Cretaceous birds and avian phylogeny

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Cretaceous birds and avian phylogeny

ANDRZEJ ELZANOWSKI

Abstract

This paper contains a phylogenetic appraisal of the skeletal evidence for the relationships between the major lineages of birds. The Ornithurae, Carinatae, and Neornithes are redefined cladistically. The Enantiornithes are probably monophyletic on the evidence of four likely synapomorphies. An enantiornithine specimen from the Rio Colorado Formation, Argentina, reveals a temporal pattern of ossification very similar to that in *Gobipteryx*, demonstrating that superprecocial flight was characteristic of Enantiornithes. Additional preparation of one of the *Gobipteryx* skulls revealed the primitive (reptilian) choanal fenestra in front of what was previously identified as the only choanal fenestra and what now turns out to represent the subsidiary palatal fenestra of the theropods. This fenestra accommodates the choanae in all known neornithines. The paleognaths are probably a sister group of all extant neognaths, with *Struthio* as the first extant branch. The one-piece pterygoid may be another synapomorphy of the paleognaths. Several braincase characters found in most of the paleognaths and neognaths but absent in *Phaethon*, *Fregata*, Procellariiformes, *Hesperornis*, *Enaliornis* and all earlier birds seem to have evolved more than once in the neornithine birds.

Key words: Cretaceous; Aves; Ornithurae; Carinatae; Enantiornithes; Palaeognathae; Neognathae; *Gobipteryx; Hesperornis; Struthio;* phylogeny; skull.

Kurzfassung

Die Arbeit enthält eine phylogenetische Bewertung der osteologischen Belege für die Verwandtschaft zwischen den Hauptentwicklungslinien der Vögel. Die Ornithurae, Carinatae und Neornithes werden kladistisch neu bestimmt. Vier wahrscheinliche Synapomorphien sprechen für die Monophylie der Enantiornithes. Ein Vertreter dieser Gruppe aus der Rio Colorado Formation, Argentinien, zeigt ein ähnliches Zeitmuster der Ossifikation wie *Gobipteryx*, woraus hervorgeht, daß ein superprecociales Flugvermögen für die Enantiornithes kennzeichnend war. Genauere Präparation eines der *Gobipteryx*-Schädel brachte primitive (reptilienhafte) innere Nasenöffnungen zutage; sie liegen vor einer Öffnung, die zuvor als Choana angesehen wurde, sich nun aber als das subsidiäre Gaumenfenster der Theropoda erweist. Dieses Fenster faßt die Choanae bei allen bekannten Neornithes. Die Paläognathen sind wahrscheinlich die Schwestergruppe aller rezenten Neognathen, mit *Struthio* als erstem Seitenast. Das ungeteilte Pterygoid kann eine weitere Synapomorphie der Paläognathen sein. Verschiedene Strukturen des Hirnschädels, die bei *Phaethon*, *Fregata*, Procellariiformes, *Hesperornis*, *Enaliornis* und allen früheren Vögeln fehlen, scheinen sich mehrfach bei den Neornithes entwickelt zu haben.

Schlagwörter: Kreide; Aves; Ornithurae; Carinatae; Enantiornithes; Palaeognathae; Neognathae; *Gobipteryx; Hesperornis; Struthio;* Phylogenie; Schädel.

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Introduction

The primary concern of this paper is with the skeletal evidence for the relationships among the major avian lineages, with an emphasis on the enantiornithine and neornithine birds. Some character definitions draw on those by CRACRAFT (1986) and GAUTHIER (1986) but the assignments of synapomorphy levels are mine and frequently differ from theirs.

This paper is not intended as a review of the Cretaceous record of birds. Consequently, many fragmentary avian fossils of minor phylogenetic significance are left out of consideration.

Ornithurae

The Ornithurae include Sinornis (SERENO & RAO, 1992) and the Carinatae. The Ornithurae are more advanced than Archaeopteryx (WELLNHOFER, 1992) in having (O1) the pygostyle; (O2) furcula with hypocleidium; (O3) scapula and coracoid unfused in the adults; (O4) scapula long, narrow, and tapering distally; (O5) strut-like coracoid; (O6) ulna approximately twice as thick as radius; (O7) ischium not forked distally; (O8) fibula greatly reduced in length; (O9) lack of the fifth metatarsal; and (O10) eight or fewer free caudal vertebrae.

Due to only a preliminary description of Sinornis, the following characters, as well as the remaining nine leg (free limb) skeleton characters listed by GAUTHIER (1986: p. 13-14), cannot be at present reliably assigned to either Ornithurae or Carinatae: body of premaxillae fused; nasal process of the premaxilla approaches frontal; mandibular symphysis; dentary forked posteriorly; lack of hyposphenes and hypantra; more than 5 synsacral vertebrae; prominent ventral (internal) tuberosity separated from humeral head by capital groove; dorsal (external) condyle of the ulna semilunate; and preacetabular portions of ilia closely appressed in the midline and in contact with at least some sacral neural spines.

Carinatae

The carinates are more advanced than Sinornis in having (C1) sternal keel (Carina sterni), (C2) metacarpals and carpals fused into the carpometacarpus, (C3) a prominent antitrochanter above the acetabulum, (C4) pubis without the distal foot-shaped expansion, and (C5) in lacking gastralia. The carinates include Cathayornis (ZHOU et al. 1992), Concornis (SANZ & BUSCALIONI, 1992), Enantiornithes (ELZANOWSKI, 1977, 1981; WALKER, 1981) and Neornithes. Cathayornis, Concornis, and

many Neornithes have two pairs of sternal notches, whose presence may be another synapomorphy of the carinates. The Enantiornithes and Neornithes alone are known to share (C6) fused pelvis, (C7) at least nine synsacral vertebrae, and (C8) coracoid with the acrocoracoid process.

In addition, the premaxilla of the carinates has palatal processes, i.e., the caudal extensions of the palatal shelves which, in contrast with the shelves themselves, are separated from the jaw margin. These processes seem to be present in Gobipteryx (Fig. 2A) and are definitely so in all neornithines including Hesperornis (ELZANOWSKI, 1991: fig. 3). The palatal processes of the premaxilla are very extensive in the non-struthioniform paleognaths and smaller in Struthio (HOFER, 1949: fig. 15A; WEBB, 1957: fig. 5) and the neognaths, e.g., in the galliforms (HOFER, 1949: fig. 3B; Jollie, 1957: fig. 3), Otididae, Ciconiidae (HOFER, 1949), and passerines (BOCK, 1960). In Struthio and the neognaths these processes fuse with the maxilla and the maxillary process of the palatine, which makes their presence difficult to ascertain in adults. The phylogenetic status of this character cannot be determined at present as the palatal aspect of the premaxilla remains unknown in both Archaeopteryx and Sinornis.

Enantiornithes

There can hardly be a better testimony to the rapid progress of avian paleontology than the story of Gobipteryx. After being denied the avian status (BRODKORB, 1976), paradoxically in a paper where another enantiornithine bird (Alexornis) was misidentified, Gobipteryx is now known to represent the Enantiornithes, a well-defined group of Mesozoic birds (MARTIN, 1983) with a world-wide distribution (MOLNAR, 1986). A striking feature of the Enantiornithes is the advanced structure of their pectoral skeleton combined with the apparent primitivism of their unfused metacarpals (BRETT-SURMAN & PAUL, 1985), the latter showing prodigious diversity of locomotory adaptation. At least the first three of the following characters seem unique and thus possibly apomorphic for Enantiornithes:

E1. The hind major metacarpal of at least the same strength (thickness and width) as the front major metacarpal. Among living birds, the hind major metacarpal was found to equal or even exceed in size the front major metacarpal only at the cartilaginous stage in a few embryos of Apteryx (PARKER, 1891: 95-96, fig. 17/262), which may be nothing more than a case of adventitious variation in the development of a vestigial organ.

E2. External condyle of the humerus transversely orien#ted.

E3. Medial condyle of the tibiotarsus markedly broader than the lateral condyle, which is a configuration distinctly different from that found in the theropods or any other bird (MOLNAR, 1986).

E4. Metatarsal IV thinner (anteroposteriorly) than metatarsals II and III (CHIAPPE, 1992).

?E5. Possibly holapomorphic for Enantiornithes is the lack of teeth, if *Gobipteryx* is representative for the entire group in this respect as well. Teeth persisted in the avian phylogeny all the way to the Neornithes.

Insofar as the primitive ornithuran coracoid of *Sinornis* and Enantiornithes combines the modern slender, strut-like form with the lack of the procoracoid process, it seems to be a morphological intermediate between the coracoids of *Archaeopteryx* and Neornithes. Similarly, the square, truncated profile of the humeral head may be a morphological intermediate between *Archaeopteryx* and Neornithes. This shape results from the lack of embayments defining the articular head, the dorsal (external) tuberosity, and the deltopectoral crest. The dorsal tuberosity is absent in *Archaeopteryx* and more or less pronounced in the Neornithes.

The large, flat, laterally projecting deltopectoral crest of Enantiornithes (ELZANOWSKI, 1981: 167; MARTIN, 1983: 310) may be a primitive carinate character as well, as this form has apparently been inherited by *Ichthyornis* and *Ambiortus* which are close to the ancestry of Neornithes. A deltopectoral crest not unlike that of Enantiornithes is present in *Wyleyia*, which may represent a bird (HARRISON, 1991), a theropod (NORMAN, 1990) or an intermediate maniraptoran. However, the deltopectoral crest is more or less deflected on the dorsal side in all extant Neornithes, *Archaeopteryx*, and most of the theropods.

The fragmentary skulls of *Gobipteryx* (ELZANOWSKI, 1977) are so far the only source of information on the cranial anatomy of Enantiornithes. My reexamination of the referred *Gobipteryx* skull (ZPAL MgR-I/32) after its additional preparation revealed a complete separation of the nasal opening from the maxillary sinus (Fig. 1A). The dividing bar or lamina probably forms part of the maxilla although no dividing suture could be positively identified. Contrary to the previous reconstruction, the culmen is very thin above the nasal opening.

Another feature revealed by the additional preparation of the same specimen is the presence of a large primitive (reptilian) choanal fenestra which is only caudally bordered by the palatines (Fig. 1B); rostrally and rostrolaterally it is probably enclosed by the palatal processes of the premaxilla, if one of them was correctly identified in the left nasal opening (Fig. 1A). Farther caudally, between the palatine and

vomeral crura that embrace the pterygoids, there is another, narrow fenestra, the only one identified previously. This is apparently the subsidiary palatal fenestra of the theropods (see OSTROM, 1990) which has been considered to be a synapomorphy of the theropod clade (Coelurosauria) that gave rise to birds (GAUTHIER, 1986). Although this is probably incorrect since the fenestra is known to occur outside this clade (e.g., in some carnosaurs), it is clearly a distinctive theropod character that was present in the avian ancestors as confirmed by its presence in *Archaeornithoides* (ELZANOWSKI & WELLNHOFER, 1992).
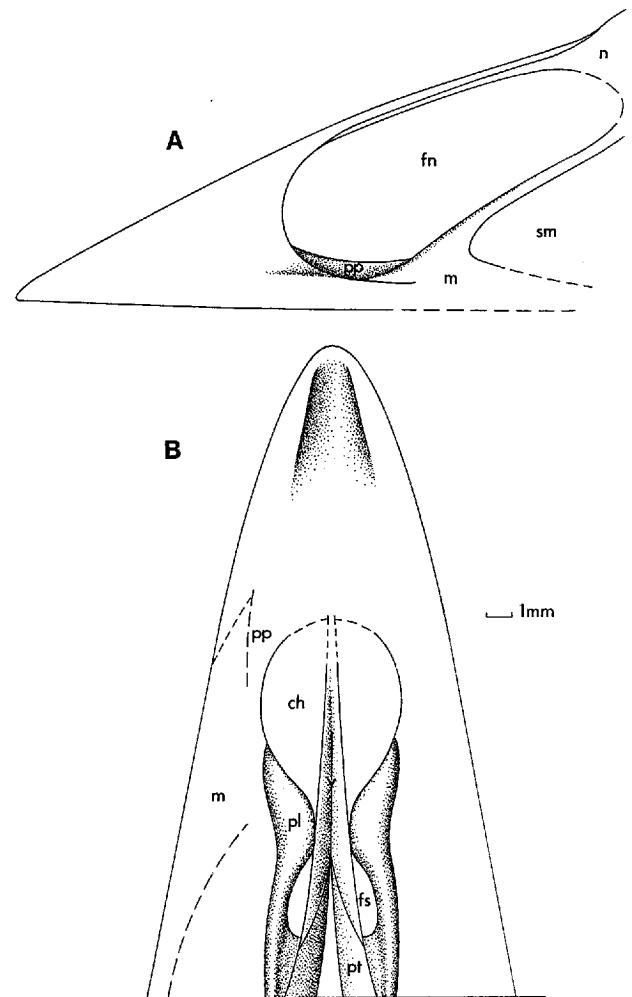

Fig. 1: *Gobipteryx minuta*, revised reconstructions of the upper jaw in lateral (A) and ventral (B) views, based primarily on the referred skull ZPAL MgR-I/32. Abbreviations: ch, primitive (reptilian) choanal fenestra; fn, nasal opening; fs, subsidiary palatal fenestra; m, maxilla; n, nasal; pl, palatine; pp, palatal process of the premaxilla; pt, pterygoid; sm, maxillary sinus; v, vomer.

The location of choanae in *Gobipteryx* is uncertain. The subsidiary palatal fenestrae of *Gobipteryx* are small and seem to open dorsally to the antorbital sinus (which, of course, does not necessarily mean that they opened to anything in vivo). Whatever the position of the choanae in *Gobipteryx*, the fenestration of its palate suggests that the choanal fenestra of Neornithes either corresponds to or incorporates the subsidiary palatal fenestra. The choanae of Neornithes extend far caudally where they are laterally enclosed by the palatines rather than the maxillae.

Another ancestral feature of the enantiornithine palate is the hooked ectopterygoid, hitherto known only in the theropods. A small, previously unidentified bone, which has been found in association with the left pterygoid in the holotype skull of *Gobipteryx* (ELZANOWSKI, 1977: fig.1/2 "LPT(?)" and fig.1/3), bears a striking resemblance to the lateral hook of the theropod ectopterygoid (Fig. 2), which has been identified in the Eichstätt specimen of *Archaeopteryx* (WELLNHOFER, 1974).

Fig. 2: *Gobipteryx minuta*, holotype skull ZPAL MgR-I/12, the lateral (jugal) process of the left ectopterygoid in dorsal view.

A comparison of the tetraradiate theropod palatine, as found in the dromaeosaurids and Archaeornithoides (ELZANOWSKI & WELLNHOFER, 1992), with that of *Gobipteryx* suggests that two processes, vomeral and jugal, were lost in birds, that the maxillary process expanded rostrad (to become the premaxillary process in the neognaths), and that the pterygoid process developed (at least in the neognaths) a rostral spine, which is probably not homologous to the vomeral process of theropods.

The coracoid (# 56/11915) described from the locality Dzharakuduk, Taikarshin Formation (Coniacian), Usbekistan (NESOV & BORKIN, 1983: fig. 4) is essentially identical with that of *Gobipteryx* (Fig. 3). The complete bone was some 25 mm long, indicating a bird of the size of a lapwing (*Vanellus vanellus*), which perfectly agrees with the size estimate of *Gobipteryx* based on the adult skulls (ELZANOWSKI, 1977).

An enantiornithine tibiotarsus (# 3472) has been subsequently described from the same locality (Dzharakuduk) under the name of *Sazavis prisca* (NESOV & YARKOV, 1989: fig. 1/2). This bone is some 5 mm wide at the distal end, which leads to approximately the same bird size estimate as does the coracoid length. Most probably the coracoid # 56/11915 and the tibiotarsus # 3472 from Dzharakuduk belong to the same representative of the family Gobipterygidae, if not of the genus *Gobipteryx*.
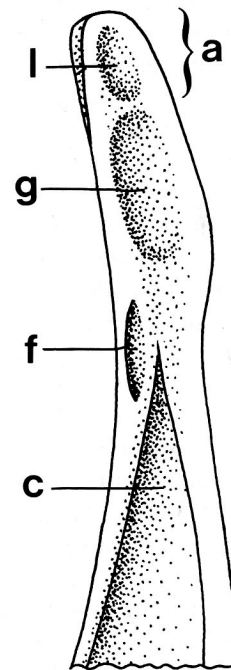

Fig. 3: *Gobipteryx minuta*, a semidiagrammatic reconstruction of the right coracoid in the referred embryonic skeleton ZPAL MgR-I/34, as originally intended for ELZANOWSKI (1981). Abbreviations: a, acrocoracoid process; c, dorsal concavity (= posterior coracoidal concavity in BOCK & McEVEY, 1969); f, supracoracoid foramen; g, glenoid ?and scapular facet; l, impression of the acrocoracohumeral ligament.

The enantiornithine specimen MUCPv-142 from the Rio Colorado Formation, Argentina (CHIAPPE, 1991: fig. 3A; CHIAPPE, 1992: fig. 2) is strikingly similar, in both the morphology and preservation, to the specimen ZPAL MgR-I/33, that is, to the less ossified of the two major embryonic skeletons of *Gobipteryx* (ELZANOWSKI, 1981: fig. 2 and pl. 42). The humerus/forearm/carpometacarpus ratios are essentially identical in the two specimens: 1/1.15/0.54 in ZPAL MgR-I/33 and 1/1.12/0.52 in MUCPv-142. In both specimens, the articular ends of limb bones are selectively missing and the pectoral skeleton with

dorsal vertebrae are distinctly better preserved than the remaining skeleton, the pelvis being absent altogether. This demonstrates that MUCPv-142 is a very young specimen. It seems to be referable to the order Gobipterygiformes. CHIAPPE (1992) assigned it to the family Avisauridae which may prove identical with the Gobipterygidae since the tarsometatarsus of *Gobipteryx* remains unknown.

The striking difference in the ossification between the pectoral and pelvic limb indicates the superprecocial development of flight, that is, the ability to fly immediately after hatching, as first proposed for *Gobipteryx* (ELZANOWSKI, 1981). Building in ovo a ready for use flight apparatus in addition to, rather than instead of, the ambulatory one, amounts to high energy costs of development, comparable to those incurred by the living megapodes (Megapodiidae). This in turn favors male incubation that has been proposed to be primitive for birds (ELZANOWSKI, 1985; VAN RHIJN, 1990, 1991) and may have persisted in the paleognaths.

The late embryonic skeletons of *Gobipteryx* and the Rio Colorado specimen demonstrate that the early carinates hatched with the pelvis and leg bones strongly retarded by comparison to the shoulder girdle and wing bones. This was probably due to the energetic trade-off between the rapid development of the two locomotory systems, which is responsible for the staggering, in a reverse order, of rapid growth phases of the leg and wing in today's birds. It seems, therefore, likely that the superprecocial development of powered flight was accompanied by the slowing down of the development of the leg and thus its retardation at hatching. Since legs of primitive birds certainly had to be used from the first minute after hatching, this was conducive to paedomorphosis and adaptive modifications of the immature leg. The stunning diversity of the hindlimb adaptations in Enantiornithes, involving shifts in the mutual positions of metatarsals, suggests an adaptive diversification of the juvenile leg skeleton. If primitive-looking pelvic limb characters of the early carinates appear at the immature stages of all birds, they are as likely to be paedomorphic as to be primitive.

Iberomesornis from the Lower Cretaceous of Las Hoyas, Spain, has been portrayed as an intermediate form between *Archaeopteryx* and all more advanced birds because of the unfused pelvis and tibiotarsus, and the count of 11 dorsal vertebrae (SANZ & BONAPARTE, 1992). In fact, *Iberomesornis* may still be closely related to the Enantiornithes. In addition to the similarity of the distal end of the humerus, noted by SANZ & BONAPARTE (1992), *Iberomesornis* has high neural spines of the dorsal vertebrae as in *Gobipteryx*, and the forearm bones longer than the humerus as in all Enantiornithes. Such intramembral proportions seem to

be derived among the ornithurans as the humerus and forearm are of equal length in both *Sinornis* and *Cathayornis*. The number of dorsals is not known in Enantiornithes but is known to reach 10 in some neognaths and both the number of presacral vertebrae in birds and their division into the cervicals and dorsals are highly variable. Lastly, the late fusion of the pelvis and leg bones or the lack of it in the early carinates may have been consequent upon superprecocial development of the flight apparatus, which calls into doubt the phylogenetic significance of this character alone.

Neornithes

The monophyly of Neornithes is demonstrable with the following synapomorphies uniting *Hesperornis* (MARSH, 1880, ELZANOWSKI, 1991), the paleognaths (PYCRAFT, 1900; BOCK, 1963; MÜLLER 1961a; MÜLLER, 1963) whose postcranial anatomy is best represented by the lithornithids (HOUDE & HAUBOLD, 1987; HOUDE, 1988; PETERS, 1988), and the extant neognaths (PYCRAFT, 1901; BELLAIRS & JENKIN, 1960; BOCK & MCEVEY, 1969):

N1. Coracoid with the procoracoid process and a distinct scapular socket.

N2. Humerus with the articular head (caput humeri) separated from the deltopectoral crest and dorsal tuberosity.

N3. Humerus with lateral extension of ventral tuberosity (crus dorsale tuberculi medialis).

N4. Ulna with quill knobs indicating the attachment of secondaries to the bone. The quill knobs are present in most although not all flying neornithines including *Ichthyornis*, but consistently absent in pre-neornithine birds including *Archaeopteryx*, *Sinornis*, and *Iberomesornis*.

N5. Ilium so lengthened as to overlap at least the most caudal ribs.

N6. Tarsometatarsal ossifications, including distal tarsals and metatarsals, completely fused to each other.

N7. Tarsometatarsus with hypotarsus.

N8. Ectopterygoid absent.

N9. Choanal fenestra (the former subsidiary palatal fenestra) is open rostrally. Only in *Apteryx* is this fenestra rostrally closed by the palatines that converge onto the vomer, which makes it strikingly similar to the subsidiary palatal fenestra of *Gobipteryx*. This is probably a case of homoplasy that may be due to the transverse compacting of the kiwi palate.

Only tentatively assigned to the neornithine level are four following cranial characters (?N10-?N13), the state of which cannot be ascertained in the Enantiornithes:

?N10. Vomer does not articulate with the premaxilla in the neognaths and *Struthio*, which is in contrast with the theropods where the vomer articulates with the body of the premaxilla (or its palatal shelf) far rostrally. Even if originally present in *Hesperornis*, the vomer probably did not articulate with the premaxilla as this is strongly concave, making an articulation with a median palatal element difficult to imagine. In the non-struthioniform paleognaths the vomer contacts the long palatal processes of the premaxilla which are probably apomorphic and thus this contact is probably derived as well (see PG'1).

?N11. Maxilla has two caudomedial processes, the medial palatine process and the lateral palatine process, both well pronounced in *Hesperornis* (ELZANOWSKI, 1991: fig. 3). The medial palatine process, also known as the maxillopalatine process (MÜLLER, 1963), separates the body of the maxilla from the vomer in the neognaths and *Struthio*. It is absent or vestigial in the non-struthioniform paleognaths (see PG'3). The lateral palatine process carries the maxillary process of the palatine. This process is small or vestigial in the neognaths, big in the non-struthioniform paleognaths (see PG'4), and intermediate in *Struthio*. Only a single caudomedial process of the maxilla seems to be present in *Archaeopteryx*.

?N12. The pterygoid is divided into two parts, the hemipterygoid (mesopterygoid, anteropterygoid) and the main caudal part, called posteropterygoid (JOLLIE, 1957). Among the neognaths the hemipterygoid is lacking in the Anseriformes, Galliformes, Falconidae and Alcidae (SUSCHKIN, 1899; PYCRAFT, 1901; JOLLIE, 1977: 228=128). Based on a slight differentiation of texture, JOLLIE (1957) interpreted the caudal part of the palatine in *Gallus* as a vestige of the hemipterygoid although ERDMANN (1940) did not find any indication of it. The hemipterygoid apparently fails to separate from the caudal part in the piciforms including Picidae (PARKER, 1875; KRASSOWSKY, 1936; pers. obs.), *Notharchus macrorhynchus*, and *Megalaima virens* (PYCRAFT, 1901), although in *Megalaima virens* some discontinuity between the hemipterygoid and the caudal part seems to be present (DE BEER, 1956: fig. 9/2). More importantly, a separate hemipterygoid has been figured in *Megalaima asiatica* (PARKER, 1876: fig.23/5) and reported to be present at least in some specimens of *Megalaima haemacephala, Lybius vieilloti, Pogoniulus atroflavus* and *Semnornis ramphastinus* (MANUCCI & SIMONETTA, 1979; SIMONETTA, pers. comm.). No trace of fragmentation of the pterygoid has ever been observed in any of the paleognaths and this despite detailed studies of the skull ossification in *Apteryx, Dromaius, Rhea*, and *Struthio* (PARKER, 1866; PARKER, 1891; WEBB, 1957; MÜLLER, 1963; LANG, 1956). In contrast with those neognaths that lack the

hemipterygoid, the pterygoid of non-struthioniform paleognaths extends to the vomer, as in *Gobipteryx*, theropods and ancestral tetrapods, which prima facie suggests that the paleognathous pterygoid represents the entire undivided reptilian pterygoid. This conflicts, however, with the distribution of other characters and other evidence, which suggests that the pterygoid of paleognaths may correspond to the posteropterygoid alone (see below).

?N13. The otic process of the quadrate has two heads (or at least their traces). Stratigraphically, the oldest record of the two-headed quadrate comes from *Enaliornis* which has an unquestionable prootic cotyla for the medial head (ELZANOWSKI & GALTON, 1991). The two heads are bulky and leave little if any space for the dorsal pneumatic recess in *Ichthyornis* (MARSH, 1880: fig. 28, WITMER 1990: figs 5A, 5C), *Hesperornis* (MARSH, 1880: fig. II/6), and *Fregata* (WITMER, 1990: fig. 4). In most of the other neognaths, the prootic and squamosal heads are widely separated by an intrusion of the dorsal pneumatic recess (see, e.g., LOWE, 1926: fig. II/3-6). In *Phaethon*, the condyles stand alone but are not separated by the extension of the tympanic recess (pers. obs). The quadrate heads are reduced but still separated by a more or less distinct intercapitular incisure in the anseriforms, gastornithiforms (ANDORS, 1992: table 2) and phasianids but not other galliforms (HOFER, 1945). Although the paleognaths are known to have a single temporal head, some of them, including *Rhea* (LOWE, 1926) and two genera of tinamous (*Saiff*, 1988), show a shallow but distinct division of the otic process, which is better accounted for by an unequal suppression of the formerly bipartite head than by the convergent deviation from the primitive lack of any division.

In addition to the characters known to be present in all or most of the neornithines including *Hesperornis*, the paleognaths, and the neognaths, the two latter taxa alone share a number of characters that show opposite states in at least one of the primitive, toothed or probably toothed neornithines:

N'1. Scapula with the glenoid facet facing dorsally (latero-cranio-dorsally) rather than being nearly perpendicular to the scapular blade as in *Ambiortus* (pers. obs.).

N'2. Carpometacarpus with a pronounced extensor process, which seems to be poorly developed or absent in *Ambiortus*.

N'3. Tarsometatarsus with the distal foramen completely closed. The tarsals III and IV are unfused distally to this foramen in *Ichthyornis* (MARSH, 1880: figs. 33/9 and 33/11), *Baptornis* (MARSH, 1880, figs. 37 and 39; MARTIN & TATE, 1976: fig.16), *Enaliornis* (SEELEY, 1876: fig. 27/24) and *Gansus* (HOU & LIU, 1984: fig. 3).

N'4. Triradiate mandibular articulation of the quadrate, which is present in most but not all of the neornithines. Primitive birds inherited from the theropods the quadrate with two transversely aligned mandibular condyles, medial and lateral, without any prominent rostrocaudal projections. Such quadrate is known in *Gobipteryx* (ELZANOWSKI, 1977), *Baptornis* (MARTIN & TATE, 1976: fig. 1) and *Ichthyornis* (MARSH, 1880: text-fig. 28, WITMER, 1990: figs 5A, 5C), and was probably present in *Archaeopteryx*. In the majority of neornithines the mandibular articulation of the quadrate is distinctly tricondylar due to the presence of the caudal condyle. In some of them it is essentially bicondylar but triradiate owing to a caudal extension of the lateral condyle as in *Phaethon* (pers. obs.), Pteroclidae (LOWE, 1926: fig. II/6), *Apteryx*, lithornithids (HOUDE, 1988: fig. 8), and tinamous (LOWE, 1926: fig. II/2; ELZANOWSKI, 1987: fig. 3). Among the extant neornithines, only the pigeons have two plain condyles without any caudal extension (LOWE, 1926: fig. II/5).

N'5. Humerus with the deltopectoral crest deflected dorsally rather than flat and projecting laterally as in *Ambiortus* and *Ichthyornis*.

N'6. Scapula with the acromion less prominent by comparison to that of *Ambiortus*, *Apatornis* and Enantiornithes. Contrary to KUROCHKIN (1985) and HOUDE (1988), I do not find the acromion of *Ambiortus* similar to that of lithornithids where it curves laterad, conferring a distinctive convex, medial profile to the rostral end of the bone. This is the situation in the scapula referred by MARSH (1880: figs. 29/9, 29/11) to *Ichthyornis victor*. The acromion of *Ambiortus* and that referred to *Apatornis gently* turns mediad in continuation of the curvature of the scapular blade, as in most other birds.

N'7. Tibiotarsus with the bony supratendinal bridge, which is absent in *Ichthyornis*, *Apatornis*, and *Hesperornis*; most of the paleognaths except for kiwi, moa, and tinamous; and in a few neognaths including parrots, some owls (Tytonidae) and some grebes.

N'8. Absence of teeth. The teeth of *Ichthyornis*, except for the most caudal ones, are separated by the interdental septa which is a mode of tooth implantation more primitive than in *Hesperornis*.

N'9. Premaxilla is fused with the maxilla in the neognaths and *Struthio* but only syndesmotically connected to the maxilla in the non-struthioniform paleognaths. Since the lack of fusion is obviously primitive for birds and the bones are not fused in *Hesperornis*, the condition in the non-struthioniform paleognaths is either primitive or reversed.

N'10. Pterygoids of neognaths and paleognaths (with a partial exception of *Apteryx*) converge onto the parasphenoid rostrum far caudally, at the level of the pterygopalatine articulation, whereas in the theropods,

Gobipteryx and *Hesperornis* the pterygoids converge gradually to meet one another and/or the vomer far rostrally, in front of the parasphenoid rostrum. Even if the hemipterygoids of *Hesperornis* were slightly more convergent than represented in the reconstruction (ELZANOWSKI, 1991), any abrupt convergence comparable to that in modern neornithines is geometrically impossible because of their very length.

The prominent pterygoid processes of the sphenoid could be another synapomorphy of advanced neornithines, possibly correlated with the caudal convergence of their pterygoids. Alternatively, their lack may be an autapomorphy of *Hesperornis*. These processes are prominent in the theropods, paleognaths and many neognaths, suggesting that this is a plesiomorphic feature of the neornithines and probably all birds. The homology of pterygoid processes in reptiles and birds except for the anseriforms and galliforms is supported by their development in similar positions (WEBER, 1990). However, a developmental evidence alone does not permit a distinction between homology and homoiology (that is, nonhomologous similarity of homologous structures) and the morphological gaps between the relevant fossils are big enough to warrant skepticism.

Two details of the avian braincase, the dorsal rim of the supraoccipital and the exit of the ninth and tenth cranial nerves, show pronounced, taxonomically consistent differences. Unfortunately, their polarities cannot be at present determined with any certainty. The supraoccipital is split dorsally below the parietal in all juvenile neognaths but only in the part underlapping the parietal in *Enaliornis* (ELZANOWSKI & GALTON, 1991). The dorsal fissure reflects paired origins of the tectum synoticum from two procartilaginous strips in the neognaths (TOERIEN, 1971). In contrast, the tectum is unpaired and the supraoccipital is correspondingly undivided at any stage in all paleognaths including the ostrich and tinamous (MÜLLER, 1963; WEBB, 1957; pers. obs.). The supraoccipital is not reported to be of paired origins in any of the extant major groups of reptiles (BELLAIRS & KAMAL, 1981), although in the crocodiles the epiotic cartilages, that fuse with the tectum, meet in the midline under the parietal (PARKER, 1885: fig. 70/VI). A similar morphology could possibly account for the situation observed in *Enaliornis*. However, there is no indication of the epiotic elements meeting in the midline in the extant birds (JOLLIE, 1957).

The glossopharyngeus nerve leaves the skull separately from the vagus nerve through a separate foramen in most neognaths (WEBER, 1990) including *Fregata* and many Procellariiformes, some of which have a marginal notch for this nerve (SAIFF, 1974). In *Phaethon* and Diomedeidae this nerve issues out of the skull through the recessus scalae tympani without an

external opening of its own (SAIFF, 1974; SAIFF, 1978). There is no separate glossopharyngeal foramen in *Enaliornis* (ELZANOWSKI & GALTON, 1991) and *Hesperornis* (ELZANOWSKI, 1991) and their vagus foramen is in a marginal position, which, together with the braincase similarities to *Phaethon* and Procellariiformes, suggests that the separation of the two nerve exits dates back to the origins of Neornithes or earlier. The glossopharyngeus leaves the skull by the same foramen as the vagus in the paleognaths (MÜLLER, 1961a; SAIFF, 1988) although in some specimens of the ostrich there is a pair of foramina on one or both sides of the skull (WEBB, 1957). This is reminiscent of the crocodiles where the two nerves exit by two separate openings located close to each other in the Foramen jugulare externum (MÜLLER, 1967: fig. 27). The theropod braincases are customarily represented with a joint exit for the IX and X nerves, but this is a mere extrapolation from the crocodiles. Not even a guess at the primitive avian condition is possible on the present evidence.

Primitive neornithines

The oldest clearly identifiable fossil neornithine bird is *Ambiortus* from the end of Early Cretaceous (KUROCHKIN, 1985). Two generic names, *Ichthyornis* and *Apatornis*, have been applied to a collection of Late Cretaceous bones containing at least one genus of primitive, toothed neornithines. MARSH's (1880) presentation of this material may reach the distinction of being the most confusing chapter of avian paleontology and hardly any other material of fossil birds is in greater need of revision. Despite dramatic differences in the structure of scapulae, coracoids, carpometacarpi and synsacra, that suggest members of two distinct orders (HOWARD, 1955), MARSH viewed all birds represented in his *Ichthyornis-Apatornis* collection as closely related members of a single family Ichthyornithidae in his "Odontotormae" and, consequently, used scapulae, coracoids and tibiotarsus assigned to *Apatornis* in the skeletal mount of *Ichthyornis victor* (MARSH, 1880: pl. 34). On this assumption, the presence of one element was considered to be a default, whereby only the presence of two different elements had to be accounted for. This assumption makes MARSH's assignments of the referred material unreliable unless there is an evident similarity to the type specimen of *Ichthyornis dispar*. This is the type species of the genus and, fortunately, MARSH deliberately kept its description clean. The holotype of I. dispar includes braincase, lower jaw, a few vertebrae, synsacrum, a fragment of sternum, ventral fragment of the coracoid, complete humerus, complete ulna, a proximal fragment of the radius, a

distal fragment of the carpometacarpus, femur and tibiotarsus. The species *Apatornis celer* is based on a fragment of the synsacrum YPM 1451, but this species is known primarily from the referred specimen YPM 1734 that does not contain either the synsacrum or pelvis. Neither the association with the type synsacrum nor the differences from the Ichthyornis, as defined by reference to the type specimen of *Ichthyornis* dispar, are clear. MARSH's material has never been revised. The subsequently published fragmentary finds of Ichthyornis are confined to the wing bones and isolated vertebrae (NESOV, 1990; PARRIS & ECHOLS 1992; see OLSON, 1985, for a review of older record).

The name *Ichthyornis* applies to a primitive, toothed neornithine. The name *Apatornis* may apply to a more advanced neornithine possibly related to *Telmabates* (HOWARD, 1955). MARSH's assignments of those bones that are not well represented in the type specimen of *Ichthyornis* dispar, such as the scapulae, are likely to be wrong; they are used here as temporary labels pending the overdue revision.

The neornithine relationships of *Ambiortus* and *Ichthyornis* are demonstrated by the presence of the procoracoid process and scapular socket of the coracoid, the articular head of the humerus set off from the external tuberosity and deltopectoral crest, and the presence of quill knobs on the ulna, at least on the bone referred to *Ichthyornis validus* (MARSH, 1880: 153 and pl. 30). Their primitivism within the *Neornithes* is indicated by the opposite character states to N'1-N'2 and N'5-N'6 for *Ambiortus* and N'3-N'8 for Ichthyornis and/or *Apatornis*.

Baptornis cannot be at present classified with any confidence due to the lack of the cranial material (except for the quadrate and the caudal end of the mandible) and the postcranial anatomy strongly moulded by the diving specialization. *Baptornis* has long been known to differ from other Cretaceous divers. As was customary in old-fashioned avian paleontology, it was classified, faute de mieux, with modern birds, either loons or grebes. MARTIN & TATE (1976) rejected these clearly unwarranted classifications and, based on a description mixed with alternating rather than systematic comparisons to mosasaurs, *Ichthyornis, Hesperornis* and a few recent diving birds, replaced them by an equally unwarranted assignment of *Baptornis* to the hesperornithiforms. This conclusion is not supported by a single good synapomorphy of Hesperornithidae and Baptornithidae and ignores both the well-known convergence in the diving adaptations of birds and striking differences between *Baptornis* and *Hesperornis* in the proportions of the pelvis and the structure of the leg bones, in particular of the patella and tarsometatarsus, which persist despite their similar swimming specialization. The two genera consistently differ in all preserved

parts including the mandibular articulation of the quadrate, which is bicondylar in Baptornis and triradiate in Hesperornis. The wing and shoulder girdle bones are utterly dissimilar in the two genera, the ulna of *Baptornis* showing an intriguing similarity to that of theropods (MARTIN & TATE, 1976). One of the most telling differences is between the virtual lack of the procoracoid process *in* Baptornis and its expanded size in *Hesperornis*. Although MARTIN & TATE identified a small projection as a vestigial procoracoid process in *Baptornis*, this does not correspond in either shape or position to the procoracoid in *Hesperornis*. Since the wing of *Hesperornis* is much more reduced than that of *Baptornis*, the procoracoid processes would have to be subject to two opposite allometric trends, had these two genera evolved from a neornithine ancestor with an average sized process.

The most diagnostic parts of the skeleton of *Enaliornis*, including the palate, pectoral girdle, and wing skeleton remain unknown. Some details of the braincase suggest the brain structure to be more primitive than in any known neornithine. The structure of the tympanic cavity is likely to be primitive for the Ornithurae or Carinatae in being comparable to *Archaeopteryx, Hesperornis,* and primitive marine neognaths (ELZANOWSKI & GALTON, 1991). The assignment of *Enaliornis* to the hesperornithiforms (MARTIN, 1983) solely on the basis of possibly similar diving habits and despite the lack of a single good synapomorphy is unwarranted.

Hesperornis is primitive among the *Neornithes* in having the opposite character states to the potential synapomorphies N'7-N'10. In *Hesperornis* (MARSH, 1880: fig. II/6b) and a few neognaths, such as *Pelecanus* (HOFER, 1945: fig. 12F), the two quadrate heads are approximately at the same level. In most of the neognaths the lateral (squamosal) head projects distinctly higher dorsally than the medial (prootic) head. The opposite is true of *Phaethon* (pers. obs.), and *Ichthyornis* (MARSH, 1880: text-fig. 28; WITMER, 1990: fig. 5).

Neognaths

The following suite of characters demonstrates the monophyly of Neognathae:

NG1. The pterygopalatine joint, that incorporates the more or less reduced intrapterygoid joint, is movable and slides on the parasphenoid rostrum. In the reptiles, *Hesperornis* and paleognaths the pterygoid and palatine articulate by a suture.

NG2. All braincase sutures are obliterated in the grown up neognaths whereas the frontoparietal and fronto-pleurosphenoidal sutures remain open in the tinamous and lithornithids. Although all sutures tend to

ultimately obliterate in the ratites, this is possibly one more peramorphic result of their hypermorphic development (ELZANOWSKI, 1988). Since all braincase sutures remain open in *Archaeopteryx* and at least the frontoparieteal suture in *Hesperornis*, the paleognathous condition seems to be primitive.

NG3. Ilioischiadic fenestra is broadly closed caudally in the neognaths, but open in paleognaths except for *Rhea* where a narrow bridge grows near, but not from, the end of the ilium and connects it to the ischium at its mid-length. This bridge may or may not be homologous to the caudalmost ilioischiadic fusion of the neognaths. A similar bridge has probably been present in *Palaeotis* (PETERS, 1988).

NG4. Ascending process of the immature tibiotarsus fuses to the calcaneum in the neognaths (including *Larus*) but remains attached to the astragalus in the paleognaths including the ostrich (McGOWAN, 1985). However, no data for the primitive marine neognaths (see below) are available, which makes the level of synapomorphy of this excellent character somewhat uncertain.

Paleognaths

The following characters provide evidence for the monophyly of Palaeognathae:

PG1. Pygostyle small or vestigial. This seems to be one of the few good synapomorphies of the paleognaths as the presence of a reduced pygostyle in the flying lithornithids is against functional expectations. The pygostyle is big in both *Sinornis* and *Cathayornis*, and is present in the Enantiornithes as well.

PG2. Quadrate without a distinct or any division of the otic process into two heads (the lateral and the medial). This may possibly be a consequence of the immobilization of the quadrate and thus may be correlated with PG3.

PG3. Zygomatic process extends close to the mandibular articulation and braces the quadrate laterally (BOCK, 1963). The zygomatic process provides the brace for the quadrate, preventing the shocks transmitted by the pterygopalatine bars from disarticulating the quadrate (PETERS, 1987). In contrast, the zygomatic process of most neognaths does not reach beyond half the length of the otic process of the quadrate or, even if it does, as in the Otididae and some coraciiforms, it slants rostrally to the otic process without bracing it.

?PG4. Premaxilla with a single (unpaired) frontal process (PYCRAFT, 1900). This process is paired in the neognaths as it is the theropods, *Archaeopteryx*, *Hesperornis* which suggests that the neognathous condition is primitive. However, in the embryonic

Gobipteryx skeletons the process does not show any trace of division (ELZANOWSKI, 1981) and the split half length of the process in the referred adult skull (ELZANOWSKI, 1977) may represent a break as the process seems to be undivided farther caudally.

?PG5. Furcula without hypocleidium which is present in a number of primitive birds including *Sinornis*, *Cathayornis* and *Iberomesornis*. However, KUROCHKIN (1985) reported the absence of hypocleidium in *Ambiortus*.

?PG6. If paleognaths derive from the neornithines with a fragmented pterygoid, which is a likely possibility (see below), then the lack of the hemipterygoid is another major synapomorphy of all paleognaths and their monopartite pterygoid homologous to the posteropterygoid of *Hesperornis* and the neognaths. Consistent with this possibility is the fact that the pterygoids of paleognaths converge onto the parasphenoid rostrum far caudally as they do in the neognaths (N'10). A complete reduction of the hemipterygoid in a single lineage seems perfectly plausible as it happened in some neognaths (see discussion under ?N12). However, the apomorphic interpretation of the one-piece pterygoid of the paleognaths is a corollary rather than a premise of the proposed phylogenetic reconstruction. At the level of primary character analysis, the paleognathous pterygoid is at least as likely to represent the entire reptilian pterygoid as the neognathous posteropterygoid.

?PG7. Another consequence to the branching of paleognaths after *Hesperornis* would be the synapomorphic interpretation of their rhynchokinesis and associated characters such as a continuous orbital and nasal septum (BOCK, 1963). Neognathous rhynchokinesis is almost certainly a derived condition among the neornithines as *Hesperornis* is now positively known to be prokinetic (BÜHLER et al. 1988). However, since paleognathous rhynchokinesis probably evolved independently of neognathous rhynchokinesis (ZUSI, 1984), a possibility of its being primitive cannot be ruled out in the absence of any reliable information on cranial kinesis in pre-neornithine birds.

The evidence for the monophyly of the non-struthioniform paleognaths alone turns out to be stronger than that for the monophyly of all paleognaths. The following characters are probably synapomorphic for the non-struthioniform paleognaths:

PG'1. Premaxilla with long palatal processes that articulate with the vomer and, in common with the palatal shelves of the maxilla, close the rostral palatal fenestra. The palatal processes of comparable size are definitely absent from the premaxillae of *Gobipteryx* and *Hesperornis*.

?PG'2. Maxilla with broad palatal shelves which, in common with the palatal processes of the premaxilla, enclose the rostral palatal fenestra. The broad palatal shelves of the maxilla are present in *Hesperornis* and thus could be symplesiomorphic in the non-struthioniform paleognaths. However, the pneumatization pattern of these shelves is substantially different from that in the neognaths, which casts doubts on the homology of pneumatic sinuses of paleognaths and neognaths (WITMER, 1990:337).

PG'3. Maxilla with the medial palatine processes absent or vestigial. The vestige of this process is present in the juvenile *Rhea* (MÜLLER, 1963: fig. 3) and the adult *Casuarius* (pers. obs.), indicating the this process is indeed reduced rather than plesiomorphically absent.

PG'4. Maxilla with the prominent lateral palatine process, which correlates with the shortness of the maxillary process of the palatine, suggesting that the latter character is derived as well.

The plesiomorphic background provided by Cretaceous birds emphasizes the basic division between the struthioniform and non-struthioniform paleognaths which is also strongly pronounced in the skeleton and musculature of the tongue (BOCK & BÜHLER, 1990). The opposites to the characters PG'1-PG'3 and the presence of N'9 make the ostrich palate morphologically intermediate between the neognathous and paleognathous types. The position of the nasal gland in the ostrich differs from that in both the rhea and tinamous (TECHNAU, 1936) and its bony setting is reminiscent of neognaths such as Ergilornithidae and *Burhinus* (OLSON, 1985:158, and pers. comm.). If the paleognaths are monophyletic, as they seem to be, then the neognathous similarities of the ostrich provide strong evidence for its being the plesiomorphic sister group of the remaining paleognaths. This conclusion is contrary to the hitherto prevailing opinion that the ostrich is the most derived among the paleognaths. If it were, then N'9 and the opposites to PG'1-PG'3 would have to be accounted for as being convergent on the neognaths, which seems particularly unlikely in the case of maxillopalatines (the opposite to PG'3) as there is no reason, either comparative or functional, to suspect the convergent origins of this unique structure. In keeping with the cranial evidence, the ostrich has the best developed pygostyle among the paleognaths (DE BEER, 1956: fig. 5/2) as well as an empty space between the vomer and the pterygoid, which may have accommodated the hemipterygoid in its ancestors.

Braincase similarities of paleognaths and neognaths

Extensive comparisons of the braincases of *Enaliornis*, *Hesperornis* and members of 66 extant

nonpasserine families (ELZANOWSKI & GALTON, 1991; ELZANOWSKI, 1991) revealed a striking similarity in the distribution of the following five characters:

Nb'1. Basal plate separated from the tympanic cavity by the sphenooccipital jugamentum which is a perpendicular bony lamina that connects the basisphenoid and exooccipital at the ventral margin of the tympanic fossa (ELZANOWSKI, 1987) and thus bridges the gap deriving from the metotic fissure. Since the jugamentum supports the postmeatic membrane that largely closes the tympanic fossa, and itself separates the tympanic fossa from the carotids in the parabasal fossa, it may possibly be involved in the insulation of the tympanic cavity against unwanted noise. It is absent in *Phaethon*, *Fregata*, Procellariiformes, *Scopus*, Phoenicopteridae, many Charadriiformes (including the auks) and all more primitive birds (ELZANOWSKI & GALTON, 1991). The jugamentum is present in most of the living paleognaths (PYCRAFT, 1900: 173; MÜLLER, 1961a: 289) but poorly developed in *Apteryx* and absent in *Casuarius* (pers. obs.).

Nb'2. Internal carotid and stapedial arteries are at least partly enclosed in bony tubes in most of the neognaths and all paleognaths. The carotid tubes are absent in *Phaethon, Fregata,* Procellariiformes, Sulidae, Pelecanidae, Ciconiidae and *Scopus* (GADOW & SELENKA, 1891; SAIFF, 1988). The arterial tubes evolved independently in birds and mammals as a protection against, or an internal adaptation to, the noise from the pulsation of arteries (PACKER, 1987). This raises a possibility of the convergent appearance of the arterial tubes among birds as well.

Nb'3. Pharyngotympanic (eustachian, auditive) tubes are enclosed in the cranial base in most of the neognaths and paleognaths (GADOW & SELENKA, 1891). Among neognaths they remain completely open lateroventrally in the Diomedeidae, Procellariidae, Ardeidae, and *Scopus* and only partly closed in *Phaethon, Fregata,* Hydrobatidae, Pelecanoididae, Phalacrocoracidae, Pelecanidae, Ciconiidae, and *Balaeniceps* (SAIFF, 1988). Among paleognaths the tubes are entirely open only in *Casuarius* and *Dinornis* (PYCRAFT, 1900). The tubes are not enclosed in bone in *Hesperornis* and the theropods, which suggests the primitivism of this condition among birds, but are enclosed in the crocodiles, which may be an independent development in this group despite views to the contrary (TARSITANO, 1985). What is beyond any doubt is that the bony walls of the tympanic cavity expanded independently in the archosaurian and mammalian clades despite considerable differences in morphological settings. The tendency towards closing of the pharyngotympanic tubes in birds may be correlated with the expansion of the basiparasphenoid (= basitemporal) ossification (JOLLIE, 1957) which

seems to contribute to the ventral wall of the canals. The closed tubes of neognaths, but not paleognaths, open rostrally in the midline to a single anthrum tubarum. There is a strong interspecies and intraspecies variation in the ways and degrees the tubes are enclosed in bone and the associated details of the cranial base, e.g., in the Anhingidae (SAIFF, 1978). This variation, which cannot be reflected in the simple digitization into none, partial, and complete closure, suggests that the closing of the pharyngotympanic tubes occurred many times independently in avian evolution.

Nb'4. The medial cotyla for the quadrate articulation is more or less pedunculate, i.e., supported by an otic peduncle (LOWE, 1926: "opisthotic columella"; BUTENDIECK & WISSDORF, 1982: "pila prootica") and set off from the caudal wall of the tympanic fossa by the length of this peduncle in most of the neognaths and all paleognaths. A long peduncle is present in the paleognaths, Turnicidae, Pedionomidae, Galliformes, Jacanidae, *Rostratula,* most Scolopacidae and Mergini among Anatidae (pers. obs). A broad and short peduncle is present in the Otididae, *Cariama, Psophia,* Gruidae, *Aramus,* Rallidae, *Heliornis,* and some Podicipedidae (pers. obs.). In contrast, the medial cotyla is sessile and situated in the caudalmost position in the tympanic fossa in all toothed birds and all Pelecaniformes, all Procellariiformes, Ciconiiformes (including *Scopus* and Cathartidae), many Charadriiformes including Alcidae, Phoenicopteridae, Spheniscidae, Gaviidae, Ardeidae, many Falconiformes, Pteroclidae and some Podicipedidae. A great diversity in the development of the otic peduncle within the Podicipedidae and Scolopacidae reveals a potential for convergent evolution of this structure.

Nb'5. No separate recess, named suprarecessal compartment (ELZANOWSKI & GALTON, 1991) in the tympanic cavity dorsal to the cochlear fenestra. The suprarecessal compartment is well-identifiable in *Phaethon, Fregata,* and Diomedeidae and may be present in other procellariiforms, Sulidae, and Ciconiidae. This puzzling detail is listed here because of the similarity of its taxonomic distribution and anatomical location with the four other characters but will be left out of the further discussion.

Phaethon, Fregata, and Procellariiformes are consistently similar to *Hesperornis* and *Enaliornis* in showing the opposites of all five characters. The opposites of Nb'1-Nb'4 seem to be primitive among birds as they are present in *Hesperornis, Enaliornis, Archaeopteryx,* and the theropods. The majority of the neognaths and paleognaths share the characters Nb'1-Nb'5, whereas the remaining neognath taxa including the ciconiiforms, herons, charadriiforms, and the complement of pelecaniforms, show a variety of

intermediate combinations. Since the charadriiforms are obviously unrelated to the pelecaniform-ciconiiform assemblage, the observed distribution of the characters states Nb'1-Nb'5 reveals a pattern indicative of mosaic evolution, suggesting that the sphenooccipital jugamentum, arterial tubes, bony pharyngotympanic tubes and otic peduncle either evolved or were lost more than once among birds.

There is a likely functional reason for the independent evolution of at least some of these structures. It has been demonstrated in mammals that the bony arterial tubes provide acoustic insulation of the middle ear (PACKER, 1987) and this may possibly be true of the sphenooccipital jugamentum and bony pharyngotympanic tubes. Whereas the inland birds rely on hearing in locating food and predators, sea birds are permanently exposed to high levels of background noise from wind and waves and rely on hearing primarily if not exclusively for social communication, which is mediated by harsh vocalizations. Therefore, reducing the endogenous noise, arterial or otherwise, may be of less importance for the sea birds and their tolerance toward this noise may be greater than it is in the inland birds. However, this functional attribution may account for the convergent reversals to, as well as the selective retention of, the opposites to Nb'1-Nb'3 in the sea birds such as *Phaethon*, *Fregata*, and Procelariiformes. These taxa may have retained the primitive condition because the functional demands that are responsible for the adaptive trend among the inland birds are absent in the marine environment.

The selective retention seems to be more likely than the convergent reversals for at least two reasons. Firstly, the opposites of Nb'1-Nb'4 are not limited to the sea birds, but occur, in various mosaic combinations, in a few non-marine taxa such as *Casuarius* (no jugamentum and pharyngotympanic tubes), Ciconiidae (medial quadrate cotyla sessile, no jugamentum and carotid tubes), *Scopus* (medial quadrate cotyla sessile, no jugamentum, carotid tubes, and pharyngotympanic tubes), Ardeidae (medial quadrate cotyla sessile, no pharyngotmpanic tubes), some Scolopacidae (medial quadrate cotyla sessile, no jugamentum), *Attagis* (no jugamentum), Cathartidae, most falconiforms, and Pteroclidae (medial quadrate cotyla sessile). This makes it difficult to attribute the opposites of Nb'1-Nb'4 to a single or a few environmentally correlated selective pressures.

Secondly, if the opposites of Nb'1-Nb'3 were due to reversals in the pelecaniforms, ciconiiforms, herons and charadriiforms, why should they be consistently absent from the other neognaths? This argument does not apply with the same strength to the sessile medial quadrate cotyla (the opposite of Nb'4) that shows a broader distribution, but still a more or less

pedunculate condition is consistently maintained in the majority of neognathous orders.

The pronouncedly polarized distribution of the characters states Nb'1-Nb'5, with a few unrelated intermediate groups, is reminiscent of that of mammalian characters in the anagenetic succession from the early therapsids to mammals, with a variety of mosaic character combinations in the late therapsids. A considerable individual variation of characters Nb'1-Nb'3, which is particularly strong for the bony pharyngotympanic tubes, suggests the paradaptive nature of interspecies differences and thus the possibility of independent evolution of otherwise similar structures (BOCK, 1974).

The expansion of bone in and around the tympanic cavity is one among the many examples of independently evolved cranial similarities of mammals and birds. Another is the incorporation of the squamosal into the braincase wall. The chondrocrania of mammals and birds show several homoplastic similarities including three additional commissures, the processus recessus in the metotic fissure, the counterpart of the mammalian fissura supraoccipitocapsularis (MÜLLER, 1961b; STARCK, 1969), and the backward leaning of the occipital arches (DE BEER, 1937). The potential for homoplasy in the braincase evolution probably results from the similarity of spatial constraints imposed by the brain expansion, and the similarity of functional demands such as those of hearing. The homoplasy in the skull structure of higher vertebrates may, therefore, be causally correlated with the parallel improvements in the performance of their major functions including metabolic rate, thermoregulation, cognition and motivation, all of which either enable or depend on the cerebral expansion.

The origins of paleognaths

The character states opposite to NG1-NG4 suggest that the paleognaths branched off prior to all living neognaths, which is consistent with the bulk of nonskeletal evidence (for references see HOUDE, 1988; SIBLEY & AHLQUIST, 1991). This allows two possibilities, the dichotomy hypothesis and the early branching hypothesis. The dichotomy hypothesis (Fig. 4) proposes that the paleognaths are the sister group of the neognaths. It requires the premaxilla-maxilla fusion (N'9) to be lost in the non-struthioniform paleognaths or convergent in the ostrich and the one-piece pterygoid to be a paleognathous synapomorphy (?PG6).

However, since the primitivism of the unsegmented pterygoid may still appear as the most straightforward

ARCHAEOPTERYX SINORNIS CONCORNIS CATHAYORNIS ENANTIORNITHES AMBIORTUS ICHTHYORNIS HESPERORNIS STRUTHIO OTHER PALEOGNATHS

PG'1-PG'4
↓N'9

PG1-PG6

NEOGNATHAE
NG1-NG4

E1-E4

N'7-N'10

N'3-N'4 ←? ↑

N'5-N'6

N'1-N'2

N1-N9*
NEORNITHES

C6-C8

C1-C5
CARINATAE

O1-O10
ORNITHURAE

AVES

Fig. 4: The proposed phylogeny of birds with the most likely variant of the origins of paleognaths (the dichotomy hypothesis). The down-pointing arrow marks reversal. Boxed are characters whose presence cannot be determined and/or is phylogenetically irrelevant (e.g., due to reduction of the wing). The broken line indicates a tentative placement of *Ichthyornis. Patagopteryx* (ALVARENGA & BONAPARTE, 1992) should probably be placed between Carinatae and Neornithes (CHIAPPE, this symposium). All characters are discussed in the text, those of the neornithines are in addition summarized as follows:

Neornithes*: N1. Coracoid with procoracoid process and a distinct scapular socket; N2. Caput humeri separated from the deltopectoral crest and dorsal tuberosity; N3. Humerus with a lateral limb of ventral tuberosity; N4. Quill knobs present; N5. Ilium overlaps the most caudal ribs. N6. Tarsometatarsus completely fused; N7. Hypotarsus; N8. Ectopterygoid absent; N9. Choanal fenestra open rostrally. See text for another four possible neornithine apomorphies.

Advanced Neornithes: N'1. Scapular glenoid faces dorsally; N'2. Carpometacarpus with pronounced extensor process; N'3. Tarsometatarsus with distal foramen completely closed; N'4. Quadrato-mandibular articulation triradiate; N'5. Deltopectoral crest deflected; N'6. Acromion moderately prominent; N'7. Tibiotarsus with supratendinal bridge; N'8. Teeth absent; N'9. Premaxilla and maxilla fused; N'10. Pterygoids converge caudally.

Neognathae: NG1. Pterygopalatine articulation slides on the rostrum; NG2. Braincase sutures obliterate upon maturation; NG3. Ilioischiadic fenestra closed caudally; NG4. Ascending process fuses to calcaneum.

Paleognathae: PG1. Pygostyle small or vestigial; PG2. Quadrate capitula absent or vestigial; PG3. Zygomatic process braces the quadrate laterally; ?PG4. Hypocleidium absent; ?PG5. One-piece pterygoid; ?PG6. Rhynchokinesis.

Non-struthioniform paleognaths: PG'1. Palatal processes of premaxilla long, articulate with the vomer; ?PG'2. Palatal shelves of maxilla broad; PG'3. Medial palatine (= maxillopalatine) processes of maxilla absent or vestigial; PG'4. Lateral palatine process of maxilla prominent and maxillary process of palatine short.

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* Due to the fragmentary material of the early neornithines, the unresolved *Ichthyornis-Apatornis* tangle, and the reduction of the wing skeleton in *Hesperornis*, the phylogenetic status of each of the eight neornithine characters (N1-N8) cannot be reliably established for single genera.

interpretation, the branching of the paleognaths prior to *Hesperornis* (and possibly *Enaliornis*) remains a serious although less likely alternative that will be referred to as the early branching hypothesis. This hypothesis would necessitate an independent appearance of characters N'7-N'10 in the neognaths and paleognaths, which includes the independent reduction of teeth. More importantly, the reptilian interpretation of the paleognathous pterygoid immediately identifies the non-struthioniform palate as more primitive than the ostrich palate. In conjunction with the paleognathous monophyly, this would require the ostrich's maxillopalatines, premaxilla-maxilla fusion, and separation of vomer from the pterygoid to be convergent on the neognaths. Furthermore, if the non-struthioniform palate were primitive within the paleognaths, the medial bending of the pterygoids and the pronounced caudal shift of the entire palate would be difficult to account for as being synapomorphic. For all these reasons, the early branching hypothesis appears to be less likely than the dichotomy hypothesis.

Although there is good evidence for the independent evolution of the braincase characters Nb'1-Nb'4 in the paleognaths and neognaths, their presence could still be adduced in support of the late branching of paleognaths from the advanced neognaths. The late branching hypothesis would require four additional reversals (of NG1-NG4) in the paleognaths, including the evolutionary loss of the movable joint between the palatine and posteropterygoid. Since this joint is literally pivotal to the function of the jaw apparatus and thus highly conserved throughout the neognaths, it is unlikely to be lost. Also, the neognathous ancestry of the paleognaths is contradicted by most of the non-osteological evidence that consistently points to the branching of all paleognaths prior to all living neognaths. Finally, the origin of paleognaths from within the neognaths could be demonstrated only by likely synapomorphies with a single neognathous sister taxon, none of which has ever been found despite over a century of continuous search. All in all, the neognathous ancestry of paleognaths is very unlikely on present evidence.

The contradictions inherent to the paleognathous origins may reflect the nature of underlying evolutionary events. Comparisons of the neognathous and lithornithid skeletons reveal a disparity in the differences between the cranial and the postcranial or, alternatively, the axial and appendicular, morphology. In terms of the postcranial skeleton the lithornithids are generally more primitive than are the neognaths and make an almost perfect sister group of the neognaths. The only exception is the reduction of the pygostyle, which remains puzzling in flying, nonaquatic birds.

In contrast, the differences in cranial morphology, including the musculature (ELZANOWSKI, 1987), between the neognaths and paleognaths are so dramatic as to make the definition of the neornithine skull very scanty. This contrast suggests a rapid rebuilding of the cranial architecture in the evolution of the neornithines. Some of the cranial differences between the neognaths and paleognaths, in particular the bifid-undivided differences of the supraoccipital and the frontal process of the premaxilla, may be due to an anteroposterior shift in the expression of homeotic genes. In the skulls of transgenic mice with the Hox-4.2 gene expressed more rostrally than in normal mice, the basioccipital is rostrally bifid, the exoccipital and supraoccipital reduced and the palatal processes of the maxilla remain unfused (LUFKIN et al., 1992). The analogy is admittedly remote since the basioccipital is of vertebral (neocranial) origins and the supraoccipital is an amniote neomorph. However, very little is known so far about the impact of homeotic genes on single skull bones. The amazing constancy of the bifid condition in the juvenile neognaths and of its opposite in the paleognaths suggests a rechanneling of the underlying developmental process, which cannot be accounted for by any functional requirements. To be reckoned with in this context is a possibility that the paradoxical reduction of the pygostyle in the paleognaths may be a side effect of the tandem shift in the expression of homeotic genes. Whatever its developmental mechanism, the origins of either paleognathous or neognathous lineage seem to involve a major cranial remodelling.

Acknowledgements

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