0), present (1). This character was proposed as a synapomorphy of palaeognathous birds by Parkes and Clark (1966). Its absence in *Rhynchotus rufescens* (Tinamidae) is here considered autapomorphic for this taxon.

41. Mandible, os coronioideum: present (0), absent (1). The loss of a coronoid bone was proposed to be a synapomorphy of Neornithes relative to *Ichthyornis* (e.g., Cracraft, 1988, p. 344).

42. Mandible, ossified symphysis mandibulae: absent (0), present (1).

43. Mandible, dorsal surface of symphysis essentially flat (Clarke, 2002, character 44): no (0), yes (1).

44. Mandible, long and strongly mediolaterally compressed processus retroarticularis: absent (0), present (1). The presence of this character in some Passeriformes (e.g., Sturnidae, Icteridae) is here considered autapomorphic for these taxa. This character was considered to be synapomorphic for Galloanseres by Cracraft (1988) and Cracraft and Clarke (2001).

45. Mandible, processus medialis, long, narrow, and dorsally oriented: no (0), yes (1). This character was listed as a synapomorphy of Galloanseres by Cracraft and Clarke (2001, character 41).

46. Atlas, well-developed, narrow processus ventralis: absent (0), present (1).

47. Atlas, foramina transversaria: absent (0), present (1).

48. Axis, corpus with pneumatic foramina on lateral sides (Fig. 6B): no (0), yes (1).

49. Axis, foramina transversaria (Fig. 6A): present (0), absent (1).

50. Axis, processus costales (Fig. 6B): present (0), absent (1).

51. Axis, osseous bridge from processus transversus to processus articularis caudalis: absent (0), present (1).

52. Third cervical vertebra, osseous bridge from processus transversus to processus articularis caudalis (Fig. 6D): absent (0), present (1).

53. At least 7th and 8th cervical vertebra, osseous bridge from processus costalis to midsection of corpus vertebrae (Fig. 6F): no (0), yes (1).

54. Fourth to seventh cervical vertebrae strongly elongate and processus spinosus forming a marked ridge: no (0), yes (1). This character was proposed as a synapomorphy of Phoenicopteridae and Podicipedidae by Mayr (2004).

55. Number of praesacral vertebrae (all vertebrae cranial to synsacrum): 18–19 (0), 20–22 (1), 23 or more (2). This character was coded as ordered.

56. Several thoracic vertebrae fused to a notarium: no (0), yes (1). Ericson (1997, character 25) erroneously

coded a notarium as present for Anatidae and Anhimidae; in only very few Anatidae two or three thoracic vertebrae are (often incompletely) fused.

57. Thoracic vertebrae: at least part of series with subround, central articular surfaces (e.g., amphicoelous/opisthocoelous) that lack the dorsoventral compression and saddle-shaped articular surface seen in heterocoelous vertebrae (0), series completely heterocoelous (1).

58. Caudalmost praesacral vertebrae with deep lateral excavations: no (0), yes (1). (see Clarke, 2002, p. 408, Ericson, 1997, character 23). A deep lateral concavity is present in the early Tertiary stem group galliform taxon *Paraortygoides* (Clarke, 2002, p. 407; Dyke and Gulas, 2002, fig. 3).

59. Posterior caudal vertebrae with well-developed processus haemales (Fig. 6H): no (0), yes (1).

60. Pygostyle, discus pygostyli: absent (0), present (1).

61. Pygostyle, corpus perforated at caudoventral end (Fig. 6G): yes (0), no (1).

62. Furcula, extremitas omalis with strongly developed, laterally protruding facies articularis acrocoracoidae: no (0), yes (1). Within the Strigiformes, this character is absent in *Tyto*.

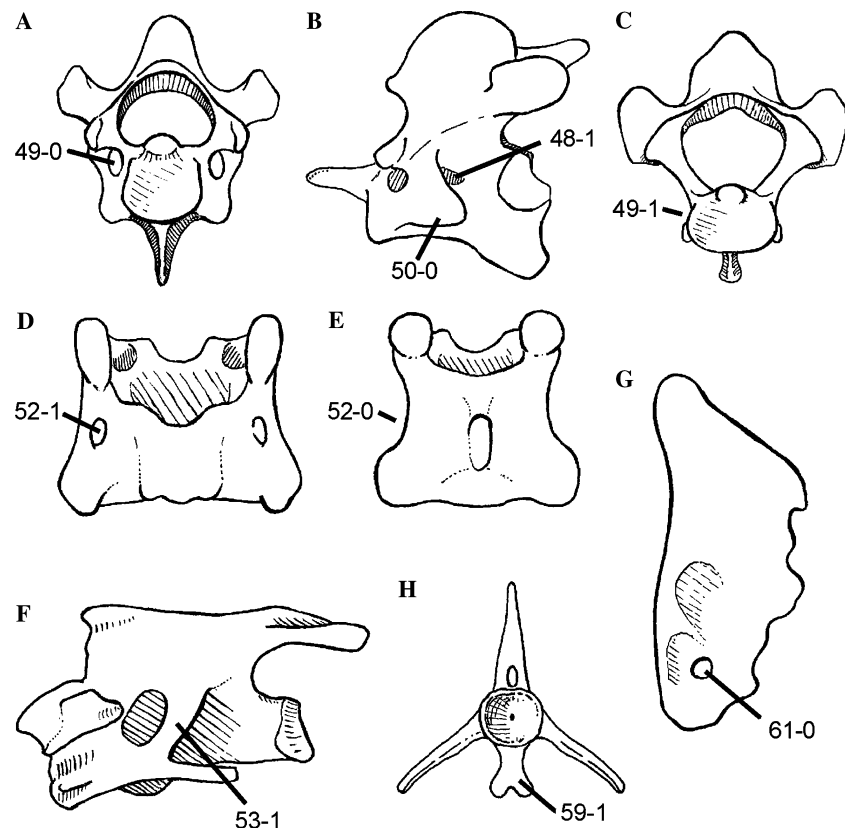


Fig. 6. Some vertebral characters and character states included in the analysis and not figured in previous studies (numbers refer to Appendix A): Axis in cranial (A, C) and lateral (B) view, third cervical vertebra in dorsal view (D, E), fifth cervical vertebra in lateral view (F), pygostyle in lateral view (G), and last free caudal vertebra in cranial view (H). (A, B, E) *Rhynchotus rufescens* (Tinamidae, Tinamiformes); (C, D) *Elanus leucurus* (Accipitridae, Falconiformes); (F) *Tauraco fischeri* (Musophagidae, Musophagiformes); (G) *Falco cherrug* (Falconidae, Falconiformes); and (H) *Columba palumbus* (Columbidae, Columbiformes). Not to scale.

63. Furcula, apophysis furculae: not as follows (0), abutting with an articular facet at the apex carinae of the carina sterni (fused with the apex carinae in *Balaenicipitidae* and *Fregatidae*, see Mayr, 2003a) (1). We consider the fusion of the furcula with the apex carinae in the *Gruinae* (absent in *Balearica*) to be non-homologous to this character.

64. Coracoid, facies articularis clavicularis dorso-ventrally wide and roofing the sulcus supracoracoideus, tuberculum brachiale well developed and strongly ventromedially protruding (Fig. 7D): no (0), yes (1).

65. Coracoid, foramen nervi supracoracoidei (Fig. 7B): present (0), absent (1). Within the *Ciconiidae*, a foramen nervi supracoracoidei is present in *Leptoptilos*. See Mayr et al. (2003, character 29), concerning the presence of this character in *Accipitridae* and *Falconidae*, Mayr (2002b) concerning its presence in fossil stem group representatives of the *Psittaciformes*, and Mayr (2002d) concerning its presence in fossil *Coliiformes*.

66. Coracoid, ?pneumatic foramen directly below facies articularis scapularis which does not penetrate shaft (Fig. 7A): absent (0), present (1). It is uncertain whether this foramen is homologous to the foramen nervi supracoracoidei. Within the *Cuculidae*, this character is present in *Coua*.

67. Coracoid, impressio musculi sternocoracoidei on dorsal surface of extremitas sternalis with pneumatic foramina (Fig. 7B): no (0), yes (1). Within the *Rallidae*, the character is present in *Himantornis* (Olson, 1973, fig. 2). Although present in many extant *Cracidae* and *Phasianidae*, this character is absent in stem group representatives of the *Galliformes* (Mourer-Chauviré, 1992) and has accordingly been coded as absent for this taxon.

68. Coracoid fused with scapula: no (0), yes (1).

69. Sternum, sulci coracoidei crossed (Ericson, 1997, character 34): absent (0), present (1). In the *Opisthocomidae* the coracoids are fused to the sternum and thus this character could not be evaluated. Contrary to

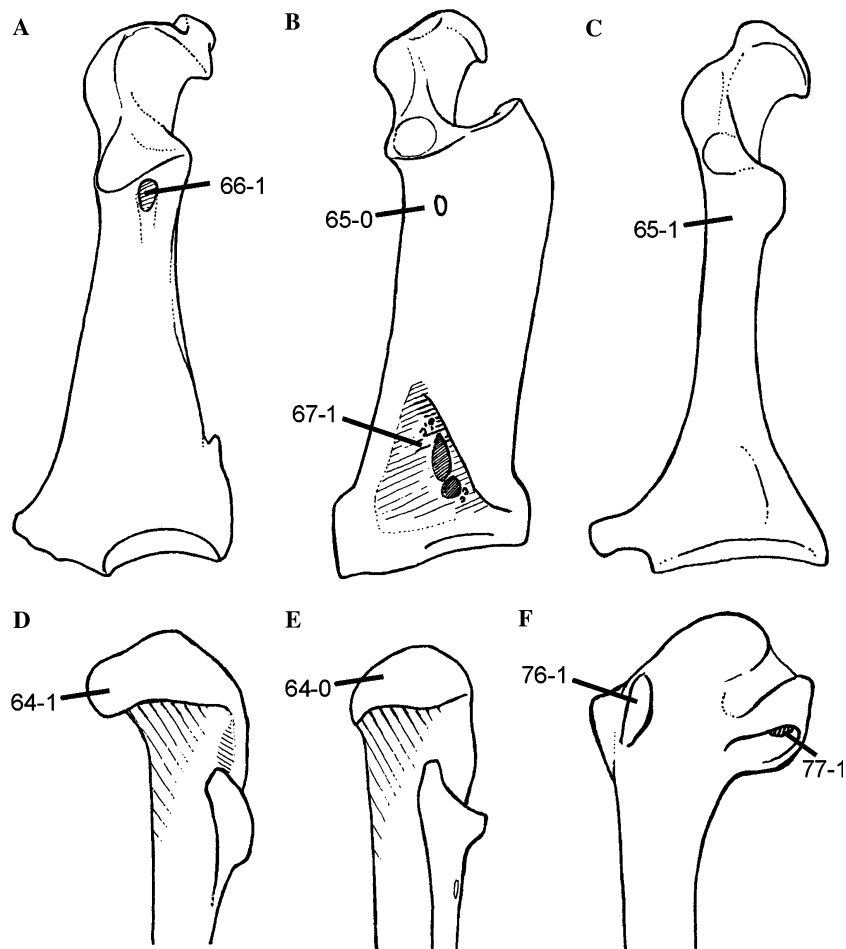


Fig. 7. Dorsal aspect of left coracoid (A–C), medial aspect of extremitas omalis of right coracoid (D, E), and caudal surface of proximal end of left humerus (F) to illustrate some characters and character states used in this study (numbers refer to Appendix A). (A) *Tinamus solitarius* (Tinamidae, Tinamiformes); (B) *Psophia crepitans* (Psophiidae, “Gruiformes”); (C) *Eurypyga helias* (Eurypygidae, “Gruiformes”); (D) *Numenius arquata* (Scolopacidae, Charadriiformes); (E) *Plegadis falcinellus* (Threskiornithidae, “Ciconiiformes”); and (F) *Chalcophaps stephani* (Columbidae, Columbiformes). Not to scale.

Ericson (1997), we found it to be absent in the Burhinidae. Within the Gruidae crossed sulci are present in *Balearica* but absent in the Gruinae.

70. Sternum, well-developed, blade-like spina externa rostri: absent (0), present (1).

71. Sternum, number of processus costales: 3–4 (0), 5–6 (1), 7–8 (2). This character was coded as ordered.

72. Sternum, facies visceralis with numerous pneumatic foramina along midline and lateral margins: no (0), yes (1).

73. Sternum, caudal margin: with four notches/fenestrae (0), with two notches/fenestrae (1) or without notches/fenestrae (2). In some Falconidae (e.g., *Microhierax caerulescens*, see Jollie, 1977, p. 201) the notches are completely reduced which we here consider autapomorphic for these taxa.

74. Ribs, processus uncinati: present, not fused to ribs (0), present, fused to ribs (1), absent (2). The presence of fused uncinate processes was proposed as a synapomorphy of Neornithes by Cracraft (1988, p. 344).

75. Humerus short and stocky with crista deltopectoralis strongly protruding and triangular: no (0), yes (1). The humerus of extant Psittacidae resembles that of Columbidae and Pteroclididae. However, the derived state of this character, although present within crown group Psittaciformes, is not present in any parts of the stem lineage (Mayr, 2002b); thus, it was coded as absent.

76. Humerus, tuberculum dorsale greatly elongated proximo-distally (Fig. 7F): no (0), yes (1). This character is present in extant Psittacidae, but see Mayr (2002b) concerning its absence in fossil stem group representatives of the Psittaciformes. Due to its highly apomorphic morphology, the humerus of Hesperornithidae, Rheidae, Apterygidae, and Spheniscidae cannot be coded for this character.

77. Humerus, foramina pneumatica at bottom of fossa pneumotricipitalis (or corresponding area in taxa without such fossa, Fig. 7F): absent (0), present (1). The absence of this feature in some diving Anatidae (e.g., *Aythya marila*, *Melanitta fusca*) is here considered to be derived, accordingly the character was coded as absent for the Anatidae. The presence of pneumatic foramina in the humerus was proposed as a synapomorphy of Neornithes by Cracraft (1988, p. 344).

78. Humerus, marked oval depression at attachment site of musculus scapulohumeralis cranialis (see Mayr, 2004, fig. 2; Olson and Feduccia, 1980a: fig. 27): absent (0), present. This character was proposed of a synapomorphy of Phoenicopteridae and Podicipedidae by Mayr (2004).

79. Humerus, fossa musculi brachialis not present or very indistinct: yes (0), no (1). Due to its highly apomorphic morphology, the humerus of Hesperornithidae, Rheidae, Apterygidae, and Spheniscidae cannot be coded for this character.

80. Humerus, fossa musculi brachialis very deep and sharply delimited: no (0), yes (1). This character was proposed as a synapomorphy of the taxon (Trogonidae + Steatornithidae) by Mayr (2003b). Due to its highly apomorphic morphology, the humerus of Hesperornithidae, Rheidae, Apterygidae, and Spheniscidae cannot be coded for this character.

81. Humerus, well-developed sulcus scapulotricipitalis: absent (0), present (1). Due to its highly apomorphic morphology, the humerus of Hesperornithidae, Rheidae, Apterygidae, and Spheniscidae cannot be coded for this character.

82. Ulna, distinctly exceeding humerus in length: no (0), yes (1).

83. Ulna, proximal end dorsoventrally compressed and cranioventrally inflected (Ericson, 1997, character 61): yes (0), no (1). Due to its highly apomorphic morphology, the ulna of Hesperornithidae, Rheidae, Apterygidae, and Spheniscidae cannot be coded for this character.

84. Ulna, distal end with marked depressio radialis: no (0), yes (1). Due to its highly apomorphic morphology, the ulna of Hesperornithidae, Rheidae, Apterygidae, and Spheniscidae cannot be coded for this character.

85. Carpometacarpus, os metacarpale minus strongly bowed, delimiting a large spatium intermetacarpale (Fig. 8B): no (0), yes (1). Within Galliformes, a strongly bowed os metacarpale minus is absent in the Megapodiidae, the sister taxon of Cracidae and Phasianidae, and in Eocene stem group representatives (see Mayr (2000a,b)); accordingly this character has been coded as absent for Galliformes.

86. Carpometacarpus, proximal end of os metacarpale minus dorsoventrally wide and strongly deflected ventrally (Ericson, 1997, character 65): no (0), yes (1). Contrary to Ericson (1997), we found the ventral deflection of the os metacarpale minus to be absent in the Psophiidae.

87. Os carpi ulnare with crus longum greatly abbreviated (Fig. 8D): no (0), yes (1). This character was proposed as a synapomorphy of the taxon (Cuculidae + Musophagidae) by Hughes (2000).

88. Os carpi ulnare, tuberculum at area of insertion of ligamentum humerocarpale (Fig. 8C; character 63 of Ericson, 1997): no (0), yes (1).

89. Phalanx proximalis digiti majoris elongate and craniocaudally narrow (ratio length to craniocaudal width more than 4.5): no (0), yes (1). This character was proposed of a synapomorphy of Phoenicopteridae and Podicipedidae by Mayr (2004).

90. Pelvis greatly elongated and strongly compressed mediolaterally, midsection of dorsal part of cristae iliacae dorsales reduced: no (0), yes (1). The shared derived morphology of the pelvis was proposed as a synapomorphy of Gaviidae and Podicipedidae by Cracraft

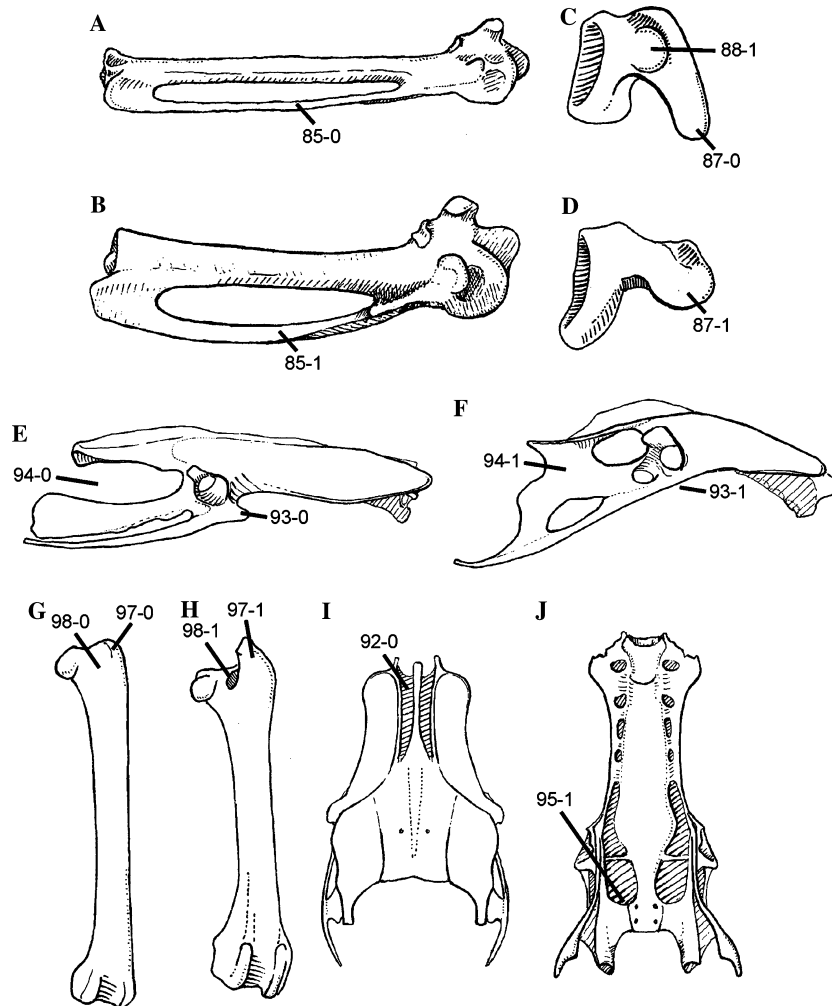


Fig. 8. Ventral aspect of right carpometacarpus (A, B), right os carpi ulnare (C, D), lateral (E, F), dorsal (I), and ventral (J) view of the pelvis, and left femur (G, H) to illustrate some postcranial characters and character states used in this study (numbers refer to Appendix A). (A) *Anthropoides virgo* (Gruidae, "Gruiformes"); (B) *Psophia crepitans* (Psophiidae, "Gruiformes"); (C) *Haematopus ostralegus* (Haematopodidae, Charadriiformes); (D) *Corythaixoides zonurus* (Musophagidae, Musophagiformes); (E) *Crypturellus cinnamomeus* (Tinamidae, Tinamiformes); (F) *Turdus merula* (Turdidae, Passeriformes); (G) *Eurystomus glaucurus* (Coraciidae, Coraciiformes); (H) *Psophia crepitans* (Psophiidae, "Gruiformes"); (I) *Turdus merula* (Turdidae, Passeriformes); and (J) *Laterallus melanophaius* (Rallidae, "Gruiformes"). Not to scale.

(1988, p. 349). The caudal part of the synsacrum of the Rheidae is reduced and the number of synsacral vertebrae is thus uncertain.

91. Pelvis, number of vertebrae ankylosed in synsacrum: 9–10 (0), 11–12 (1), 13–14 (2), 15–16 (3), and 17–18 (4). This character was coded as ordered.

92. Pelvis, cristae iliacae dorsales largely or completely fused cranially with crista spinosa of synsacrum, thus forming a closed canalis iliosynsacralis: no (0), yes (1).

93. Pelvis, tubercula praeacetabularia (Fig. 8E): large (0), absent or vestigial (1). Within Galliformes, the tubercula praeacetabularia are vestigial in the Tetraoninae (Phasianidae) which we consider to be a derived feature of this taxon.

94. Pelvis, foramen ilioischadicum caudally closed (Fig. 8F): no (0), yes (except Rheidae) (1), yes (condition in Rheidae) (2). We consider the condition in Rheidae

established (e.g., Lee et al., 1997) as derived within Palaeognathae and, thus, non-homologous to that of neognathous birds.

95. Pelvis, deeply excavated recessus caudalis fossae (Fig. 8J): absent (0), present (1). It is uncertain whether the morphology in Balaenicipitidae and Otididae is equivalent to the deep recessus treated here or is best considered a non-topologically equivalent pneumatic opening (see Ericson, 1997, character 31).

96. Femur, short and stout, ratio length to diameter in midsection less than 9.0: no (0), yes (1). This character was proposed as a synapomorphy of Phoenicopteridae and Podicipedidae by Mayr (2004).

97. Femur, crista trochanteris markedly projected cranially (Fig. 8H): no (0), yes (1).

98. Femur, pneumatic foramen at cranio-lateral side of proximal end (Fig. 8H): absent (0), present (1).

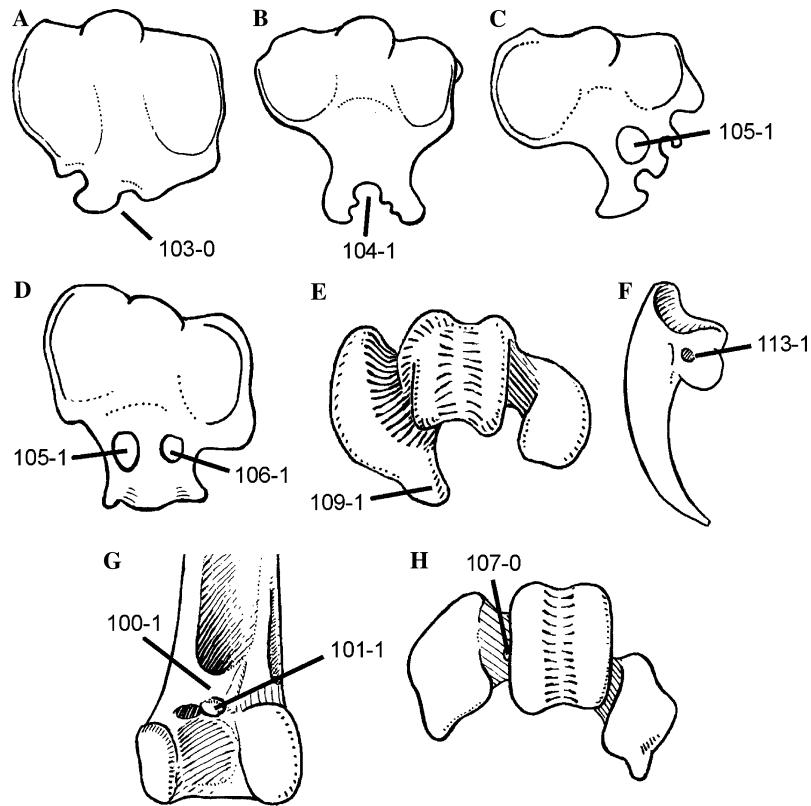


Fig. 9. Proximal end of right tarsometatarsus in proximal view (A–D), distal end of right tarsometatarsus in distal view (E, H), distal end of left tibiotarsus in cranial view (G), and claw (F) to illustrate some postcranial characters and character states used in this study (numbers refer to Appendix A). (A) *Tinamus solitarius* (Tinamidae, Tinamiformes); (B) *Plegadis falcinellus* (Threskiornithidae, “Ciconiiformes”); (C) *Columba palumbus* (Columbidae, Columbiformes); (D) *Guira guira* (Cuculidae, Cuculiformes); (E) *Guira guira* (Cuculidae, Cuculiformes); (F) *Psophia crepitans* (Psophiidae, “Gruiformes”); (G) *Tinamus solitarius* (Tinamidae, Tinamiformes); and (H) *Elanus leucurus* (Accipitridae, Falconiformes). Not to scale.

99. Tibiotarsus, cristae cnemiales markedly protruding proximally (Mayr, 2004, fig. 3): no (0), yes (1). The presence of this character in some diving Anatidae (e.g., *Oxyura* and *Melanitta*) is here considered autapomorphic for these taxa.

100. Tibiotarsus, distal end, ossified pons supratendineus (Fig. 9G): absent (0), present (1). Within Neornithes, an ossified pons supratendineus is absent in many Ratites, Opisthocomidae, some Podicipedidae, Strigiformes, some Psittaciformes, Steatornithidae, Nyctibiidae, and Bucerotidae. The presence of an ossified supratendinal bridge was proposed as a synapomorphy of Neornithes relative to *Ichthyornis* by Gauthier (1986) and Cracraft (1988, p. 344).

101. Tibiotarsus, prominent tubercle latero-distal to pons supratendineus (or corresponding area in taxa without supratendinal bridge; Fig. 9G): absent (0), present (1). Within the Rallidae this character is present in, e.g., *Aramides saracura*.

102. Tibiotarsus, distal rim of condylus medialis distinctly notched: no (0), yes (1). Within the Ciconiidae, this character is absent in *Leptoptilos*.

103. Tarsometatarsus, hypotarsus with well-developed cristae/sulci: no (0), yes (1).

104. Tarsometatarsus, hypotarsus with cristae medialis et lateralis hypotarsi strongly protruding and delimiting a marked sulcus through which all flexor tendons pass (Fig. 9B; this sulcus encompasses bony canals in Gaviidae, Podicipedidae): no (0), yes (1). Cracraft (1988, p. 352) proposed this character, in a slightly modified form, as a synapomorphy of a taxon including Phoenicopteridae, Threskiornithidae, and Ciconiidae.

105. Tarsometatarsus, hypotarsus, tendon of musculus flexor digitorum longus enclosed in bony canal (Fig. 9C; furrow/canal no. 1 of Strauch, 1978, 320): no (0), yes (1). Homology of tendinal furrows/canals was deduced from position of bony canals. This character is present in the Psittacidae, but see Mayr (2002b) concerning the hypotarsus of fossil stem group representatives of the Psittaciformes.

106. Tarsometatarsus, hypotarsus, tendon of musculus flexor hallucis longus enclosed in bony canal (Fig. 9D; furrow/canal no. 4 of Strauch, 1978, 320): no (0), yes (1). Homology of tendinal furrows/canals was deduced from position of bony canals and is uncertain for Gaviidae. This character is present in the Psittacidae, but see Mayr (2002b) concerning its absence in fossil stem group representatives of the Psittaciformes.

107. Tarsometatarsus, canalis interosseus distalis (Fig. 9H): present (0), absent (1). This canal opens into the incisura intertrochlearis lateralis and is not to be confused with the foramen vasculare distale.

108. Tarsometatarsus, trochlea metatarsi II plantarily deflected and distal end reaching much less far distally than distal end of trochlea metatarsi IV: yes (0), no (1).

109. Trochlea metatarsi IV with large trochlea accessoria (typical of fully zygodactyl feet; Fig. 9E): no (0), yes (1).

110. Hallux: not as follows (0), greatly reduced (proximal phalanx very short, measuring less than half of the length of the proximal phalanx of third toe) or completely absent (1). Within Galliformes, a long hallux is present in stem lineage representatives (Mayr, 2000b) and presumably basal (e.g., Mayr, 2000b) extant taxa like Megapodiidae and Cracidae, and we assume a long hallux to be primitive within the taxon.

111. Three anterior toes connected by web over their entire length: no (0), yes (1). Within Recurvirostridae, webbed feet occur in *Cladorhynchus*; see Mayr (2003a) concerning the rudimentary webbing in the Fregatidae.

112. Hallux included in webbed foot: no (0), yes (1). This character was coded as unknown for Spheniscidae and Procellariidae in which the toes are connected by a web but the hallux is greatly reduced.

113. Osseous claws, pair of canals lateral and medial to tuberculum extensorium (Fig. 9F): absent (0), present (1).

114. Claw of third toe distinctly pectinate on its medial side: no (0), yes (1). See Mayr (2003a) concerning the condition in *Balaeniceps*.

115. Musculus iliotibialis lateralis, pars acetabularis: present (0), absent (1); (after McKittrick, 1991, character 3).

116. Musculus iliofemoralis externus (“D” muscle in the formula of George and Berger, 1966, Tab. IX.1): present (0), absent (1); (after McKittrick, 1991, character 7).

117. Musculus femorotibialis externus, distal head: present (0), absent (1); (after McKittrick, 1991, character 8).

118. Musculus flexor cruris lateralis, pars accessoria (“Y” muscle in the formula of George and Berger, 1966, Tab. IX.1): present (0), absent (1); (after McKittrick, 1991, character 12).

119. Musculus flexor cruris lateralis, pars pelvica (“X” muscle in the formula of George and Berger, 1966, Tab. IX.1): present (0), absent (1); (after McKittrick, 1991, character 13).

120. Musculus caudofemoralis, pars caudalis (“A” muscle in the formula of George and Berger, 1966, Tab. IX.1): present (0), absent or poorly developed (1); (after McKittrick, 1991, character 15). The absence of this muscle in *Eudromia* (Tinamidae) and *Meleagris* (Phasianidae) is here considered autapomorphic for these taxa.

121. Musculus caudofemoralis, pars pelvica (“B” muscle in the formula of George and Berger, 1966, Tab. IX.1): present (0), absent (1); (after McKittrick, 1991, character 16). The absence of this muscle in some Procellariidae is here considered autapomorphic for this taxon.

122. Musculi obturatorii medialis et lateralis fused distally: yes (0), no (1); (after McKittrick, 1991, character 26).

123. Musculus iliofemoralis internus: present (0), absent (1); (after McKittrick, 1991, character 27).

124. Musculus iliotrochantericus medius (“C” muscle in the formula of George and Berger, 1966, Tab. IX.1): present (0), absent (1); (after George and Berger, 1966; Hoff, 1966; McKittrick, 1991; Vanden Berge, 1970).

125. Musculus ambiens: present (0), absent (1); (after Gadow, 1893; McKittrick, 1991, character 29).

126. Musculus ambiens, extent of origin: limited to tuberculum praeacetabulare (0), extending from tuberculum praeacetabulare to pubis (1), one origin tuberculum praeacetabulare and one from pubis (2); (after McKittrick, 1991, character 30).

127. Musculus gastrocnemius, number of heads: one (0), two (1); (after McKittrick, 1991, character 34).

128. Tendon of musculus extensor digitorum longus sending branch to hallux: no (0), yes (1); (after Berman, 1984; Berman and Raikow, 1982; McKittrick, 1991, character 39).

129. Musculus gastrocnemius, fourth head: absent (0), present (1); (after McKittrick, 1991, character 35; Vanden Berge, 1970). Cracraft (1988, 352) proposed this character as a synapomorphy of a taxon including Phoenicopteridae, Threskiornithidae, and Ciconiidae.

130. Musculus fibularis longus, branch to flexor perforatus digiti III: present (0), absent (1); (after McKittrick, 1991, character 42).

131. Musculus flexor perforans et perforatus digiti III, vinculum: present (0), absent (1); (after McKittrick, 1991, character 44).

132. Musculus flexor perforans et perforatus digiti II, origin from ansa iliofibularis: no (0), yes (1); (after McKittrick, 1991, character 47).

133. Musculus plantaris (“F” muscle in the formula of George and Berger, 1966, Tab. IX.1): present (0), absent (1); (after McKittrick, 1991, character 49).

134. Musculus flexor hallucis longus, tendon to hallux: present (0), weak or absent (1); (after McKittrick, 1991, character 51).

135. Musculus flexor hallucis longus and musculus flexor digitorum longus, type of arrangement. See George and Berger (1966, 447) for description of types I–VIII, and Berman (1984) for description of type X (coded 9, following McKittrick, 1991); (after McKittrick, 1991, character 52).

136. Musculus flexor hallucis longus, number of heads: one (0), two (1), three (2); (after McKittrick, 1991, character 53).

137. *Musculus popliteus* (“G” muscle in the formula of George and Berger, 1966, Tab. IX.1): present (0), absent (1); (after McKittrick, 1991, character 57).

138. *Musculus extensor hallucis longus*: present (0), absent or vestigial (1); (after McKittrick, 1991, character 60).

139. Accessory *musculus hallucis longus*: present (1), absent (0); (after McKittrick, 1991, character 62).

140. Wing: diastataxic (0), eutaxic (1); (after Mitchell, 1913; Sibley and Ahlquist, 1990, 217f; Stephan, 1970). The presence of an eutaxic wing in *Rollandia microptera* (Podicipedidae), few Rallidae, and *Micropsitta* (Psittacidae) is here considered autapomorphic for these birds (see also Bostwick and Brady, 2002).

141. Wing, number of primaries: 10 (0), 11 (1); (e.g., Stresemann, 1927–34). This character was proposed as a synapomorphy of Phoenicopteridae and Podicipedidae by Mayr (2004).

142. Large and naked gular pouch: absent (0), present (1).

143. Beak with well-defined cere surrounding narial openings (feathered in some Psittacidae): absent (0), present (1).

144. Oil gland: tufted (0), minutely tufted (only vestigial feather remains present)/naked (1); (after Johnston, 1988). The Otididae lack an oil gland.

145. *Medulla spinalis*, cornu dorsale of substantia grisea (dorsal horn of spinal grey matter): “leiocerate,” i.e., smooth and rounded (0), “schizocerate,” i.e., markedly inflected, “split-horned” (1); (after Woodbury, 1998). The “leiocerate” type is found in other amniotes and thus probably is primitive within birds (Woodbury, 1998).

146. Enzyme malate dehydrogenase with unusually slow motility (55% as fast as that of galliform birds): no (0), yes (1); (after Kitto and Wilson, 1966; this character is unique to charadriiform birds).

147. Eggshell: not as follows (0), covered with layer of microglobular material of amorphous calcium carbonate (1); (after Mikhailov, 1995).

148. Eggs covered with a chalky layer of amorphous calcium phosphate: no (0), yes (1); (after Mikhailov, 1995). This character was proposed as a synapomorphy of Phoenicopteridae and Podicipedidae by Mayr (2004).

Appendix B. Character matrix of 148 morphological characters for the 46 taxa included in this study (see Appendix A for character definitions)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
<i>Apsaravis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
<i>Hesperornis</i>	0	0	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Ichthyornis</i>	0	0	?	0	0	0	0	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Rheidae	1	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Apterygidae	1	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tinamidae	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galliformes	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	0	1	0
Anhimidae	1	0	1	0	0	0	0	0	0	0	1	1	0	?	0	1	1	0	1	1	1	1	0	1	0
Anatidae	1	0	2	0	0	0	0	0	0	0	1	1	0	?	0	0	1	0	1	1	1	1	0	1	0
Opisthocomidae	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0
Podicipedidae	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	1	1	1	1	0	0
Phoenicopteridae	1	0	2	1	0	0	0	0	0	0	1	0	0	?	1	1	0	0	1	0	1	1	1	0	0
Threskiornithidae	1	0	0	1	0	1	0	0	0	0	1	1	0	0	1	1	0	0	1	1	0	1	1	0	0
Cariamidae	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	1	1	1	1	1	0	0
Strigiformes	1	1	0	0	1	0	0	1	0	0	0	0	1	0	1	1	0	1	?	?	?	1	0	0	0
Recurvirostridae	1	0	0	0	0	1	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	1	0	0	1
Burhinidae	1	0	0	0	0	0	0	0	0	0	0	0	0	?	1	1	0	0	0	1	0	1	1	0	0
Accipitridae	1	1	0	0	0	0	0	1	0	0	0	0	01	0	1	1	0	0	1	1	1	1	1	0	0
Falconidae	1	1	0	0	0	0	0	1	0	0	0	0	1	0	1	1	0	0	0	1	0	1	1	0	0
Sagittariidae	1	1	0	0	0	0	0	1	0	0	01	0	1	0	0	1	0	1	?	?	?	1	0	0	0
Cuculidae	1	0	0	0	0	0	0	1	0	0	1	0	0	1	1	1	0	1	?	?	?	1	1	0	0
Musophagidae	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0
Cathartidae	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	?	?	?	1	0	0	0
Gaviidae	1	0	0	0	0	0	0	0	0	0	0	0	0	?	0	1	0	0	0	1	1	1	1	0	1
Spheniscidae	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	1	0	1
Phaethontidae	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0
Fregatidae	1	1	0	1	0	0	1	?	1	0	0	0	0	?	0	1	1	0	1	1	0	1	1	0	0
Phalacrocoracidae	1	1	0	1	1	0	1	?	1	0	1	0	0	?	1	1	01	1	?	?	?	1	1	0	0
Balaenicipitidae	1	1	0	1	1	0	1	?	0	0	1	0	0	?	1	1	1	1	?	?	?	1	1	0	0
Eurypygidae	1	0	0	0	0	1	0	0	0	0	0	1	0	?	1	1	0	0	0	1	0	1	1	0	0
Ardeidae	1	0	0	0	0	0	0	0	0	0	01	0	0	0	1	1	0	0	0	1	1	1	1	0	0

Appendix B. (continued)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Ciconiidae	1	0	0	0	0	0	0	0	0	0	1	1	0	?	1	1	0	1	?	?	?	1	1	0	0
Procellariidae	1	1	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	1
Otididae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	1	1	1	0	0
Pteroclididae	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	?	?	?	1	0	0	0
Columbidae	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1	?	?	?	1	0	0	0
Rallidae	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1	1	1	1	0	0
Psophiidae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	1	0	0
Gruidae	1	0	0	0	0	0	0	0	0	0	0	01	1	0	1	1	0	0	0	0	1	1	1	0	0
Steatornithidae	1	1	0	0	1	0	0	1	0	0	1	1	0	0	0	0	1	1	?	?	?	1	0	0	0
Psittaciformes	1	1	0	0	1	0	0	1	0	0	1	0	01	0	0	1	0	1	?	?	?	1	1	0	0
Coliidae	1	0	0	0	0	0	0	1	0	0	1	1	0	1	0	1	0	1	?	?	?	1	1	0	0
Trogonidae	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0	0
Aegothelidae	1	1	0	0	0	0	0	0	0	0	?	?	0	0	1	0	0	0	0	0	0	1	0	0	0
Coraciidae	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	1	0	1	1	0	1	1	0	0
Passeriformes	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
<i>Apsaravis</i>	?	?	?	?	?	?	?	?	?	0	0	?	?	?	?	?	1	?	0	?	?	?	?	?	?
<i>Hesperornis</i>	0	0	?	0	1	0	0	1	0	0	0	0	0	?	0	?	0	0	0	0	0	0	0	?	?
<i>Ichthyornis</i>	0	0	?	01	0	0	?	?	0	0	0	0	0	?	?	0	0	0	0	0	0	0	1	0	?
Rheidae	0	0	0	0	0	1	1	0	0	0	1	0	0	?	1	1	1	1	0	0	0	0	0	0	0
Apterygidae	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1	1	0
Tinamidae	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	1	1	1	0	0	0	0	1	0	0
Galliformes	1	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	1	0	1	1	0	0	0	01	1
Anhimidae	1	0	0	1	0	0	1	1	1	1	0	0	1	0	0	1	1	0	1	1	0	01	1	0	0
Anatidae	1	1	0	1	0	0	1	1	1	1	0	0	1	0	0	1	1	0	1	1	0	01	01	0	0
Opisthocomidae	0	0	0	1	0	1	1	0	1	0	1	0	0	0	0	1	1	0	0	0	0	1	1	0	1
Podicipedidae	0	0	0	1	1	0	1	0	1	0	0	1	0	0	0	1	1	0	0	0	1	0	0	0	01
Phoenicopteridae	0	1	0	1	1	0	1	0	1	0	0	1	0	0	0	1	1	0	1	0	1	0	1	1	1
Threskiornithidae	0	1	0	1	1	0	1	0	1	0	0	1	0	0	0	1	1	0	0	0	01	0	1	1	0
Cariamidae	0	0	0	1	0	1	1	0	1	0	1	0	0	0	0	1	1	0	0	0	0	0	1	0	1
Strigiformes	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	1	1	0	0	1	0	0	0	1	1
Recurvirostridae	0	1	0	1	0	0	1	0	1	0	0	1	0	0	0	1	1	0	1	0	0	0	0	1	1
Burhinidae	0	0	0	1	0	0	1	0	1	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0
Accipitridae	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	1	1	0	0	1	0	0	0	1	0
Falconidae	0	0	0	1	0	0	1	0	1	0	0	01	0	0	0	1	1	0	0	1	0	0	0	1	1
Sagittariidae	0	0	0	1	0	0	1	1	1	0	1	0	0	0	0	1	1	0	0	1	1	1	0	0	1
Cuculidae	0	0	0	1	0	01	1	0	1	0	01	0	0	0	0	1	1	0	0	1	0	0	0	01	0
Musophagidae	0	0	0	1	0	1	1	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	01	1
Cathartidae	0	0	1	1	1	0	1	0	1	0	0	1	0	0	0	1	1	0	0	1	0	0	0	01	1
Gaviidae	0	0	0	1	1	0	1	0	1	0	0	1	0	0	0	1	1	0	0	0	1	0	0	1	1
Spheniscidae	0	0	0	1	1	0	1	1	1	1	0	1	0	0	0	1	1	0	0	0	0	0	0	1	1
Phaethontidae	0	0	0	1	1	0	1	1	1	0	0	0	0	0	0	1	1	0	0	0	1	0	1	1	1
Fregatidae	0	0	1	1	1	0	1	1	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	1	1
Phalacrocoracidae	0	0	0	1	1	0	1	1	1	0	0	1	0	0	0	1	1	0	0	1	1	0	0	1	0
Balaenicipitidae	0	0	1	1	0	1	1	0	1	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0	1
Eurypygidae	0	0	0	1	0	1	1	1	1	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0	1
Ardeidae	0	0	0	1	0	0	1	1	1	01	0	1	0	0	0	1	1	0	0	0	0	0	1	0	1
Ciconiidae	0	0	01	1	1	0	1	0	1	0	1	1	0	0	0	1	1	0	0	0	0	01	1	0	0
Procellariidae	0	0	1	1	1	0	1	1	1	0	01	1	0	0	0	1	1	0	0	0	1	0	0	1	1
Otididae	0	0	0	1	0	1	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1
Pteroclididae	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	1	1	0	1	1	0	0	0	1	1
Columbidae	0	0	0	1	0	1	1	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1
Rallidae	0	0	0	1	0	1	1	0	1	01	0	1	0	0	0	1	1	0	0	0	0	0	0	1	1
Psophiidae	0	0	0	1	0	0	1	0	1	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	1
Gruidae	0	1	0	1	0	1	1	1	1	0	1	1	0	0	0	1	1	0	0	0	0	0	1	0	0
Steatornithidae	0	0	0	1	0	0	1	1	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1
Psittaciformes	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	1	1
Coliidae	0	0	0	1	0	1	1	1	1	0	1	0	0	0	0	1	1	0	0	0	1	0	0	1	1
Trogonidae	0	0	0	1	0	0	1	1	1	0	0	0	0	1	0	1	1	0	0	1	0	0	0	1	1
Aegothelidae	0	0	0	1	0	0	1	1	1	0	1	0	0	0	0	1	1	0	0	0	1	0	0	1	1
Coraciidae	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	01	1	01
Passeriformes	0	0	0	1	0	01	1	0	1	0	0	0	0	0	0	1	1	0	0	1	0	0	0	1	1

Appendix B. (continued)

	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	
<i>Apsaravis</i>	?	?	?	?	12	?	0	0	0	0	0	?	?	0	0	0	0	0	0	?	?	?	?	?	0	
<i>Hesperornis</i>	0	0	0	0	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	
<i>Ichthyornis</i>	0	0	?	0	12	?	0	1	?	0	0	0	0	0	0	0	0	0	1	0	1	0	?	?	0	
Rheidae	0	0	0	0	1	0	1	0	0	0	0	?	?	0	0	0	0	1	0	0	0	0	2	0	0	
Apterygidae	0	1	0	0	1	0	1	0	0	0	0	?	?	0	0	0	0	1	0	0	0	0	1	0	0	
Tinamidae	01	0	0	0	1	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	
Galliformes	0	1	0	0	1	1	1	01	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	1	0	
Anhimidae	01	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0	1	0	0	0	2	0	1	2	0	
Anatidae	0	1	0	0	1	0	1	0	1	0	1	0	0	0	1	0	0	0	0	01	12	0	1	1	0	
Opisthocomidae	1	1	0	0	1	1	1	0	1	0	0	1	0	0	1	1	1	0	?	?	1	1	1	1	0	
Podicipedidae	0	0	0	1	2	1	1	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	1	0	0	
Phoenicopteridae	0	0	0	1	2	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	
Threskiornithidae	0	1	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	
Cariamidae	0	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	1	1	0	1	1	0	
Strigiformes	0	1	0	0	0	0	1	0	1	0	0	01	0	0	0	0	0	0	01	0	1	0	0	1	0	
Recurvirostridae	0	1	0	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	1	1	0	0	1	0	
Burhinidae	0	1	1	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	1	1	0	0	1	0	
Accipitridae	0	01	0	0	01	0	1	0	1	0	0	1	0	0	0	0	0	0	01	01	1	0	1	1	0	
Falconidae	0	1	0	0	01	1	1	0	1	0	0	1	0	0	0	0	0	0	1	1	1	0	1	1	0	
Sagittariidae	1	1	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	1	1	2	1	0	
Cuculidae	0	1	01	0	0	0	1	0	1	0	1	0	0	0	1	01	0	0	0	1	0	0	01	1	0	
Musophagidae	0	1	1	0	0	0	1	0	1	1	0	1	0	0	0	0	0	0	1	1	01	0	0	1	0	
Cathartidae	0	1	0	0	1	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	
Gaviidae	0	0	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	2	0	1	0	0	
Spheniscidae	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	
Phaethontidae	0	1	0	0	2	0	1	0	1	?	?	0	1	0	0	0	0	0	1	1	1	0	2	1	0	
Fregatidae	0	1	0	0	0	0	1	0	1	1	0	?	1	0	1	0	0	0	0	0	1	1	2	1	0	
Phalacrocoracidae	0	0	0	0	2	0	1	0	1	1	0	1	1	0	1	0	0	0	1	0	1	0	1	1	0	
Balaenicipitidae	0	0	0	0	1	0	1	0	1	0	1	1	1	0	0	0	0	0	1	0	1	1	1	1	0	
Eurypygidae	0	0	0	0	2	1	1	0	1	0	1	0	0	0	1	0	0	0	1	1	1	0	1	1	0	
Ardeidae	0	0	0	0	2	0	1	0	1	0	1	0	0	0	1	0	0	0	1	1	0	0	1	1	0	
Ciconiidae	0	1	0	0	1	0	1	0	1	0	0	0	1	0	01	0	0	0	01	0	1	1	1	1	0	
Procellariidae	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	1	1	1	01	0	1	0	
Otididae	01	01	0	0	1	0	1	0	0	0	1	0	0	0	1	1	0	0	0	0	1	0	0	1	0	
Pteroclididae	0	1	0	0	1	1	1	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	1	
Columbidae	0	0	0	0	0	1	1	0	1	0	1	0	0	0	1	0	0	0	0	01	0	0	01	1	1	
Rallidae	0	01	0	0	12	0	1	0	1	0	1	0	0	0	0	0	01	0	0	1	1	0	1	1	0	
Psophiidae	0	0	0	0	2	1	1	0	0	0	1	0	0	0	0	0	1	0	0	0	2	1	2	1	0	
Gruidae	0	0	0	0	2	1	1	0	0	0	1	0	0	0	0	0	0	1	0	01	0	2	1	2	1	0
Steatornithidae	0	0	0	0	0	1	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	1	1	0	
Psittaciformes	0	01	01	0	0	0	1	0	1	0	1	0	0	0	01	0	0	0	1	1	1	0	1	1	0	
Coliidae	0	1	1	0	0	0	1	0	1	1	0	0	0	0	01	0	0	0	0	1	0	0	0	1	0	
Trogonidae	0	0	0	0	0	0	1	0	1	1	1	0	0	0	1	0	0	0	0	1	0	0	0	1	0	
Aegothelidae	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	
Coraciidae	1	1	1	0	0	0	1	0	1	1	1	0	0	0	1	0	0	0	0	1	1	0	0	1	0	
Passeriformes	0	1	0	0	0	0	1	0	1	1	1	0	0	0	1	0	0	0	0	1	1	0	1	1	0	
	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	
<i>Apsaravis</i>	0	0	0	0	0	0	0	1	?	0	0	0	?	0	0	0	0	1	0	0	0	0	?	?	0	
<i>Hesperornis</i>	?	0	0	?	?	?	0	?	?	?	?	?	?	?	1	2	0	0	0	0	1	0	0	0	0	
<i>Ichthyornis</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	01	0	1	0	0	0	0	0	0	0	
Rheidae	?	0	0	?	?	?	0	?	?	0	0	?	?	?	0	?	1	0	2	0	0	0	0	0	0	
Apterygidae	?	0	0	?	?	?	0	?	?	0	0	?	?	?	0	23	1	0	0	0	0	0	0	0	1	
Tinamidae	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	1	0	0	1	
Galliformes	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	3	1	0	1	1	0	1	01	0	1	
Anhimidae	0	1		0	0	1	0	1	1	0	0	0	0	0	0	4	1	1	1	0	1	0	1	0	1	
Anatidae	0	1	0	1	0	1	0	1	01	1	0	0	0	0	0	34	1	0	1	0	01	0	0	0	1	
Opisthocomidae	0	1	0	1	1	1	0	1	0	0	1	0	0	0	0	3	1	1	1	1	0	0	0	0	0	
Podicipedidae	0	0	1	1	0	1	0	1	1	0	0	0	0	1	1	4	0	1	1	0	1	0	0	1	01	
Phoenicopteridae	0	1	1	1	0	1	0	1	1	0	0	0	0	1	0	2	1	1	1	1	0	1	1	1	1	
Threskiornithidae	0	1	0	1	0	1	1	1	0	0	0	0	0	0	0	3	1	1	1	0	0	1	0	0	1	
Cariamidae	0	1	0	1	0	1	0	0	0	1	1	0	0	0	0	2	1	1	1	1	0	1	0	0	1	
Strigiformes	0	1	0	1	0	1	1	1	0	0	0	0	0	0	0	2	1	1	1	1	0	0	0	0	0	
Recurvirostridae	0	0	0	1	0	1	1	1	0	0	0	0	1	0	0	2	0	1	1	0	0	1	0	1	1	

Appendix B. (continued)

	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100
Burhinidae	0	0	0	1	0	1	1	1	0	0	0	0	1	0	0	3	0	1	1	0	0	1	0	0	1
Accipitridae	0	1	0	1	0	1	1	1	1	0	0	0	0	0	0	2	1	1	1	0	0	0	1	0	1
Falconidae	0	1	0	1	0	1	1	1	1	0	0	0	0	0	0	12	1	1	1	0	0	1	1	0	1
Sagittariidae	0	1	0	1	1	1	0	1	0	0	0	0	0	0	0	2	1	1	1	1	0	1	1	0	1
Cuculidae	0	1	0	1	0	1	0	1	0	01	01	1	0	0	0	1	01	01	1	01	0	0	0	0	1
Musophagidae	0	1	0	1	0	1	0	1	0	1	1	1	0	0	0	2	0	0	1	1	0	0	1	0	1
Cathartidae	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0	2	1	1	1	0	0	1	1	0	1
Gaviidae	0	0	0	1	0	1	0	1	0	0	0	0	0	0	1	4	0	1	1	0	1	0	0	1	1
Spheniscidae	0	0	0	?	?	?	0	?	?	0	0	0	0	0	0	1	0	1	1	0	0	0	0	1	1
Phaethontidae	0	1	0	1	0	1	1	1	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1
Fregatidae	0	1	0	1	0	1	1	1	0	0	0	0	0	1	0	2	0	1	1	0	1	0	0	0	1
Phalacrocoracidae	0	0	0	1	0	1	1	1	0	0	0	0	0	1	0	3	1	1	1	0	0	0	0	1	1
Balaenicipitidae	0	1	0	1	0	1	1	1	0	0	0	0	0	0	0	3	1	1	1	?	0	0	0	0	1
Eurypygidae	0	1	0	1	0	1	1	1	0	0	0	0	0	0	0	2	0	1	1	0	0	0	0	0	1
Ardeidae	0	1	0	1	0	1	1	1	0	0	0	0	0	0	0	2	1	1	1	0	0	0	0	0	1
Ciconiidae	0	1	0	1	0	1	1	1	01	0	0	0	01	0	0	3	1	1	1	0	1	1	1	0	1
Procellariidae	0	0	0	1	1	0	0	1	0	0	0	0	0	1	0	2	0	1	1	0	0	0	0	1	1
Otididae	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	3	0	1	1	?	1	1	1	0	1
Pteroclididae	1	1	0	1	0	1	1	1	0	1	0	0	0	0	0	2	0	1	1	0	0	1	0	0	1
Columbidae	1	1	0	1	0	1	1	1	0	1	0	0	1	0	0	2	0	1	1	0	0	1	0	0	1
Rallidae	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	4	1	1	1	1	0	1	0	0	1
Psophiidae	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	3	1	1	1	1	0	1	0	0	1
Gruidae	0	1	0	1	0	1	1	1	0	0	0	0	0	0	0	3	1	1	1	1	0	1	0	0	1
Steatornithidae	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0
Psittaciformes	0	1	0	1	0	1	1	1	1	0	0	0	0	0	0	2	1	1	1	0	0	0	0	0	01
Coliidae	0	1	0	1	0	1	01	1	0	1	0	0	0	0	0	1	0	1	1	0	0	0	0	1	1
Trogonidae	0	1	0	1	1	1	1	1	0	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1
Aegothelidae	0	1	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1
Coraciidae	0	1	0	1	0	1	1	1	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1
Passeriformes	0	1	0	1	0	1	1	1	0	0	0	01	0	0	0	1	0	1	1	0	0	0	0	0	1
	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	121	122	123	124	125
<i>Apsaravis</i>	0	1	0	0	0	0	1	0	0	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hesperornis</i>	0	0	0	0	0	0	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ichthyornis</i>	0	0	0	0	0	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rheidae	0	0	0	0	0	0	0	1	0	1	0	0	0	0	?	?	?	0	0	1	0	?	?	?	0
Apterygidae	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tinamidae	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Galliformes	0	0	1	0	1	0	0	0	0	0	0	0	01	0	0	0	0	0	0	0	0	0	0	0	0
Anhimidae	0	0	1	0	0	0	0	1	0	0	0	0	0	0	?	?	?	0	0	?	?	?	?	?	0
Anatidae	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	1	0	0	0
Opisthocomidae	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Podicipedidae	0	1	1	1	1	?	0	0	0	1	0	0	0	0	1	1	1	1	0	1	0	0	0	0	1
Phoenicopteridae	1	1	1	1	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0
Threskiornithidae	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Cariamidae	0	0	0	0	0	0	0	1	0	1	0	0	0	0	?	?	?	?	?	1	?	?	?	?	0
Strigiformes	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	1	0	1	0	0	0	1
Recurvirostridae	0	1	1	0	0	0	0	0	0	1	01	0	0	0	?	?	?	?	?	?	?	?	?	?	0
Burhinidae	0	1	1	0	0	0	0	1	0	1	0	0	0	0	?	?	?	?	?	1	?	?	?	?	0
Accipitridae	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	1	1	0	1	1	0	0	0
Falconidae	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	1	1	0	1	1	0	0	0
Sagittariidae	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
Cuculidae	0	0	1	0	1	1	0	1	1	0	0	0	0	0	0	1	1	0	0	01	1	0	1	1	0
Musophagidae	0	0	1	0	1	0	0	1	0	0	0	0	0	0	?	0	?	0	0	?	0	?	1	1	0
Cathartidae	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	01	1	1	0	0	0
Gaviidae	0	0	1	1	1	?	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Spheniscidae	0	0	0	0	0	0	1	1	0	1	1	?	0	0	0	0	01	1	0	0	0	0	0	0	0
Phaethontidae	0	0	1	1	0	0	0	1	0	0	1	1	0	0	?	?	?	0	0	?	1	?	?	?	?
Fregatidae	0	0	1	0	1	0	0	1	0	0	0	1	0	1	0	0	1	1	1	1	1	0	0	?	0
Phalacrocoracidae	0	0	1	0	1	1	0	1	0	0	1	1	0	1	0	0	1	1	0	0	1	?	0	0	0
Balaenicipitidae	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1
Eurypygidae	0	0	1	0	0	0	0	1	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?
Ardeidae	0	0	1	0	1	01	0	1	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	1
Ciconiidae	1	01	1	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0

Appendix B. (continued)

	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	121	122	123	124	125
Procellariidae	0	1	1	0	0	0	0	0	0	1	1	?	0	0	0	0	0	1	1	0	0	0	0	0	0
Otididae	0	0	1	0	1	0	0	1	0	1	0	0	0	0	?	?	?	?	0	1	?	?	?	?	0
Pteroclididae	0	0	1	0	1	0	0	0	0	1	0	0	0	0	?	?	?	?	?	?	0	?	?	?	0
Columbidae	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Rallidae	01	0	1	0	01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Psophiidae	1	1	1	0	0	0	0	1	0	0	0	0	0	0	?	?	?	?	?	1	?	?	?	?	0
Gruidae	1	1	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0
Steatornithidae	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1	?	0	0	1
Psittaciformes	0	0	1	0	0	0	1	1	1	0	0	0	01	0	1	0	0	0	0	0	1	1	0	0	0
Coliidae	0	0	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	1
Trogonidae	0	0	1	0	1	1	1	1	0	0	0	0	0	0	1	1	?	1	?	?	?	?	?	0	1
Aegothelidae	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0	1	0	?	?	0	1	?	0	0	1
Coraciidae	0	0	1	0	1	0	1	1	0	0	0	0	0	0	01	1	0	0	0	0	1	0	0	0	1
Passeriformes	0	0	1	0	1	1	1	1	0	0	0	0	01	0	01	1	0	0	0	0	1	1	0	0	1
	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148		
<i>Apsaravis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Hesperornis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Ichthyornis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
Rheidae	?	?	0	?	?	?	1	?	1	4	?	?	?	?	?	?	0	0	1	0	0	0	0	0	
Apterygidae	0	0	0	0	0	1	0	01	1	2	0	1	0	0	?	?	0	0	1	?	0	0	0	0	
Tinamidae	0	0	0	0	0	0	0	0	0	1	0	0	01	0	1	0	0	0	0	0	0	0	0	0	
Galliformes	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	
Anhimidae	?	?	?	0	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	?	0	0	0	0	
Anatidae	12	01	0	0	0	01	0	0	01	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	
Opisthocomidae	0	0	0	0	0	1	1	0	0	1	0	0	0	0	1	0	0	0	0	1	?	0	0	0	
Podicipedidae	?	1	0	0	1	1	0	0	1	4	0	0	1	?	0	1	0	0	0	1	0	0	1	0	
Phoenicopteridae	0	0	0	1	0	0	0	0	1	4	0	0	1	0	0	1	0	0	0	?	0	0	1	0	
Threskiornithidae	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	
Cariamidae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0	0	1	?	?	0	0	0	
Strigiformes	?	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	0	1	1	1	0	0	0	0	
Recurvirostridae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	1	1	0	0	0	
Burhinidae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	1	1	0	0	0	
Accipitridae	0	0	0	0	0	1	0	1	0	3	1	0	0	0	0	0	0	1	0	?	0	0	0	0	
Falconidae	0	0	0	0	0	1	0	0	0	3	1	0	0	0	0	0	0	1	0	1	0	0	0	0	
Sagittariidae	0	0	0	0	0	0	0	1	0	3	1	0	0	0	0	0	0	1	0	?	?	0	0	0	
Cuculidae	1	0	0	0	0	1	1	0	0	1	0	0	0	0	1	0	0	0	1	0	0	01	0	0	
Musophagidae	1	?	?	?	?	0	?	?	?	?	?	?	?	?	1	0	0	0	0	1	0	0	0	0	
Cathartidae	0	0	0	0	0	0	1	0	0	5	1	0	0	0	0	0	0	1	1	1	0	0	0	0	
Gaviidae	1	1	0	0	1	0	1	0	1	4	0	0	1	?	0	0	0	0	0	1	0	0	0	0	
Spheniscidae	1	0	0	0	0	1	1	0	1	2	0	0	1	0	?	?	0	0	0	?	0	1	0	0	
Phaethontidae	?	?	0	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	1	0	0	0	0	
Fregatidae	0	0	0	0	0	1	0	0	0	5	0	0	0	0	0	0	1	0	0	?	?	1	0	0	
Phalacrocoracidae	0	0	0	0	0	?	0	0	0	2	1	0	0	0	0	0	1	0	0	1	?	1	0	0	
Balaenicipitidae	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	?	?	1	0	0	
Eurypygidae	?	?	0	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	1	1	?	0	0	0	
Ardeidae	?	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0	01	0	0	
Ciconiidae	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	?	0	0	0	0	
Procellariidae	1	0	0	0	0	1	0	0	0	4	0	0	1	?	0	0	0	0	0	?	0	0	0	0	
Otididae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	?	1	0	0	0	0	
Pteroclididae	?	?	?	0	?	0	?	1	?	?	?	?	?	?	0	0	0	0	1	1	0	0	0	0	
Columbidae	0	0	0	0	0	0	0	0	0	1	0	0	0	1	01	0	0	1	1	0	0	0	0	0	
Rallidae	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
Psophiidae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0	0	0	0	?	0	0	0	
Gruidae	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Steatornithidae	?	0	?	0	?	0	0	0	0	?	0	1	0	0	0	0	0	0	1	1	?	0	0	0	
Psittaciformes	?	0	1	0	1	1	1	1	0	9	0	1	0	1	0	0	0	1	0	1	0	0	0	0	
Coliidae	?	0	1	0	1	1	0	1	0	5	1	1	0	1	1	0	0	0	0	1	?	0	0	0	
Trogonidae	?	?	0	?	0	?	?	0	0	8	?	1	?	?	1	0	0	0	1	1	0	0	0	0	
Aegothelidae	?	0	?	0	?	1	0	0	0	?	0	1	0	0	0	0	0	0	1	1	?	0	0	0	
Coraciidae	?	0	0	0	1	1	0	0	0	5	1	0	0	?	0	0	0	0	1	1	0	0	0	0	
Passeriformes	?	?	0	0	0	1	0	0	0	7	12	1	01	0	1	0	0	0	1	0	0	0	0	0	

Polymorphic characters are coded as such, unknown character states are indicated by "?".

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