

Morphological evidence for sister group relationship between flamingos (Aves: Phoenicopteridae) and grebes (Podicipedidae)

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Received January 2003; accepted for publication July 2003

A recent molecular analysis strongly supported sister group relationship between flamingos (Phoenicopteridae) and grebes (Podicipedidae), a hypothesis which has not been suggested before. Flamingos are long-legged filter-feeders whereas grebes are morphologically quite divergent foot-propelled diving birds, and sister group relationship between these two taxa would thus provide an interesting example of evolution of different feeding strategies in birds. To test monophyly of a clade including grebes and flamingos, I performed a cladistic analysis of 70 morphological characters which were scored for 17 taxa. Parsimony analysis of these data supported monophyly of the taxon (Podicipedidae + Phoenicopteridae) and the clade received high bootstrap support. Previously overlooked morphological, oological and parasitological evidence is recorded which supports this hypothesis, and which makes the taxon (Podicipedidae + Phoenicopteridae) one of the best supported higher-level clades within modern birds. The phylogenetic significance of some fossil flamingo-like birds is discussed. The Middle Eocene taxon *Juncitarsus* is most likely the sister taxon of the clade (Podicipedidae + (Palaelodidae + Phoenicopteridae)) although resolution of its exact systematic position awaits revision of the fossil material. Contrary to previous assumptions, it is more parsimonious to assume that flamingos evolved from a highly aquatic ancestor than from a shorebird-like ancestor. © 2004 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2004, 140, 157–169.

ADDITIONAL KEYWORDS: evolution – fossil birds – *Juncitarsus* – Palaelodidae – phylogeny.

INTRODUCTION

Avian higher-level systematics is only poorly understood and in particular, the phylogenetic affinities of flamingos (Phoenicopteridae) are among the ‘most controversial and long-standing problems’ (Sibley & Ahlquist, 1990). These birds show a strange mosaic of a duck-like beak with stork-like legs and were indeed considered to be most closely related to either anseriform or ciconiiform birds by earlier authors (see the review of the history of avian classification in Sibley & Ahlquist, 1990). Neither of these hypotheses, however, has been convincingly supported with derived characters and the evidence has been critically discussed by Olson & Feduccia (1980a).

There is strong morphological and molecular support for monophyly of Galloanseres to the exclusion of the Phoenicopteridae (e.g. Sibley & Ahlquist, 1990;

Livezey, 1997; van Tuinen, Sibley & Hedges, 2000; Livezey & Zusi, 2001; this study), and monophyly of Phoenicopteridae and Anseriformes was not supported by the study of Mindell *et al.* (1997). The only cladistic analysis which did support sister group relationship between Phoenicopteridae and Anseriformes was by Ericson (1997) who did not, however, list the characters supporting this result. Re-analysis of the data by Ericson, Parsons & Johansson (2001) did not support monophyly of the taxon (Phoenicopteridae + Anseriformes).

Cracraft (1981) considered a clade comprising flamingos, storks and ibises as only ‘moderately well-defined’, and most of the few synapomorphies supporting sister group relationship between storks and flamingos (Cracraft, 1988) are characters of the hindlimb and might well be functionally related to the elongated legs of these birds.

Olson & Feduccia (1980a) suggested that the Phoenicopteridae are most closely related to the charadriiform stilts and avocets (Recurvirostridae). These

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authors did not evaluate the proposed synapomorphies in a cladistic context and the assumed relationships were not depicted in some kind of phylogenetic tree. As already discussed by Cracraft (1981), there is considerable character conflict with this hypothesis, which has not been supported by subsequent analyses (e.g. Sibley & Ahlquist, 1990; Livezey & Zusi, 2001), because flamingos lack many derived characters that support inclusion of the Recurvirostridae in a clade with other charadriiform birds such as gulls (Laridae).

Recently, a completely new hypothesis on flamingo relationships was set up by van Tuinen *et al.* (2001), who analysed mitochondrial and nuclear DNA sequences as well as DNA-DNA hybridization data and found strong support for sister group relationship between flamingos and grebes (Podicipedidae). Although both DNA-DNA hybridization studies and mitochondrial sequence data have been considered problematic for the study of higher level relationships among birds (e.g. Houde, 1987; Lanyon, 1992; Groth & Barrowclough, 1999), the study of van Tuinen *et al.* (2001) is notable for its high statistical support and the high degree of congruence between these different data sets.

A closer relationship between flamingos and grebes has not been proposed before, and grebes were traditionally (e.g. Fürbringer, 1888; Beddard, 1898) considered to be most closely related to loons (Gaviidae). With the exception of Cracraft (1982, 1988), most recent authors have considered the shared derived similarities between Podicipedidae and Gaviidae to be due to convergence, and the systematic affinities of grebes to be uncertain (Sibley & Ahlquist, 1990).

Whereas flamingos are long-legged, wading filter-feeders, grebes are foot-propelled diving birds which mainly feed on fish and small arthropods (del Hoyo, 1992; Llimona & del Hoyo, 1992). As noted by van Tuinen *et al.* (2001), sister group relationship between grebes and flamingos would thus provide an interesting example of evolution of divergent feeding strategies among birds.

Van Tuinen *et al.* (2001) stated that flamingos and grebes 'show no resemblance', but no detailed morphological comparisons between these taxa have ever been made. The single cladistic analysis of morphological data that included both flamingos and grebes is an analysis of cranial and vertebral characters by Livezey & Zusi (2001), which resulted in sister group relationship between flamingos and a taxon including grebes, loons, penguins (Spheniscidae) and procellariiform birds. However, these authors considered the results of their study to be preliminary and the position of flamingos not to be convincing; derived characters supporting the resulting phylogeny were not listed.

Here, I test the hypothesis of a flamingo–grebe sister group relationship by a cladistic analysis of 70 morphological characters, and present previously overlooked morphological, oological and parasitological evidence for its support.

METHODS

TAXA AND CHARACTERS

Apart from representatives of all other higher avian taxa, skeletons of the following taxa have been examined in the collection of Forschungsinstitut Senckenberg (SMF). Tinamidae: *Crypturellus (cinnamomeus, obsoletus, parvirostris, undulatus)*, *Nothura boraciquira*, *Rhynchotus rufescens*, *Tinamus solitarius*. Galliformes: Cracidae: *Crax (alector, daubentoni)*, *Pipile jacutinga*, *Nothocrax urumutum*; Phasianidae: *Agriocharis ocellata*, *Chrysolophus pictus*, *Crossoptilon auritum*, *Gallus gallus*, *Lagopus lagopus*, *Lyrurus tetrax*, *Numida meleagris*, *Pavo cristatus*, *Phasianus colchicus*, *Tetrao urogallus*, *Tetrastes bonasia*, *Tragopan satyra*. Anseriformes: Anhimidae: *Anhima cornuta*, *Chauna chavaria*; Anatidae: *Aix sponsa*, *Anas platyrhynchos*, *Anser anser*, *Aythya fuligula*, *Calonetta leucophrys*, *Cygnus olor*, *Dendrocygna viduata*, *Melanitta nigra*, *Oxyura jamaicensis*, *Somateria mollissima*, *Tadorna tadorna*. Podicipedidae: *Aechmophorus (clarkii, occidentalis)*, *Podiceps (cristatus, grisegena)*, *Tachybaptus ruficollis*. Gaviidae: *Gavia (immer, stellata)*. Spheniscidae: *Spheniscus (demersus, humboldti, magellanicus)*, *Pygoscelis papua*, *Eudyptes chrysolome*, *Aptenodytes patagonicus*. Balaenicipitidae: *Balaeniceps rex*. Ciconiidae: *Anastomus lamelligerus*, *Ciconia (abdimii, ciconia, nigra)*, *Leptoptilus crumeniferus*, *Mycteria (ibis, leucocephala)*. Threskiornithidae: *Eudocimus ruber*, *Geronticus eremita*, *Hagedashia hagedash*, *Lophotibis cristata*, *Platalea (alba, leucorodia)*, *Plegadis falcinellus*, *Threskiornis (aethiopicus, melanocephalus)*. Phoenicopteridae: *Phoenicopterus (chilensis, ruber)*, *Phoeniconaias (minor)*. Procellariiformes: Procellariidae: *Bulweria bulwerii*, *Daption capense*, *Fulmarus glacialis*, *Procellaria aequinoctialis*, *Pterodroma (hypoleuca, neglecta)*, *Puffinus puffinus*; Diomedidae: *Diomedea melanophrys*; Hydrobatidae: *Oceanodroma* sp. Cathartidae: *Coragyps atratus*, *Cathartes aura*, *Sarcoramphus papa*, *Vultur gryphus*. Cariamidae: *Cariama cristata*. Ardeidae: *Agamia agami*, *Ardea (cinerea, herodias)*, *Ardeola grayi*, *Botaurus stellaris*, *Cochlearius cochlearius*, *Egretta garzetta*, *Ixobrychus minutus*, *Nycticorax nycticorax*. Opisthocomidae: *Opisthocomus hoazin*. Recurvirostridae: *Recurvirostra avosetta*, *Himantopus himantopus*. Laridae: *Larus (argentatus, canus, marinus, ridibundus)*, *Sterna (hirundo, sandvicensis)*.

Although the phylogenetic affinities of some fossil taxa are briefly discussed, revision of the fossil record of flamingo-like birds was beyond the scope of this study and these were not included in the cladistic analysis.

Coding of the osteological characters is based on personal study, and all non-osteological characters were taken from the literature. Anatomical terminology follows Baumel & Witmer (1993) and Vanden Berge & Zweers (1993).

PHYLOGENETIC ANALYSIS

Seventy morphological characters of 17 ingroup taxa were coded for the phylogenetic analysis with PAUP 3.1 (Swofford, 1993) (see character matrix in Appendix 2). The shortest tree was found with the heuristic search option. The consistency index (CI), retention index (RI) and rescaled consistency index (RC) were calculated. The robustness of the tree was tested with a bootstrap analysis of 1000 replicates.

Three characters were coded as ordered. Two of these concern vertebrae counts which were grouped to avoid an overly great influence on the analysis (which would have strengthened monophyly of Phoenicopteridae and Podicipedidae). Calculation with all characters unordered did not change the resulting tree topology.

OUTGROUP

Due to the poorly resolved higher-level phylogeny of birds, choice of an appropriate outgroup has proved difficult. Outgroup comparisons were initially made with the palaeognathous Tinamidae, which were established as the sister taxon of neognathous birds by most recent phylogenetic analyses (e.g. Groth & Barrowclough, 1999; Livezey & Zusi, 2001). This analysis confirmed monophyly of Galloanseres to the exclusion of the Phoenicopteridae. A second analysis was then performed using Tinamidae, Galliformes and Anseriformes as outgroup taxa.

RESULTS

PHYLOGENETIC ANALYSIS

Cladistic analysis of the character matrix in Appendix 2 with PAUP 3.1 resulted in three most parsimonious trees, the consensus tree of which is shown in Figure 1. In all the resulting trees, Phoenicopteridae was optimized as sister taxon of Podicipedidae, and this clade received a bootstrap support of 80%. Monophyly of (Galliformes + Anseriformes) and (Recurvirostridae + Laridae), to the exclusion of the Phoenicopteridae, received high bootstrap support of

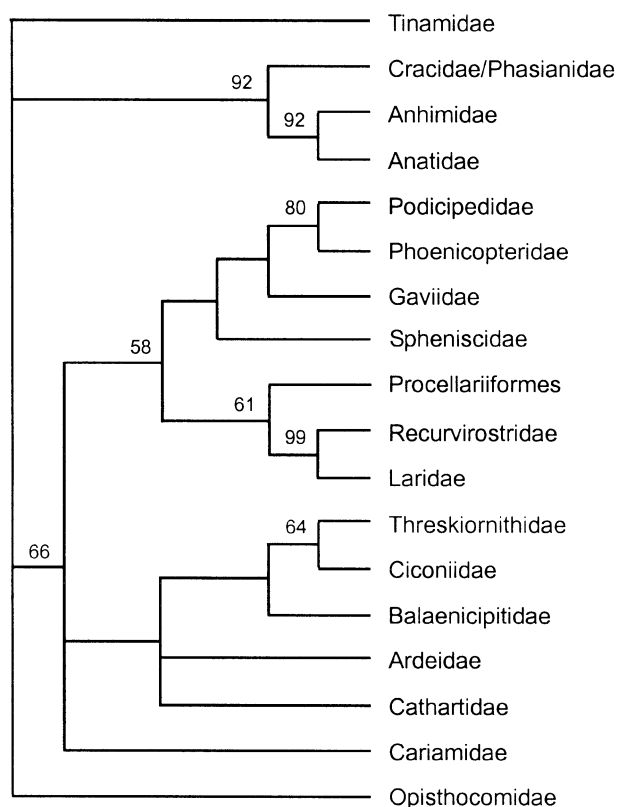


Figure 1. Strict consensus tree of three most parsimonious trees resulting from a cladistic analysis of the character matrix in Appendix 2 (Length = 197, CI = 0.39, RI = 0.56, RC = 0.21). Bootstrap values of more than 50% are indicated above the internodes.

92% and 99%, respectively. Sister group relationship between Threskiornithidae and Ciconiidae was supported with a bootstrap value of 64%. Three other taxa received weak bootstrap support (see Fig. 1). An analysis with Phasianidae/Cracidae and the two anseriform taxa as additional outgroup taxa did not change the resulting tree topology.

SYNAPOMORPHIES OF THE TAXON (PHOENICOPTERIDAE + PODICIPEDIDAE)

In all the resulting trees, the following characters were optimized as synapomorphies of the taxon (Phoenicopteridae + Podicipedidae); the numbers in parentheses refer to character numbers in Appendix 1:

(30) At least fourth to seventh cervical vertebrae strongly elongate, processus spinosus forming a marked ridge (CI = 1.0). The shape of the cervical vertebrae of flamingos is very characteristic and strongly resembles that of grebes.

(31) At least 23 praesacral vertebrae (all vertebrae cranial to synsacrum) (CI = 0.5). In flamingos, there

are 23 praesacral vertebrae, in grebes the number varies from 23 (e.g. *Tachybaptus ruficollis*) to 26 (e.g. *Podiceps grisegena*); in most other birds there are between 18 and 21 praesacral vertebrae.

(32) At least four thoracic vertebrae fused to a notarium (CI = 0.25). In flamingos, four vertebrae are fused, in grebes the number varies between four and five (Storer, 1982). A notarium is absent in other taxa that were previously considered to be related to the Phoenicopteridae (Anseriformes, Ciconiidae and Recurvirostridae).

(41) Humerus with a marked oval depression at insertion site of musculus scapulohumeralis cranialis (CI = 1.0). This character was regarded by Olson & Feduccia (1980a) to be a unique feature of flamingos (including the fossil taxa *Juncitarsus* and *Palaelodidae*), but it is also present in grebes (Fig. 2).

(44) Ulna, distal end with marked depressio radialis (CI = 0.333).

(46) Phalanx proximalis digiti majoris very elongate and narrow craniocaudally (ratio length to craniocaudal width more than 4.5, see Fig. 2) (CI = 0.5).

(56) Tibiotarsus, distal rim of condylus medialis distinctly notched (CI = 0.5). This character was noted as synapomorphy of the taxon (Phoenicopteridae + Ciconiidae) by Cracraft (1988) and as a shared derived feature of the taxon (Phoenicopteridae + Recurvirostridae) by Olson & Feduccia (1980a); it is also present in the Podicipedidae.

(62) Musculus ilirotibialis lateralis, pars acetabularis absent (CI = 0.5). This muscle is reduced in few other avian taxa (McKittrick, 1991).

(63) Musculus caudofemoralis, pars caudalis absent (CI = 0.333). This muscle is completely reduced in only

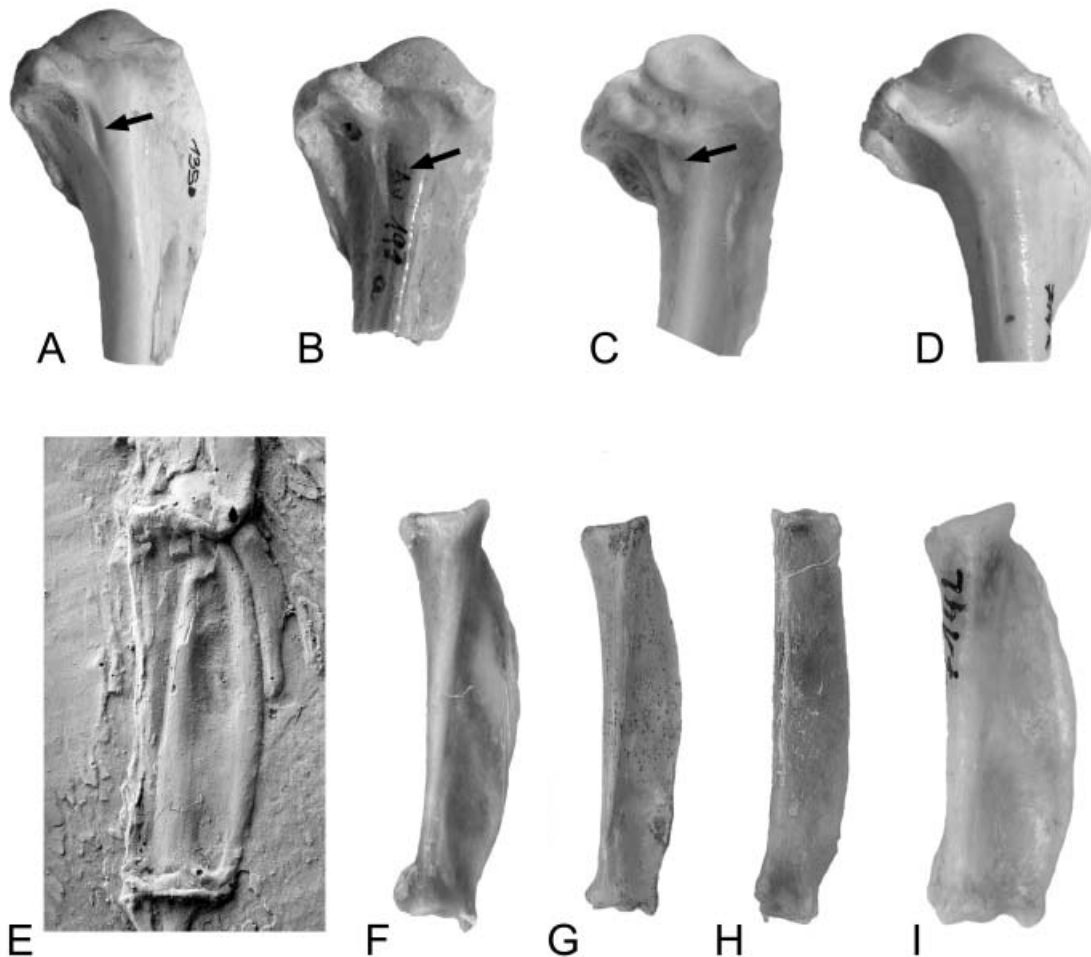


Figure 2. Proximal end of right humerus (A–D) and proximal phalanx of major digit (E–I) in comparison. (A) *Phoenicopterus chilensis* (Phoenicopteridae); (B) *Palaelodus* sp. (Palaelodidae, SMF Av 191a); (C) *Tachybaptus ruficollis* (Podicipedidae); (D) *Eudocimus ruber* (Threskiornithidae); (E) *Juncitarsus merkei* (cast of holotype in SMF, coated with ammonium chloride); (F) *Phoenicopterus ruber* (Phoenicopteridae); (G) *Palaelodus* sp. (Palaelodidae, SMF Av 274g); (H) *Aechmophorus occidentalis* (Podicipedidae); (I) *Eudocimus ruber* (Threskiornithidae). The arrows indicate the marked depression at the attachment site of musculus scapulohumeralis cranialis (character 41). Not to scale.

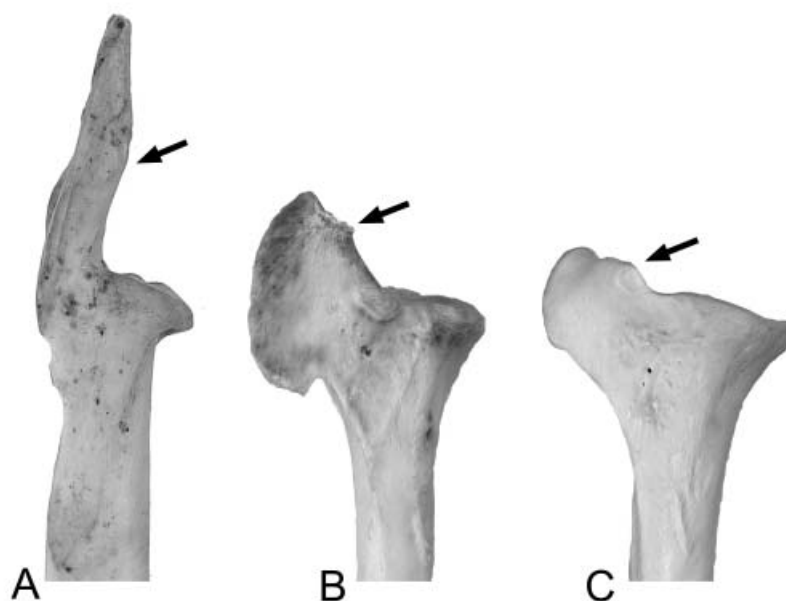


Figure 3. Right tibiotarsus, proximal end in comparison. (A) *Podiceps cristatus* (Podicipedidae); (B) *Phoenicopterus ruber* (Phoenicopteridae); (C) *Ciconia ciconia* (Ciconiidae). The arrows indicate the cnemial crest (character 55). Not to scale.

a few other avian taxa; it is, however, poorly developed in Ciconiidae, Ardeidae, Threskiornithidae and Balaenicipitidae (McKittrick, 1991).

(68) Wing with 11 primaries (CI = 0.5). Eleven primaries otherwise occur only in storks (Ciconiidae). Ironically, Olson & Feduccia (1980a) noted that the 'taxonomic distribution of this character strongly suggests independent derivation in all instances [grebes, flamingos, and storks]'.

(69) Eggs covered with a chalky layer of amorphous calcium phosphate (CI = 1.0). This character otherwise occurs only in some galliform birds (Megapodiidae, Mikhailov, 1995). The eggs of few other taxa (Balaenicipitidae, Scopidae, many Pelecaniformes, Spheniscidae and some Cuculidae) are covered with a layer of amorphous calcium carbonate (Mikhailov, 1995).

DISCUSSION

As shown by van Tuinen *et al.* (2001) and in this study, monophyly of the taxon (Phoenicopteridae + Podicipedidae) is supported by molecular, morphological and oological evidence, which makes it one of the best supported higher-level clades within modern birds. Virtually none of the morphological characters presented above has been recognized as potential synapomorphies of a flamingo-grebe clade before, although the derived similarities shared by flamingos and grebes are difficult to explain by convergence, given the very different living habits of both taxa.

Grebes and flamingos are parasitized by a taxon of cestodes, the Amabiliidae, which is unique to these two taxa (Storer, 2000). Cestodes have a high degree of host specificity (Olson & Feduccia, 1980a; Storer, 2000), and the presence of a taxon which is found exclusively in grebes and flamingos is further evidence for their close relationship.

The earliest, well preserved fossils of grebes are from Miocene deposits (Švec, 1982, 1984; Olson, 1985, 1995), but they are very similar to modern Podicipedidae and thus do not contribute to an understanding of the phylogenetic relationships of the group. Flamingo-like birds, however, are known from earlier deposits and have a fairly extensive fossil record (see Olson & Feduccia, 1980a).

Van Tuinen *et al.* (2001) hypothesized that evolution of grebes and flamingos started from an ancestor with a 'typical shorebird habitus and lifestyle', and based this assumption on the morphology of the Middle Eocene *Juncitarsus* which was thought to provide an evolutionary link between flamingos and shorebirds (Olson & Feduccia, 1980a; Peters, 1987). Except for the strongly elongated tarsometatarsus, however, all characters that were listed as evidence for phoenicopterid affinities of *Juncitarsus* by Olson & Feduccia (1980a) are also present in the Podicipedidae. Moreover, *Juncitarsus* lacks several of the derived characters which define monophyly of the clade (Podicipedidae + Phoenicopteridae). Most notably, a notarium is either completely absent (Olson & Feduccia, 1980a) or consists of only two vertebrae (Peters, 1987),

the proximal phalanx of the second digit is not greatly elongated and narrow (Fig. 2), and the hindtoe is not strongly reduced as in extant Podicipedidae and Phoenicopteridae (Fig. 4). Assessment of the exact systematic position of *Juncitarsus* awaits revision of the fossil material, which is beyond the scope of this study. However, if this taxon can be shown to be closely related to grebes and flamingos, it is most likely the sister taxon of a clade including Phoenicopteridae and Podicipedidae.

The Palaelodidae, another taxon of early Tertiary flamingo-like birds, are known from numerous skeletal remains from the Tertiary of Europe, both Americas, and Australia (Olson & Feduccia, 1980a; Cheneval, 1983; Alvarenga, 1990; Boles, 1991). Shared derived characters which support monophyly of Palaelodidae and Phoenicopteridae to the exclusion of the Podicipedidae include a well developed spina externa sterni with a slightly bifurcate tip and very deep mandibular rami, which Cheneval & Escuillié (1992) mentioned as evidence for the presence of a primitive filter-feeding apparatus in palaelodids. Palaelodids also resemble flamingos in many aspects of their overall osteology, but detailed comparisons with grebes have not yet been made. Most parts of the

skeleton, especially the wing bones, are equally similar to the corresponding elements of grebes (Fig. 2).

Most interesting with regard to flamingo evolution is the fact that the 'foot bones of *Palaelodus* show many similarities with those of a foot-propelled diving bird such as *Podiceps*' (Cheneval & Escuillié, 1992), e.g. the tarsometatarsus is mediolaterally compressed, the hypotarsus is complex and some flexor tendons are enclosed in bony canals (the arrangement of which is, however, slightly different, see Fig. 5). Olson & Feduccia (1980a) assumed that palaelodids 'may have occupied a more duck-like swimming niche than do typical flamingos', whereas Cheneval & Escuillié (1992) noted that palaelodids 'have been better diving birds than swimming birds'. However, some of the characters that the latter authors listed as diving adaptations of the Palaelodidae are also present in the Phoenicopteridae, i.e. a 'short femur with a double articulation in the region of the acetabulum' and a 'long tibiotarsus with a very well-developed cnemial crest' (Fig. 4). Contrary to virtually all modern diving birds, the humerus of palaelodids was pneumatic, as evidenced by the presence of pneumatic foramina, which also makes it unlikely that these birds were specialized divers.

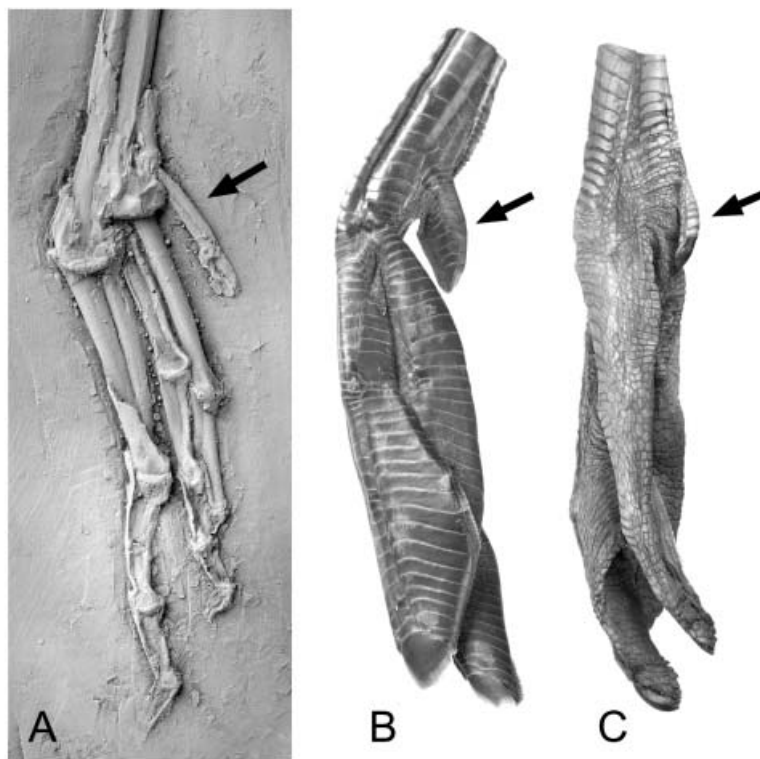


Figure 4. Right foot in comparison. (A) *Juncitarsus merkeli* (cast of holotype in SMF, coated with ammonium chloride); (B) *Podiceps cristatus* (Podicipedidae); (C) *Phoenicopterus ruber* (Phoenicopteridae, figure reversed to facilitate comparison). The arrows point to the hallux (character 59); note the comparatively well-developed hindtoe in *Juncitarsus*. Not to scale.

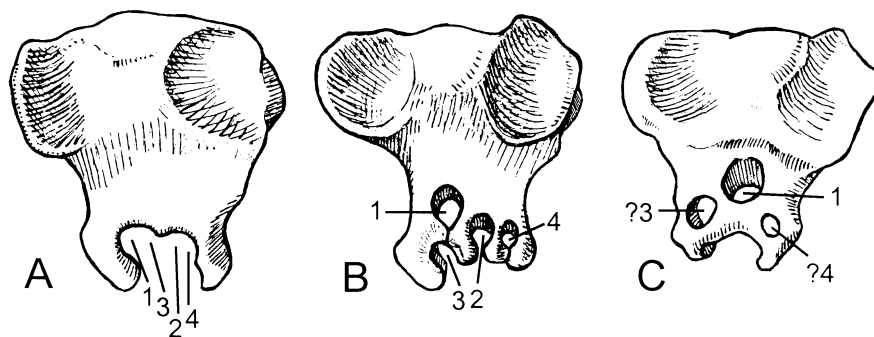


Figure 5. Hypotarsus in comparison. (A) *Phoenicopterus chilensis* (Phoenicopteridae); (B) *Palaelodus* sp. (Palaelodidae, SMF Av182c); (C) *Aechmophorus occidentalis* (Podicipedidae). Not to scale. The numerals indicate the furrows/canals for the tendons of: 1, musculus flexor digitorum longus; 2, musculus flexor perforatus digiti II; 3, musculus flexor perforans et perforatus digiti II; 4, musculus flexor hallucis longus. Homology of tendineal furrows/canals was verified against spirit specimens for Phoenicopteridae (J. Bosch, pers. comm.) and deduced from position of bony canals for the other taxa. Note that identification of tendineal furrows/canals departs from Strauch (1978: fig. 29). Not to scale.

Irrespective of whether palaelodids were adapted to swimming or diving, they were unquestionably highly aquatic birds. Recognition of sister group relationship between flamingos and grebes shows that an aquatic way of living is present in two successive sister taxa of modern flamingos, Podicipedidae and Palaelodidae. It is thus more parsimonious to assume that an aquatic way of living is primitive for the clade (Podicipedidae + Palaelodidae + Phoenicopteridae) than to assume that it evolved independently in stem group representatives of Podicipedidae and Palaelodidae, particularly as extant flamingos still occasionally feed while swimming (del Hoyo, 1992). The shared similarities in the foot structure of grebes and palaelodids are best interpreted as plesiomorphic resemblances which were already present in the last common ancestor of Podicipedidae, Palaelodidae and Phoenicopteridae.

Contrary to the assumption of Olson & Feduccia (1980a), Peters (1987) and van Tuinen *et al.* (2001), flamingos thus probably did not evolve from a shore-bird-like ancestor but from a highly aquatic one, and the long-legged wading habit of modern flamingos apparently evolved in the stem lineage of the Phoenicopteridae.

ACKNOWLEDGEMENTS

I thank S. Tränkner (Forschungsinstitut Senckenberg) for taking the photographs, and P. Ericson (Swedish Museum of Natural History) and an anonymous referee for reviewing the manuscript.

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8. Os palatinum, well developed crista ventralis: absent (0), present (1).
9. Os palatinum, pars lateralis: absent or very small (0), present and well developed (1). Cracraft (1988) listed a palatinum which is 'poorly developed posteriorly' as a synapomorphy of Galloanseres.
10. Ossa palatina fused along midline: no (0), yes (1) (Ericson, 1997: character 8).
11. Vomer: caudal end more or less deeply cleft: yes (0), no (1). This character was coded as unknown in taxa in which the vomer is reduced.
12. Basipterygoid articulation in adulthood: present (0), absent (1). Within the Procellariiformes, these processes are well developed in the Procellariidae but absent or vestigial in Diomedidae and Hydrobatidae.
13. Basipterygoid process short, facet for articulation with pterygoid large and oval: 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. Unfortunately, he did not include the Anhimidae in his study for which reason I only coded the morphological differences in the basipterygoid articulation of Galloanseres and other neognathous birds.
14. Os frontale, marked depressions for supraorbital salt glands; absent (0), present (1). Based on the phylogeny of Livezey (1986), I consider the presence of this character in some marine Anatidae to be apomorphic for these taxa and accordingly coded the character.
15. Cranium, fonticuli occipitales in adult birds: absent (0), present (1).
16. 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). These characters were coded as two separate characters by Cracraft (1988) and Cracraft & Clarke (2001), but I agree with Ericson (1996) that they are part of a single character complex.
17. Tuba auditiva (eustachian tube) completely ossified ventrally: yes (0), no (1).
18. Marked processus parasphenoidales mediales: absent (0), present (1). Within Procellariiformes, this character is absent in the Hydrobatidae.
19. Well-developed, (caudo-) ventrally protruding processus paroccipitales: absent (0), present (1). Within Procellariiformes, this character is absent in the Hydrobatidae.

APPENDIX 1. CHARACTER DESCRIPTIONS

OSTEOLOGICAL CHARACTERS

Skull

- Upper beak, marked furrow rostral of nasal opening ('nasal groove' of Cottam, 1957): absent (0), present (1).
- Upper beak, lamellae for filter feeding: absent (0), vestigial (1), present (2). This character was coded as ordered; see Olson & Feduccia (1980b: fig. 6) concerning the presence of vestigial lamellae in the Anhimidae.
- Ossa maxillaria, processus maxillopalatinus dorso-ventrally high and inflated structure: no (0), yes (1).
- Palate directly desmognathous, i.e. processus maxillopalatini of ossa maxillaria fused along midline: absent (0), present (1).
- Os lacrimale, well-developed descending process which touches or nearly touches the jugal bar: present (0), absent (1).
- Os lacrimale, descending process: not as follows (0), fused with os ectethmoidale, both bones forming a large fenestra (1) (see also Strauch, 1978: figs 5, 7C). Within Procellariiformes, this character is absent in the Diomedidae.
- Os ectethmoidale vestigial or absent: no (0), yes (1).

20. Quadratum, processus oticus, eminentia articularis (see Weber & Hesse, 1995): absent (0), present (1).
21. Quadratum, condylus medialis, markedly concave articular surface (Strauch, 1978: character 11): absent (0), present (1)
22. Quadratum, condylus caudalis very small or absent: yes (0), no (1).
23. Quadratum, condylus lateralis ('external mandibular condyle' of Cracraft, 1988) large and with greatest extension in mediolateral direction; articular surface of mandible 'with single anteroposterior [= rostrocaudal] ridge' and 'lacking posteromedial [= caudomedial] and lateral walls' (Cracraft & Clarke, 2001: characters 39 and 40): no (0), yes (1). In concordance with Ericson (1996) I consider these features to be part of a single character complex. Usually, the condylus lateralis has its greatest extension in rostrocaudal direction.
24. Mandible, long and strongly mediolaterally-compressed processus retroarticularis: absent (0), present (1). This character was considered to be synapomorphic for Galloanseres by Cracraft (1988) and Cracraft & Clarke (2001).
25. Mandible, processus medialis, long, narrow, and dorsally-oriented: no (0), yes (1). This character was listed as a synapomorphy of Galloanseres by Cracraft & Clarke (2001: character 41).

Vertebrae

26. Atlas, well-developed, narrow processus ventralis: absent (0), present (1).
27. Axis, foramina transversaria: present (0), absent (1).
28. Axis, processus costales: present (0); absent (1).
29. Third cervical vertebra, osseous bridge from processus transversus to processus articularis caudalis: present (0), absent (1).
30. Fourth to seventh cervical vertebrae strongly elongate and processus spinosus forming a marked ridge: no (0), yes (1).
31. 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.
32. Several thoracic vertebrae fused to a notarium: no (0), yes (1). Although a notarium is present in the Tinamidae, this character is unquestionably a derived feature within Neornithes (Storer, 1982).

Postcranial skeleton

33. Coracoid, facies articularis clavicularis dorso-ventrally wide and roofing the sulcus supracoracoideus, tuberculum brachiale well developed and strongly ventromedially-protruding: no (0), yes (1).
34. Coracoid, processus procoracoideus well developed with tip markedly deflected towards extremitas omalis: no (0), yes (1).
35. Coracoid, foramen nervi supracoracoidei: present (0), absent (1). Within the Ciconiidae, a foramen nervi supracoracoidei is present in *Leptoptilos* (incompletely closed medially in some specimens).
36. Coracoid, impressio musculi sternocoracoidei on dorsal surface of extremitas sternalis with large pneumatic opening: no (0), yes (1).
37. 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. Within the Ciconiidae, this character is present in *Ciconia abdimii* but absent in *C. nigra*, *C. ciconia* and *Leptoptilos crumeniferus*.
38. Caudal margin of sternum: with four notches (0), with two notches (1).
39. Ribs, processus uncinati: present, not fused to ribs (0), present, fused to ribs (1), absent (2).
40. Humerus, foramina pneumatica at bottom of fossa pneumotricipitalis: present (0), absent (1). The absence of pneumatic foramina in some diving Anatidae (e.g. *Aythya marila*, *Melanitta fusca*) is here considered to be derived. Within Procellariiformes, pneumatic foramina are present on the humerus of the Diomedidae.
41. Humerus, marked oval depression at attachment site of musculus scapulohumeralis cranialis (Fig. 2, Olson & Feduccia, 1980a: fig. 27): absent (0), present. This character is well developed in fossil flamingos of the taxon Palaelodidae and in extant *Phoenicopterus chilensis*; in *P. ruber* and *Phoeniconaias minor* it is very indistinct.
42. Humerus, processus supracondylaris dorsalis greatly enlarged: no (0), yes (1).
43. Ulna, distinctly exceeding humerus in length: no (0), yes (1).
44. Ulna, distal end with marked depressio radialis: no (0), yes (1).
45. Carpometacarpus, os metacarpale minus distinctly bowed and spatium intermetacarpale wide: no (0), yes (1). A distinctly bowed os metacarpale minus is present in Cracidae and Phasianidae, but absent in Megapodiidae and stem group representatives of Galliformes (Mourer-Chauviré, 1992; Mayr, 2000), and has accordingly been coded as absent.
46. Phalanx proximalis digiti majoris elongate and craniocaudally-narrow (ratio length to craniocaudal width more than 4.5): no (0), yes (1).
47. Pelvis greatly elongated and strongly compressed mediolaterally, midsection of dorsal part of cristae iliacae dorsales reduced, postacetabular ilium

- much longer than praeacetabular ilium: no (0), yes (1). The shared derived morphology of the pelvis was proposed as a synapomorphy of Gaviidae and Podicipedidae by Cracraft (1988).
48. Pelvis, number of vertebrae ankylosed in synsacrum: 11–12 (0), 13–14 (1), 15–16 (2), 17–18 (3). This character was coded as ordered.
 49. Pelvis, tubercula praeacetabularia: large (0), absent or vestigial (1). Within Cracidae/Phasianidae, the tubercula praeacetabularia are vestigial in the Tetraoninae (Phasianidae) which I consider to be a derived feature of this taxon, based on current phylogenies of galliform birds (e.g. Dyke, Gulas & Crowe, 2003).
 50. Pelvis, marked recessus caudalis fossae: absent (0), present (1). Due to the fact that the foramen ilioischadicum is not closed caudally, the condition in the Tinamidae cannot be compared with that of the other ingroup taxa.
 51. Femur, short and stout (ratio length to diameter in midsection less than 9.0): no (0), yes (1).
 52. Femur, crista trochanteris marked: no (0), yes (1).
 53. Femur, pneumatic foramen at cranio-lateral side of proximal end: absent (0), present (1).
 54. Tibiotarsus, cristae cnemiales markedly protruding proximally (Fig. 3): no (0), yes (1). This character was proposed as a synapomorphy of the taxon (Podicipedidae + Gaviidae) by Cracraft (1988); it is also present, though in a somewhat less exaggerated form, in the Phoenicopteridae. Within Anatidae, it is present in some diving taxa such as *Oxyura* and *Melanitta*.
 55. Tibiotarsus, prominent tubercle latero-distal to pons supratendineus: absent (0), present (1). This character was listed as a synapomorphy of a taxon including Phoenicopteridae, Threskiornithidae and Ciconiidae by Cracraft (1988) but I could not confirm its presence in the Threskiornithidae.
 56. Tibiotarsus, distal rim of condylus medialis distinctly notched: no (0), yes (1). Within the Ciconiidae, this character is absent in *Leptoptilos*.
 57. Tarsometatarsus, hypotarsus, cristae medialis et lateralis hypotarsi strongly protruding and delimiting a marked sulcus through which all flexor tendons pass (this sulcus encompasses bony canals in Gaviidae, Podicipedidae and the early Tertiary flamingo-like taxa *Juncitarsus* and *Palaelodidae*): no (0), yes (1). Cracraft (1988) proposed this character, in a slightly modified form, as a synapomorphy of a taxon including Phoenicopteridae, Threskiornithidae and Ciconiidae.
 58. Tarsometatarsus, trochlea metatarsi II reaching much less far distally than trochlea metatarsi IV: yes (0), no (1).
 59. Hallux greatly reduced (proximal phalanx very short, measuring much less than half of the length of the proximal phalanx of third toe) or completely absent (Fig. 4): no (0), yes (1). Within Galliformes, a long hallux is present in presumably basal (e.g. Mayr, 2000) taxa like Megapodiidae and Cracidae, and I assume a long hallux to be primitive within the taxon. Although a well-developed hallux is absent in the Tinamidae, its presence is unquestionably plesiomorphic for Neornithes (as it is present in Mesozoic non-Neornithes).

MYOLOGICAL AND OTHER CHARACTERS

60. Three anterior toes: not as follows (0), connected by web over their entire length (1), lobed (2).
61. Musculus iliotibialis medialis: absent (0), present (1); (after McKittrick, 1991). This muscle has only been reported for flamingos and *Cladorhynchus* (Recurvirostridae) (Olson & Feduccia, 1980a).
62. Musculus iliotibialis lateralis, pars acetabularis: present (0), absent (1); (after McKittrick, 1991).
63. Musculus caudofemoralis, pars caudalis ('A' muscle in the formula of George & Berger, 1966: Tab. IX.1): present (0), absent or poorly developed (1); (after McKittrick, 1991). The absence of this muscle in *Eudromia* (Tinamidae) and *Meleagris* (Phasianidae) is here considered autapomorphic for these taxa.
64. Musculus caudofemoralis, pars pelvica ('B' muscle in the formula of George & Berger, 1966: tab. IX.1): present (0), absent (1); (after McKittrick, 1991). The absence of this muscle in few Procellariiformes (*Bulweria*, *Nesofregatta*, *Pelecanoides*) is here considered autapomorphic for these taxa.
65. Musculus ambiens: present (0), absent (1); (after Olson & Feduccia, 1980a; McKittrick, 1991). The absence of this muscle in few Procellariiformes (*Fregatta*, *Nesofregatta*, *Pelecanoides*) is here considered autapomorphic for these taxa.
66. Musculus gastrocnemius, fourth head: absent (0), present (1); (after Vanden Berge, 1970; McKittrick, 1991). Cracraft (1988) proposed this character as a synapomorphy of a taxon including Phoenicopteridae, Threskiornithidae and Ciconiidae.
67. Wing: diastataxic (0), eutaxic (1); (after Mitchell, 1913; Stephan, 1970; Sibley & Ahlquist, 1990: 217f.).
68. Wing, number of primaries: 10 (0), 11 (1); (e.g. Stresemann, 1927–34).
69. Eggs covered with a chalky layer of amorphous calcium phosphate: no (0), yes (1); (after Walters, 1994; Mikhailov, 1995).
70. Enzyme malate dehydrogenase with unusually slow motility (55% as fast as that of galliform birds): no (0), yes (1); (after Kitto & Wilson, 1966; this character is unique to charadriiform birds).

APPENDIX 2

Character matrix of 70 morphological characters for the 17 ingroup taxa included in this study (see Appendix 1 for character definitions). Polymorphic characters are coded as such, unknown character states are indicated by "?".

Taxa	Characters																								
	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
Tinamidae	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Cracidae/Phasianidae	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0	1	0	0	0	1	0	0	1	1	1
Anhimidae	0	1	1	1	1	0	1	0	1	1	1	0	1	0	0	1	0	0	0	1	0	0	1	1	1
Anatidae	0	2	1	1	1	0	1	0	0	1	1	0	1	0	1	1	0	0	0	1	0	0	1	1	1
Podicipedidae	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	0	0	1	1	0	1	0	1	0	0
Phoenicopteridae	0	2	1	1	0	0	1	1	1	1	1	1	0	0	1	0	0	1	1	0	1	1	0	1	0
Threskiornithidae	1	0	1	1	1	0	0	1	1	1	1	1	1	0	0	1	0	0	1	1	0	1	1	0	0
Ciconiidae	0	0	1	1	1	0	1	1	1	1	1	1	0	0	0	0	1	1	1	0	1	1	0	0	0
Ardeidae	0	0	1	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0
Balaenicipitidae	1	0	1	1	0	0	1	1	1	1	?	1	0	0	0	0	1	0	0	0	1	1	0	0	0
Procellariiformes	1	0	0	0	0	0	1	0	1	0	0	0	1	0	0	1	0	1	0	1	0	0	0	0	0
Gaviidae	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	0	0	1	1	0	1	1	0	0	0
Spheniscidae	1	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	1	1	1	1	0	0	0	0
Opisthocomidae	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Cariamidae	0	0	1	1	1	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0
Cathartidae	0	0	0	0	0	1	0	1	1	0	?	0	0	0	0	0	1	1	1	0	1	1	0	0	1
Recurvirostridae	0	0	0	0	1	1	0	1	1	0	0	0	0	1	1	0	0	0	0	0	1	1	0	1	0
Laridae	0	0	0	0	1	1	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0

Taxa	Characters																																																	
	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																									
Tinamidae	0	0	0	1	0	1	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	3	0	?																									
Cracidae/Phasianidae	0	0	1	0	0	1	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	2	0	0																									
Anhimidae	0	0	0	0	0	12	0	0	0	0	1	0	1	2	0	0	0	0	1	0	0	0	3	1	1																									
Anatidae	0	0	0	0	0	12	0	0	0	1	0	0	1	1	0	0	0	0	0	1	0	0	23	0	0																									
Podicipedidae	1	0	0	1	1	2	1	0	0	1	0	0	1	0	1	1	0	0	1	0	1	1	3	1	0																									
Phoenicopteridae	1	0	1	1	1	2	1	0	0	0	0	1	1	1	0	1	0	0	1	0	1	0	2	1	0																									
Threskiornithidae	0	1	0	0	0	0	1	1	0	1	0	0	1	0	1	0	0	0	1	0	0	0	2	1	1																									
Ciconiidae	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	0	1	0	1	0	0	2	1	1																										
Ardeidae	0	0	1	1	0	2	0	0	0	1	0	1	1	1	0	0	0	1	0	0	0	1	1	1																										
Balaenicipitidae	0	0	1	1	0	1	0	0	1	0	0	1	1	1	0	0	0	1	0	0	0	2	1	1																										
Procellariiformes	1	1	1	0	0	1	0	0	0	0	0	1	0	1	0	1	0	1	0	0	1	0	1	1	0																									
Gaviidae	1	1	1	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	3	1	0																									
Spheniscidae	0	1	1	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	?	0	0	0	0	1	0																									
Opisthocomidae	0	0	1	0	0	1	1	0	0	1	1	?	1	1	0	0	0	0	0	1	0	0	2	1	1																									
Cariamidae	0	0	1	0	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0	1	0	0	1	1	1																									
Cathartidae	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	1	0																									
Laridae	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	0	1	1	0	0	0	0	1	1	0																									
Recurvirostridae	0	1	1	0	0	0	0	1	1	0	0	0	0	1	1	0	1	1	0	0	0	0	1	1	0																									

APPENDIX 2 *Continued*

Taxa	Characters																			
	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70
Tinamidae	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0
Cracidae/Phasianidae	0	1	01	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Anhimidae	1	0	1	0	0	0	0	1	0	0	0	?	?	?	0	0	0	0	0	0
Anatidae	01	0	0	01	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Podicipedidae	1	0	0	1	0	1	1	0	1	2	0	1	1	0	1	0	0	1	1	0
Phoenicopteridae	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	1	0	1	1	0
Threskiornithidae	0	1	0	0	0	1	1	1	0	0	0	0	1	0	0	1	0	0	0	0
Ciconiidae	1	1	1	0	1	01	1	1	0	0	0	1	1	1	0	1	0	1	0	0
Ardeidae	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0
Balaenicipitidae	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	?
Procellariiformes	0	0	0	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Gaviidae	1	0	0	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0
Spheniscidae	0	0	0	1	0	0	0	1	1	1	0	0	0	0	0	0	?	?	0	0
Opisthocomidae	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	?
Cariamidae	0	1	0	0	0	0	0	1	1	0	0	?	1	?	0	?	1	0	0	?
Cathartidae	0	1	1	0	0	0	0	1	0	0	0	0	01	1	0	0	0	0	0	0
Recurvirostridae	0	1	0	1	0	1	0	0	1	01	01	?	0	0	0	?	0	0	0	1
Laridae	0	1	0	1	0	1	0	0	1	1	0	0	0	1	0	0	0	0	0	1