

## The phylogenetic affinities of the Shoebill (*Balaeniceps rex*)

Gerald Mayr

Forschungsinstitut Senckenberg, Sektion für Ornithologie, Senckenberganlage 25,  
D-60325 Frankfurt/M., Germany; E-mail: Gerald.Mayr@senckenberg.de

### Summary

The phylogenetic affinities between the shoebill (*Balaenicipitidae*) and pelecaniform and ciconiiform birds are analysed. A cladistic analysis of 54 anatomical characters resulted in monophyly of the taxon (*Scopidae* + (*Balaenicipitidae* + *Steganopodes* (sensu Cracraft 1985))) and showed both *Ciconiiformes* and *Pelecaniformes* to be polyphyletic. Derived characters which support the resulting phylogeny are discussed. Monophyly of the taxon (*Scopidae* + (*Balaenicipitidae* + *Steganopodes*)) is better supported by morphological evidence than monophyly of the taxon (*Procellariiformes* + (*Phaethontidae* + *Steganopodes*)) which was established by Cracraft (1985). The shared derived characters of *Scopidae*, *Balaenicipitidae* and *Steganopodes* are furthermore less easily explained by convergent evolution than by the few characters which support monophyly of the taxon (*Phaethontidae* + *Steganopodes*). The *Phaethontidae* share derived characters with the *Procellariiformes*, which might support a sister group relationship between the two taxa.

**Keywords:** Phylogeny, *Balaenicipitidae*, *Scopidae*, *Pelecaniformes*, *Ciconiiformes*, *Procellariiformes*, osteology.

### Zusammenfassung

#### Die phylogenetischen Beziehungen des Schuhschnabels (*Balaeniceps rex*)

Die phylogenetischen Beziehungen zwischen dem Schuhschnabel (*Balaenicipitidae*) und pelecaniformen und ciconiiformen Vögeln werden untersucht. Eine kladistische Analyse von 54 anatomischen Merkmalen resultierte in Monophylie des Taxons (*Scopidae* + (*Balaenicipitidae* + *Steganopodes* (sensu Cracraft 1985))) und ergab, dass sowohl *Ciconiiformes* als auch *Pelecaniformes* polyphyletisch sind. Abgeleitete Merkmale, welche den resultierenden Stammbaum begründen, werden diskutiert. Monophylie des Taxons (*Scopidae* + (*Balaenicipitidae* + *Steganopodes*)) ist besser gestützt durch morphologische Merkmale, als die von Cracraft (1985) begründete Monophylie des Taxons (*Procellariiformes* + (*Phaethontidae* + *Steganopodes*)). Die gemeinsamen abgeleiteten Merkmale von *Scopidae*, *Balaenicipitidae* und *Steganopodes* lassen sich darüber hinaus weniger leicht durch Konvergenz erklären, als die wenigen Merkmale, welche Monophylie des Taxons (*Phaethontidae* + *Steganopodes*) begründen könnten. Die *Phaethontidae* teilen abgeleitete Merkmale mit den *Procellariiformes*, welche eine Schwestergruppenbeziehung zwischen beiden Taxa stützen könnten.

## Introduction

The shoebill (*Balaeniceps rex*) is the sole living representative of the Balaenicipitidae and today only occurs in remote swamps of east-central Africa. It is a fairly rare and, despite its popular appeal in zoological gardens, rather poorly studied solitary bird which feeds on fishes and small vertebrates (see Elliott 1992). Although it is generally classified within the Ciconiiformes, together with storks (Ciconiidae), herons (Ardeidae), ibises (Threskiornithidae) and the hamerkop (Scopidae) (del Hoyo et al. 1992), there is no consensus about the phylogenetic affinities of the shoebill.

Gould (1852) regarded *Balaeniceps* as an aberrant pelican, but subsequent authors especially noted morphological similarities to herons (Bartlett 1861, Parker 1861, Beddard 1888, Gadow 1893) and the African hamerkop, *Scopus umbretta* (Reinhardt 1861, Giebel 1873). Böhm (1930) thought that *Balaeniceps* was more closely related to storks than to herons but did not make comparisons with *Scopus*. The idea of a closer affinity between Balaenicipitidae and peleaniform birds was revived by Cottam (1957) who, curiously, also omitted *Scopus* from her comparisons because "there is no point in comparing one genus of doubtful affinities with another"; for the same reason she did not make comparisons with the peleaniform Phaethontidae. Cottam (1957) did not clearly state to which peleaniform taxon she considered *Balaeniceps* to be most closely related, but indicated that it should be placed "possibly near the Pelecanidae". On the basis of a study of the middle ear region Saiff (1978) also concluded that the shoebill was more closely related to peleaniform than to ciconiiform birds, and Olson (1979) noted that "it appears possible that the Balaenicipitidae, Scopidae and Ciconiidae may represent a more or less natural assemblage having affinities with the Pelecaniformes". However, Feduccia (1977) thought that the Balaenicipitidae were the sister taxon of the Ciconiidae because both taxa shared a similar derived morphology of

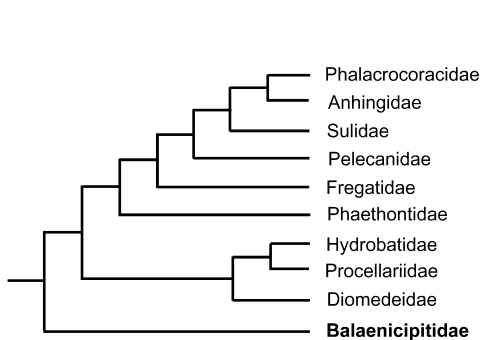
the columella (ear ossicle). Cracraft (1981, 1985, 1988) also regarded the similarities between *Balaeniceps* and pelicans as convergences and assumed that the shoebill was the sister taxon of herons. Cracraft (1985) performed a cladistic analysis of the Pelecaniformes in which he also included the shoebill but no ciconiiform birds. Rea (1983) considered Balaenicipitidae, Scopidae, Threskiornithidae, Ciconiidae and Cathartidae (New World vultures) to be closely related. A cladistic analysis of characters of the hind limb musculature by McKittrick (1991) resulted in monophyly of Balaenicipitidae and Ardeidae, and these two taxa were widely separated from other ciconiiform and from peleaniform birds (the Scopidae were not included in the analysis which yielded several very unlikely results as, for example, paraphyly of ducks and geese, Anatidae). Mikhailov (1995), on the other hand, investigated the eggshell microstructure of the shoebill and found derived similarities to that of *Scopus* and most peleaniform birds. An analysis of 20 morphological characters by Siegel-Causey (1997) showed a taxon including Balaenicipitidae, Fregatidae and Pelecanidae to be monophyletic; the corresponding clade received, however, weak bootstrap support and the analysis was mainly restricted to peleaniform taxa. A cladistic analysis of characters of the skull and the vertebral column by Livezey & Zusi (2001) resulted in monophyly of Balaenicipitidae and Pelecanidae (pelicans); characters supporting the resulting phylogeny were, however, not given and the results of this study were explicitly considered by the authors to be preliminary.

In recent years, several molecular studies have addressed the relationships between *Balaeniceps* and peleaniform birds. The results of their DNA-DNA hybridisation studies led Sibley & Ahlquist (1990) to include *Balaeniceps* in the Pelecanidae. An analysis of DNA-DNA hybridisation data and mitochondrial DNA sequences by Hedges & Sibley (1994) also resulted in monophyly of the taxon (Balaenicipitidae + Pelecanidae), as did an analy-

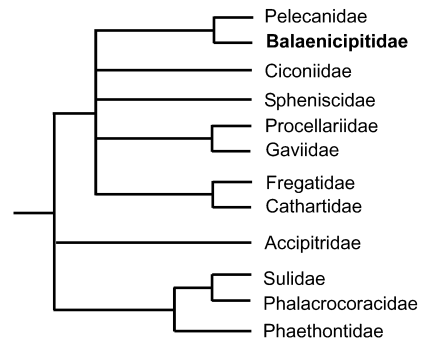
sis of mitochondrial and cytochrome b sequences by Siegel-Causey (1997) (Fig. 1). An analysis of DNA-DNA hybridisation data, as well as nuclear and mitochondrial DNA sequences by van Tuinen et al. (2001) supported monophyly of the taxon (Scopidae + (Balaenicipitidae + Pelecanidae)) (Fig. 1).

The fossil record of the Balaenicipitidae is very poor and consists of fragmentary remains

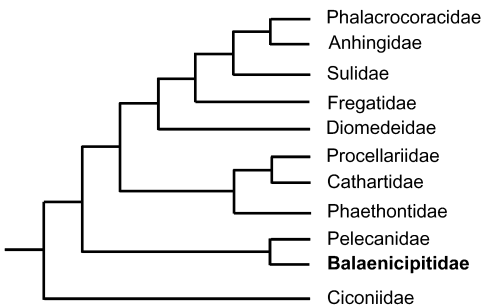
from the Oligocene of Egypt (Rasmussen et al. 1987) and the Miocene of Tunisia and Pakistan (Harrison & Walker 1982), which do not contribute to an understanding of the affinities of these birds. Assessment of the phylogenetic position of the Balaenicipitidae is further obscured by the fact that neither monophyly of the traditional Ciconiiformes (as defined above) nor of the Pelecaniformes, i. e. a clade



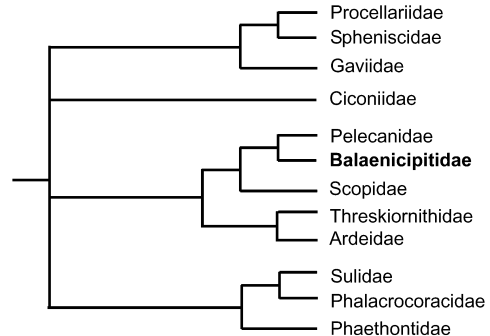
Cracraft (1985: fig. 8A)



Hedges & Sibley (1994: fig. 3)



Siegel-Causey (1997: fig. 6.2)



van Tuinen et al. (2001: fig. 2)

**Fig. 1.** Recent hypotheses on the phylogenetic relationships of the Balaenicipitidae in comparison. The phylogenies are based on analyses of morphological characters (Cracraft 1985), DNA sequences of the mitochondrial 12S rRNA and 16S rRNA genes (Hedges & Sibley 1994), DNA sequences of the mitochondrial 12S rRNA and 16S rRNA genes and cytochrome b nucleotide sequences (Siegel-Causey 1997), and DNA sequences of the c-mos proto-oncogene exon, G3PDH intron 11, and complete 12S rRNA, tRNA<sup>Val</sup> and 16S rRNA genes (van Tuinen et al. 2001).

**Abb. 1.** Neuere Hypothesen über die Verwandtschaftsbeziehungen der Balaenicipitidae im Vergleich. Die Stammbäume basieren auf Analysen morphologischer Merkmale (Cracraft 1985), DNA-Sequenzen mitochondrialer 12S rRNA- und 16S rRNA-Gene (Hedges & Sibley 1994), DNA-Sequenzen mitochondrialer 12S rRNA- und 16S rRNA-Gene und Cytochrom-b-Nukleotid-Sequenzen (Siegel-Causey 1997), sowie DNA-Sequenzen des c-mos proto-oncogene exon, des G3PDH intron 11 und vollständiger 12S rRNA-, tRNA<sup>Val</sup>- und 16S rRNA-Gene (van Tuinen et al. 2001).

including Phaethontidae (tropicbirds), Fregatidae (frigatebirds), Pelecanidae (pelicans), Sulidae (boobies and gannets), Phalacrocoracidae (cormorants) and Anhingidae (darters), has been conclusively established (see Sibley & Ahlquist 1990 and discussion below). The present study is the first cladistic analysis of the phylogenetic relationships of *Balaeniceps* to cover a wide range of morphological data, includes representatives of all ciconiiform and pelecaniform families, and lists the derived characters which support the resulting phylogeny.

### Material and methods

Skeletons of the following taxa were examined in the collection of the Forschungsinstitut Senckenberg and of the Université Claude Bernard, Lyon: Tinamidae: *Crypturellus cinnamomeus*, *C. obsoletus*, *C. parvirostris*, *C. undulatus*, *Nothura boraquira*, *Rhynchotus rufescens*, *Tinamus solitarius*. Ardeidae: *Agamia agami*, *Ardea cinerea*, *A. goliath*, *A. herodias*, *A. purpurea*, *Ardeola grayii*, *A. ralloides*, *Botaurus stellaris*, *Butorides striatus*, *Cochlearius cochlearius*, *Egretta alba*, *E. garzetta*, *E. gularis*, *E. sacra*, *E. thula*, *Ixobrychus minutus*, *Nycticorax nycticorax*. Scopidae: *Scopus umbretta*. Balaenicipitidae: *Balaeniceps rex*. Ciconiidae: *Anastomus lamelligerus*, *Ciconia abdimii*, *C. ciconia*, *C. nigra*, *Leptoptilos crumeniferus*, *Mycteria ibis*, *M. leucocephala*. Threskiornithidae: *Eudocimus ruber*, *Geronticus eremita*, *Hagedashia hagedash*, *Lophotibis cristata*, *Platalea ajaja*, *P. alba*, *P. leucorodia*, *Plegadis falcinellus*, *Threskiornis aethiopicus*, *Th. melanocephala*. Phaethontidae: *Phaethon* cf. *lepturus* (subfossil bones). Fregatidae: *Fregata spec.*. Pelecanidae: *Pelecanus occidentalis*, *P. onocrotalus*, *P. rufescens*. Sulidae: *Sula bassana*, *S. sula*, *S. cf. dactylatra*. Phalacrocoracidae: *Phalacrocorax aristotelis*, *Ph. auritus*, *Ph. carbo*, *Ph. gaimardi*, *Ph. harrisi*, *Ph. olivaceus* (skull), *Ph. penicillatus*. Anhingidae: *Anhinga anhinga*. Diomedidae: *Diomedea melanophrys*. Procellariidae: *Bulweria bulwerii*, *Calonectris diomedea*, *Daption capensis*, *Fulmarus glacialis*, *Macronectes giganteus* (skull), *Procellaria aequinoctialis*, *Pterodroma hypoleuca*, *P. neglecta*, *Puffinus puffinus*. Hydrobatidae: *Oceanodroma castro*, *O. leucorhoa*. Specimens of the

procellariiform Pelecanoididae unfortunately were not available for study.

Most non-osteological characters were taken from the literature. Anatomical terminology follows Baumel & Witmer (1993) and Vanden Berge & Zweers (1993), if not otherwise indicated. Following Cracraft (1985), the term Steganopodes is used for the taxon including Fregatidae, Pelecanidae, Sulidae, Phalacrocoracidae and Anhingidae.

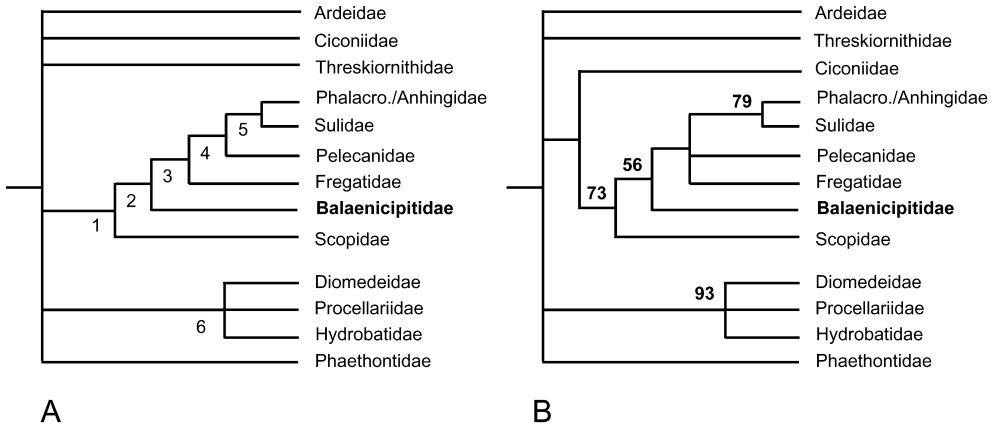
A phylogenetic analysis with the cladistic software PAUP, version 3.1 (Swofford 1993) was performed on a data set of 54 anatomical characters (see Appendices for character descriptions and character matrix). Two characters were coded as "ordered". The shortest tree was found with the "branch-and-bound" search option and the analysis was run in the accelerated transformation (ACCTRAN) mode. The consistency index (CI), retention index (RI) and rescaled consistency index (RC) were calculated and the robustness of the tree was tested with a bootstrap analysis of 1000 replicates.

Most behavioural characters included in the analysis of Cracraft (1985) were omitted from this study because homology with similar behavioural patterns in pelecaniform, procellariiform and ciconiiform birds in many cases is uncertain (van Tets 1965). Outgroup comparisons were made with the palaeognathous Tinamidae, which are generally considered to be the sister taxon of neognathous birds (Groth & Barrowclough 1999, Livezey & Zusi 2001).

### Results

#### Results of the phylogenetic analysis with PAUP 3.1

Analysis of the character matrix in Appendix II with PAUP 3.1 resulted in ten most parsimonious trees, the consensus tree of which is shown in Fig. 2B. This analysis supported monophyly of the taxon (Scopidae + (Balaenicipitidae + Steganopodes)) which received a bootstrap support of 73 %. Monophyly of the taxon (Balaenicipitidae + Steganopodes) received a weak bootstrap support of 56 %, monophyly of the Steganopodes did not receive any bootstrap support. In seven of the resulting trees, the Pelecanidae are the sister group of the clade (Sulidae + Phalacrocoraci-



**Fig. 2.** **A:** The phylogeny proposed in this study; derived characters supporting the numbered nodes are listed in the text. **B:** Consensus tree of ten most parsimonious trees resulting from an analysis of the character matrix in Appendix II with PAUP 3.1 (Length = 126, CI = 0.48, RI = 0.52, RC = 0.30); the bold values indicate the bootstrap support of the respective nodes (1000 replicates, see also text).

**Abb. 2.** **A:** Der hier vorgestellte Stammbaum; abgeleitete Merkmale, welche die nummerierten Verzweigungspunkte stützen sind im Text aufgeführt. **B:** Konsensus-Stammbaum von zehn aus der Analyse der Merkmalstabelle in Anhang II mit PAUP 3.1 resultierenden sparsamsten Stammbäumen (Länge = 126, CI = 0.48, RI = 0.52, RC = 0.30); die fettgedruckten Ziffern geben die Bootstrap-Werte an (1 000 Wiederholungen, siehe Text).

dae/Anhingidae), in three trees the Fregatidae are the sister taxon of this clade, which is, however, supported by a single derived character only (character 53 in Appendix I; other characters were optimised as derivative reversals into the primitive state). The clade including Pelecanidae, Sulidae, Phalacrocoracidae and Anhingidae was retained in the bootstrap analysis and got a support of 61 %. The Phaethontidae were optimised as sister taxon of the Procellariiformes in nine of the resulting trees, in one tree their position was unresolved; bootstrap analysis did not support sister group relationship between Phaethontidae and Procellariiformes.

In contrast to the studies of Cracraft (1985: therein Fig. 6, 7, 8B) and Siegel-Causey (1997: therein Fig. 6.2), monophyly of the Procellariiformes (Hydrobatidae, Procellariidae and Diomedeidae) was highly corroborated with a bootstrap value of 93 %.

Monophyly of Scopidae, Balaenicipitidae and Steganopodes (Fig. 2A, node 1)

Monophyly of Scopidae, Balaenicipitidae and the Steganopodes (Fregatidae, Pelecanidae, Sulidae, Phalacrocoracidae and Anhingidae) is supported by the following derived characters (the numbers refer to Appendix I):

(1) Upper beak, praemaxilla with sharply hooked tip (Fig. 3). Since the diet of the hamerkop does not significantly differ from that of storks and herons, the presence of a hooked praemaxilla appears to be of phylogenetic rather than functional significance. The absence of this character in the Anhingidae and its weak development in the Sulidae is here considered to be due to the highly derived feeding technique of these birds (see Appendix I).

(4) Upper beak, praemaxilla with marked furrow distal of nasal opening (Fig. 3). The absence of this character in the Anhingidae is here considered autapomorphic for that taxon



**Fig. 3.** Skull in comparison. A, *Balaeniceps rex* (Balaenicipitidae); B, *Scopus umbretta* (Scopidae). The arrows indicate the marked furrow distal of the nasal opening. Note to Scale.

**Abb. 3.** Schädel im Vergleich. A, *Balaeniceps rex* (Balaenicipitidae); B, *Scopus umbretta* (Scopidae). Die Pfeile markieren die deutliche Rinne distal der Nasenöffnung. Nicht im selben Maßstab.

and is probably connected with the unique feeding technique of these birds (see Appendix I).

(5) Skull, ossified septum nasale present. This character does not occur in other putatively related taxa.

(10) Skull, ossa palatina fused along their midline. This character is found in few other unrelated taxa, e. g. toucans (Ramphastidae), hornbills (Bucerotidae) and frogmouths (Podargidae) (not to be confused with the desmognathous palate in which the processus maxillopalatini are fused).

(22) Furcula, extremitas omalis with strongly developed, laterally protruding facies articularis acrocoracoidea which articulates with a distinct ovoid facies articularis clavicularis of the coracoid (Fig. 4). Olson (1984) noted that the ovoid facies articularis clavicularis of the coracoid distinguishes *Scopus* from "all other avian [taxa] except the Balaenicipitidae and Pelecaniformes (within which the Phaethontidae are exceptional in lacking this character and the modern Fregatidae have it

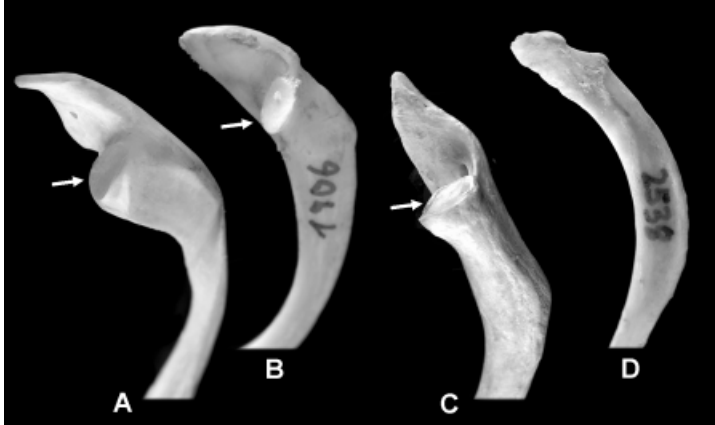
obliterated by fusion with clavicle)". According to my observations, the fac. art. clavicularis is also strongly protruding in owls (Strigidae), hawks (Accipitridae) and falcons (Falconidae), but in these taxa its shape is different from that in the above-listed taxa. The condition of this character in the Fregatidae needs further study (see Appendix I).

(28) Sternum, dorsal surface with numerous pneumatic foramina along midline and lateral margins (Fig. 5). The absence of this character in Phalacrocoracidae and Anhingidae is here considered to be autapomorphic for these taxa; underlying the phylogeny in Fig. 2A, this assumption is more parsimonious than that of a convergent origin of this character in Scopidae, Balaenicipitidae, Fregatidae, Pelecanidae and Sulidae.

(38) Tarsometatarsus, hypotarsus with tendon of musculus flexor digitorum longus and m. flexor hallucis longus enclosed in bony canal (Fig. 6). The absence of this character in the Fregatidae, in which there is only a single large canal for m. flexor digitorum longus,

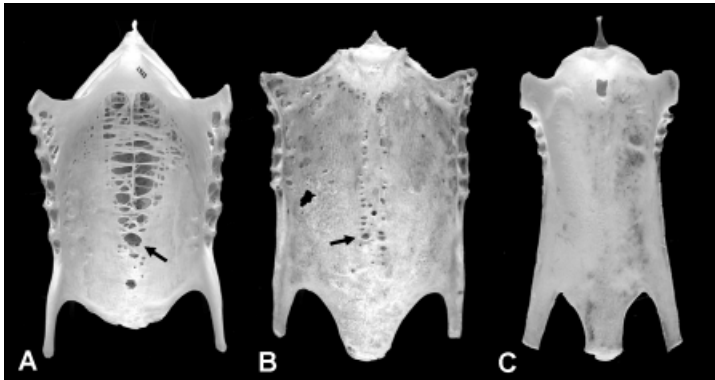
might be related to the fact that in frigatebirds the tarsometatarsus is extremely abbreviated. The tendons of both muscles are also enclosed in bony canals in several “higher land birds” (e. g. most zygodactyl and some perching

birds) but rarely among the more basal Neornithes. In the Phalacrocoracidae there is only a groove but no canal, which is here considered to be a derivative reversal into the primitive state.



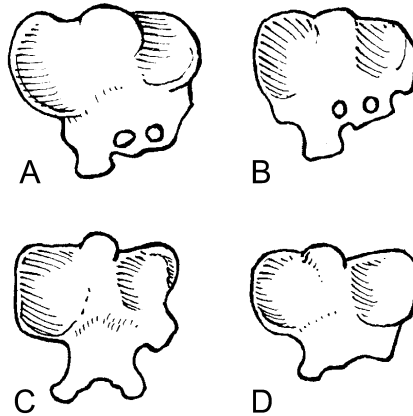
**Fig. 4.** Furcula, right extremitas omalis in comparison. **A:** *Balaeniceps rex* (Balaenicipitidae); **B:** *Scopus umbretta* (Scopidae); **C:** *Sula bassana* (Sulidae); **D:** *Agamia agami* (Ardeidae, represents the primitive condition). The arrow indicates the strongly protruding facies articularis acrocoracoidea. Not to scale.

**Abb. 4.** Furcula, rechte Extremitas omalis im Vergleich. **A:** *Balaeniceps rex* (Balaenicipitidae); **B:** *Scopus umbretta* (Scopidae); **C:** *Sula bassana* (Sulidae); **D:** *Agamia agami* (Ardeidae, primitiver Merkmalszustand). Der Pfeil markiert die weit hervorstehende Facies articularis acrocoracoidea. Nicht im selben Maßstab.



**Fig. 5.** Dorsal view of sterna in comparison. **A:** *Balaeniceps rex* (Balaenicipitidae); **B:** *Scopus umbretta* (Scopidae); **C:** *Agamia agami* (Ardeidae). The arrow indicates the pneumatic foramina along the midline. Not to scale.

**Abb. 5.** Dorsalansicht des Sternums im Vergleich. **A:** *Balaeniceps rex* (Balaenicipitidae); **B:** *Scopus umbretta* (Scopidae); **C:** *Agamia agami* (Ardeidae). Der Pfeil markiert die pneumatischen Öffnungen entlang der Mittellinie. Nicht im selben Maßstab.



**Fig. 6.** Hypotarsus, proximal end in comparison. **A:** *Balaeniceps rex* (Balaenicipitidae); **B:** *Sula bassana* (Sulidae); **C:** *Ciconia abdimii* (Ciconiidae); **D:** *Rhynchotus rufescens* (Tinamidae, probably the primitive morphology of the hypotarsus). In A and B the tendons of musculus flexor digitorum longus and m. flexor hallucis longus are enclosed in bony canals. Not to scale.

**Abb. 6.** Hypotarsus, proximales Ende im Vergleich. **A:** *Balaeniceps rex* (Balaenicipitidae); **B:** *Sula bassana* (Sulidae); **C:** *Ciconia abdimii* (Ciconiidae); **D:** *Rhynchotus rufescens* (Tinamidae, wahrscheinlich die primitive Morphologie des Hypotarsus). In A und B sind die Sehnen des Musculus flexor digitorum longus und des M. flexor hallucis longus von einem knöchernen Kanal umgeben. Nicht im selben Maßstab.

(41) Musculus expansor secundariorum vestigial or completely absent. This muscle is also reduced in the Phaethontidae and a number of other taxa, none of which, however, seem to be closely related to the Balaenicipitidae (Gadow 1891).

(54) Eggshell covered with a layer of microglobular material (amorphous form of calcium carbonate). This character is otherwise known only from some herons, penguins (Spheniscidae) and some cuckoos (Cuculidae); in a few other taxa (Podicipediformes, Phoenicopteriformes and the galliform Megapodiidae) the layer consists of calcium phosphate (Mikhailov 1995). In *Balaeniceps* and the Steganopodes the chalky covering of the egg is also macroscopically visible (Walters 1994).

Characters (1), (4), (5), (10), (22) and (38) were also listed by Cottam (1957) as evidence for the peleaniform affinities of *Balaeniceps*. Technau (1936) further noted a great resemblance in the position of the salt gland and the

morphology of the nasal cavity of *Scopus* and the Steganopodes.

Monophyly of Balaenicipitidae and Steganopodes (Fig. 2A, node 2)

Monophyly of Balaenicipitidae, Fregatidae, Pelecanidae, Sulidae, Phalacrocoracidae and AnHINGIDAE is supported by the following derived characters:

(2) External narial openings greatly reduced or completely absent. In very few other avian groups are the external narial openings as greatly reduced as in the above-listed taxa.

(23) Furcula, apophysis furculae abutting with an articular facet at the apex carinae of carina sterni (completely fused with the apex carinae in Balaenicipitidae, Pelecanidae and Fregatidae). This character also occurs in the Ciconiidae.

This node received only weak bootstrap support in the analysis with PAUP 3.1 (Fig. 2B).



Monophyly of Steganopodes to the exclusion of the Balaenicipitidae (Fig. 2A, node 3)

Monophyly of the Steganopodes is supported by the following derived characters, none of which is present in *Balaeniceps*:

(6) Conchae nasales greatly reduced or completely absent. This feature appears to be unique to the Steganopodes; it is absent in the Phaethontidae (Technau 1936).

(15) Recessus tympanicus dorsalis enlarged, situated rostrally or laterally to the articular facets of the quadrate (Saiff 1978).

(44) Musculus flexor cruris lateralis, pars accessoria absent. This character occurs in several other avian taxa and certainly evolved several times independently (McKittrick 1991).

(47) Naked gular pouch present.

(50) Hallux included in webbed foot (Fig. 7). This character otherwise only occurs in the Phaethontidae and is traditionally used to define the Pelecaniformes (see discussion).

(51) Young naked at hatching. This character is unquestionably derived in neornithine birds but occurs in many other taxa.

Monophyly of Pelecanidae, Sulidae, Phalacrocoracidae and Anhingidae (Fig. 2A, node 4)

Monophyly of Pelecanidae, Sulidae, Phalacrocoracidae and Anhingidae is in concordance with most other studies of morphological data (Lanham 1947, Cracraft 1985) and is supported by:

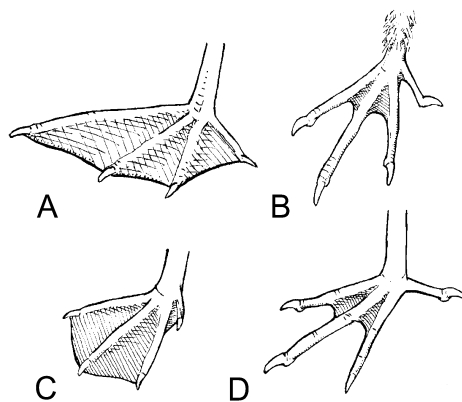
(12) Vomer absent.

(27) Sternum, caudal portion of carina sterani reduced, apex carinae strongly cranially protruding. This character evolved convergently in the Diomedidae.

(37) Tibiotarsus, distal end bent medially, condylus medialis protruding farther distally than condylus lateralis.

(48) Three anterior toes webbed over their entire length (Fig. 7). This character occurs in several other aquatic birds and certainly evolved several times independently.

(52) Eggs incubated beneath feet. This character is unique among extant birds.



**Fig. 7.** Feet in comparison (slightly schematic and not to scale). **A:** Phalacrocoracidae (cormorants); **B:** Fregatidae (frigatebirds); **C:** Phaethontidae (tropicbirds); **D:** Scopidae (hamerkop).

**Abb. 7.** Füße im Vergleich (leicht schematisch und nicht im selben Maßstab). **A:** Phalacrocoracidae (Kormorane); **B:** Fregatidae (Fregattvögel); **C:** Phaethontidae (Tropikvögel); **D:** Scopidae (Hammerkopf).

Monophyly of Sulidae, Phalacrocoracidae and Anhingidae (Fig. 2A, node 5)

Monophyly of Sulidae, Phalacrocoracidae and Anhingidae is supported by the following derived characters:

(11) Os palatinum an almost completely flat horizontal plate. This feature is unique among extant birds.

(14) Processus paroccipitales protruding in caudal direction. Usually, these processes project ventrally.

(16) Fossae temporales extending to midline of cranium. Usually these fossae are much less developed.

(19) Quadratum, processus orbitalis reduced. This feature is found in very few other birds (e. g. parrots and swifts), none of which is closely related to the above-mentioned taxa.

Sulidae, Phalacrocoracidae and Anhingidae further share a number of unique derived behavioural similarities (van Tets 1965, Cracraft 1985) and a derived number of 12 or 13 scleral ossicles (Warheit et al. 1989). Monophyly of this taxon also is corroborated by virtually all molecular analyses (Hedges & Sibley 1994, Siegel-Causey 1997, Farris et al. 1999, van Tuinen et al. 2001).

Monophyly of Procellariiformes (Fig. 2A, node 6)

Monophyly of the Procellariiformes has not been seriously questioned so far and is supported by the following derived characters:

(3) External nostrils tubular. This feature is unique to the Procellariiformes.

(17) Fossae glandulae nasales very marked and situated on dorsal surface of supraorbital margin of orbitae.

(26) Coracoid, extremitas sternalis, processus lateralis greatly elongated.

(34) Humerus, large and strongly protruding processus supracondylaris dorsalis present.

(36) Tibiotarsus, proximal end, cristae cnemiales strongly proximally protruding. This feature is also found in other aquatic birds,

such as loons (Gaviidae) and grebes (Podicipedidae).

(49) Hallux greatly reduced and consisting of a single phalanx only.

## Discussion

Since virtually all of the derived characters shared by Scopidae, Balaenicipitidae and the Steganopodes (Fregatidae, Pelecanidae, Sulidae, Phalacrocoracidae and Anhingidae) are absent in the Phaethontidae, the position of the Balaenicipitidae heavily depends on whether the traditional Pelecaniformes, i. e. the taxon comprising Phaethontidae and Steganopodes, are monophyletic.

Cracraft (1988) listed 11 characters in order to support monophyly of the Pelecaniformes, none of which, however, convincingly supports his hypothesis. The “loss of supraorbital depressions” (for the salt glands) clearly is primitive within neornithine birds (see below and Technau 1936), and the “mediopalatine processes [= crista ventralis]” are not “ankylosed or fused” in the Phaethontidae. The “relatively large ilio-ischiatic fenestra” is poorly defined and is not larger in the Fregatidae than, for example, in Scopidae and Balaenicipitidae. A “deep, broad ligamental furrow of humerus” occurs in many other neornithine taxa and is absent in the Pelecanidae and Sulidae (see Appendices). The “totipalmate foot” (hallux turned medially and all four toes connected by a web) is traditionally used to define the Pelecaniformes (Beddard 1898, Lanham 1947) but shows considerable variation within the taxon in that the hallux is quite short in the Phaethontidae (long in the other pelecaniforms, as well as in Scopidae and Balaenicipitidae), and the webbing is very rudimentary in the Fregatidae (the web between the anterior toes is of similar extension to that of, for example, the Scopidae; see Fig. 7). Webbing of the three anterior toes occurs in numerous unrelated avian taxa (e. g. ducks, flamingos and gulls) and it is thus not unlikely that inclusion of the hallux into the

web also evolved more than once (in penguins, for example, the vestigial hallux is also turned medially and connected to the second toe by an incipient web, see also Sibley & Ahlquist 1990). The feathered “gular pouch” of the Phaethontidae is very inconspicuous (and might even not be present at all, see Sibley & Ahlquist 1990); homology of this character within the Pelecaniformes was questioned by Sibley & Ahlquist (1990) and Siegel-Causey (1997). The “prelanding call” was first considered to be a synapomorphy of the Pelecaniformes by van Tets (1965) who noted that “probably all the Pelecaniformes” have a “prelanding display”. However, until this feature is better defined and its occurrence outside the Pelecaniformes is safely excluded, it also is of questionable phylogenetic value. The “relatively horizontal preacetabular ilium” occurs in many other avian taxa including Balaenicipitidae and Scopidae, the “internal condyle of tibio-tarsus” is “greatly enlarged relative to [the] external” in almost all extant birds, and the “greatly foreshortened tarsometatarsus” is absent in the Pelecanidae and Phalacrocoracidae (Cracraft 1985: tab. 1; moreover this bone exhibits a completely different morphology in Phaethontidae, Fregatidae and Anhingidae). The young also “feed by sticking heads down gullet of adult” in penguins (Cracraft 1985) and the young of many other birds at least introduce their beak into that of the adults when being fed (van Tets 1965). Moreover, according to Howell (in Sibley & Ahlquist 1990), the adults of the Fregatidae regurgitate food into the throat of the young.

Sibley & Ahlquist (1990) and Hedges & Sibley (1994) added the position of the salt glands within the orbitae, on the ventral side of the supraorbital margin, as another possible synapomorphy of the Pelecaniformes. However, the salt glands are not situated within the orbitae in the Phaethontidae (Technau 1936, Siegel-Causey 1990) nor do they share any derived similarities with the salt glands of the Steganopodes (Technau 1936). According to Technau (1936) the salt glands are in a

“praeorbital” position in the Sulidae, Phalacrocoracidae, Anhingidae, Fregatidae and Scopidae (and in numerous other unrelated taxa such as Columbidae, Podargidae and Coraciidae), in an “interorbital” position in the Pelecanidae and Ciconiidae (and others, such as Psittacidae and Strigidae), and in an “interorbital-exorbital” position in the Phaethontidae (and others, such as Caprimulgidae and Upupidae). The position of the salt glands in pelecaniform birds thus appears to be of little phylogenetic value, so much the less since Technau (1936) considered the “praeorbital” position to be primitive. Because of a greatly modified narial region, the Balaenicipitidae lack salt glands (Technau 1936). Hedges & Sibley (1994) further stated that all Pelecaniformes lack incubation patches, but according to Orta (1992) in the Fregatidae these are even present in both parents.

Monophyly of the Pelecaniformes also is not supported by any molecular analysis (Sibley & Ahlquist 1990, Hedges & Sibley 1994, Siegel-Causey 1997, van Tuinen et al. 2001).

Cracraft (1985) further listed six characters in order to support monophyly of Procellariiformes and Pelecaniformes to the exclusion of the Balaenicipitidae. However, again, none of these characters is present in all pelecaniform and procellariiform taxa: the “mediopalatine processes” are not “enlarged toward the pterygo-palatine joint” in the Fregatidae and Phalacrocoracidae (Cracraft 1985: tab. 1; since I found it difficult to code this character into discrete character states, it is not included in the present analysis); the “upper tympanic recess” [= recessus tympanicus dorsalis] is not “greatly enlarged” in the Hydrobatidae and some Procellariidae (see Appendices); the bony nostrils are not “greatly reduced” in the Phaethontidae and Procellariiformes (see Appendices); the rostrum of the Phaethontidae lacks a “long nasal groove” and a terminal hook (see Appendices); and the crista deltopectoralis (“deltoid crest”) of the humerus is not “triangular in shape and projecting to a sharp point” in the Hydrobatidae, Pelecanidae,

Sulidae, Phalacrocoracidae and Anhingidae (see Cracraft 1985 and Appendices).

The traditional (*sensu del Hoyo et al. 1992*) Ciconiiformes are even more poorly defined than the Pelecaniformes, since not a single unique derived character has ever been presented in order to show monophyly of this taxon. All characters listed by Beddard (1898) are either plesiomorphic (e.g., “oil gland feathered”, “aftershaft present”) or present in many other taxa, including most Pelecaniformes (e.g., desmognathous palate). Rea (1983) listed numerous characters in order to establish a taxon including Balaenicipitidae, Scopidae, Threskiornithidae, Ciconiidae and Cathartidae but did not distinguish between primitive and derived character states. He explicitly stated that his phylogenetic conclusions were based on “overall similarity” and in his long list I could not find any derived character which convincingly supports his classification (many characters are present in virtually all neognathous birds, e.g. “functional primaries 10 or 11”, others are clearly primitive and of no phylogenetic value, e.g. “conspicuous gallbladder present”). Cracraft (1981) also considered the Ciconiiformes (in which he included the flamingos) to be monophyletic but noted that the supporting evidence is “more circumstantial”. Citing Vanden Berge (1970), he mentioned a single muscular character, the poor separation of *musculus iliotrochantericus medius* from *m. iliotr. cranialis* (“anterior”), in order to support his hypothesis. However, this character appears to be absent in at least some Ciconiidae (Vanden Berge 1970), is unknown for the Scopidae (which were not investigated by Vanden Berge 1970), and absent in *Balaeniceps* (Vanden Berge (1970) notes that in this taxon there is a “fairly definite line of separation” between these muscles; see also Olson 1982 for a critique of Cracraft’s classification).

Summarising the above, current evidence thus more convincingly supports monophyly of the taxon (Scopidae + (Balaenicipitidae + Steganopodes)) than monophyly of the taxon (Phaethontidae + Steganopodes). Accordingly,

the Ciconiiformes as currently recognized (del Hoyo et al. 1992) are polyphyletic and the Procellariiformes are not the sister taxon of the Pelecaniformes (contrary to Cracraft 1985). Resolving the exact systematic position of the Phaethontidae was beyond the scope of this study. Tropicbirds share several derived characters with the Procellariiformes (e.g. the straight shaft and triangular crista deltopectoralis of the humerus, and the complete webbing of the anterior toes) but whether these similarities are indeed synapomorphic needs to be evaluated in a more comprehensive study which also includes other taxa that were considered to be related to the Procellariiformes as, for example, penguins (Sibley & Ahlquist 1990).

As detailed in the introduction, virtually all molecular analyses supported monophyly of the taxon (Balaenicipitidae + Pelecanidae), which is not in concordance with the morphological evidence presented in this study. Monophyly of the shoebill and pelicans would imply either that the above-listed 11 derived characters which, at two different hierarchical levels, are shared by Pelecanidae, Sulidae, Phalacrocoracidae and Anhingidae evolved independently in pelicans or that they were secondarily reversed into the primitive condition in *Balaeniceps* (which, for example, does not show any traces of webs between the toes). However, most molecular studies were either based on the DNA-DNA hybridisation technique or used sequences of mitochondrial genes. The methodology employed in DNA-DNA hybridization studies is a comparison of “median similarity or dissimilarity” (Sibley & Ahlquist 1990) rather than a strict cladistic analysis of derived characters and has for this reason been criticised by several authors (Houde 1987, Lanyon 1992, Harshman 1994). Its limitations are shown by the fact that it does not support sister group relationship between Phalacrocoracidae and Anhingidae (Sibley & Ahlquist 1990, van Tuinen et al. 2001), which share a number of unique derived characters as, for example, an ossified “occipital style” at the cau-

dal end of the cranium. Mitochondrial genes on the other hand probably evolve too rapidly to be useful in the detection of basal divergences among birds (Groth & Barrowclough 1999). The analysis of Hedges & Sibley (1994) was critically evaluated by Farris et al. (1999), who concluded that the data “are too poorly constructed to provide well-supported resolution of any larger divisions of the in-group”.

Siegel-Causey (1997) listed a single morphological character that supports monophyly of a taxon including Pelecanidae, Fregatidae and Balaenicipitidae, i. e. the fusion of the furcula with the apex carinae of the sternum. This character in isolation is of questionable phylogenetic significance since the furcula abuts to an articulation facet of the carina sterni in all pelecaniform birds as well as in the Ciconiidae; fusion could thus easily have occurred several times independently. Cottam (1957) noted that within the Ciconiidae the furcula is fused to the apex carinae in some specimens of *Leptoptilos*. Livezey & Zusi (2001) did not give the characters supporting their phylogeny which also resulted in sister group relationship of Balaenicipitidae and Pelecanidae, within a monophyletic taxon Pelecaniformes. However, these authors did not include postcranial characters in their analysis and if there are convergent similarities between the shoebill and pelicans, they are likely to be due to the huge bill of these taxa and thus mainly effect the characters studied by these authors, i. e. the skull and the vertebral column.

Cracraft (1985) considered the derived similarities between *Balaeniceps* and pelecaniform birds to be due to “mechanical responses to similarities in feeding behaviour”. However, apart from the fact that, for example, the shared derived eggshell structure cannot be explained in this way, most of the above-listed characters are also present in *Scopus*, which has very different living and feeding habits from those of *Balaeniceps* and pelecaniform birds (del Hoyo et al. 1992). Moreover, Cracraft (1985) did not mention characters which

more convincingly support assignment of *Balaeniceps* to any of the “ciconiiform” birds, and omitted from his analysis one of the most characteristic characters shared by Balaenicipitidae, Scopidae and the Steganopodes, the laterally protruding facies articularis acrocoracoidea of the furcula. Webbing of toes occurs in many unrelated aquatic birds (see above), but it is difficult to explain by convergence the above-listed derived characters of the pectoral girdle in birds with such different flight styles as hamerkops, shoebills and gannets.

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## Appendices

### Appendix I. Character descriptions.

- Upper beak, praemaxilla with sharply hooked tip (Fig. 3; Cottam 1957): absent (0), present (1). The beak of extant adult Sulidae has a slight terminal hook only, which might be connected with the characteristic plunge-diving of boobies and gannets. Because a hook is present in hatchlings of the Sulidae (Cottam 1957), I assume its weak development in adult Sulidae to be derived and accordingly coded the character as present. Likewise, the absence of this character in the Anhingidae is probably due to the unique foraging method of these birds (spear-fishing); I assume that the beak was hooked in the last common ancestor of Phalacrocoracidae and Anhingidae and also coded the character as present for this taxon.
- External narial openings greatly reduced or completely absent: no (0), yes (1).
- External nostrils tubular: no (0), yes (1). This character is unique to the Procellariiformes.
- Upper beak, marked furrow distal of nasal opening (Fig. 3; “nasal groove” of Cottam 1957): no (0), yes (1). As noted by Beddard (1898), this furrow “is suggestive of a recently closed, more elongated nostril, like that of the cranes” (which indeed occurs in some juvenile pelecaniforms, see Fig. 9 in Olson 1977). The absence of this character

- in the Anhingidae is here considered to be autapomorphic for this taxon and connected with its foraging behaviour (see above). The furrow in Ardeidae is much wider and shallower than that in the other taxa.
5. Skull, ossified septum nasale: absent (0), present (1).
  6. Conchae nasales greatly reduced or completely absent: no (0), yes (1); (after Technau 1936).
  7. Os ectethmoidale: not as follows (0), vestigial (1), completely reduced (2). The Ardeidae show a great variation in the size of the os ectethmoidale (see Figs. 6–8 in Payne & Rislely 1976); I consider a well-developed bone primitive for the taxon and accordingly coded it with “0” (see also Cracraft 1968 for a survey on the morphology of the ectethmoid within extant birds). This character was coded as ordered.
  8. Ossa maxillaria, processus maxillopalatini greatly enlarged and spongy: no (0), yes (1).
  9. Os palatinum, pars choanalis very deep in dorso-ventral direction: no (0), yes (1).
  10. Ossa palatina fused along their midline (Fig. 1 in Cottam 1957): no (0), yes (1). The ossa palatina appear to be completely fused in the specimens of *Fregata* I investigated (three skulls in the collection of the Forschungsinstitut Senckenberg); Cracraft (1985) found them to be only caudally (“posteriorly”) fused.
  11. Os palatinum an almost completely flat horizontal plate: no (0), yes (1). This character is unique to Sulidae, Anhingidae and Phalacrocoracidae.
  12. Vomer: present (0), absent (1).
  13. Well-developed processus basiptygoidei that articulate with the ossa pterygoidea: present (0), absent (1). In the Hydrobatidae and Pelecanidae rudimentary processus basiptygoidei are present which do not, however, articulate with the ossa pterygoidea.
  14. Processus paroccipitales protruding in caudal direction: no (0), yes (1).
  15. Recessus tympanicus dorsalis: not as follows (0), greatly enlarged and situated rostrally to the articular facets of the quadrate (1), enlarged and situated laterally to the articular facets of the quadrate (2) (Saiff 1978). Usually the recessus tympanicus is small and situated between the articular facets of the quadrate. This character was incorrectly coded as present for the Hydrobatidae by Cracraft (1985) (see also Saiff 1978); it is further absent in some Procelariidae (e. g. *Bulweria bulwerii*).
  16. Fossae temporales extending to midline of cranium: no (0), yes (1).
  17. Fossae glandulae nasales very marked and situated on dorsal surface of supraorbital margin of orbitae: no (0), yes (1).
  18. Quadratum, condylus medialis: not as follows (0), with marked, rostrally projecting, concave articular surface (1), with rather indistinct, laterally projecting, concave articular surface (2). This character was referred to as either “lateral groove”, “lateral concavity”, “incurved surface”, or “anterior lip” by Bock (1960) who considered it a medial brace for protection of the mandible.
  19. Quadratum, processus orbitalis reduced: no (0), yes (1).
  20. Columella tubular (Fig. 1 in Feduccia 1977): no (0), yes (1).
  21. 8th–11th cervical vertebrae: processus carotici ankylosed along midline, forming an osseous canal: no (0), yes (1).
  22. Furcula, extremitas omalis with strongly developed, laterally protruding facies articularis acrocoracoidea which articulates with a distinct ovoid facies articularis clavicularis of the coracoid (Fig. 4): no (0), yes (1). The extremitates omales of furcula and coracoid are fused in the Fregatidae, but according to Cottam (1957), the presence of this character can be “inferred from the sutures” in juvenile speci-



- mens; Olson (1977), however, found it absent in Eocene stem group representatives of the *Fregatidae* and I have coded it as unknown.
23. Furcula: apophysis furculae: not as follows (0), abutting with an articular facet at the apex carinae of the carina sterni (1), fused with the apex carinae of the carina sterni (2). This character was coded as ordered.
  24. Coracoid, foramen nervi supracoracoidei: absent (0), present (1). Within the *Ciconiidae*, a foramen nervi supracoracoidei occurs in *Leptoptilos*.
  25. Coracoid, tip of processus procoracoideus bent towards extremitas omalis: no (0); yes (1).
  26. Coracoid, extremitas sternalis, processus lateralis greatly elongated: no (0), yes (1).
  27. Sternum, caudal portion of carina sterni reduced, apex carinae strongly cranially protruding: no (0), yes (1).
  28. Sternum, dorsal surface with numerous pneumatic foramina along midline and lateral margins (Fig. 5): no (0), yes (1).
  29. Sternum, distal margin, trabecula mediana very short, reaching much less far distally than trabeculae laterales: no (0), yes (1).
  30. Humerus, shaft straight: no (0), yes (1). Usually the shaft of this bone is more or less sigmoidally bowed.
  31. Humerus, proximal end, sulcus transversus very deep, long and rectangular-shaped: no (0), yes (1).
  32. Humerus, crista deltopectoralis strongly protruding and triangular: no (0), yes (1).
  33. Humerus, crista deltopectoralis strongly reduced: no (0), yes (1).
  34. Humerus, large and strongly protruding processus supracondylaris dorsalis present: no (0), yes (1).
  35. Phalanx proximalis digiti majoris with well-developed processus internus indicis (terminology after Stegmann 1963): no (0), yes (1).
  36. Tibiotarsus, proximal end, cristae cnemiales strongly proximally protruding: no (0), yes (1).
  37. Tibiotarsus, distal end bent medially, condylus medialis protruding farther distally than condylus lateralis: no (0), yes (1).
  38. Tarsometatarsus, hypotarsus with tendon of musculus flexor digitorum longus and m. flexor hallucis longus enclosed in bony canal (Fig. 6): no (0), yes (1).
  39. Tarsometatarsus, hypotarsus without cristae intermediae, crista lateralis separated from crista medialis by a deep sulcus: no (0), yes (1).
  40. Tarsometatarsus, hypotarsus with crista medialis strongly protruding: no (0), yes (1).
  41. Musculus expansor secundariorum vestigial or completely absent: no (0), yes (1); (after Forbes 1882, Beddard 1898, Mitchell 1913).
  42. Musculus ambiens: present (0), extremely vestigial or absent (1); (after Beddard 1884, Vanden Berge 1970, McKittrick 1991).
  43. Musculus gastrocnemius, fourth head: absent (0), present (1); (after Beddard 1884, Vanden Berge 1970, McKittrick 1991).
  44. Musculus flexor cruris lateralis, pars accessoria ("Y" muscle in the formula in Tab. IX.1 of George & Berger 1966): present (0), absent (1); (after McKittrick 1991).
  45. Musculus caudofemoralis, pars pelvica ("B" muscle in the formula Tab. IX.1 of George & Berger 1966): present (0), absent (1); (after Beddard 1884, McKittrick 1991).
  46. Powder down patches on back of rump: absent (0), present (1); (after Beddard 1898, Mitchell 1913). The presence of powder down patches was one of the major reasons for considering *Balaeniceps* related to the *Ardeidae* (Bartlett 1861). However, there are only two powder down patches in the former but four to eight in herons (Mitchell 1913).

- 47. Gular pouch: absent (0), very inconspicuous and feathered (1), large and naked (2). The homology of the gular pouch of pelecaniform birds is uncertain (Sibley & Ahlquist 1990, Siegel-Causey 1997).
- 48. Three anterior toes: not as follows (0), only proximal part webbed (1), webbed over their entire length (2). In many Ardeidae a short web is present between the fourth and the third toe, but absent between the third and second toe; *Balaeniceps* lacks any webs between the toes.
- 49. Hallux greatly reduced and consisting of a single phalanx only: no (0), yes (1). Usually the hallux has to phalanges.
- 50. Hallux included in webbed foot (Fig. 7): no (0), yes (1). This character is generally considered to be a synapomorphy of the Pelecaniformes.
- 51. Young at hatching: downy (0), naked (1).
- 52. Eggs incubated beneath feet: no (0), yes (1); (Cracraft 1985). This character was incorrectly coded by Siegel-Causey (1997) who assumed it to be present in Fregatidae and Balaenicipitidae (Elliot 1992, Orta 1992).
- 53. Claw of third toe distinctly pectinate on its medial side: no (0), yes (1). Although some authors considered the claw of the third toe of *Balaeniceps* to be incipiently pectinate (Giebel 1873, Mitchell 1913), I could not find any traces of pectination in the specimens available to me (three skins in the collection of the Forschungsinstitut Senckenberg).
- 54. Eggshell covered with layer of microglobular material (amorphous form of calcium carbonate): no (0), yes (1) (Mikhailov 1995).

Appendix II. Character matrix of 54 morphological characters for the 14 taxa included in this study (see Appendix I for character definitions). Unknown character states are indicated by “?”. Tinamidae were used for outgroup comparison.

	characters																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Tinamidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ardeidae	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	12	0	0
Ciconiidae	0	0	0	0	0	0	12	1	1	0	0	0	1	0	0	0	0	1	0	1
Threskiornithidae	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0
Diomedidae	1	0	1	1	0	0	0	0	1	0	0	0	1	0	1	0	1	1	0	0
Hydrobatidae	1	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0
Procellariidae	1	0	1	1	0	0	0	0	0	0	0	0	0	0	01	1	1	1	0	0
Scopidae	1	0	0	1	1	0	1	1	1	1	0	0	1	0	0	0	0	1	0	0
Balaenicipitidae	1	1	0	1	1	0	2	1	1	1	0	0	1	0	0	0	0	2	0	1
Phaethontidae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	?
Fregatidae	1	1	0	1	1	1	1	0	0	1	0	0	1	0	1	0	0	0	0	0
Pelecanidae	1	1	0	1	1	1	2	1	1	1	0	1	1	0	2	0	0	0	0	?
Phalacro./Anhingidae	1	1	0	1	1	1	0	0	0	01	1	1	1	1	12	1	0	2	1	0
Sulidae	1	1	0	1	1	1	2	0	0	1	1	1	1	1	1	1	0	2	1	0

	characters																			
	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Tinamidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ardeidae	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Ciconiidae	0	0	1	01	1	0	0	1	0	0	1	0	0	0	1	0	0	0	1	0
Threskiornithidae	01	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0
Diomedeidae	0	0	0	1	0	1	1	1	1	1	0	1	0	1	1	1	0	0	0	0
Hydrobatidae	0	0	0	1	0	1	0	0	0	1	0	0	0	1	1	1	0	0	0	0
Procellariidae	0	0	0	1	0	1	0	01	0	1	0	1	0	1	1	1	0	01	0	0
Scopidae	0	1	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	1	0	0
Balaenicipitidae	1	1	2	1	1	0	0	1	1	0	1	0	1	0	1	0	0	1	0	1
Phaethontidae	0	0	1	1	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0
Fregatidae	0	?	2	0	0	0	0	1	1	1	1	1	0	0	1	0	0	0	0	0
Pelecanidae	1	1	2	1	1	0	1	1	0	0	0	0	1	0	1	0	1	1	0	1
Phalacro./Anhingidae	0	1	1	0	0	0	1	0	1	0	1	0	1	0	01	0	1	01	0	1
Sulidae	1	1	1	0	1	0	1	1	1	0	0	0	1	0	1	0	1	1	0	1

	characters													
	41	42	43	44	45	46	47	48	49	50	51	52	53	54
Tinamidae	0	0	0	0	0	01	0	0	0	0	0	0	0	0
Ardeidae	0	1	0	0	1	1	0	0	0	0	1	0	1	01
Ciconiidae	0	01	1	0	1	0	0	1	0	0	01	0	0	0
Threskiornithidae	0	0	1	0	0	0	0	1	0	0	01	0	0	0
Diomedeidae	1	0	0	1	0	0	0	2	1	0	0	0	0	0
Hydrobatidae	0	0	0	01	0	0	0	2	1	0	0	0	0	0
Procellariidae	1	0	0	1	0	0	0	2	1	0	0	0	0	0
Scopidae	1	1	1	0	1	0	0	1	0	0	0	0	1	1
Balaenicipitidae	1	1	0	0	1	1	0	0	0	0	0	0	0	1
Phaethontidae	1	?	?	0	1	0	1	2	0	1	0	0	0	0
Fregatidae	1	0	0	1	1	0	2	1	0	1	1	0	1	1
Pelecanidae	1	1	?	1	1	0	2	2	0	1	1	1	0	1
Phalacro./Anhingidae	1	0	0	1	1	0	2	2	0	1	1	1	1	1
Sulidae	1	0	0	1	1	0	2	2	0	1	1	1	1	1