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Cenozoic mystery birds – on the phylogenetic affinities of bony-toothed birds (Pelagornithidae)

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The extinct Cenozoic bony-toothed birds (Pelagornithidae) are characterized by the occurrence of unique spiky projections of the osseous jaws and are among the most distinctive neornithine taxa. Earlier authors considered these marine birds to be most closely related to 'Pelecaniformes' or Procellariiformes, but recent phylogenetic analyses resulted in a sister group relationship to Anseriformes. This latter hypothesis was, however, coupled with a non-monophyly of galloanserine or even neognathous birds, which is not supported by all other current analyses. The character evidence for anseriform affinities of pelagornithids is thus reassessed, and it is detailed that the alleged apomorphies cannot be upheld. Pelagornithids lack some key apomorphies of galloanserine birds, and analysis of 107 anatomical characters did not support anseriform affinities, but resulted in a sister group relationship between Pelagornithidae and Galloanseres. By retaining a monophyletic Galloanseres, this result is in better accordance with widely acknowledged hypotheses on the higher-level phylogeny of birds. The (Pelagornithidae + Galloanseres) clade received, however, only weak bootstrap support, and some characters, such as the presence of an open frontoparietal suture, may even support a position of Pelagornithidae outside crown-group Neognathae.

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Introduction

There are few Cenozoic birds that depart as much from the common avian morphology as pelagornithids, the 'bony-toothed' birds. Pelagornithidae include some of the largest volant birds with wingspans above five metres; their beak is also equipped with numerous bony projections, and the skull morphology differs in several other respects from that of most extant neornithine birds (e.g., Harrison & Walker 1976; Bourdon *et al.* 2010; Mayr & Rubilar-Rogers 2010).

Pelagornithids are now known from all continents except Australia, and from sediments dating from the late Palaeocene to the latest Pliocene (e.g., Olson 1985; Mourer-Chauviré & Geraads 2008; Mayr 2009a; Bourdon *et al.* 2010). As even the earliest species exhibit the characteristic morphology of the group, the origin of bony-toothed birds almost certainly goes back into the Cretaceous.

Although these spectacular birds buzzed the literature for decades, their osteology remained very poorly known. Recently, however, abundant material of Palaeogene pelagornithids has been described (Bourdon *et al.* 2010; see also Mayr & Smith 2010) as well as a largely complete skeleton of one of the largest Neogene species (Mayr & Rubilar-Rogers 2010). Still not all aspects of pelagornithid osteology are well established, but after these new discoveries, pelagornithids certainly rank among the better known Cenozoic avian taxa. Their phylogenetic affinities nevertheless remain controversial.

Bony-toothed birds lack three of the neornithine apomorphies listed by Cracraft & Clarke (2001), i.e., a bony mandibular symphysis, three mandibular condyles of the quadrate, and a cranially deflected crista deltopectoralis of the humerus, but an assignment to the neornithine Neognathae is well supported by the morphology of the palatopterygoid joint and the derived morphology of the hypotarsus, which exhibits well-developed sulci for the tendons of the flexor muscles of the toes. Tackling the affinities of bony-toothed birds within Neognathae, however, is less straightforward.

Virtually all recent analyses support a division of neognathous birds into two clades, Galloanseres, including Galliformes and Anseriformes, and Neoaves, which comprise the remaining taxa (e.g., Ericson *et al.* 2006; Livezey & Zusi 2007; Hackett *et al.* 2008; Mayr 2011). Whereas Galloanseres are characterized by a number of derived osteological features (e.g., Cracraft & Clarke 2001; Mayr & Clarke 2003; Livezey & Zusi 2007), a morphological characterization of Neoaves remains difficult. Proposed apomorphies mainly concern soft tissue anatomy and include the reduction of a phallus and the morphology of the neoptile feathers (Montgomerie & Briskie 2007; Brennan *et al.* 2008; Mayr 2008a; Foth 2011). The only osteological apomorphy of Neoaves pertains to the morphology of the palatinum, which exhibits a well-developed crista ventralis (Mickoleit 2004; Mayr 2008b).

As detailed by Olson (1985), most earlier workers considered pelagornithids to be most closely related to the polyphyletic neoavian 'Pelecaniformes'. Similarities to procellariiform birds were, however, also noted (e.g., Harrison & Walker 1976), and to reflect the uncertain affinities of pelagornithids, Howard (1957) erected the taxon Odontopterygiformes. So far, however, advocates of 'pelecaniform' or procellariiform affinities of bony-toothed birds did not present explicit hypotheses on the interrelationships between these fossil birds and their presumed extant relatives.

Bourdon (2005) performed the first cladistic analysis including bony-toothed birds and concluded that they are the sister taxon of Anseriformes. She proposed the new taxon Odontoanserae for the clade including Pelagornithidae and Anseriformes, and for the first time depicted a phylogenetic tree including bony-toothed birds. By not recovering a monophyletic Galloanseres, however, Bourdon's (2005) analysis conflicts with all other recent phylogenetic studies (e.g., Ericson *et al.* 2006; Hackett *et al.* 2008; Mayr 2011), and she noted that a constrained tree with a monophyletic Galloanseres 'implies that none of the derived characters of the Odontoanserae is valid' (Bourdon 2005: 589). New data obtained from a well-preserved and largely complete pelagornithid skeleton from the Miocene of Chile further show that pelagornithids lack derived features of Galloanseres, such as retroarticular processes of the mandible and an eminentia articularis of the quadrate (Mayr & Rubilar-Rogers 2010).

Bourdon (2011) conducted another analysis, which included Mesozoic non-neornithine birds (*Ichthyornis* and *Hesperornis*) and produced an even less likely result in that Galliformes resulted as sister taxon of palaeognathous birds, thus rendering not only Galloanseres but also Neognathae non-monophyletic groups.

Knowledge of the exact phylogenetic position of pelagornithids is critical for an understanding of the evolution of the morphological features that set them apart from other birds. The aim of the present study is to re-evaluate the character evidence listed by Bourdon (2005) and to present a phylogenetic hypothesis that is in better accordance with well-supported and generally accepted hypotheses on the higher-level phylogeny of birds.

Material and methods

Osteological terminology follows Baumel & Witmer (1993). The data matrix comprises 22 ingroup taxa and 107 morphological characters. Because of the hypothesized position of Pelagornithidae on the stem lineage of Anseriformes, Dromornithidae, putative Anseriformes from the Cenozoic of Australia were added to the ingroup taxa, which were scored after the descriptions and illustrations in Murray & Vickers-Rich (2004). Also included are the Sylviornithidae, putative Galliformes from the Holocene of New Caledonia, which were scored after Poplin & Mourer-Chauviré (1985) and Mourer-Chauviré & Balouet (2005). The early Cenozoic Gastornithidae were not included, as a meaningful character scoring is not possible without restudy of the actual material, which is beyond the scope of the present study. Outgroup comparisons were made with the Mesozoic non-neornithine taxa *Apsaravis*, *Hesperornis*, and *Ichthyornis*. The character matrix (see Appendices) is based on the revised and emended data set of Mayr & Clarke (2003).

The phylogenetic analysis was performed with the heuristic search modus of NONA 2.0 (Goloboff 1993) through the WINCLADA 1.00.08 interface (Nixon 2002), using the commands hold 10000, mult*1000, hold/10, and max*. All characters were coded as nonadditive. Consistency index (CI) and retention index (RI) were calculated, as well as bootstrap support values with 1000 replicates, three searches holding one tree per replicate, and TBR branch swapping without max*.

Bourdon *et al.* (2010) synonymized the pelagornithid taxa *Odontopteryx* and *Dasornis*, but following Mayr & Zvonok (in press), they are kept separate in the present study.

Institutional Abbreviations: BMNH, The Natural History Museum, London; MNHN, Museo Nacional de Historia Natural, Santiago de Chile, Chile; SMF, Forschungsinstitut Senckenberg, Frankfurt am Main, Germany; SMNK, Staatliches Museum für Naturkunde Karlsruhe, Germany.

Results of phylogenetic analysis

The analysis resulted in four most parsimonious trees (Length = 314, CI = 0.38, RI = 0.60), the strict consensus tree of which is shown in Fig. 1. Pelagornithidae were recovered as sister taxon of a clade including Sylviornithidae, Dromornithidae, and crown-group Galloanseres, but this topology was not retained in the bootstrap analysis. A clade including Pelagornithidae and galloanserine birds is supported by the following two characters (numbers refer to the character list in the appendix):

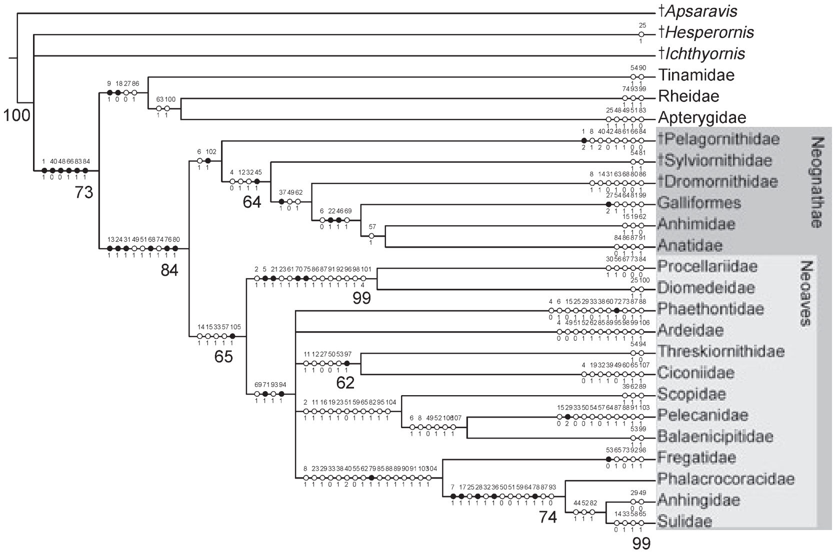

Fig. 1 Strict consensus tree of four most parsimonious trees (Length = 314, CI = 0.38, RI = 0.60) resulting from the analysis of the data matrix. Apomorphies and character states are listed on the internodes (numbers refer to the character list in Appendix 1); filled circles represent strict apomorphies, open circles homoplastic ones. Bootstrap support values are indicated below the internodes. Extinct taxa are marked with a dagger.

(6) Skull, distinct nasofrontal hinge, i.e., caudal part of beak markedly set off by a furrow against rostral part of cranium. The character optimization implies a reversal into the primitive state in crown-group Galloanseres (see Discussion).

(102) Impressio musculi adductoris mandibulae externus, pars coronoidea in medial position.

The clade including Sylviornithidae, Dromornithidae, and crown-group Galloanseres also received a low bootstrap of 64%. Monophyly of crown-group Galloanseres to the exclusion of Pelagornithidae is, however, well supported by the following characters, which were optimized as apomorphies of three successive nodes:

(12) Os lacrimale without well-developed processus orbitalis which touches or nearly touches the jugal bar (compare Figs 2H and 5B). This character was optimized as an apomorphy of a clade including Sylviornithidae, Dromornithidae, and crown-group Galloanseres.

(22) Cranium, basiparasphenoid plate inflated, rounded, broad, and meeting the parasphenoid rostrum at a very acute angle; ostia canalis carotici et opthalmici externi situated in a well-marked depression (listed as a galloanserine apomorphy by Cracraft & Clarke 2001). This character was optimized as an apomorphy of crown-group Galloanseres.

(32) Quadratum, processus oticus with eminentia articularis (Fig. 2C, D; tuberculum subcapitulare of Elzanowski *et al.* 2000). This character was identified as a galloanserine apomorphy by Elzanowski & Stidham (2010), but also occurs in few other taxa (see Mayr & Clarke 2003). It was here optimized as an apomorphy of a clade including Sylviornithidae, Dromornithidae, and crown-group Galloanseres.

(37) Quadratum, processus orbitalis with well-developed crista orbitalis (Fig. 2C, D). This character was identified as a galloanserine apomorphy by Elzanowski & Stidham (2010). It was here optimized as an apomorphy of a clade including Dromornithidae and crown-group Galloanseres.

(45) Mandible with strongly elongated, blade-like processus retroarticularis (Fig. 2J). This character was listed as a galloanserine apomorphy by Cracraft & Clarke (2001). In the present analysis, it was optimized as an apomorphy of a clade including Sylviornithidae, Dromornithidae, and crown-group Galloanseres.

(46) Mandible, processus medialis, long, narrow, and dorsally oriented. This character was listed as a galloanserine apomorphy by Cracraft & Clarke (2001). In this study, it was optimized as an apomorphy of crown-group Galloanseres.

Four other characters that were optimized as apomorphies of crown-group Galloanseres or a Dromornithidae/crown-group Galloanseres clade either represent reversals into the primitive state (49: axis, presence of foramina transversaria; 6: loss of nasofrontal hinge) or exhibit homoplasy (62: coracoid, loss of foramen nervi supracoracoidei; 69: humerus, presence of well-developed sulcus scapulotricipitalis). Recovery of another character as an apomorphy of a Sylviornithidae/Dromornithidae/crown-group Galloanseres clade (4: upper beak, loss of marked furrow rostral

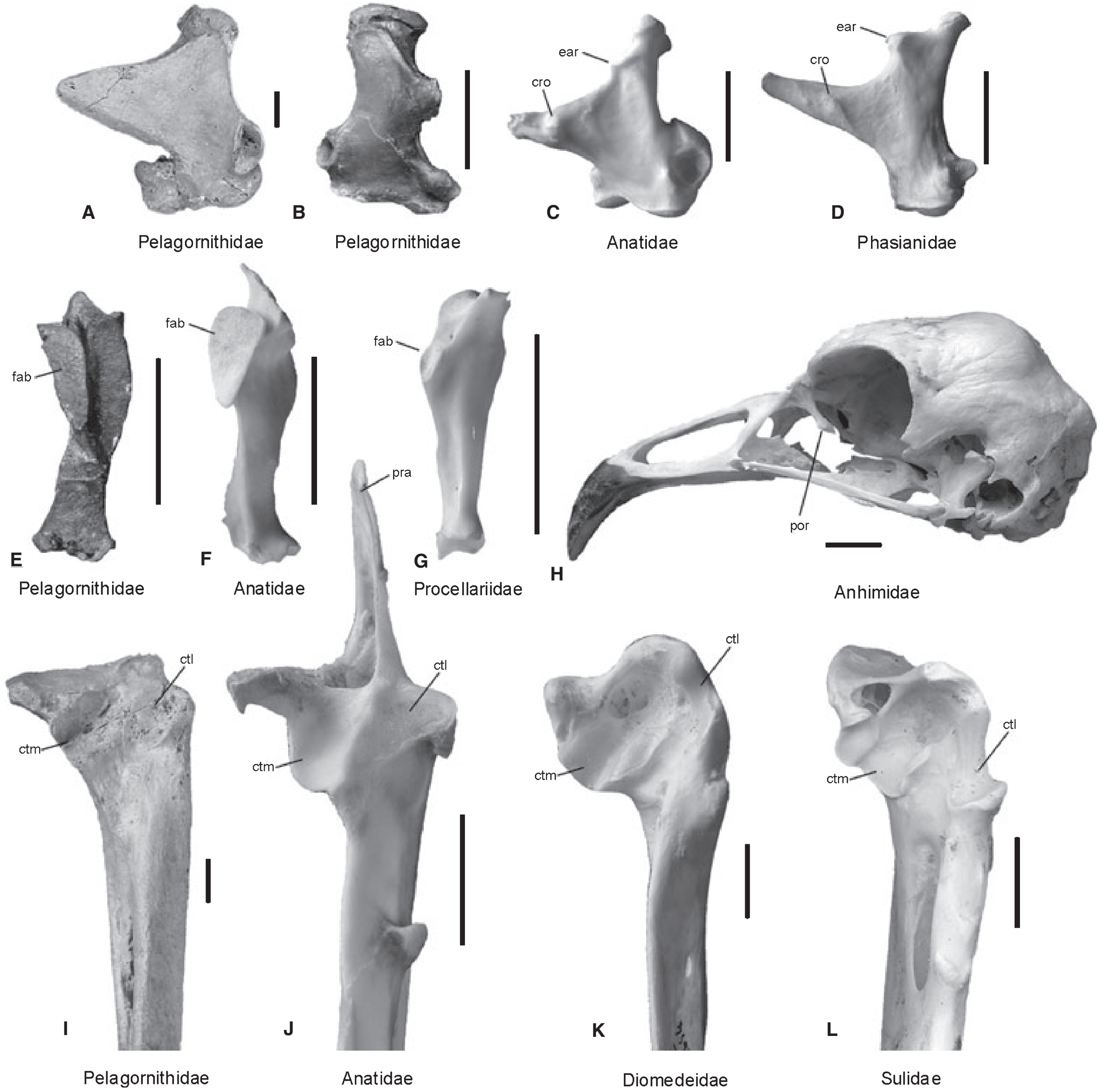

Fig. 2 A–D. Left (A, C, D) and right (B) quadratum in comparison. —A. *Pelagornis chilensis* from the Miocene of Chile (Pelagornithidae; MNHN SGO.PV 1061). —B. *Odontopteryx toliapica* from the early Eocene London Clay in England (Pelagornithidae; BMNH 44096). —C. *Cygnus olor* (Anseriformes, Anatidae). —D. *Tetrao urogallus* (Galliformes, Phasianidae). —E–G. Left pterygoid in comparison. —E. *O. toliapica* (Pelagornithidae; BMNH 44096). —F. *C. olor*. —G. *Fulmarus glacialoides* (Procellariiformes, Procellariidae). —H. Skull of *Chauna torquata* (Anseriformes, Anhimidae). —I–L. Proximal end of mandible (dorsal view) in comparison. —I. *P. chilensis* (MNHN SGO.PV 1061). —J. *C. olor*. —K. *Diomedea antipodensis* (Procellariiformes, Diomedeidae). —L. *Morus bassanus* ('Pelecaniformes', Sulidae). cro, crista orbitalis; ctl, cotyla lateralis; ctm, cotyla medialis; ear, eminentia articularis, fab, facies articularis basipterygoidea; por, processus orbitalis of os lacrimale; pra, processus retroarticularis. The scale bars equal 10 mm.

of nasal opening) is an artefact of the restricted taxon sampling of the study.

Monophyly of the neoavian taxa included in the analysis received a bootstrap support of 65% and is supported by five characters, of which the following three are considered significant:

(14) Os palatinum with crista ventralis (Fig. 3E).

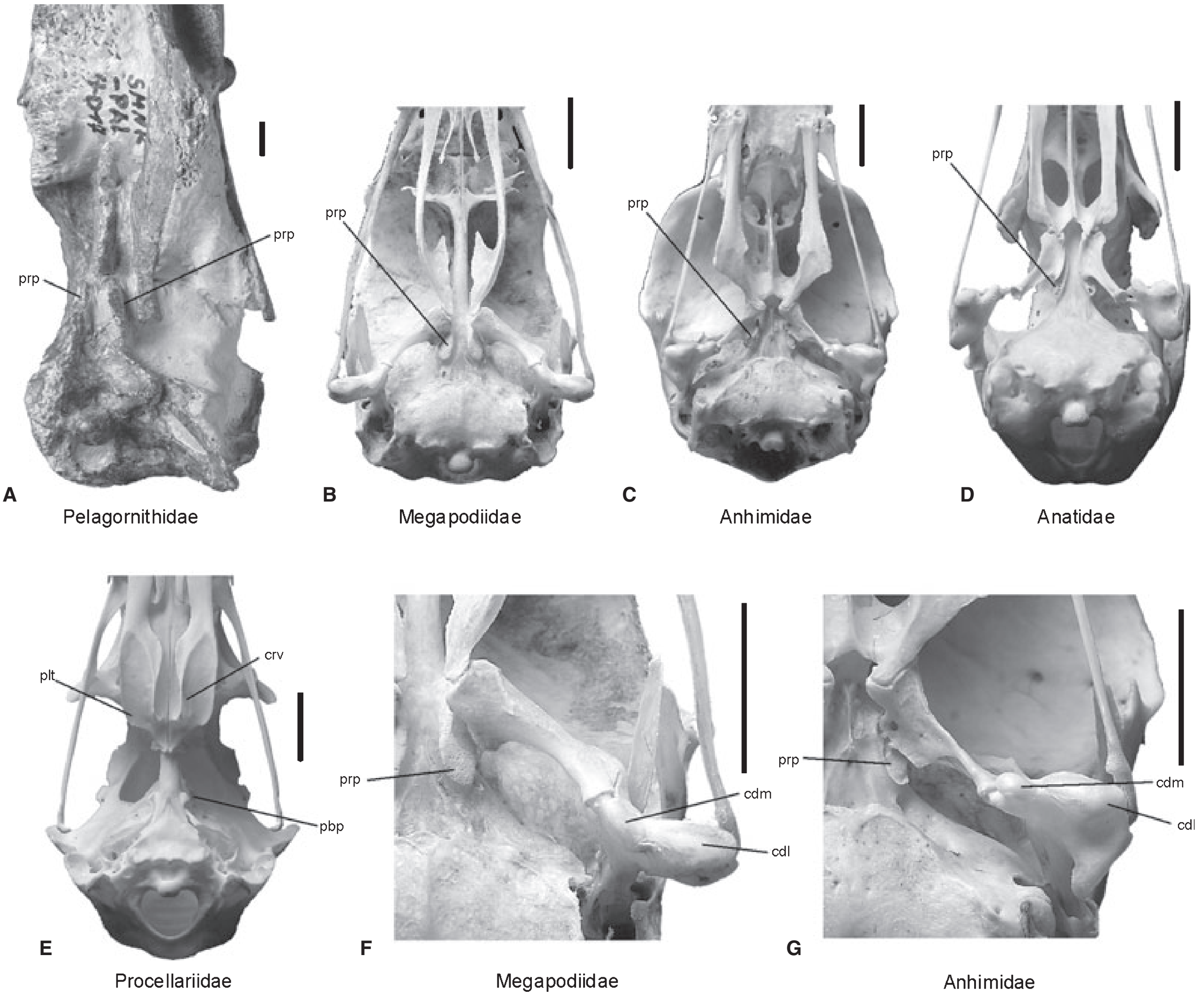

Fig. 3 A–E. Skulls in ventral view. —A. *Dasornis emuinus* from the early Eocene London Clay in England (Pelagornithidae; SMNK-PAL 4017). —B. *Alectura lathami* (Galliformes, Megapodiidae). —C. *Chauna torquata* (Anseriformes, Anhimidae). —D. *Chloephaga picta* (Anseriformes, Anatidae). —E. *Fulmarus glacialoides* (Procellariidae, Procellariiformes). —F, G. Detail of Quadrate/pterygoid articulation and basipterygoid process of *A. lathami* (F) and *C. torquata* (G). cdl, condylus lateralis; cdm, condylus medialis; crv, crista ventralis; pbp, processus basipterygoideus, plt, pars lateralis; prp, processus rostropterygoideus. The scale bars equal 10 mm.

(15) Os palatinum with well-developed pars lateralis (Fig. 3E).

(105) Loss of phallus.

Optimization of two other characters as neoavian apomorphies (33: quadratum, condylus medialis with marked, rostrally or laterally projecting, concave articular surface; 57: posterior caudal vertebrae with well-developed processus haemales) is an artefact of the restricted taxon sampling of the analysis (see, e.g., Mayr & Clarke 2003).

Concerning the interrelationships of the extant 'pelecaniform' taxa, the analysis is in basic agreement with the results of recent molecular studies, which support a polyphyletic 'Pelecaniformes', with Fregatidae as sister taxon of Suloidea (Sulidae, Phalacrocoracidae, Anhingidae) and with Pelecanidae being nested in a clade including the 'ciconiiform' Scopidae and Balaenicipitidae (Ericson *et al.* 2006; Hackett *et al.* 2008; Mayr 2011). A (Fregatidae + Suloidea) clade also resulted from an analysis by Smith (2010), but the present study is the first analysis of morphological data that supports a clade including Pelecanidae, Balaenicipitidae, and Scopidae. This latter clade was not retained in the bootstrap analysis but is supported by 11 homoplastic characters, of which the following five characters do not occur in other 'pelecaniform' birds:

(11) Ossa maxillaria, processus maxillopalatini greatly enlarged, inflated, and spongy.

(19) Os pterygoideum very short, measuring as much or less than maximum width of processus mandibularis of quadratum.

(65) Sternum, facies visceralis with numerous pneumatic foramina along midline and lateral margins.

(82) Tarsometatarsus, hypotarsus, tendon of musculus flexor hallucis longus enclosed in bony canal.

(95) Loss of musculus ambiens.

Five other characters that were recovered as apomorphies of this node also occur in Fregatidae and Suloidea and thus do not serve to support non-monophyly of the traditional 'Pelecaniformes' (2: upper beak, praemaxilla with sharply hooked tip; 16: ossa palatina fused along midline; 23: tubae auditivae not completely ossified ventrally; 59: furcula, extremitas omalis with strongly developed, laterally protruding facies articularis acrocoracoidea; 104: eggshell covered with layer of microglobular material of amorphous calcium carbonate). A further character (51: third cervical vertebra without osseous bridge from processus transversus to processus articularis caudalis) shows too much homoplasy among the taxa included in the analysis to be of great significance.

The following characters support a (Fregatidae + Suloidea) clade, which received a bootstrap support of 74%:

(29) Recessus tympanicus dorsalis greatly enlarged and situated rostrally to the articular facets of the quadrate (absent in Anhingidae).

(38) Apparatus hyobranchialis lacking os urohyale.

(40) Mandible of adult birds with synovial intraramal joint between os spleniale and os angulare formed by internal ossification associated with Meckel's cartilage (Zusi & Warheit 1992).

(55) Caudalmost thoracic vertebrae platy- or opisthocoelous.

(62) Coracoid without foramen nervi supracoracoidei.

(79) Tarsometatarsus very short and stocky, ratio distal width: length more than 0.3.

(85) Tarsometatarsus, trochlea metatarsi II distinctly longer than trochlea metatarsi IV, reaching as far distally as trochlea metatarsi III.

(89) Claw of third toe distinctly pectinate on its medial side.

Other characters that were recovered as apomorphies of this node also occur in Pelecanidae (8: external narial openings greatly reduced or completely absent; 23: tubae auditivae not completely ossified ventrally; 88: hallux included in webbed foot; 91: musculus flexor cruris lateralis without pars accessoria; 103: presence of large and naked gular pouch; 104: eggshell covered with layer of microglobular material of amorphous calcium carbonate). A further character is unknown for Pelecanidae (90: musculus femorotibialis externus without distal head), and another (33: quadratum, condylus medialis, marked, rostrally or laterally projecting, concave articular surface) represents a reversal into the primitive condition and exhibits homoplasy within the clade. Fregatidae and Suloidea also share a patella with a marked sulcus/canal for the tendon of the ambiens muscle (Mayr 2011; the character was not included in the present study), and further apomorphies of a Fregatidae/Suloidea clade were listed by Smith (2010).

The analysis does not support the current views on the affinities of Sylviornithidae and Dromornithidae. *Sylviornis* was classified into Galliformes by Poplin & Mourer-Chauviré (1985) and Mourer-Chauviré & Balouet (2005), and derived osteological features that support this hypothesis include the presence of a notarium and hypotarsus morphology. With respect to some features, *Sylviornis* is, however, clearly distinguished from extant Galliformes, such as the fused ossa palatina and the presence of a foramen nervi supracoracoidei. Dromornithidae were assumed to be anseriform birds by Murray & Vickers-Rich (2004: 156), who listed two features in support of a sister group relationship to the Anhimidae. At least one of these, however, the alleged absence of uncinate processes seems to be erroneous, as Murray & Vickers-Rich (2004: figs 44 and 60) depicted ribs with articulation facets, which actually indicate the presence of uncinate processes (see also Olson 2005). The exact affinities of sylviornithids and dromornithids were beyond the scope of this study, so much the more as no firsthand examination of the material was made. Concerning these taxa, the results of the analysis may thus reflect inadequate character sampling rather than the true phylogeny.

Character evidence for Bourdon's (2005) Odontoanserae

Bourdon (2005) listed fourteen characters in support of a sister group relationship between Pelagornithidae and Anseriformes, twelve of which she considered to be unique for a (Pelagornithidae + Anseriformes) clade. Only three of these latter characters were included in the present analysis, because I found the character descriptions of the others to be problematic, i.e. either difficult to comprehend or not restricted to the taxa in question. In particular, several of the allegedly anseriform character states are also present in Megapodiidae, the sister taxon of the other crown-group Galliformes, and are thus likely to be plesiomorphic for Galloanseres. The following twelve characters were identified by Bourdon (2005) as strict apomorphies of a (Pelagornithidae + Anseriformes) clade:

(1) Impressio musculi adductoris mandibulae externus, pars coronoidea in medial position. Zusi & Livezey (2000:

178) detailed that this muscle impression is not laterally exposed in most Anseriformes (except Mergini). However, these authors also noted that Megapodiidae also exhibit the derived, medially displaced muscle impression (Fig. 4A; Zusi & Livezey 2000: 185), which may thus be plesiomorphic for Galloanseres. The character was included in the present analysis (character 102 in the Appendix 1), but contra Bourdon (2005), who scored the feature as absent for all galliform birds, Galliformes were coded polymorphic.

(2) Processus rostropterygoideus with basal support. Bourdon (2005) noted that Pelagornithidae and Anseriformes share slightly elevated rostropterygoid processes, whereas these processes are sessile in galliform birds. However, the morphology of the rostropterygoid processes of Megapodiidae closely corresponds with that of the anseriform Anhimidae (Fig. 3F, G), and elevated basipterygoid processes are also present in Sylviornithidae (Mourer-Chauviré & Balouet 2005: fig. 3d). Homology of the anseriform and pelagornithid condition may have further been enforced as this character was coded as ordered by Bourdon (2005), thus biasing the analysis towards an evolutionary path with the galliform state as a precursor of the anseriform one. Rostropterygoid processes were included in the present analysis (character 20 in the Appendix 1), but no distinction was made between elevated and sessile conditions (as the elevated condition is present in Sylviornithidae and Dromornithidae, the resulting tree topology suggests that it is plesiomorphic for Galloanseres).

(3) Os quadratum with two condyli, condylus medialis situated rostral of condylus lateralis. A bicondylar quadrate is considered an apomorphy of Galloanseres (e.g., Cracraft & Clarke 2001), and was included in the analysis (character 35 in the Appendix 1). However, although Phasianidae and Anatidae are distinguished by the rostral extent of the condylus medialis, no difference was found between Anhimidae and Megapodiidae (Fig. 3F, G). Because these taxa are the sister groups of the other crown-group Anseriformes and Galliformes, respectively, it is likely that the configuration of their mandibular condyles is plesiomorphic for Galloanseres.

(4) Tibiotarsus with wide incisura intercondylaris; condylus medialis rostrally protruding and narrower than condylus lateralis. This character complex occurs in many unrelated neornithine taxa (contra Bourdon 2005 it is present in Phoenicopteridae, Ciconiidae, and Threskiornithidae; Fig. 4I). In Charadriiformes, it is found in Recurvirostridae, but absent in Turnicidae. Because of the high degree of homoplasy and the difficulties involved in the scoring of intermediate states, this character is considered to be of little phylogenetic significance and not included in the analysis.

(5) Basicranium with wide platform lateral of lamina parasphenoidalis. Description of this character was modified by Bourdon (2011: 223) into 'os exoccipitale, processus paroccipitalis: strongly protruding caudoventrally, caudally convex, with wide lateral side for origin of musculus depressor mandibulae; the processus is continuous with stout processus lateralis parasphenoidalis and ala parasphenoidalis so that the cavitas tympanica is deeply recessed'. Bourdon (2011: 233) noted that the character is absent in Anhimidae, a condition she considered autapomorphic for screamers. However, by not coding Anseriformes polymorphic, the analysis was actually biased towards recognition of this character as a synapomorphy of Pelagornithidae and Anseriformes. The corresponding part of the basicranial area of Anhimidae and Megapodiidae is very similar (Fig. 3), and I consider the resemblances between Pelagornithidae and Anatidae to be of convergent origin. The character was thus not included in the present analysis.

(6) Well-developed os mesethmoidale with deep depression for concha caudalis. Contrary to Bourdon's (2005) scoring, this character is present in non-anseriform extant taxa included in her analysis, such as Spheniscidae (e.g., *Spheniscus demersus*; Fig. 4B). Because it is further not comparable in most 'pelecaniform' birds, in which the conchae caudales are reduced (except Phaethontidae; Technau 1936), it was not included in the present analysis.

(7) Proximal extremity of ulna 'with strongly convex facies caudodorsalis showing impressio musculi scapulotricipitalis in distodorsal position; cotyla dorsalis with pointed extremity; depression for meniscus radioulnaris poorly developed' (Bourdon 2005: 588). This character complex also occurs in Phoenicopteridae, Ardeidae, and Threskiornithidae, whose proximal ulna is very similar to that of anseriform birds. I could not determine which of the features may be a synapomorphy of Pelagornithidae and Anseriformes and did not include the character in the analysis.

(8) Ulna, 'proximal continuation of sulcus intercondylaris forming a wide surface bounded ventrally by long sinuous ridge' (Bourdon 2005: 588). I could not comprehend the meaning of the character description, and the character was not included in the present analysis. Bourdon (2011) noted that it is absent in Anhimidae and assigned Anseriformes and Pelagornithidae different states; homology of the anseriform and pelagornithid condition was then enforced by coding the character as ordered, thus biasing the analysis towards homology of the anseriform and pelagornithid character states.

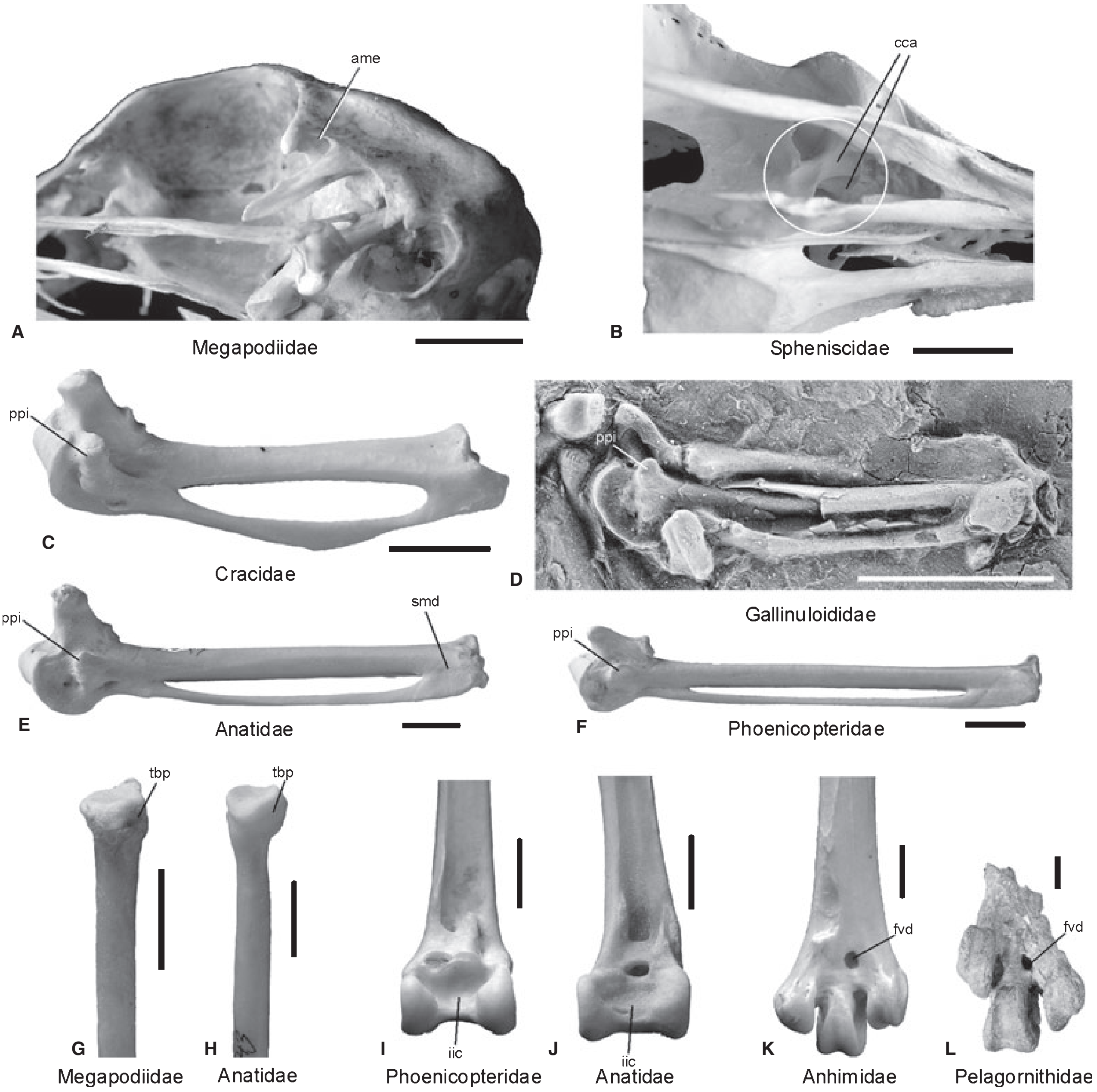

Fig. 4 A. Detail of the skull of *Alectura lathami* (Galliformes, Megapodiidae) to show the medially situated impressio musculi adductoris mandibulae externus, pars coronoidea. —B. Detail of the skull of *Spheniscus demersus* (Sphenisciformes) to illustrate the presence of well-developed depressions for conchae caudales. —C–F. Left carpometacarpus in comparison. —C. *Pipile jacutinga* (Galliformes, Cracidae). —D. *Paraortygoides messelensis* from the middle Eocene of Messel in Germany (Galliformes, Gallinuloididae; SMF-ME 3663a). —E. *Chloephaga picta* (Anatidae, Anseriformes). —F. *Phoeniconaias minor* (Phoenicopteriformes). —G, H. Proximal end of right radius of *A. lathami* (G) and *C. picta* (H). —I, J. Distal end of left tibiotarsus of *Phoenicopterus ruber* (Phoenicopteriformes) (I) and *C. picta* (J). —K, L. Distal end of right tarsometatarsus of *Chauna torquata* (K) and *Dasornis emuinus* (L) from the early Eocene London Clay in England (Pelagornithidae; BMNH A 894). ame, impressio musculi adductoris mandibulae externus, pars coronoidea; cca, rostral end of os mesethmoidale (encircled) with depressions of conchae caudales; fvd, foramen vasculare distale; iic, incisura intercondylaris; ppi, processus pisiformis; smd, symphysis metacarpalis distalis; tbp, tuberculum bicipitale. The scale bars equal 10 mm.

(9) Radius 'ventral border of cotyla humeralis convex, prominent and continuous with caudal edge of tuberculum bicipitale, surface dorsal to the latter and distal to facies articularis ulnaris flat and triangular' (Bourdon 2005: 588). I also had difficulties to recognize the significance of this character complex and found the proximal radius of Megapodiidae and Anseriformes to be quite similar (Fig. 4G, H). The character was not included in the analysis.

(10) Carpometacarpus 'processus pisiformis prominent, with proximal border reaching trochlea carpalis and rostral [distal] border extending far distally' (Bourdon 2005: 588). Although this character was considered unique for Anseriformes and Pelagornithidae by Bourdon (2005), the morphology of the processus pisiformis of Anatidae is essentially the same as that of stem group Galliformes (Fig. 4D), and is thus likely to be plesiomorphic for Galloanseres. The character was not included in the present analysis.

(11) Carpometacarpus with 'long symphysis metacarpalis distalis with os metacarpale minus close to os metacarpale majus; the latter shows median ridge that curves caudally at distal extremity; high and well-defined caudal protuberance on facies articularis digitalis major' (Bourdon 2005: 588). This character actually represents a complex of different characters, which refer to features of the distal carpometacarpus. The morphology of the distal carpometacarpus of Anatidae is essentially the same as that of Phoenicopteridae (Fig. 4F), for which this character complex was coded absent by Bourdon (2005). The character was not included in the present analysis.

(12) Tarsometatarsus, 'trochlea metatarsi III elongated, plantarly prominent, pointed at the tip, slightly oblique; low foramen vasculare distale with recessed plantar opening' (Bourdon 2005: 588). This character also represents a complex of different characters, referring to the shape of the trochlea metatarsi III and the foramen vasculare distale. An elongate trochlea metatarsi III is characteristic for many neornithine birds, and among the taxa included in Bourdon's (2005) analysis present in Phoenicopteridae. Contrary to Bourdon's (2005) scoring, the plantar opening of the foramen vasculare distale is not recessed in Anhimidae and the pelagornithid *Dasornis* (Fig. 4K, L). The character was not included in the present analysis.

Discussion

Regarding the extant taxa, the results of the present analysis agree well with current phylogenies derived from molecular data (e.g., Ericson *et al.* 2006; Hackett *et al.* 2008; Mayr 2011). The analysis also confirms Bourdon's (2005, 2011) hypothesis that pelagornithids are outside Neoaves, but does not support anseriform affinities.

Closer affinities between bony-toothed birds and Procellariiformes or any of the 'pelecaniform' taxa are not convincingly indicated by osteological data. Although the wing and pectoral girdle bones of pelagornithids resemble those of the procellariiform Diomedeidae (Mayr & Smith 2010), these similarities can be attributed to convergence. Diomedeidae are nested within crown-group Procellariiformes (e.g., Hackett *et al.* 2008), and pelagornithids lack derived features shared by albatrosses and other procellariiform birds, such as a supraorbital position of the nasal glands, a well-developed processus supracondylaris of the humerus (which is primitively absent in the extinct Diomedeoididae and Oceanitinae; Mayr 2009b) and strongly protruding cristae cnemiales (tibiotarsus). At best, bony-toothed birds may thus be the sister taxon of Procellariiformes, but no derived characters have yet been reported that would support this hypothesis.

Pelagornithids also lack derived characters shared by Pelecanidae, Scopidae and Balaenicipitidae, such as a laterally protruding facies articularis acrocoracoidea of the furcula and fused palatine bones. Derived characters of the Fregatidae/Suloidea clade, which are absent in bony-toothed birds, include the fusion of the palatine bones, the short tarsometatarsus with a distally protruding trochlea metatarsi II, and the lack of a foramen nervi supracoracoidei on the coracoid. Olson (1985: 200) spearheaded the intraorbital position of glandulae nasales in support of 'pelecaniform' affinities of pelagornithids, but this feature is absent in early Palaeogene Pelagornithidae (*Odontopteryx* and *Dasornis*; Bourdon *et al.* 2010: 53). As detailed by Zusi & Warheit (1992), pelagornithids also share a well-developed intraramal joint with the taxa of the Fregatidae/Suloidea clade, which in the extant species is formed by an internal ossification in or around Meckel's cartilage. The developmental origin of the intraramal joint of pelagornithids is, however, unknown, and only the joint of Sulidae approaches that of pelagornithids in the degree of its development (Zusi & Warheit 1992). Bony-toothed birds further share with Fregatidae, Suloidea and other 'pelecaniform' birds the presence of longitudinal furrows along the upper beak, which run from the nostrils to the tip of the bill and are indicative of a compound rhamphotheca (Fig. 5; nasolabial groove of Hieronymus & Witmer 2010). Adult 'pelecaniform' birds have very small narial openings, but it is notable that juveniles exhibit long nostrils, and these also occur in stem lineage representatives of Phaethontidae and Fregatidae (Fig. 5; Olson 1977). Although this hypothesis needs to be corroborated by futures studies, it is likely that the rostral furrows of 'pelecaniform' birds are due to the fact that the stem species of these birds had long narial openings. The rostral furrows of bony-toothed birds, by contrast, extend to the

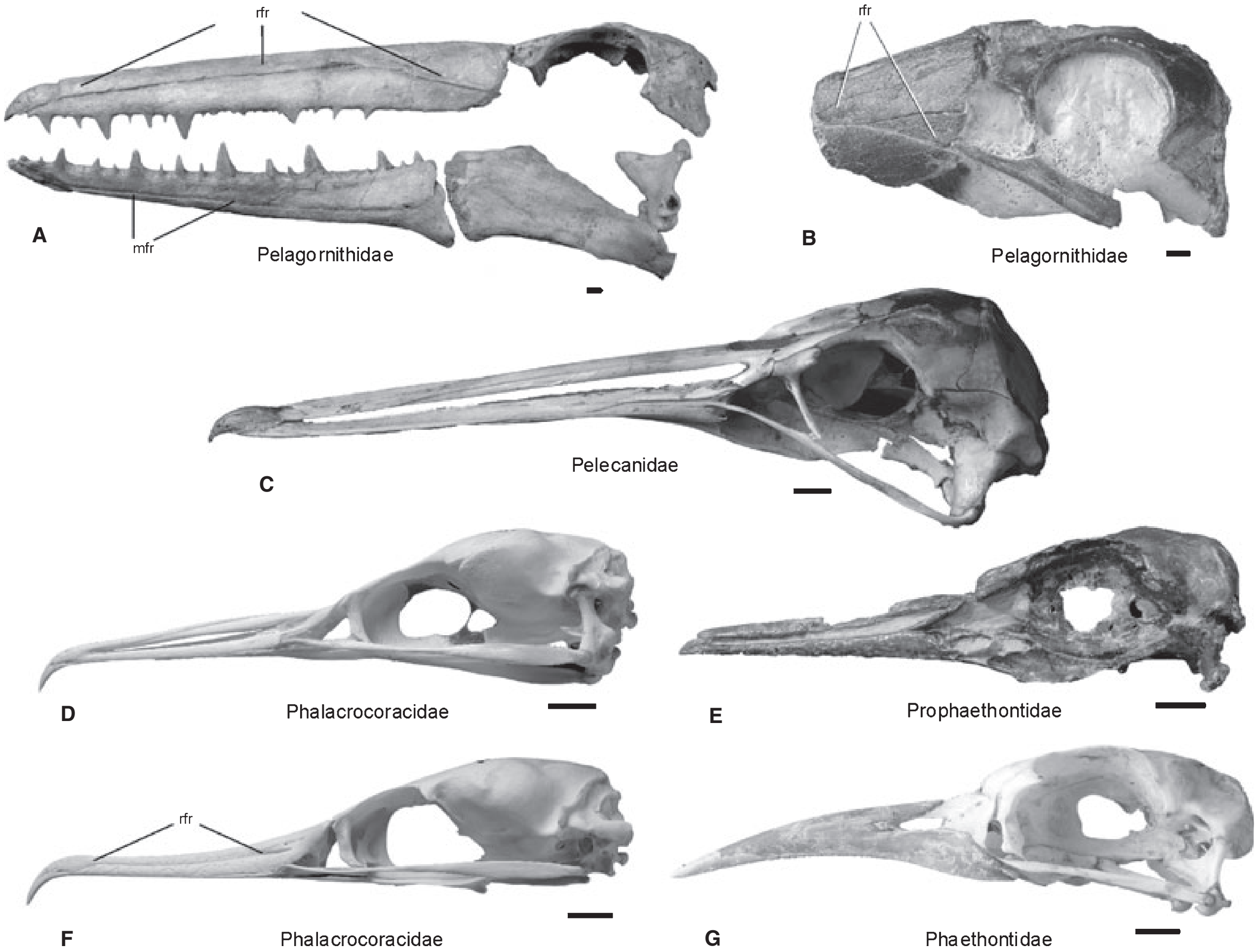

Fig. 5 Skulls in comparison. —A. *Pelagornis chilensis* from the Miocene of Chile (Pelagornithidae; MNHN SGO.PV 1061). —B. *Dasornis emuinus* from the early Eocene London Clay in England (Pelagornithidae; SMNK-PAL 4017). —C. Juvenile *Pelecanus occidentalis* ('Pelecaniformes', Pelecanidae) with long nostrils. —D. Juvenile *Phalacrocorax carbo* ('Pelecaniformes', Phalacrocoracidae) with long nostrils. —E. *Prophaethon shrubsolei* from the early Eocene London Clay in England (Prophaethontidae; BMNH A 683) with long nostrils. —F. Adult *P. carbo*. —G. *Phaethon aethereus* ('Pelecaniformes', Phaethontidae). mfr, mandibular furrow; rfr, rostral furrow (nasolabial groove). The scale bars equal 10 mm.

jugal arch (Fig. 5), which makes an association with long nostrils less likely; the Neogene *Pelagornis* further exhibits a distinct culminolabial groove that delimits a praemaxillary nail (Hieronymus & Witmer 2010; Mayr & Rubilar-Rogers 2010).

A position of Pelagornithidae outside Neoaves is supported by two plesiomorphic features of the palatine bone: the absence of a crista ventralis and the poorly developed pars lateralis (Mayr 2008b). As detailed in the results section, pelagornithids lack several key apomorphies of crown-group Galloanseres, and the analysis does not support anseriform affinities but resulted in a sister group relationship to a clade including Sylviornithidae, Dromornithidae, and crown-group Galloanseres. Only two characters were, however, optimized as apomorphies of a (*Pelagornis* + Galloanseres) clade, one of which, the presence of a marked nasofrontal hinge, is of limited phylogenetic significance because of its widespread distribution among birds and absence in most crown-group Galloanseres.

Pelagornithids share with Galloanseres a bicondylar quadrate (Bourdon 2005) and very shallow mandibular cotylae (Fig. 2I, J). These two characters are generally regarded as galloanserine apomorphies (e.g., Cracraft & Clarke 2001). They were, however, not optimized as such in the analysis, as both are also present in *Ichthyornis* and *Hesperornis* and may thus be plesiomorphic for Neornithes (the proximal end of the mandible of pelagornithids is particularly similar to that of *Ichthyornis*; compare Fig. 2I with Elzanowski *et al.* 2000: fig. 4 and Clarke 2004: fig. 28).

Rostropterygoid processes, another character widely accepted as a galloanserine apomorphy, were likewise not identified as a synapomorphy of Pelagornithidae and Galloanseres in the analysis, because their origin in the stem lineage of neognathous birds is an equally parsimonious assumption with the taxon sampling of the analysis and the resulting tree topology. However, identification of rostropterygoid process as a galloanserine apomorphy is well established, because Weber (1993) studied the ontogeny of avian basipterygoid processes and detailed that rostropterygoid processes, which develop through apposition of the pterygoid on the parasphenoid, are an evolutionary novelty of Galloanseres and not homologous to other avian basipterygoid processes, which develop from an early embryonic quadratopolar commission.

The basipterygoid processes of bony-toothed birds are more elongated and less ovate than those of crown-group Galloanseres (Fig. 3). Although the ontogenetic development of these processes is unknown, I concur with Bourdon (2005) that their position and morphology suggests homology with rostropterygoid processes and thus galloanserine affinities of bony-toothed birds. Likewise, the large facies articularis basipterygoidea of the pterygoid bone closely corresponds with that of galloanserine birds (Fig. 2E, F). A sister group relationship between Pelagornithidae and Anseriformes is, however, not well based, and a position of bony-toothed birds outside crown-group Galloanseres is in better agreement with the osteology of these birds.

Still, however, galloanserine affinities of pelagornithids are not strongly supported and some plesiomorphic morphological traits distinguish them from all other neognathous taxa. One such feature is the presence of an open frontoparietal suture, which, apart from pelagornithids, is only found in Mesozoic taxa outside Neornithes and in the palaeognathous Lithornithidae, Palaeotididae, and Tinamidae (Houde & Haubold 1987; Elzanowski & Galton 1991). Based on the result of the present analysis, occurrence of this feature in pelagornithids must be considered a secondary reversal into the plesiomorphic condition. If, however, an open suture can be shown to be plesiomorphic for palaeognathous birds (the exact affinities of Lithornithidae and Palaeotididae are uncertain; see Mayr 2009a), it may well also have been present in the stem species of Neognathae. In this case its occurrence in pelagornithids would represent a retained plesiomorphic feature supporting a position of these birds outside crown-group Neognathae. Another possibly plesiomorphic feature that distinguishes bony-toothed birds from all Neognathae, is the occurrence of neurovascular furrows along the mandibles (Fig. 5A), which also occur in Mesozoic non-Neornithes, Lithornithidae (Houde 1988), and Apterygidae.

Future studies will also have to address the origin and evolutionary significance of the pseudoteeth, which certainly are the most intriguing feature of pelagornithids. These hollow bony outgrowths of the jaws are very different from true avian teeth, which are situated in alveoles and have an enamel-covered crown. In being mere outgrowths of the jaw bones, pseudoteeth more closely resemble the enlarged fangs of some anurans (e.g., Fabrezi & Emerson 2003), which are, however, not hollow and not serially repeated. Because of their resemblance to true teeth in serial occurrence and regular size pattern, Mayr & Rubilar-Rogers (2010) hypothesized that pseudoteeth may be homologous to true avian teeth on a molecular level, i.e. that genes that regulate the development of true avian teeth may also be involved in the formation of pseudoteeth.

Pseudoteeth underwent little change in the more than 50 million years of pelagornithid evolution, and the selective forces that led to the evolution of such unique structures remain enigmatic. It is assumed that bony-toothed birds fed on soft-bodied marine invertebrates, such as squid (Olson 1985), and the morphologies of the cervical vertebrae and the labyrinth indicate that they carried their head in a near-vertical position (Milner & Walsh 2009; Mayr & Rubilar-Rogers 2010). If bony-toothed birds thus captured prey by skimming the sea surface, the pseudoteeth may have functioned as prey trap rather than grasping devices. Tooth-like, albeit much smaller tomial projections otherwise only occur in the anseriform *Thambetochen xanion* from the Holocene of Hawaii (see Olson & James 1991; Mayr 2009a). Such projections may thus have been licensed either by particularities of a galloanserine-like feeding apparatus, such as the gliding jaw joint (e.g., Weber & Hesse 1995), or by a genetic potential that was lost in neoavian birds.

An issue of possible significance for pelagornithid affinities finally concerns the identity of the enigmatic large eggs from the Miocene or Pliocene of Lanzarote (Canary Islands). These fossils were described as ratite eggs by Rothe (1964) and Sauer & Rothe (1972), but Garcia-Talavera (1990) hypothesized that they actually stem from bony-toothed birds. The Lanzarote eggs represent two types that were classified as struthionid and aepyornithid (Sauer & Rothe 1972). Their shells exhibit a ratite-like microstructure, which differs from the prismatic type of neognathous birds (Rothe 1964: fig. 7). However, a ratite-like eggshell microstructure also occurs in the Eocene *Ornitholithus*-type eggshell, which is considered to stem from the anseriform Gastornithidae (e.g., Mikhailov 1991).

Identification of fossil eggshell types is further not always straightforward, and a ratite-like eggshell morphotype is also found in some extant neognathous taxa, such as Cuculiformes and Piciformes (Hirsch *et al.* 1997). In the absence of bones associated with these eggs, future analyses of the eggshell microstructure of the Lanzarote eggs are needed to clarify whether these exhibits unambiguous derived features of ratite eggs (e.g., Patnaik *et al.* 2009). If the Lanzarote eggs can be shown to be from neognathous birds, a pelagornithid origin is likely and may call into question the identification of other 'aepyornithid' eggshell fragments that were found in North African localities.

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Appendix 1 Description of characters included in the phylogenetic analysis

1. Teeth: present (0), absent (1), 'pseudoteeth' present (2).
2. Upper beak, praemaxilla with sharply hooked tip: no (0), yes (1).
3. Upper beak, lamellae for filter feeding: absent (0), vestigial (1), well developed (2).
4. Upper beak, marked furrow rostral of nasal opening (nasolabial groove of Hieronymus & Witmer 2010): absent (0), present (1).
5. Rhamphotheca forming tubular external nostrils: no (0), yes (1).
6. Skull, distinct nasofrontal hinge, i.e., caudal part of beak markedly set off by a furrow against rostral part of cranium: absent (0), present (1). In Anhimidae, a nasofrontal hinge is present in *Chauna* but absent in *Anhima*. In Sylviornithidae and some Dromornithidae (*Dromornis* and *Bullockornis*), the beak is completely separated from the rostrum. As this character is, however, absent in the dromornithid *Genyornis*, it is likely to be the result of convergent evolution.
7. Os suprajugale: absent (0), present (1). This small ossicle is situated dorsal of the rostral end of the os jugale; it is separated from the latter in Phalacrocoracidae but fused with the os jugale in Sulidae and Anhingidae. I could not confirm its presence in Phaethontidae, Pelecanidae, and Fregatidae (contra Livezey & Zusi 2006: character 720).
8. External narial openings greatly reduced or completely absent: no (0), yes (1).
9. Os mesethmoidale reaching rostrally markedly beyond nasofrontal hinge: no (0), yes (1).
10. Ossa maxillaria, processus maxillopalatini fused along their midline, i.e., palate desmognathous: no (0), yes (1).
11. Ossa maxillaria, processus maxillopalatini greatly enlarged, inflated, and spongy: no (0), yes (1).
12. Os lacrimale, well-developed processus orbitalis which touches or nearly touches the jugal bar: yes (0), no (1).
13. Articulatio pterygopalatina sliding on rostrum parasphenoidale: no (0), yes (1). Presence of this character is an apomorphy of Neognathae (e.g., Elzanowski 1995).
14. Os palatinum, crista ventralis: absent (0), present (1).
15. Os palatinum, pars lateralis: absent or very small (0), present and well developed (1).
16. Ossa palatina fused along midline: no (0), yes (1). Coding of Phalacrocoracidae differs from Mayr (2005); in that, this character was scored as absent rather than variable. Presence of fused ossa palatina in *Cochlearius* (Ardeidae) is here considered autapomorphic for this taxon.
17. Both ossa palatina forming a flat plate with virtually no dorsoventral extension: no (0), yes (1).
18. Os palatinum and os pterygoideum fused: yes (0), no (1).
19. Os pterygoideum very short, measuring as much or less than maximum width of processus mandibularis of quadratum: no (0), yes (1).
20. Basipterygoid articulation in adulthood: present, not as follows (0), present, rostropterygoid articulation with large and ovoid articular facet for pterygoid (1), absent (2).
21. Os frontale, dorsal surface with marked depressions for supraorbital salt glands: absent (0), present (1).
22. Cranium, basiparasphenoid plate inflated, rounded, broad, and meeting the parasphenoid rostrum at a very acute angle; ostia canalis carotici et opthalmici externi situated in a well marked depression: no (0), yes (1).
23. Tubae auditivae completely ossified ventrally: yes (0), no (lateral osseous wall lacking) (1). The condition in Sulidae is uncertain, and tubae auditivae seem to be absent.
24. Tubae auditivae: paired and lateral (0), paired and close to/adjacent on cranial midline or single rostral opening (tuba auditiva communis) (1).
25. Marked processus parasphenoidales mediales: absent (0), present (1).
26. Fronto-parietal suture in adult birds: open or incompletely ossified (0), closed (1). Note that Bourdon erroneously scored a closed sutura frontoparietalis for Pelagornithidae (see Mayr 2008b; Bourdon *et al.* 2010).
27. Processus zygomaticus: present, variably developed (0), absent or vestigial (1), as before; but ossified aponeurosis zygomatica present (2). Zusi & Livezey (2000) detailed that a processus zygomaticus is vestigial in adult Galliformes. Whether the process in

Sylviornithidae represents a true processus zygomaticus or an ossified aponeurosis zygomatica is unknown.

28. Number of scleral ossicles: 14 or more (0), 12 or 13 (1); (after Warheit *et al.* 1989; Livezey & Zusi 2006; and own. obs.).
29. 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 dorsalis is small and situated between the articular facets of the quadrate.
30. Fossae temporales very marked and extending to midline of cranium: no (0), yes (1).
31. Quadratum, processus oticus, two well-separated heads for articulation with os squamosum and os prooticum: absent (0), present (1). Absence of this character in the galliform Phasianidae clearly represents an apomorphy of the taxon, as Megapodiidae and Cracridae exhibit a two-headed quadrate.
32. Quadratum, processus oticus, eminentia articularis (tuberculum subcapitulare of Elzanowski *et al.* 2000): absent (0), present (1).
33. Quadratum, condylus medialis, marked, rostrally or laterally projecting, concave articular surface: absent (0), present (1).
34. Quadratum, condylus lateralis with large and caudally prominent facies articularis quadratojugalis caudalis (terminology after Elzanowski & Stidham 2010; 'posterior buttress for quadratojugal' of Andors 1992: fig. 10): no (0), yes (1).
35. Quadratum, condylus caudalis: present (0), absent (1).
36. Quadratum, processus orbitalis greatly reduced in size: no (0), yes (1).
37. Quadratum, processus orbitalis, well-developed crista orbitalis: absent (0), present (1). Presence of a crista orbitalis was identified as an apomorphy of Galloanseres by Elzanowski & Stidham (2010).
38. Apparatus hyobranchialis, os urohyale: present, rod-shaped (0), vestigial or absent (1). This character is coded unknown for Rheidae and Anhingidae, of which no hyoid bones were available for study.
39. Mandible, ventral portion of rami mandibulae caudal of pars symphysialis medially inflected, so that mandible forms a deep trough: no (0), yes (1).
40. Mandible of adult birds with synovial intraramal joint between os spleniale and os angulare: absent (0), present, formed by splenial and angular bones (1), present, formed by internal ossification associated with Meckel's cartilage (2); after Zusi & Warheit (1992).
41. Mandible, os coronoideum: present (0), absent (1).
42. Mandible, ossified symphysis mandibulae: absent (0), present (1).
43. Mandible, two marked grooves on ventral surface of symphysis: absent (0), present (1). This character was coded as unknown for Hesperornithidae, Ichthyornithidae, and Pelagornithidae, which lack an ossified mandibular symphysis.
44. Mandible, dorsal surface of symphysis essentially flat: no (0), yes (1). This character was coded as unknown for Hesperornithidae, Ichthyornithidae, and Pelagornithidae, which lack an ossified mandibular symphysis.
45. Mandible, strongly elongated, blade-like processus retroarticularis: absent (0), present (1).
46. Mandible, processus medialis, long, narrow, and dorsally oriented: no (0), yes (1).
47. Mandible, cotylae of caudal end very shallow, without caudomedial and lateral walls and separated by rostrocaudally oriented crista intercotylaris: yes (0), no (1).
48. Mandible, marked neurovascular furrow along lateral surfaces: absent (0), present (1).
49. Axis, foramina transversaria: present (0), absent (1).
50. Axis, processus costales: present (0), absent (1).
51. Third cervical vertebra, osseous bridge from processus transversus to processus articularis caudalis: absent (0), present (1).
52. 8th–11th cervical vertebrae: processus carotici ankylozed along midline, forming an osseous canal: no (0), yes (1). In Ciconiidae, the processus carotici are ankylozed in *Mycteria*, nearly so in *Ephippiorhynchus*, and separated in *Leptoptilos*, *Ciconia*, and *Anastomus*.
53. Number of praesacral vertebrae (all vertebrae cranial to synsacrum): 19 (0), 20–22 (1), 23 or more (2). Concerning Pelecanidae, the three caudalmost thoracic vertebrae that are fused with the synsacrum were included in the vertebral count.
54. Several thoracic vertebrae fused to a notarium: no (0), yes (1).
55. Thoracic vertebrae: at least part of series platycoelous or opisthocoelous, i.e., with subround, central articular surfaces that lack the dorsoventral compression and saddle-shaped articular surface seen in heterocoelous vertebrae (0), series completely heterocoelous (1). This character was scored as unknown for Pelecanidae, in which the caudalmost thoracic vertebrae are fused.
56. Caudalmost praesacral vertebrae with deep lateral excavations: no (0), yes (1).
57. Posterior caudal vertebrae with well-developed processus haemales: no (0), yes (1).

58. Pygostyle, corpus perforated at caudoventral end: yes (0), no (1).
59. Furcula, extremitas omalis with strongly developed, laterally protruding facies articularis acrocoracoidea: no (0), yes (1). Because of the fusion of coracoid and furcula, the presence of this articulation facet cannot be established for extant Fregatidae. It is, however, absent in *Limnofregata*, an Eocene stem group representative of frigatebirds (Olson 1977; Smith 2010; Mayr 2011) and was thus coded as absent for Fregatidae.
60. Furcula, apophysis furculae: not as follows (0), abutting with an articular facet on the apex carinae of the sternum (1), fused with the apex carinae of the sternum (Balaenicipitidae and Fregatidae) (2), fused with the apex carinae of the sternum (Pelecanidae) (3). I consider fusion of the furcula with the apex carinae to be an autapomorphy of crown-group Pelecanidae, because this feature is absent in the early Miocene *Pelecanus gracilis* (Milne-Edwards 1867–1871; : pl. 38). Likewise, the presence of a furcula/sternum articulation in *Ardea cinerea* (Ardeidae) is here considered autapomorphic for the species. This character is variable in pelagornithids, with the furcula abutting with a sternal articular facet in Eocene species, but not in the Neogene taxon *Pelagornis* (Mayr *et al.* 2008).
61. Coracoid, extremitas sternalis, processus lateralis greatly elongated: no (0), yes (1).
62. Coracoid, foramen nervi supracoracoidei: present (0), absent (1). Bourdon (2005) erroneously considered a foramen nervi supracoracoidei to be absent in Pelagornithidae (see Mayr & Rubilar-Rogers 2010; Mayr & Smith 2010).
63. Coracoid and scapula fused to form scapulocoracoid: no (0), yes (1).
64. Scapula, acromion very long and markedly cranially projecting: no (0), yes (1). This character was coded as unknown for Rheidae. Apterygidae, and Dromornithidae, in which scapula and coracoid are fused.
65. Sternum, facies visceralis with numerous pneumatic foramina along midline and lateral margins: no (0), yes (1).
66. Humerus, crista deltopectoralis cranially deflected: no (0), yes (1). This character was coded as unknown in Hesperornis, Rheidae, Apterygidae, and Dromornithidae, in which the humerus is greatly reduced.
67. Humerus, pneumatic foramina at bottom of pneumotricipital fossa, or corresponding area in taxa without such fossa: absent (0), present (1).
68. Humerus, fossa musculi brachialis absent or very indistinct: yes (0), no (1).
69. Humerus, well-developed sulcus scapulotricipitalis: absent (0), present (1).
70. Humerus with very large processus supracondylaris dorsalis: no (0), yes (1).
71. Ulna, distinctly exceeding humerus in length: no (0), yes (1). In Phalacrocoracidae and Sulidae, the humerus/ulna length ratio is variable, with the ulna being longer than the humerus in *Sula nebouxii* and *S. leucogaster*, but distinctly shorter in *Morus bassanus*, *M. capensis*, and *Sula dactylatra*.
72. Pelvis, number of vertebrae ankylozed in synsacrum: 9–10 (0), 11–12 (1), 13–14 (2), 15–16 (3), 17–18 (4). In Pelecanidae, the vertebrae that are fused into a notarium were not included in the count.
73. Pelvis, cristae iliacae dorsales largely or completely fused with crista spinosa of synsacrum, thus forming a closed canalis iliosynsacralis: no (0), yes (1).
74. Pelvis, foramen ilioischiadicum caudally closed: no (0), yes (1).
75. Tibiotarsus, cristae cnemiales greatly enlarged and markedly protruding proximally: no (0), yes (1). Although the cristae cnemiales are proximally prominent in some taxa (e.g., Dromornithidae), but not to the degree found in procellariiform birds. The occurrence of long cnemial crests in some Anatidae (e.g., *Oxyura*) is here considered autapomorphic for these taxa.
76. Tibiotarsus, ascending process of astragalus fusing to calcaneum: no (0), yes (1). The presence of this character in the early ontogenetic development is an apomorphy of Neognathae (e.g., Elzanowski 1995).
77. Tibiotarsus, distal end, ossified pons supratendineus: absent (0), present (1).
78. Tibiotarsus, distal end medially inflected, condylus medialis protruding farther distally than condylus lateralis: no (0), yes (1). Note that coding of this character differs from Mayr (2005) concerning Pelecanidae, in which this character is present in, e.g., *Pelecanus onocrotalus* but absent in, e.g., *Pelecanus occidentalis*.
79. Tarsometatarsus: not as follows (0), very short and stocky, ratio distal width: length more than 0.3 (1).
80. Tarsometatarsus, hypotarsus with well-developed cristae/sulci: no (0), yes (1).
81. Tarsometatarsus, hypotarsus, tendon of musculus flexor digitorum longus enclosed in bony canal: no (0), yes (1). Pelagornithidae are variable concerning this character (Mayr & Rubilar-Rogers 2010; Mayr & Smith 2010), and I consider the absence of a closed canal in the Palaeogene species to be plesiomorphic.

82. Tarsometatarsus, hypotarsus, tendon of musculus flexor hallucis longus enclosed in bony canal: no (0), yes (1). Pelagornithidae are variable concerning this character (Mayr & Rubilar-Rogers 2010; Mayr & Smith 2010), and I consider the absence of a closed canal in the Palaeogene species to be plesiomorphic.
83. Tarsometatarsus, canalis interosseus distalis: absent (0), present (1).
84. Tarsometatarsus, trochlea metatarsi II plantarly deflected and distal end reaching much less far distally than distal end of trochlea metatarsi IV: yes (0), no (1). Pelagornithidae are variable concerning this character (Bourdon *et al.* 2010; Mayr & Rubilar-Rogers 2010), and I consider the presence of a deflected trochlea in the Palaeogene taxa to be plesiomorphic.
85. Tarsometatarsus, trochlea metatarsi II distinctly longer than trochlea metatarsi IV, reaching as far distally as trochlea metatarsi III: no (0), yes (1).
86. Hallux: not as follows (0), greatly reduced (proximal phalanx very short, measuring less than half of the length of the proximal phalanx of third toe) or completely absent (1).
87. Three anterior toes connected by web over their entire length: no (0), yes (1). The absence of a webbed feet in Dromornithidae can be inferred from fossil footprints (Murray & Vickers-Rich 2004).
88. Hallux included in webbed foot: no (0), yes (1). This character was coded as unknown for Procellariidae in which the toes are connected by a web but the hallux is greatly reduced.
89. Claw of third toe distinctly pectinate on its medial side: no (0), yes (1). Coding of this character by Mayr (2005) is incorrect for Anhingidae, in which the claw of the third toe is actually pectinate. In Threskiornithidae, a pectinate claw is present in *Plegadis*.
90. Musculus femorotibialis externus, distal head: present (0), absent (1); after McKitrick (1991: character 8).
91. Musculus flexor cruris lateralis, pars accessoria: present (0), absent (1); after McKitrick (1991: character 12).
92. Musculus flexor cruris lateralis, pars pelvica: present (0), absent (1); after McKitrick (1991: character 13).
93. Musculus caudofemoralis, pars caudalis: present (0), absent or poorly developed (1); after McKitrick (1991: character 15).
94. Musculus caudofemoralis, pars pelvica: present (0), absent (1); after McKitrick (1991: character 16).
95. Musculus ambiens: present (0), absent (1); after McKitrick (1991: character 29).
96. Musculus ambiens, extent of origin: limited to tuberculum praeacetabulare (0), extending from tuberculum praeacetabulare to pubis (1), one origin tuberculum praeacetabulare and one from pubis (2); after McKitrick (1991: character 30).
97. Musculus gastrocnemius, fourth head: absent (0), present (1); after McKitrick (1991: character 35).
98. Musculus flexor perforans et perforatus digiti III, vinculum: present: (0), absent (1); after McKitrick (1991: character 44).
99. Musculus flexor perforans et perforatus digiti II, origin from ansa iliofibularis: no (0), yes (41); after McKitrick (1991: character 47).
100. Musculus flexor hallucis longus, tendon to hallux: present (0), weak or absent (1); after McKitrick (1991: character 51).
101. Musculus flexor hallucis longus and musculus flexor digitorum longus, type of arrangement; after McKitrick (1991: character 52).
102. Impressio musculi adductoris mandibulae externus, pars coronoidea in medial position: no (0), yes (1); see Zusi & Livezey (2000). Coding of Pelagornithidae after Bourdon (2005).
103. Large and naked gular pouch: absent (0), present (1).
104. Eggshell: not as follows (0), covered with layer of microglobular material of amorphous calcium carbonate (1).
105. Phallus: present (0), absent (1). Reduction of the phallus in Tinamidae and phasianid Galliformes occurred independently from that of neoavian taxa (Brennan *et al.* 2008).
106. Neck in flight ('underwater flight' in penguins, respectively): stretched out (0), retracted and resting on back (1). In Ciconiidae, the neck is retracted in *Leptoptilos* but stretched out in the other taxa (after del Hoyo *et al.* 1992).
107. Syrinx, musculus tracheolateralis ('intrinsic muscles'): present (0), absent or reduced to a narrow ligament (in Balaenicipitidae) (1); after Beddard (1898).

Appendix 2 Character matrix used for the phylogenetic analysis. Extinct taxa are indicated by a dagger

	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
†*Apsaravis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?
†*Hesperornis*	0	0	?	1	?	0	?	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	?	0	1
†*Ichthyornis*	0	0	?	?	?	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?	0	0	?	01	0
Rheidae	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Apterygidae	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	1
Tinamidae	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galliformes	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0	1	0	1	0
Anhimidae	1	0	1	0	0	01	0	0	0	1	0	1	1	0	1	1	0	1	1	1	0	1	0	1	0
Anatidae	1	0	2	0	0	0	0	0	0	1	0	1	1	0	0	1	0	1	0	1	0	1	0	1	0
Threskiornithidae	1	0	0	1	0	0	0	0	0	1	1	1	1	1	1	0	0	1	0	2	0	0	0	1	0
Phaethontidae	1	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	2	0	0	0	1	1
Fregatidae	1	1	0	1	0	0	0	1	0	0	0	0	1	1	1	1	0	1	0	2	0	0	1	1	0
Phalacrocoracidae	1	1	0	1	0	1	1	1	0	1	0	0	1	1	1	0	1	1	0	2	0	0	1	1	1
Anhingidae	1	0	0	1	0	0	1	1	0	1	0	0	1	1	1	1	1	1	0	2	0	0	1	1	1
Sulidae	1	0	0	1	0	1	1	1	0	1	0	0	1	0	1	1	1	1	0	2	0	0	?	?	1
Pelecanidae	1	1	0	1	0	1	0	1	0	1	1	0	1	1	0	1	0	1	1	2	0	0	1	1	0
Scopidae	1	1	0	1	0	0	0	0	0	1	1	0	1	1	1	1	0	1	1	2	0	0	1	1	0
Balaenicipitidae	1	1	0	1	0	1	0	1	0	1	1	0	1	1	1	1	0	1	1	2	0	0	1	1	0
Ardeidae	1	0	0	0	0	0	0	0	0	01	0	0	1	1	1	0	0	1	0	2	0	0	0	1	0
Ciconiidae	1	0	0	0	0	01	0	0	0	1	1	1	1	1	1	0	0	1	1	2	0	0	01	1	0
Procellariidae	1	1	0	1	1	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	1	0	1	1	0
Diomedeidae	1	1	0	1	1	0	0	0	0	0	0	0	1	1	1	0	0	1	0	2	1	0	1	1	1
†Pelagornithidae	2	0	?	1	?	1	0	1	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	1	0
†Dromornithidae	1	0	?	0	?	1	0	1	?	1	?	1	1	1	0	?	0	1	0	1	0	0	0	1	0
†Sylviornithidae	1	0	?	0	?	1	0	0	0	?	?	1	1	0	0	1	0	1	0	1	0	0	0	1	0

	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
†*Apsaravis*	?	?	?	?	?	0	0	?	?	?	?	?	?	0	?	?	1	?	?	0	?	?	?	?	?
†*Hesperornis*	0	1	?	0	1	0	0	0	0	1	0	0	?	0	1	?	0	?	?	0	0	0	1	?	?
†*Ichthyornis*	?	?	?	?	?	0	0	0	0	1	?	?	?	0	1	0	0	?	?	0	0	0	1	0	?
Rheidae	1	0	0	0	0	0	0	0	0	0	0	0	?	0	0	1	1	1	1	0	0	1	0	0	0
Apterygidae	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0	0	1	1	1	0
Tinamidae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0	0	1	0	0	0
Galliformes	1	2	0	0	0	1	1	0	0	1	0	1	0	0	0	1	1	0	0	1	1	0	0	01	1
Anhimidae	1	1	0	0	0	1	1	0	1	1	0	1	0	0	0	1	1	0	0	1	1	0	0	0	0
Anatidae	1	1	0	0	0	1	1	0	1	1	0	1	0	0	0	1	1	0	0	1	1	0	0	0	0
Threskiornithidae	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0
Phaethontidae	1	1	0	1	0	1	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	1	0	1	1
Fregatidae	1	1	0	1	0	1	0	0	0	0	0	0	1	0	2	1	1	0	0	0	0	1	0	1	1
Phalacrocoracidae	1	1	1	1	1	1	1	0	0	0	1	0	1	0	2	1	1	0	0	0	0	1	0	1	0
Anhingidae	1	1	1	0	0	1	1	0	0	0	1	0	?	0	2	1	1	0	1	0	0	1	0	0	0
Sulidae	1	1	1	1	1	1	1	1	0	0	1	0	1	0	2	1	1	0	1	0	0	1	0	1	0
Pelecanidae	1	1	0	2	0	1	0	0	0	0	0	0	0	0	0	1	1	0	?	0	0	1	0	0	0
Scopidae	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	1	0	0	0	0	1	0	1	1
Balaenicipitidae	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	1
Ardeidae	1	1	0	0	0	1	01	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	1
Ciconiidae	1	0	0	0	0	1	1	1	0	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0
Procellariidae	1	1	0	01	1	1	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	1
Diomedeidae	1	1	0	1	0	1	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	1
†Pelagornithidae	0	1	?	0	0	1	0	0	0	1	0	0	?	0	2	1	0	?	?	0	0	0	1	1	?
†Dromornithidae	1	1	?	0	0	0	1	0	1	1	0	1	?	0	0	1	1	0	0	1	0	0	0	0	0
†Sylviornithidae	1	?	?	0	0	1	1	0	0	1	0	0	?	0	0	1	1	0	0	1	0	0	0	1	1

Appendix 2 (Continued)

	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
†*Apsaravis*	?	?	12	?	0	0	0	0	?	?	0	0	0	1	?	0	0	0	0	0	0	0	0	0	?
†*Hesperornis*	0	0	2	0	1	1	0	0	0	0	0	0	0	0	0	?	0	?	?	0	0	2	0	0	0
†*Ichthyornis*	0	?	12	?	0	1	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	01	0	0	0
Rheidae	0	0	1	0	1	0	0	0	?	?	0	1	1	?	0	?	0	?	?	0	0	?	1	1	0
Apterygidae	1	0	1	0	1	0	0	0	?	?	0	0	1	?	0	?	0	?	?	0	0	23	1	0	0
Tinamidae	0	0	1	1	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	4	0	0	0
Galliformes	1	0	1	1	1	01	0	1	0	0	0	1	0	1	0	1	1	1	1	0	0	3	1	1	0
Anhimidae	1	0	1	0	1	0	1	1	0	0	0	0	0	0	0	1	1	1	1	0	0	4	1	1	0
Anatidae	1	0	1	0	1	0	1	1	0	0	0	1	0	0	0	1	1	1	1	0	0	34	1	1	0
Threskiornithidae	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	1	1	1	1	0	1	3	1	1	0
Phaethontidae	1	0	2	0	1	0	1	1	0	1	0	0	0	0	0	1	1	1	1	0	1	1	0	1	0
Fregatidae	1	0	0	0	0	0	1	0	0	2	0	1	0	0	1	1	1	1	1	0	1	2	0	1	0
Phalacrocoracidae	0	0	2	0	0	0	1	0	1	1	0	1	0	1	0	1	0	1	1	0	1	3	1	1	0
Anhingidae	0	1	2	0	0	0	1	0	1	1	0	1	0	1	0	1	0	1	1	0	0	3	1	1	0
Sulidae	0	1	2	0	0	0	1	1	1	1	0	1	0	1	1	1	1	1	1	0	01	3	1	1	0
Pelecanidae	0	1	2	1	?	0	0	0	1	3	0	0	0	1	1	1	1	1	1	0	1	3	1	1	0
Scopidae	0	0	2	0	1	0	1	1	1	0	0	1	0	0	1	1	1	1	1	0	1	2	1	1	0
Balaenicipitidae	0	1	1	0	1	0	1	1	1	2	0	0	0	0	1	1	1	1	1	0	1	3	1	1	0
Ardeidae	0	1	2	0	1	0	1	1	0	0	0	1	0	0	0	1	1	1	1	0	1	2	1	1	0
Ciconiidae	1	01	1	0	1	0	1	0	0	1	0	01	0	0	1	1	1	1	1	0	1	3	1	1	0
Procellariidae	01	0	1	0	1	1	1	0	0	0	1	0	0	0	01	1	0	1	0	1	0	2	0	1	1
Diomedeidae	1	0	1	0	1	0	1	0	0	0	1	0	0	0	1	1	1	1	0	1	0	2	1	1	1
†Pelagornithidae	1	0	?	0	1	0	?	?	0	01	1	0	0	0	0	0	?	1	0	0	0	?	?	?	0
†Dromornithidae	?	0	2	0	1	0	0	?	?	0	0	1	1	?	0	?	1	0	0	0	0	?	?	1	0
†Sylviornithidae	?	?	?	1	?	0	?	1	?	?	?	0	0	0	?	?	1	1	?	0	?	?	?	?	0

	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	00
†*Apsaravis*	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†*Hesperornis*	0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†*Ichthyornis*	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rheidae	0	0	0	0	0	0	0	1	1	0	1	0	0	0	?	0	0	1	0	0	?	?	?	1	1
Apterygidae	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Tinamidae	0	1	0	0	0	0	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Galliformes	1	1	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Anhimidae	1	1	0	0	1	0	0	1	1	0	0	0	0	0	?	0	0	?	?	0	?	0	?	?	?
Anatidae	1	1	0	0	1	0	0	1	0	0	1	1	0	0	1	1	0	0	0	0	12	0	01	0	01
Threskiornithidae	1	1	0	0	1	0	0	1	1	0	0	0	0	01	0	0	0	1	0	0	0	1	0	0	0
Phaethontidae	1	1	0	0	1	0	0	1	1	0	0	1	1	0	?	0	0	?	1	?	?	?	?	?	?
Fregatidae	1	1	0	1	1	1	0	1	1	1	0	0	1	1	1	1	1	1	1	0	0	0	1	0	0
Phalacrocoracidae	1	1	1	01	1	1	0	1	1	1	0	1	1	1	1	1	0	0	1	0	0	0	?	0	0
Anhingidae	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	01	0	0	0	?	0	0
Sulidae	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	1	0	0	0	0	0	0
Pelecanidae	1	1	01	0	1	1	1	1	1	0	0	1	1	0	?	1	?	?	1	1	?	?	?	0	?
Scopidae	1	1	0	0	1	1	1	1	1	0	0	0	0	1	0	0	0	?	1	1	?	?	?	0	?
Balaenicipitidae	1	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0
Ardeidae	1	1	0	0	1	1	01	1	1	1	0	0	0	1	0	0	0	1	1	1	?	0	1	1	0
Ciconiidae	1	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	1	1	01	0	1	0	0	0
Procellariidae	1	1	0	0	1	01	01	1	0	0	1	1	0	0	0	1	1	0	0	0	1	0	1	0	0
Diomedeidae	1	1	0	0	1	0	0	1	1	0	1	1	0	0	0	1	1	0	0	0	1	0	1	0	1
†Pelagornithidae	1	1	0	0	1	0	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†Dromornithidae	?	1	0	0	0	0	0	1	1	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?
†Sylviornithidae	?	1	0	0	1	1	0	?	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Appendix 2 (Continued)

	01	02	03	04	05	06	07
†*Apsaravis*	?	?	?	?	?	?	?
†*Hesperornis*	?	?	?	?	?	?	?
†*Ichthyornis*	?	?	?	?	?	?	?
Rheidae	4	0	0	0	0	0	0
Apterygidae	2	0	0	0	0	0	0
Tinamidae	1	0	0	0	0	0	0
Galliformes	1	01	0	0	0	0	0
Anhimidae	?	1	0	0	0	0	0
Anatidae	2	1	0	0	0	0	0
Threskiornithidae	1	0	0	0	1	0	0
Phaethontidae	?	0	0	0	1	0	0
Fregatidae	5	0	1	1	1	0	0
Phalacrocoracidae	2	0	1	1	1	0	0
Anhingidae	2	0	1	1	1	0	0
Sulidae	1	0	1	1	1	0	0
Pelecanidae	?	0	1	1	1	1	1
Scopidae	?	0	0	1	1	0	0
Balaenicipitidae	1	0	0	1	1	1	1
Ardeidae	1	0	0	01	1	1	0
Ciconiidae	1	0	0	0	1	01	1
Procellariidae	4	0	0	0	1	0	0
Diomedeidae	4	0	0	0	1	0	0
†Pelagornithidae	?	1	?	?	?	?	?
†Dromornithidae	?	?	?	0	?	?	?
†Sylviornithidae	?	?	?	?	?	?	?