Peabody Museum
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New Observations on the Skull of *Hesperornis* with Reconstructions of the Bony Palate and Otic Region

Andrzej Elzanowski

(Received 20 April 1989)

Abstract

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Key Words

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The present paper contains a reconstruction of the bony palate and descriptions of the upper jaw bones, the cranial cavity, and occipital plate with the caudal part of cranial base, a tentative reconstruction of the tympanic fossa, and, in conjunction with the parallel study of *Enaliornis* (Elzanowski and Galton 1991), extensive comparisons to recent birds. Much information remains to be gained from the study of the remaining parts of the *Hesperornis* braincase.

Abbreviations

KUVP	Museum of Natural History, Kansas University, Lawrence
USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC
YPM	Peabody Museum of Natural History, Yale University, New Haven

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Material

The reconstruction of the palate is based on the specimens YPM 1206 and KUVP 71012; the latter was partly illustrated by Bühler et al. (1988) but remains undescribed. The description of the premaxillary is based on USNM 4978, YPM 1206, and USNM 6622. The description of the braincase is based primarily on YPM 1207. Only briefly examined was the specimen KUVP 2287, which has been illustrated (Gingerich 1976: fig. 2) and assigned to a new genus *Parahesperornis* (Martin 1984), but also remains undescribed. This specimen shows a less advanced stage of ossification than the other known skulls of the Hesperornithidae in having the exooccipital and basioccipital parts of the occipital condyle unfused, the exooccipital unfused with the sphenoid complex (left side), and the frontal unfused with the pleurosphenoid within the postorbital process (right side).

All the hesperornithid skulls are mostly or completely disarticulated. In such specimens, the thin osseous laminae connecting the palatal bones are not likely to be preserved, a point probably important for understanding of the articulations in the maxilla and palate.

Material of recent birds used for comparisons included intact skulls from 66 recent families and skulls with open cranial cavities from 36 families of nonarboreal and diurnal predatory nonpasserines listed elsewhere (Elzanowski and Galton 1991). A juvenile *Macronectes giganteus* (Procellariidae), of skull length 125 mm (71% of adult length), proved particularly comparable to *Hesperornis* in some features of the maxilla.

Maxilla and Palate

Premaxillary and Nasal

The rostral part of the premaxillary is best preserved in USNM 6622 and the remaining parts of the corpus and the frontal processes in USNM 4978 (Fig. 1). The caudal half of the corpus is divided by the median interpremaxillary suture. Shallow lateral grooves extend on the dorsal side for the caudal two-thirds of the length, become wider and deeper caudally, and exit to the nasal openings. The tomial edges are sharp and slightly decurved on the medial side. The ventral surface is strongly concave, with two asymmetrical neurovascular foramina and a median ridge at the rostral end. In the remaining part, the ventral surface is tripartite, divided into the median vault and two lateral shelves. The neurovascular canals (now squeezed) apparently run dorsal to these shelves. The shelves and the adjacent medial surfaces of the tomial edges bear shallow excavations, which accommodated the dentary teeth; these pits are distinct in both Smithsonian specimens but poorly preserved in YPM 1206. At least 13–14 pits are present on each side in USNM 4978, mostly in an alternate arrangement on the two sides. The caudalmost pit is more than 1 cm rostral to the nasal opening. Contrary to Witmer and Martin (1987: fig. 4), there is no trace of the interpremaxillary suture on the ventral surface of the premaxillary corpus, which must have been double-walled.

The interpremaxillary suture continues between and divides the frontal processes throughout their length. Rostrally, these processes are thick, and are thickest medially: each process has an approximately triangular cross section, with the bases of the triangles meeting each other in the sagittal plane. The dorsal surface of each process is convex and the ventral concave. Caudally, within the craniofacial bending zone, the processes become much thinner and flattened, starting from the level of the rostral end of the lateral palatal fenestra.

The premaxillary processes of the nasal extended to a point approximately 25 mm caudal to the rostral margin of the nasal opening. Each process of the nasal abruptly tapers to a splint of bone, which ends on the lateral margin of the culmen. Each process is vestigially bipartite because of the presence of a minuscule medial process near the end. The contact between the premaxillary and the

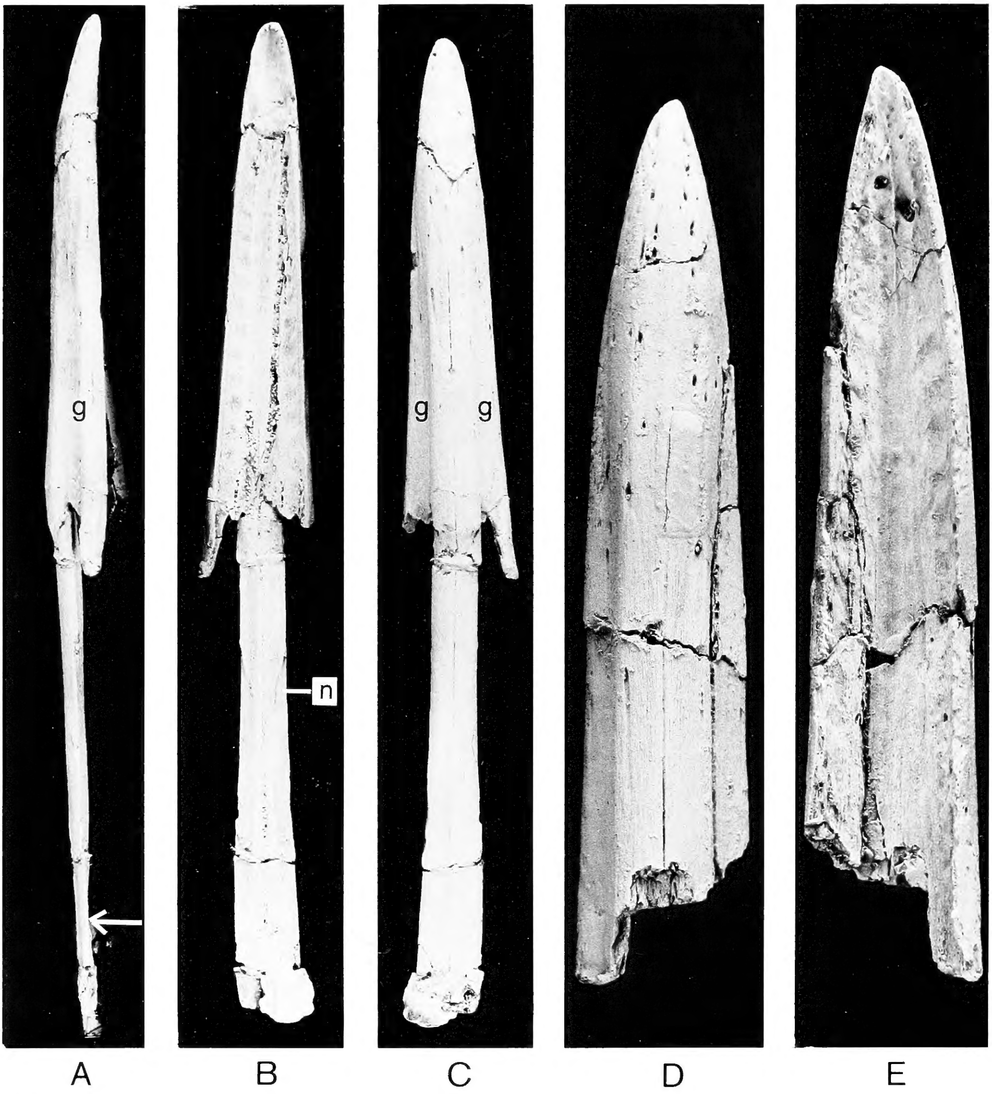

Fig. 1
Os praemaxillare. USNM 4978 in lateral (*A*), ventral (*B*), and dorsal (*C*) view; the rostral end of this specimen is replaced by plaster; arrow points to the thinnest part of the frontal processes within the craniofacial flexion zone. USNM 6622 in dorsal (*D*) and ventral (*E*) view. Abbreviations: *g* rhamphothecal groove, *n* rostral end of excavation for the premaxillary process of the nasal.

premaxillary processes of the nasal is tight, although the bones are not fused. The rostralmost fragment of the nasal (22 mm long) still remains in the excavations of the premaxillary in YPM 1206.

The maxillary processes of the premaxillary have the form of ventrally rounded slats tilted at 45° to both the frontal and the sagittal plane. Some 7–8 mm caudal to the rostral end of the nasal opening, the maxillary processes lose their sharp tomial edge; presumably, from here on, they entered the deep dorsal groove

Table 1
Measurements of the upper jaw bones (in mm).

Os praemaxillare	
Corpus, caudal end, USNM 4978 (at the rostral margins of nasal foramina)	
width	ca. 19.0
depth	ca. 10.0
Processus frontalis	
length, USNM 4978	90.0?+
width, rostrally, USNM 4978	8.4
YPM 1206	9.3
caudally, USNM 4978	10.4
depth, rostrally, USNM 4978	4.3
YPM 1206	3.7
caudally, USNM 4978	1.9
Processus maxillaris, YPM 1206	
length, preserved	22.0
estimated, minimum	30.0
width	3.0
Os maxillare, KUVP 71012	
Total length*	min. ca. 110.0
Maximum width (rostrally)*	ca. 16.0
Processus jugalis, length*	ca. 58.0
Dental groove, length*	ca. 60.0
Os palatinum, YPM 1206	
Total length**	105.0?+
Processus praemaxillaris**	53.0?+
Corpus, width at the level of choanal process	7.0
Os hemipterygoideum	
Length, KUVP 71012*	ca. 74.0
YPM 1206	65.0+
Caudal end, width, KUVP 71012*	ca. 11.0
YPM 1206	11.7

* Approximate figures based on camera lucida sketches.
** Measurements based on Marsh's (1890) plate II fig. 9, but including a small rostral piece, apparently found and added subsequently.

on the maxillary and thus the premaxillary was mostly excluded from the margin of the maxilla. In KUVP 71012 the maxillary has a shallow depression on the ventral surface of the rostral end; this depression is here interpreted as the overlap area for the palatine process, which was probably thin and fragile.

Maxillary

This bone is best preserved in KUVP 71012. In YPM 1206, both maxillaries have the jugal processes broken. The left one is flattened in the frontal plane of the bone, whereas the right one, apparently overlooked or misidentified by Gingerich (1976), is squeezed in the parasagittal plane. The left bone is preserved with three complete teeth (two in the groove, one outside), the basal part of another tooth in the groove, and a crown of a small, straight developing tooth near the groove. Only one large broken tooth is associated with the right maxillary.

The corpus of the maxillary has its medial and lateral margins approximately parallel. Caudally, the bone has three processes (Fig. 3): the dorsomedial Processus palatinus

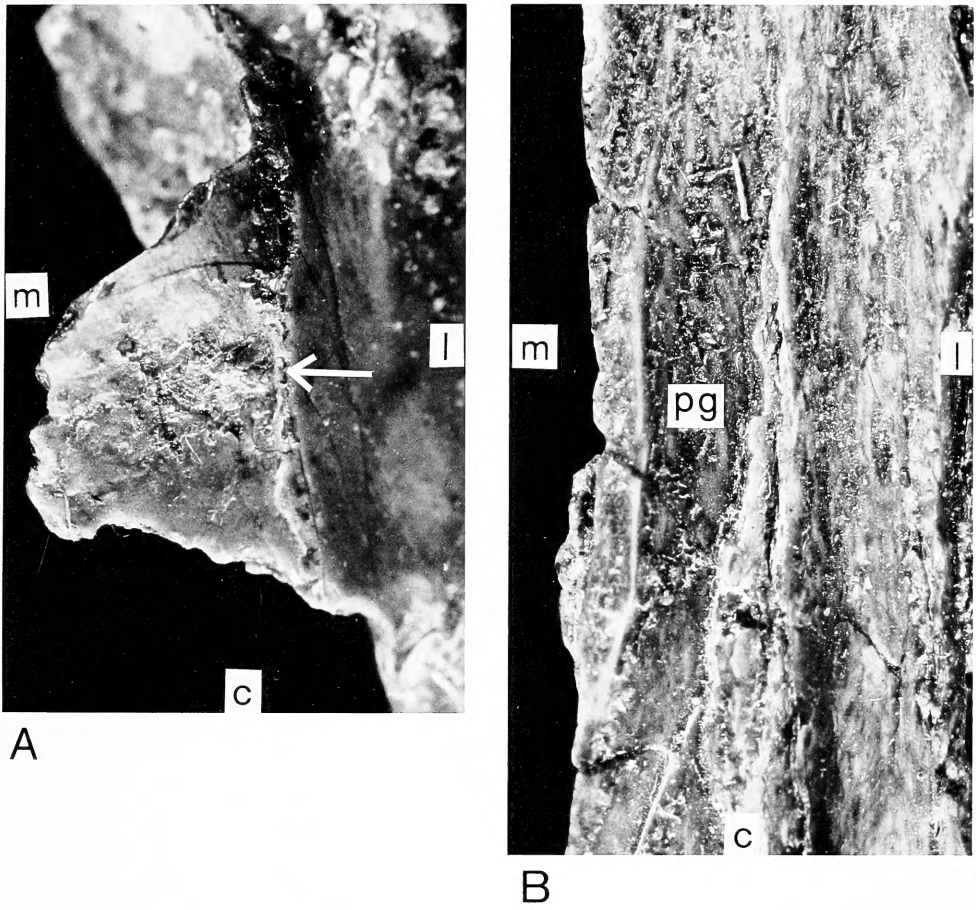

Fig. 2
YPM 1206. (*A*) Os palatinum dextrum, broken Processus choanalis in dorsal view (× 8); arrow points to the margin of the superficial bony lamina, which is missing from the process. (*B*) Os maxillare sinistrum, fragment of the ventral surface. Abbreviations: *l* lateral side, *m* medial side, *pg* groove for the palatine (× 8).

medialis (the "maxillopalatine"), which has the medial surface distinctly convex ("inflated"), as in most birds; the stout, short Processus palatinus lateralis supporting the palatine; and the flattened jugal process. The latter bears on its dorsal side (in KUVP 71012) a distinct impression of the jugal, which extends to the level of the end of the dental groove. On the dorsal side, the maxillary has a distinct groove for the nasal; in its deeper, rostral part this groove certainly also accommodated the premaxillary. The medial wall of this groove rises into the broad nasal process of the maxillary. The ventral surface of the maxillary bears, along its medial margin, a shallow groove, ca. 2.2 mm wide, which is an impression of the palatine (Fig. 2B).

Palatine

This bone was much more complete caudally at the time of Marsh's study and the length given in Table 1 includes the presently missing caudal part as represented in natural size by Marsh (1880: fig. 9, pl. 2); this illustration seems to indicate that the lateral margin of the caudal part was distinctly more dorsal than the medial margin. A small piece was apparently added at the rostral end of the premaxillary process in subsequent preparation. The choanal process is complete only in KUVP 71012.

The palatine (Fig. 3) has a long, slender premaxillary process that is well delimited from the broader corpus by an angular bend of the medial margin. The premaxillary process overlapped the maxillary throughout its length and probably reached the premaxillary. Situated at the base of the premaxillary process, on its dorsal side, is a prominent ridge that abutted against the lateral palatine process of the maxillary and the ridge rostrally extending from this process. The hook-shaped choanal process, projecting from the corpus and closing the choana caudomedially, shows in KUVP 71012 two distinct, flat articulation surfaces, the medial one for the sphenoid rostrum and/or the interorbital septum (possibly also in part for the same process of the opposite element), and the lateral one, probably for the crus of the hypothetical vomer (see below).

The palatine, at least its corpus and choanal process, has a multilayered (sandwich) structure known to strengthen flexible cranial bones in larger birds (Bühler 1981). Curiously, in both KUVP 71012 and YPM 1206, the dorsal surface of the choanal process is sharply delimited from the corpus by the edge of the superficial layer of bone, which is present on the corpus and lacking on the process (Fig. 2A).

There is a small but distinct dorsal tuberosity opposite to the choanal process, near the lateral margin of the bone. After the reconstruction of the palate (Fig. 3) had been completed, this tuberosity lay precisely at the level of the lacrimal and thus most likely marks the syndesmotic articulation with a lacrimopalatine (uncinate) bone. As in the Diomedeidae, the articulation with the lacrimopalatine is marked on the lacrimal by a shallow sinus (or a rounded incisure) in the medial margin of the ventral half of the bone (Marsh 1880: pl. II, fig. 10).

Hemipterygoid

This bone, complete in KUVP 71012, has the rostral and caudal moieties flattened at different planes, at ca. 45° to each other. The rostral end (damaged in YPM 1206) curves mediad and bears a distinct, small articulation surface on the lateral side. The caudal moiety is at least twice as wide as the rostral one, and has the ventral surface marked along the lateral margin by a slight impression, probably an attachment area for a part of the pterygoideus muscle. Caudally, the bone is obliquely truncated by a rather rough, squamous articulation surface for the pterygoid.

Pterygoid

This bone differs from the pterygoid of recent birds primarily in being much shorter, and thus more transversely oriented within the palate, and in having an enormous dorsal wing, which, as noticed by Gingerich (1976: fig. 3), partly articulated with the orbital process of the quadrate. The groove for the articulation with the hemipterygoid is rounded whereas the caudal margin of the hemipterygoid is fairly sharp (narrow) and squamous; this suggests the presence of a substantial amount of articular cartilage and absence of an articular cavity.

Reconstruction of the Palate

The four drawings published as reconstructions of the *Hesperornis* palate can hardly be considered as such. Shufeldt (1915) and Heilmann (1926) used the skull of loons (*Gavia*) as a model to interpret Marsh's (1880) figures without having seen the originals. More recent attempts (Gingerich 1973, 1976, Witmer and Martin 1987) resulted in sketches with some elements unidentifiable in the referred materials and most represented articulations, in particular those between the hemipterygoids, palatines, and maxillaries, not supported by any evidence. Gingerich (1973, 1976) represented an imaginary, complex median element (identified as the vomer, possibly a composite of right maxillary and palatine) and misrepresented the position of the hemipterygoids (misidentified as palatines). At its articulation with the pterygoid in KUVP 71012, the hemipterygoid has its lateral, not medial, margin extending further caudally and ending by a sharp angle. This point has been corrected by Witmer and Martin (1987). However, these authors misidentified the palatines as the paired vomer and represented them with the choanal processes apparently projecting in such a way as to be entirely invisible in ventral view.

The present reconstruction (Fig. 3) has been developed by reconstructing first the outlines of single elements, then combining elements with well-defined articulations (maxillary with palatine, pterygoid with quadrate) into modules, and finally by fitting together the reconstructed elements and modules and looking for osteological evidence of geometrically possible connections.

The overall primitive structure of the *Hesperornis* palate (see Comparisons below) and the presence of a large median space between the maxillaries and palatines suggest the presence of a well developed vomer. The specific evidence is provided by lateral contact surfaces (Fig. 3: *av*) on the choanal processes of the palatine, which were probably braced rostrally by a bone that could have been only a vomer. The vomer may be represented by a trough-shaped bone, preserved next to the right hemipterygoid in KUVP 2287 (see Gingerich 1976: fig. 2).

The presented reconstruction constitutes a pictorial hypothesis that can be tested by verifying the fit of the specified articular structures and confirmed or refuted by the evidence from other specimens, in particular specimens likely to contain the complete set of bones (e.g., in KUVP 2287). This reconstruction may be imprecise at three points. The first is the structure of the articulation between premaxillary and maxillary. The second is the position of the quadrate–pterygoid complex in relation to the braincase, affecting the orientation of hemipterygoid in the frontal (horizontal) plane. The range of permissible positions of the quadrate is difficult to be precisely determined from the temporoquadrate articulation surfaces alone, even if they were intact. The third uncertain point is the rostral articulation of the hemipterygoids that may have articulated with the medial palatine processes of the maxillary (maxillopalatines) as shown on Figure 3, or with the caudal bifurcation (the crura) of the hypothetical vomer that could have braced the rostral ends of the hemipterygoids as suggested by Ostrom (1969) for the corresponding parts of pterygoids in *Deinonychus*. Such a contact with the vomer would be possible if the quadrates projected somewhat more laterally and rostrally than represented on the reconstruction, since then the rostral ends of hemipterygoids would converge toward the midline.

Comparisons

The bony palate of *Hesperornis* proves quite comparable to that of other birds. The most evident differences from recent birds include the basipterygoid articulation in an extremely caudal position and without prominent pterygoid processes of the basiphenoid, the short pterygoid and long hemipterygoid, and the palatine ending far rostrally to the intrapterygoid joint. All may be accounted for by the relatively recent division of the reptilian pterygoid into two parts. This interpretation is consistent with the theropod similarities of the mandible (Gingerich 1973).

Primitive by virtue of being reptilian and present in theropods (Colbert and Russell 1969, Ostrom 1969) are at least five features: (a) presence of teeth; (b) premaxillary ventrally open; (c) premaxillary and maxillary unfused; (d) premaxillary only slightly expanded over the lateral margin of maxillary; and, (e) basipterygoid articulation in the caudal position. Characters (c) and (e) are limited to the paleognaths among the recent birds. Dispersed among paleognaths and nonpasserine neognaths, and therefore probably primitive for the Neornithes, is the presence of (f) lacrimopalatine, (g) dorsal rhamphothecal grooves on the premaxillary, and (h) well-developed lateral palatine processes of the maxillary. The only neognaths combining all three latter

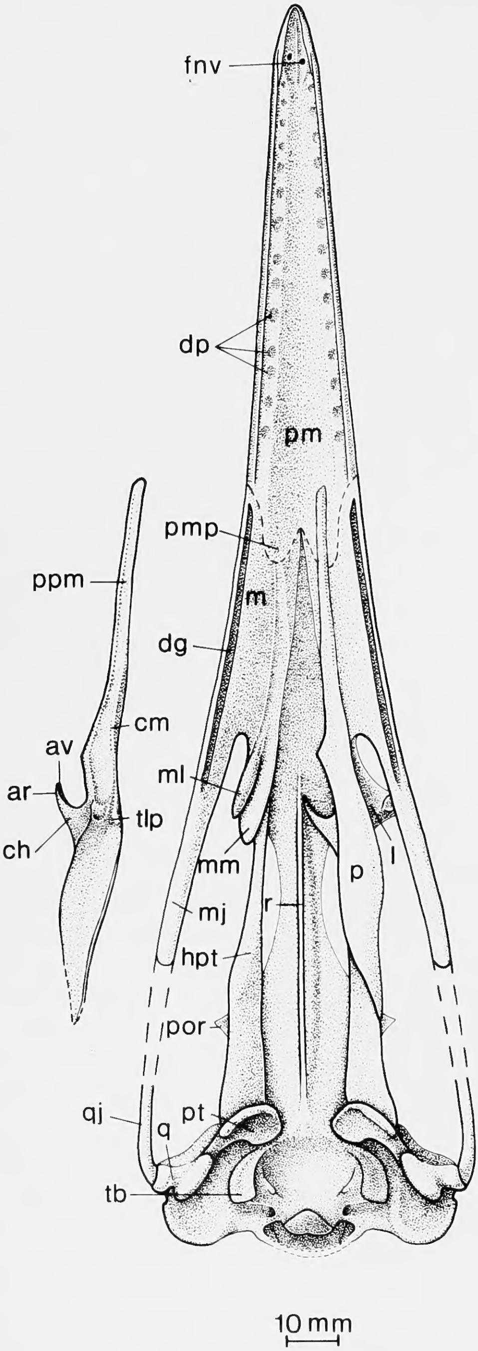

Fig. 3
Reconstruction of the bony palate in *Hesperornis* with the right palatine shown in dorsal aspect, as if it were removed from the palate and turned 180° around the long axis. This reconstruction is based on the specimens YPM 1206 and KUVP 71012, which are at least congeneric. The maximum error estimates in the rostrocaudal and transverse distances between two elements of the natural size reconstruction are 10 mm and 3 mm, respectively. Conforming to the ventral concavity of the premaxillary, the maxillaries and rostral parts of the palatines slope inwards, i.e., the medial margins of the maxillaries are more dorsal than the lateral ones. At the level of choanal process, the palatine becomes approximately horizontal. The caudal part of the palatine slopes outwards, as does the underlying rostral part of the hemipterygoid, whereas the caudal part of the hemipterygoid slopes inwards. There was probably some space enclosed between the caudal end of the palatine and the hemipterygoid; this space was certainly filled by the pterygoid muscle. The lacrimopalatine and vomer are not shown. Abbreviations: *ar* medial articulation surface on the choanal process of the palatine (for the rostrum); *av* lateral articulation surface on the choanal process of the palatine (probably for the vomer); *ch* Os palatinum, Processus choanalis; *cm* Os palatinum, Crista maxillaris; *dg* Os maxillare, dental groove; *dp* Os praemaxillare, dental pits (for the mandibular teeth); *fnv* Foramina neurovascularia; *hpt* Os hemipterygoideum; *l* Os lacrimale; *m* Os maxillare, corpus; *mj* Os maxillare, Processus jugalis; *ml* Os maxillare, Processus palatinus lateralis; *mm* Os maxillare, Processus palatinus medialis (=maxillopalatinum); *p* Os palatinum, corpus; *pm* Os praemaxillare, corpus; *pmp* Os praemaxillare, Processus palatinus (hypothetical); *por* Processus postorbitalis; *ppm* Os palatinum, Processus praemaxillaris; *pt* Os pterygoideum; *q* Os quadratum; *qj* Os quadratojugale; *r* Rostrum sphenoidale; *tb* Tuberculum basilare; *tlp* Os palatinum, Tuberculum lacrimopalatinum.

characters (f, g, h) are Procellariiformes, which, in addition, have long hemipterygoids, possibly the longest among the recent birds.

The premaxillary and the maxillary coossify in neognathous birds and in the majority of them the premaxillary has long maxillary processes that underlie the maxillaries and contribute substantial parts of the lateral (tomial) margins of the bony maxilla. The maxillary processes of the premaxillary seem to be shortest in Procellariiformes, a feature invisible in adults since these processes fuse with the maxillary. Unfortunately, the details of this contact prior to fusion remain unknown for most birds. The situation in *Hesperornis* seems best comparable to that in paleognathous birds, in which the premaxillary remains only syndesmotically connected to the maxillary and does not exclude the maxillary from the margin of the maxilla.

Premaxillary Lateral grooves on the dorsal surface of premaxillary, which reflect the division of the upper rhamphotheca into three main parts, are present in the majority of the paleognathous birds (except for two genera of tinamous, as slits in *Apteryx*), Procellariiformes, Pelecaniformes, *Scopus, Balaeniceps,* Spheniscidae, Threskiornithidae, and Rostratulidae. The grooves may be replaced by slits, entirely as in many Scolopacidae or only caudally as in Threskiornithinae.

In the majority of recent birds, the premaxillary corpus encloses a substantial space (Hesse 1907) between its dorsal and ventral (palatal) wall (the latter being frequently and incorrectly referred to as the palatine process). As in *Hesperornis,* the ventral wall is strongly concave on its palatal side and largely conforms to the dorsal wall in *Gobipteryx* (Elzanowski 1977), some Procellariiformes, Cathartidae, some large ratites (*Struthio, Rhea, Dromaius*), Galliformes, and Anatidae. The roof of the beak cavity in *Hesperornis* is quite comparable to that in a juvenile *Macronectes giganteus,* in which the rostral ends of the maxillaries assume an oblique orientation to conform to the steep walls of the premaxillary.

Maxillary Aside from the dental grooves, the maxillary of *Hesperornis* is typically avian and differs from that in most of recent birds in having a broad rostral end and a distinct lateral palatine process. In most birds, including tinamous, the maxillary tapers rostrally. The rostral end of the maxillary is broad in a juvenile *Macronectes giganteus.*

In the adult skull, the lateral palatine processes are well developed only in paleognathous birds and in some Procellariiformes, at least in the Diomedeidae (see Pycraft 1899: fig. 8, pl. 23). The drawings published by Hofer (1949: fig. 9) suggest their presence in the juvenile Ciconiidae. An apparently vestigial lateral palatine process was represented (but left unlabeled) in the hatchling of *Gallus* (Jollie, 1957: fig. 3).

Palatine The palatine is very similar to that in recent neognathous birds in having a distinct, choanal process, a distinct division between the corpus and the premaxillary process, and in details of the overlap with the maxillary. An identification of this bone as anything else would be justified only if another bone could be unequivocally identified as a palatine. The palatines were correctly identified by Marsh (1880) and mistaken for the vomer by recent students (Gingerich 1973, 1976, Witmer and Martin 1987).

The lacrimopalatine occurs in Struthionidae, Rheidae, Diomedeidae, Procellariidae, *Fregata,* some Cuculidae, Musophagidae, and Steatornithidae. In Hydrobatidae, *Pelecanoides,* and some other Cuculidae it is replaced by a ligament (Burton 1970). Such a distribution alone suggests that the presence of this bone is primitive for birds. Wellnhofer (1974) tentatively identified this ossicle in *Archaeopteryx.* As in *Hesperornis,* the palatine bears at least a slight projection for the connection with the lacrimopalatine in the Procellariiformes (personal observation).

Pterygoid Bones The hemipterygoid has been identified as a nonpalatine bone that articulated at its caudal end with the pterygoid, as revealed by KUVP 71012 (Gingerich 1976, and personal observation).

This bone has been misidentified as the vomer (Marsh, 1880) or the palatine (Gingerich 1976, Witmer and Martin 1987) despite the lack of resemblance to either. Since a postchoanal position of the vomer is unknown in any vertebrate, the vomer interpretation can be finally rejected. The palatine interpretation is not much more likely to be correct as the bone at issue is dissimilar to any avian palatine and there is another bone that shows detailed similarity to the neognathous palatine.

Furthermore, both of these two alternative interpretations identify a vomer as a pair of elements despite the fact that both theropods (Ostrom 1969) and birds have a single vomer, which in birds ossifies either from a single center (Erdmann 1940, Webb 1957) or the anlagen fuse soon after their appearance (Jollie 1957, Müller 1963). The only exception, not comparable in any other point to *Hesperornis,* are some specimens of one moa species, *Anomalopteryx didiformis* (Archey 1941: fig. 2, p. 127), which seem to have a pair of vomers, both fused to the palatine.

In view of this evidence, both the palatine and vomer interpretations are rejected. An extreme shortness of the pterygoid makes the presence of the hemipterygoid in *Hesperornis* not unexpected (Balouet 1983).

The hemipterygoid separates from the pterygoid and usually fuses with the palatine in the ontogeny of the majority of living birds except for the paleognaths, Galliformes, and Anseriformes; in a few other groups, the corresponding rostral part is present but not separated from the caudal part (Pycraft 1901). The hemipterygoid is clearly vestigial in recent birds although at least in some Procellariiformes the bone retains a considerable size: in a juvenile *Macronectes giganteus,* the hemipterygoid is at least as long as the pterygoid and shows a twist of planes comparable to that in *Hesperornis.*

The pterygoid of *Hesperornis* is dissimilar to that in any known bird. However, the dorsal wing of this bone in *Hesperornis* appears to be comparable to a dorsal ridge or flange in most other birds, the medial surface of which provides an insertion area for the M. protractor pterygoidei et quadrati. Prominent, winglike projections occur in *Diomedea* and *Gavia.*

The combined hempterygoid and pterygoid of *Hesperornis* are comparable to the whole pterygoid of *Deinonychus* (Ostrom 1969), which consists of two parts delimited by a sharp bend at the basipterygoid articulation. The hemipterygoid is similar to the long and slender rostral part of the pterygoid in *Deinonychus* in being twisted between the rostral and ventral portion and in bearing an articular surface on the lateral side of the somewhat shovel-like rostral end.

Braincase

Edinger (1951) redescribed the braincase fragment YPM 1207. Whetstone and Martin (1979) illustrated the Field Museum braincase FNMH PA219 and used it, without any prior description, for broad range comparisons with crocodiles. No serious attempts at the reconstruction of the whole braincase or detailed comparisons with other birds were ever published.

Most of the following information is derived from the asymmetrical occipital fragment YPM 1207, restored in part from pieces. The braincases of other known specimens are severely crushed, which makes most details of the original structure, including the sutures, difficult to distinguish from diagenetic damage. The interfrontal and frontoparietal sutures remain open in all specimens. The interparietal suture may have been partially obliterated in YPM 1206.

Cranial Cavity

Exposed in YPM 1207 is the ventral part of the cranial cavity (Fig. 4A), starting from the caudal wall of the tectal fossa. The preserved part of the caudal wall of this fossa (i.e., the rostral surface of the arcuate eminence) is approximately flat and somewhat irregular, which does not indicate a tight adherence of the optic lobe. The lateral wall of the fossa is very thick and thus leaves very little space for lateral expansion of the tectal fossa beyond

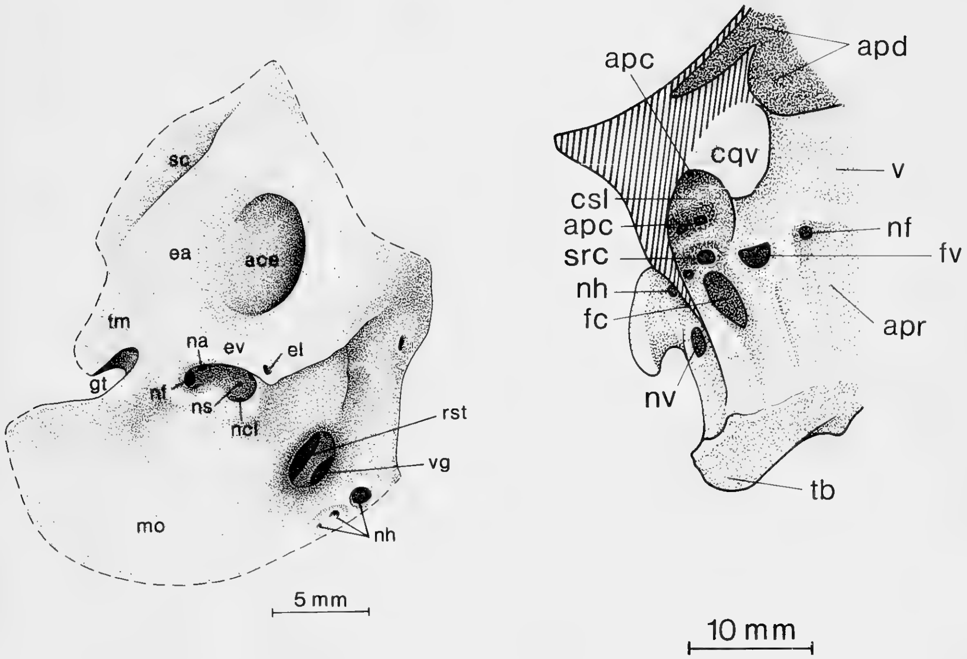

Fig. 4
YPM 1207. (*A*) Fragment of the cranial cavity. Abbreviations: *ace* Fossa auriculae cerebelli; *ea* Eminentia arcuata; *ev* Eminentia vestibularis; *el* Foramen endolymphaticum; *gt* Fossa ganglii trigemini; *mo* Fossa medullae oblongatae; *na* Foramen nervi ampullaris rostralis and Foramen nervi ampullaris lateralis; *ncl* Foramen nervorum cochlearis et lagenaris; *nf* Foramen nervi facialis internum; *nh* Foramina nervi hypoglossi; *ns* Foramen nervi saccularis; *rst* Recessus scalae tympani; *sc* Sulcus semicircularis; *tm* Fossa tecti mesencephali; *vg* Fovea ganglii vagoglossopharyngealis. (*B*) Reconstruction of the otic region. Abbreviations: *apc* Recessus pneumaticus caudalis; *apd* Recessus pneumaticus dorsalis; *apr* Recessus pneumaticus rostralis; *cqv* Cotyla quadrati medialis; *csl* Canalis semicircularis lateralis; *fc* Fenestra cochlearis; *fv* Fenestra vestibularis; *nf* Foramen nervi facialis externum; *nh* Foramen nervi hypoglossi caudale; *src* suprarecessal compartment; *tb* Tuberculum basilare; *v* preotic venous recess; *nv* Foramen nervi vagi. Hatching indicates the imaginary section, which certainly does not reflect precisely the shape of the involved structures.

the level of the trigeminal fossa. All this indicates that the tectal fossa was shallow and relatively smaller than it is in the majority of recent birds. The trigeminal fossa is elongate. Dorsal to the trigeminal fossa, a slit situated at the ventral end of the semicircular groove probably represents the Foramen venae cerebralis mediae.

The arcuate eminence, containing the rostral semicircular canal, is inclined inwards, approximately 25° from the parasagittal plane. The auricular fossa is large and has an oval entrance. At the caudal end of the vestibular eminence is the endolymphatic foramen and a tubercle with a slight crest extending dorsocaudad. Ventral to this crest and dorsal to the vagoglossopharyngeal fovea is a narrow, scarlike slit. A little pit with two internal minuscule openings lies near the lateral edge of the occipital foramen. The medullar fossa is broadest between the acoustic fossae; its bottom is only slightly concave. Contrary to Edinger (1951), three, not two, hypoglossal foramina are present, although the rostral foramen is very small. The acoustic fossae are elongate, approximately

Table 2
Measurements of the cranial cavity (YPM 1207) (in mm)

Fossa medullae oblongatae, maximum width (between the margins of acoustic fossae)	16.5
Fossa acustica	1.6 × 3.65
Foramen maxillomandibulare	1.9
Fossa auriculae cerebelli, deep part, long diameter	5.2
Fovea ganglii glossopharyngei, short (rostrocaudal) diameter	1.8
Foramen nervi hypoglossi	0.9 × 1.2
Foramen nervi vagi	1.25 × 1.7

twice the length of the height, and bipartite, with two groups of foramina: the rostral group for the facial, the rostral ampullar, and the lateral ampullar nerves; and the caudal group for the saccular, the caudal ampullar, the cochlear, and the lagenar nerves. The internal facial foramen is relatively large. The foramina for the rostral and the lateral ampullar nerves are only partly visible and the foramen for the caudal ampullar nerve is not visible in medial view.

Otic Region

The tympanic fossa and surrounding structures (Fig. 4B) are partly exposed on the right side of YPM 1207, the fossa itself being distinctly squeezed dorsoventrally. The two quadrate cotylae, the lateral (squamosal) and the medial (prootic), are adjacent to each other and caudal to, but not separated by, the dorsal pneumatic foramen. Ventral to this foramen and rostral to the medial quadrate cotyla is an excavation interpreted here as the obliterated Foramen venae cerebralis mediae and referred to as the pre-otic venous recess (Elzanowski and Galton 1991). Ventral to this recess is the caudal end of the rostral pneumatic recess, with the facial foramen in its caudodorsal corner.

The vestibular fenestra, although clearly flattened by diagenetic squeezing, suggests the original ostracode-like shape shown by Whetstone and Martin (1979: fig. 3), with the dorsal margin conspicuously straight. The vestibular fenestra is precisely ventral to the medial quadrate cotyla. The interfenestral bridge is relatively broad (not sharp). The cochlear fenestra is at least twice as high (long) as the vestibular fenestra. Dorsal to the Recessus scalae tympani and ventral to the caudal tympanic foramen, is an additional compartment—provisionally named here the suprarecessal compartment—with two small foramina perforating its bottom; it is delimited from the caudal tympanic foramen by a prominent, horizontal trabecula. The ventral end of the cochlear fenestra is extended by a short, shallow groove, probably indicative of the exit of the glossopharyngeal nerve through the Recessus scalae tympani. Ventral to the vestibular fenestra and rostral to the ventral part of the cochlear fenestra is a distinct vertical ridge.

Temporal Region and Cranial Base

The caudal region of the cranial base is well preserved in YPM 1207 (Figs. 5, 6). Marsh (1880: figs. 4, 5, pl. II) illustrated this specimen but totally ignored the foramina.

The nuchal crest extends onto the zygomatic process (YPM 1206). Situated on the occipital side of each zygomatic process (i.e., in the posttemporal position), is a horizontal pair of foramina for the branches of the Ramus occipitalis arteriae ophthalmicae externae. The occipital condyle is kidney shaped and, as revealed by KUVP 2287, built with substantial contribution from exooccipitals; as preserved in this specimen, the exooccipitals meet each other in the midline, over the basioccipital. On each side of the condyle are a distinct impression of the columellar muscle and three hypoglossal foramina (Figs. 5A, 6); the rostral hypoglossal

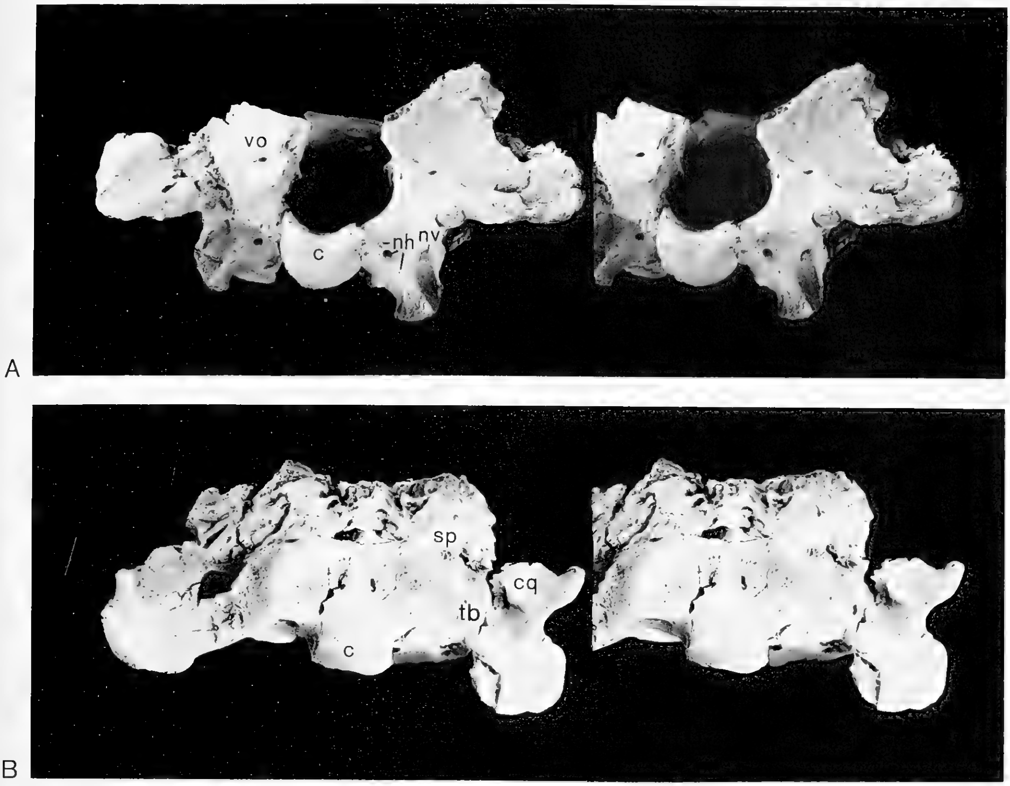

Fig. 5
Braincase fragment YPM 1207 in caudal (*A*) and ventral (*B*) view. Abbreviations: *c* Condylus occipitalis, *cq* Cotyla quadrati lateralis, *nh* Foramina nervi hypoglossi, *nv* Foramen nervi vagi, *sp* articulation surface for pterygoid, *tb* Tuberculum basilare, *vo* Foramen venae occipitalis externae.

foramen is vestigial and perforates the base of the basilar tubercle. The only other foramen lateral to the occipital condyle is the vagal foramen; absent on each side are the glossopharyngeal foramen, the carotid canal, and the sphenooccipital jugamentum.

The cranial base (Fig. 5B) does not reveal any pneumatization. The most prominent features of the cranial base are the large and deep precondylar fossa and the strong basilar tubercles in the marginal position, with their lateral slopes continuous with the wall of the tympanic cavity. Rostromedial to the left basilar tubercle of YPM 1207 is a triangular bony knob with a regular, smooth ventral surface (Fig. 5B: *sp*), which in all probability represents the pterygoid ("basipterygoid") process of the sphenoid, as indicated by Marsh (1880: fig. 4, pl. II).

Comparisons

Hesperornis shares with *Enaliornis* (Elzanowski and Galton 1991), *Phaethon*, and Diomedeidae a set of nine well-defined braincase characters (Table 3), seven of which are also present in *Fregata*. Seven (2–8) of these nine characters are certainly primitive for birds by virtue of being present in the braincase of *Archaeopteryx* (Whetstone 1983, Walker 1985) and theropods (Kurzanov 1976; Currie 1985; Raath 1985; see also Elzanowski and Galton 1991).

Fig. 6
Braincase fragment YPM 1207 in ventrolaterocaudal view. Abbreviations as in Figure 5.

Cranial Cavity Large auricular fossae, occupying the entire or almost entire area enclosed by the arcuate eminence, occur in *Enaliornis* (Elzanowski and Galton 1991), Phalacrocoracidae, Anhingidae, in most species of *Pelecanus* (except for *P. conspicillatus* and *P. onocrotalus,* which have the fossa constricted), in *Gavia,* Podicipedidae, Phoenicopteridae, and the Anseriformes including Anhimidae. In all these birds the caudal semicircular canal approaches the caudal arm of the rostral canal at very low angles and thus projects very little into the fossa. With the exception of a few anseriforms, especially the screamers, this feature appears to be correlated with the habit of feeding with the head submerged under water, which includes diving.

In most recent birds the acoustic fossa tends to be relatively shorter and more compact than in *Hesperornis.* The fossa is elongate and distinctly divided into two pits with a rostral and a caudal group of foramina, in *Enaliornis,* some specimens of *Phaethon* spp., *Diomedea, Larus, Catharacta,* some Podicipedidae, and *Grus.* However, this fossa is very variable in *Phaethon* and Podicipedidae, which makes conclusions based on single specimens uncertain.

The median ridge of the floor of the medullar fossa, certainly indicative of the division of the medulla oblongata by the Fissura mediana, is absent or poorly marked in *Hesperornis, Phaethon,* some Procellariiformes, *Fregata,* Sulidae, *Pelecanus,* Spheniscidae, *Gavia, Podiceps,* Alcidae and some other Charadriiformes including *Burhinus,* in *Mergus, Cariama, Ardea,* Gruidae, and Accipitridae. The presence and development of this ridge was found to be strongly variable at low taxonomic levels among recent birds.

Otic Region The evidence from the braincases of *Hesperornis* and *Enaliornis* confirms Walker's (1985: fig. 4) identification of

Table 3
Presence of nine braincase characters of *Hesperornis* in *Archaeopteryx* and the six most similar neornithine taxa.

	Archaeopteryx	*Enaliornis*	*Phaethon*	Diomedeidae	*Fregata*	Stercorariidae	Laridae
Prominent basilar tubercle in marginal position	2	2	2	2	0	0	2
No sphenooccipital jugamentum	(2)	2	2	2	2	0	0
No carotid canals	(2)	2	2	2	2	1	0
Exit of glossopharyng. nerve through Rec. scalae tympani	2	2	2	2	0	0	0
Suprarecessal compartment	2	2	2	2	2	0	0
Interfenestral bridge broad	2	2	2	2	2	1	1
For. n. maxillomandibularis in extreme caudal position	2	2	2	2	2	1	1
For. r. occip. art. ophth. ext. in posttemporal position	2	2	2	2	2	1	1
Nuchal crest extends onto zygomatic process	—	2	2	1	2	1	2

2 = similarity to *Hesperornis*; 0 = the opposite condition; 1 = an intermediate state; parentheses = a probable occurrence; and dash = condition not comparable. Data on *Archaeopteryx* from Walker (1985) and Whetstone (1983). For. n. = Foramen nervi; For. r. occip. art. ophth. ext. = Foramen rami occipitalis arteriae ophthalmicae externae; glossopharyng. = glossopharyngeal; Rec. = Recessus.

the vestibular fenestra, cochlear fenestra, and interfenestral bridge in the tympanic cavity of *Archaeopteryx*.

The Foramen nervi maxillomandibularis is caudal to the sphenoid (rostral tympanic) wing in *Phaethon, Fregata,* and some Procelariiformes including *Diomedea, Macronectes,* and *Fulmarus glacialis.* Aside from the presence of the sphenoid wing, the caudal position of the maxillomandibular foramen is considered primitive by comparison to *Archaeopteryx* (Walker 1985: fig. 4) and theropods including *Itemirus* (Kurzanov 1976: figs. 2, 3) and *Stenonychosaurus* (Currie 1985: figs. 4, 5).

The medial quadrate cotyla is typically sessile in *Enaliornis,* Pelecaniformes, Procellariiformes, Accipitridae, *Sagittarius, Pandion,* Ciconiidae, Cathartidae, Spheniscidae, *Gavia,* Glareolidae, *Ibidorhyncha, Dromas,* Stercorariidae, Laridae, *Rynchops,* Alcidae, most Charadriidae, *Scopus,* Phoenicopteridae, Ardeidae, Pteroclidae and some Podicipedidae, *Limosa* (Scolopacidae), some Recurvirostridae, some Burhinidae, and some Falconidae. In the majority of other birds the medial cotyla is in a more rostral position and supported caudally by a peduncle ("Pila prootica") as illustrated by Lowe (1926: "opisthotic columella"). In a few families the medial cotyla is in an intermediate position. The sessile condition and caudal position of this cotyla is almost certainly primitive since the peduncle is undoubtedly a postadaptive structure that evolved after the ventral quadrate articulation came into being and no structure comparable to the peduncle is known in the reptilian outgroup taxa. The quadrate of *Archaeopteryx* has been thought to be single-headed, but recently Haubitz et al. (1988) provided evidence for a bulky medial head. If this is the case, then the concavity in the prootic, interpreted by Walker (1985) as the "superior tympanic recess" (*str*), may represent the medial, obviously sessile cotyla for the quadrate.

The suprarecessal compartment is present in *Phaethon, Fregata,* and Diomedeidae and appears to be present in *Enaliornis.* It is variably developed in the Sulidae and in some of them is incorporated into the caudal tympanic recess. In the nondiomedeid Procellariiformes and Ciconiidae, the caudal tympanic recess is divided by an oblique rather than a horizontal septum, approximately parallel to the interfenestral crest. In *Archaeopteryx* (Walker 1985: fig. 4), there is a cavity (*pn*) between the cochlear fenestra (*fpr*) and the caudal tympanic recess (*ptr*) that corresponds in position to the suprarecessal compartment, although it is separate from the Recessus scalae tympani.

The interfenestral bridge (Crista interfenestralis) has the form of a narrow, sharp and essentially linear ridge in the majority of recent birds. As in *Hesperornis,* it is flat and relatively broad, 20–50% of the diameter of the vestibular fenestra, only in *Enaliornis,* Pelecaniformes, Procellariiformes, and Spheniscidae. In the Ciconiidae and *Scopus,* this bridge is intermediate in width. In Laridae and Stercorariidae the bridge is broad only ventrally. In *Archaeopteryx* the bridge seems to be slender (Walker 1985, but see also Whetstone 1983: fig. 7B) but not sharp. In the theropod *Stenonychosaurus* (Currie 1985: fig. 5) the bridge is broad.

Phaethon and Diomedeidae have a distinct vertical ridge, ventral to the vestibular fenestra; in Sulidae the ridge is oblique.

Temporal Region In most birds, the zygomatic process is far rostral to the lateral extension of the nuchal crest. The crest continues onto the zygomatic process in *Enaliornis,* Pelecaniformes including *Prophaethon* (Harrison and Walker 1976: pl. I, fig. C), in Ciconiidae, Spheniscidae, Laridae, *Rynchops,* some Alcidae (e.g., *Uria*), some Podicipedidae. This condition is approached in *Dromas,* Stercorariidae and many Procellariiformes including Diomedeidae, larger Procellariidae, and *Pelecanoides.* However, in *Fregata, Pelecanoides,* Pelecanidae, Ciconiidae and Spheniscidae it is only the rostral branch of the bifurcating crest that continues onto the zygomatic process. The extension of the nuchal crest onto the zygomatic process may also prove to be primitive inasmuch as it is correlated with the caudal position of the zygomatic process and quadratotemporal articulation. Nothing comparable to the zygomatic process is known in *Archaeopteryx* and theropods, in which the squamosal is not incorporated into the braincase.

A horizontal pair of foramina for the Ramus occipitalis arteriae ophthalmicae externae (and associated vessels) were found in the posttemporal position (i.e., laterally on the occipital plate), with openings close to each other, in *Enaliornis, Phaethon, Prophaethon* (Harrison and Walker 1976: pl. I. fig. E), Diomedeidae (in other procellariiforms the lateral foramen perforates the nuchal crest or is in a temporal position), *Fregata,* most Falconiformes, Ciconiidae and *Scopus* (in the latter two groups there may be only one common opening). In Laridae and Stercorariidae, the lateral opening is on, or very close to, the nuchal crest. *Archaeopteryx* has only one foramen in the posttemporal position (Walker 1985: fig. 6). In the majority of recent diving birds, the lateral foramen perforates the nuchal crest.

Cranial Base Pneumatization of the cranial base, typical for terrestrial and aerial birds, is strongly reduced or absent in other diving birds including Phalacrocoracidae, Spheniscidae, and *Pelecanoides,* but remains extensive in Podicipedidae and *Gavia,* and appears variable among the Alcidae.

Prominent basilar tubercles in the marginal position, with their lateral slopes continuous with the wall of the tympanic cavity, occur in *Enaliornis, Phaethon,* Sulidae, Phalacrocoracidae, *Anhinga,* large Procellariiformes (Diomedeidae, *Macronectes*), Spheniscidae, Laridae, and *Rynchops.* This character is considered primitive by comparison to *Archaeopteryx* (Whetstone 1983: fig. 6) and reptiles, in particular the theropod *Itemirus* (Kurzanov 1976: fig. 2, "spheno-occipital tubercles").

The sphenooccipital jugamentum is absent in *Enaliornis, Phaethon, Fregata,* Procellariiformes, Ciconiidae, *Scopus,* Phoenicopteridae, and many Charadriiformes including *Dromas, Haematopus, Chionis,* Alcidae, Recurvirostridae, Thinocoridae and some Scolopacidae. The jugamentum is poorly developed in Lari (virtually absent in many Stercorariidae), some Scolopacidae and Jacanidae, *Gavia*, Spheniscidae, and, in a different way, in Podicipedidae. The jugamentum is absent or poorly developed in all those birds with poor development of the caudal tympanic wing, which leaves the tympanic cavity open caudoventrally, as in *Enaliornis, Hesperornis, Phaethon, Fregata,* Procellariiformes, and Lari. Correlated with the lack of the jugamentum is the lack of a well delimited parabasal fossa and of the common entrance for the Arteria ophthalmica externa (stapedial artery) and Vena capitis lateralis. This character complex is considered primitive by comparison to reptiles including the small theropods *Itemirus* (Kurzanov 1976: figs. 1, 2), *Stenonychosaurus* (Currie 1985: fig. 4), and *Syntarsus* (Raath 1985: fig. 1).

The caudal ostia and canals for the internal carotids are absent in *Enaliornis, Phaethon,* Procellariiformes, and *Fregata* (Wingstrand 1951, p. 262; Saiff 1988: table 1). The canals are absent also in Sulidae, Pelecanidae, *Scopus,* and (contrary to Saiff 1988) Ciconiidae, but the entrance of the internal carotids is marked by the carotic foramen perforating the margin of the basilar plate. The canal is entirely open (i.e., only its medial wall is present) in Laridae and Stercorariidae, and it may be partly open in several other birds. The lack of carotid canals crossing the tympanic cavity is considered primitive by comparison to reptiles.

The vagal foramen is in a marginal position and the separate glossopharyngeal foramen is lacking in *Enaliornis, Phaethon,* Diomedeidae, and some Procellariidae, in all of which the glossopharyngeus exits through the Recessus scalae tympani (Saiff 1974, 1976, 1978). The lack of the glossopharyngeal foramen and the presumed exit of the nerve through the Recessus scalae tympani are considered primitive by comparison to *Archaeopteryx* (Whetstone 1983, Walker 1985) and small theropods including *Syntarsus* (Raath 1985), *Stenonychosaurus* (Currie 1985), and *Itemirus* (Kurzanov 1976).

The marginal position of the basilar tubercles and vagal foramen and the lack of the glossopharyngeal foramen, carotid canals, and sphenooccipital jugamentum may be all developmentally correlated as these features seem to result from the lack of ossification potential of the circumtympanic region of the cranial base.

Comparison to *Enaliornis* The similarity to *Enaliornis* goes beyond the set of nine characters shared with the recent taxa (Table 3). The large size of the auricular fossae is probably correlated with diving habits (Elzanowski and Galton 1991). An overall similarity of the cranial base may be due in part to the primitive braincase structure in both genera and in part to the similarity of feeding specialization. A vestigial rostral hypoglossal foramen and an open frontoparietal suture are primitive by virtue of being reptilian. The elongate and bipartite shape of the internal acoustic fossa seems to be of little systematic value (see above).

Edinger (1951) demonstrated that Marsh's (1880) interpretation of the *Hesperornis* brain as being "more reptilian in type than in any adult bird hitherto examined" is unfounded. However, it is impossible to determine whether or not *Hesperornis* had the primitive features of the *Enaliornis* brain as the braincase specimens of *Hesperornis* do not permit a reconstruction of the brain comparable to that done for *Enaliornis* (Elzanowski and Galton 1991).

The *Hesperornis* braincase differs from that of *Enaliornis* in having a more perpendicular occipital plate; an unpneumatized cranial base; shallower medullar and tectal fossae; lower dorsum sellae (judging from the broken dorsum in YPM 1207); the trigeminal fossa open to the tectal (not medullar) fossa; and much stronger muscular attachment structures on the skull roof. A more perpendicular occipital plate, a shallower medullar fossa, and the difference in connections of the trigeminal fossa suggests a more orthocranial conformation of the skull, which is a known specialization of fish-eating birds. Reduction of pneumatization certainly correlates with diving specialization. The biological significance of a small tectal fossa in *Hesperornis,* which is most comparable to that in Diomedeidae, is not clear; it may indicate a lesser importance of vision in relation to the olfactory perception, as in some Procellariiformes (Wenzel, 1973).

The cranial evidence neither contradicts nor supports, but certainly places a caveat on the hypothesis of closer genealogical relationships between *Enaliornis* and Hesperornithiformes (Martin and Tate 1976). If real, this relationship will be difficult to prove because the two taxa differ strongly in details of both the braincase and the leg bones, and certainly share both primitive features and diving specializations, the latter being inconclusive as the only or primary evidence for closer relationships. The braincases of primitive diving birds may be very similar independently of relationships.

Phylogenetic Comments

Interpretation of the skull of *Hesperornis,* as of many other fossils, is drastically limited by our ignorance of comparable details in the living forms. Nevertheless, *Hesperornis* revealed a surprisingly consistent pattern of cranial similarities to *Enaliornis* and some recent birds including *Phaethon,* Procellariiformes, and *Fregata.* These similarities are unlikely to be convergent either as external adaptations, because of being shared despite strong differences in habits, or as inertial products of developmental heterochronies because of being shared despite strong differences in size; an inertial paedomorphosis, which prima facie could be responsible for the limited ossification of the circumtympanic region of the cranial base in a group of small birds, is unlikely in *Hesperornis* and Diomedeidae, which are large and do not reveal other paedomorphic features. In the absence of counterevidence, the cranial similarities between *Hesperornis, Enaliornis,* and the named recent taxa are considered here to be homologous. The Mesozoic age of *Enaliornis* and *Hesperornis,* some evidently primitive characters such as the presence of teeth, and the comparisons to *Archaeopteryx* and theropods suggest that most, if not all, of these similarities are primitive.

The skull of *Hesperornis* is neognathous in having the intrapterygoid joint, the palatine with a slender Processus praemaxillaris and a hook-shaped Processus choanalis, the premaxillary with paired frontal processes, and in lacking the lateral bracing of the quadrate by the zygomatic process. The maximum number of the palatal characters of *Hesperornis* are present in some Procellariiformes, especially the Diomedeidae, which is consistent with the evidence from the braincase.

The only characters that are at present unique to the paleognaths (i.e., the caudal position of the basipterygoid articulation and the lack of fusion between premaxillary and maxillary) are demonstrably reptilian and thus do not provide evidence for closer relationships between paleognaths and *Hesperornis.* Instead, they support the view that the paleognaths are one of the most primitive groups of living birds, not far in the branching order from the procellariiform and *Phaethon* lineages.

The presence of reptilian and primitive neornithine characters that are absent in other neognaths suggests that the hesperornithiforms are the earliest known branch of the neognathous birds. Although very consistent, the similarities to Procellariiformes, *Phaethon,* and *Fregata* are mostly primitive and thus suggest that these are the oldest branches of living neognaths. There is very little evidence in support of closer relationships of these recent groups to the Hesperornithiformes.

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