THE PRIMITIVE FEATURES OF THE AVIAN PALATE, WITH SPECIAL REFERENCE TO MESOZOIC BIRDS

LES CARACTERES PRIMITIFS DU PALAIS AVIEN AVEC REFERENCE SPECIALE AUX OISEAUX MESOZOIQUES

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Abstract

The evolution of the avian palate has been a subject of great interest for over a century. Recently the primitive - derived sequences (i. e., character polarities) of the relevant features have become confused. Outgroup comparisons with theropod dinosaurs, crocodiles and other archosaurian reptiles suggest a number of palatal features that may be ancestral for birds. Ratites and tinamous exhibit a large number of these primitive features. Having polarized various palatal characters, we tested these polarities by examining the palates of Mesozoic birds. *Archaeopteryx*, *Gobipteryx*, and the hesperornithids were analysed. Although *Archaeopteryx* is too poorly known to reconstruct the palate, it shows a number of primitive features ; the identification of one of the bones as an ectopterygoid is questioned. *Gobipteryx* also exhibits many plesiomorphies and retains the elongate pterygoids of non-avian archosaurs. The palate of hesperornithid birds is reconstructed and shown to be widely divergent morphologically from other archosaurs ; it retains a few primitive features while showing several clear autapomorphies.

KEY-WORDS : *Archaeopteryx*, archosaur, cladistics, fossil birds, *Hesperornis*, morphology, neognathous, palaeognathous, palate, ratites.

Résumé

Depuis plus d'un siècle l'évolution du palais avien a été un problème d'un grand intérêt. Récemment les séquences «primitif-dérivé», c'est-à-dire la polarisation des caractères pour les caractères pertinents, sont devenues confuses. Les comparaisons extra-groupes (outgroup comparisons) avec certains dinosaures théropodes, les crocodiles et d'autres reptiles archosauriens suggèrent un certain nombre de caractères palatins pouvant être ancestraux pour les oiseaux. Les Ratites et les Tinamous possèdent plusieurs de ces caractères primitifs. Ayant établi la polarité de plusieurs caractères palatins, nous avons testé ces polarités en examinant le palais d'oiseaux mésozoïques. Les conditions retrouvées chez *Archaeopteryx*, *Gobipteryx* et les Hesperornithiformes ont été analysées. Bien que le palais d'*Archaeopteryx* soit trop peu connu pour permettre sa reconstitution, il possède toutefois un certain nombre de caractères primitifs ; l'identification d'un des os comme étant un ectoptérygoïde est remise en question. *Gobipteryx* présente aussi plusieurs plésiomorphies et conserve les ptérygoïdes allongés retrouvés chez les Archosaures non-aviens. Le palais des Hesperornithiformes est reconstruit et montre une grande divergence morphologique par rapport à celui d'autres Archosaures ; il conserve quelques caractères primitifs mais présente en même temps plusieurs autapomorphies distinctes.

MOTS-CLES : *Archaeopteryx*, archosaure, cladistique, *Hesperornis*, morphologie, palais néognathe, oiseaux fossiles, palais paléognathe, ratites.

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I. INTRODUCTION

In 1867 Thomas Henry Huxley based a classification of birds on palatal morphology. Since that time the avian palate has received more attention than perhaps any other aspect of avian osteology. The scientific literature on the avian palate is extensive, and throughout the past century many attempts have been made to trace the palatal evolution of birds. A discussion of the entirety of the evolution of the palate of birds is beyond the scope of this contribution, but it is instructive to investigate the earlier stages. By studying the palates of the reptiles closest to birds, i. e. the archosaurs, we can perhaps determine those features that are ancestral for birds (outgroup analysis). In this way it is possible to determine character polarities useful for phylogenetic and functional morphological analyses.

Character polarities, however, are nothing more than hypotheses and as such are subject to falsification through hypothesis-testing. One possible test of character polarities is to determine whether or not the earliest known fossils of the group exhibit the plesiomorphic features. A significant flaw in this approach is that early forms may show derived characters while later forms may show primitive characters due to differing rates of evolution between clades. Bearing this fact in mind, it is still clear that as older and older taxa are sampled, the probability of encountering primitive characters increases. Thus, while inconclusive, this technique is instructive both in elucidating character evolution in the modern forms and, often more interestingly, in determining the significance of the variance from plesiomorphy in the early forms.

In order to determine palatal plesiomorphies we will perform outgroup analysis, look at possible relationships of extant taxa, and test these hypotheses of character polarity against the palates of geologically early birds. Three orders of Mesozoic birds have palatal material sufficiently preserved to permit discussion : the Archaeopterygiformes, Gobipterygiformes, and Hesperornithiformes.

Previous work on the evolution of the avian palate has looked primarily at extant (or recently extinct) taxa—in particular the "ratites". Most studies have examined the "palaeognathous palate" of the ratites and tinamous and have considered it primitive (e.g., Huxley, 1867 ; Pycraft, 1900 ; Simonetta, 1960 ; Gingerich, 1973 ; Houde and Olson, 1981 ; Balouet, 1982 ; Rich and Balouet, 1984 ; Olson, 1985) or derived through paedomorphosis (e.g., de Beer, 1956 ; Bock, 1963 ; Cracraft, 1974, 1981).Of these, only Gingerich, Balouet, and Rich and Balouet, drew evidence from non-avian taxa.

II. NON-AVIAN ARCHOSAURS : POSSIBLE ANCESTRAL CHARACTERS

It is widely accepted that birds are derived from archosaurian reptiles. It is thus in the non-avian archosaurs that one should search for the ancestral palatal features of birds. Ideally one would need to look no further than to the immediate outgroups of birds for palatal plesiomorphies. The ancestry of birds, however, is not entirely settled. While many workers follow Huxley (1868) in considering birds the sister-taxon of coelurosaurian dinosaurs (e.g., Ostrom, 1976 ; Padian, 1982), others (e.g., Martin, 1983 a, b ; Tarsitano, 1985) consider bird/crocodile monophyly a valid hypothesis. See Martin (1983b) for a review of this problem.

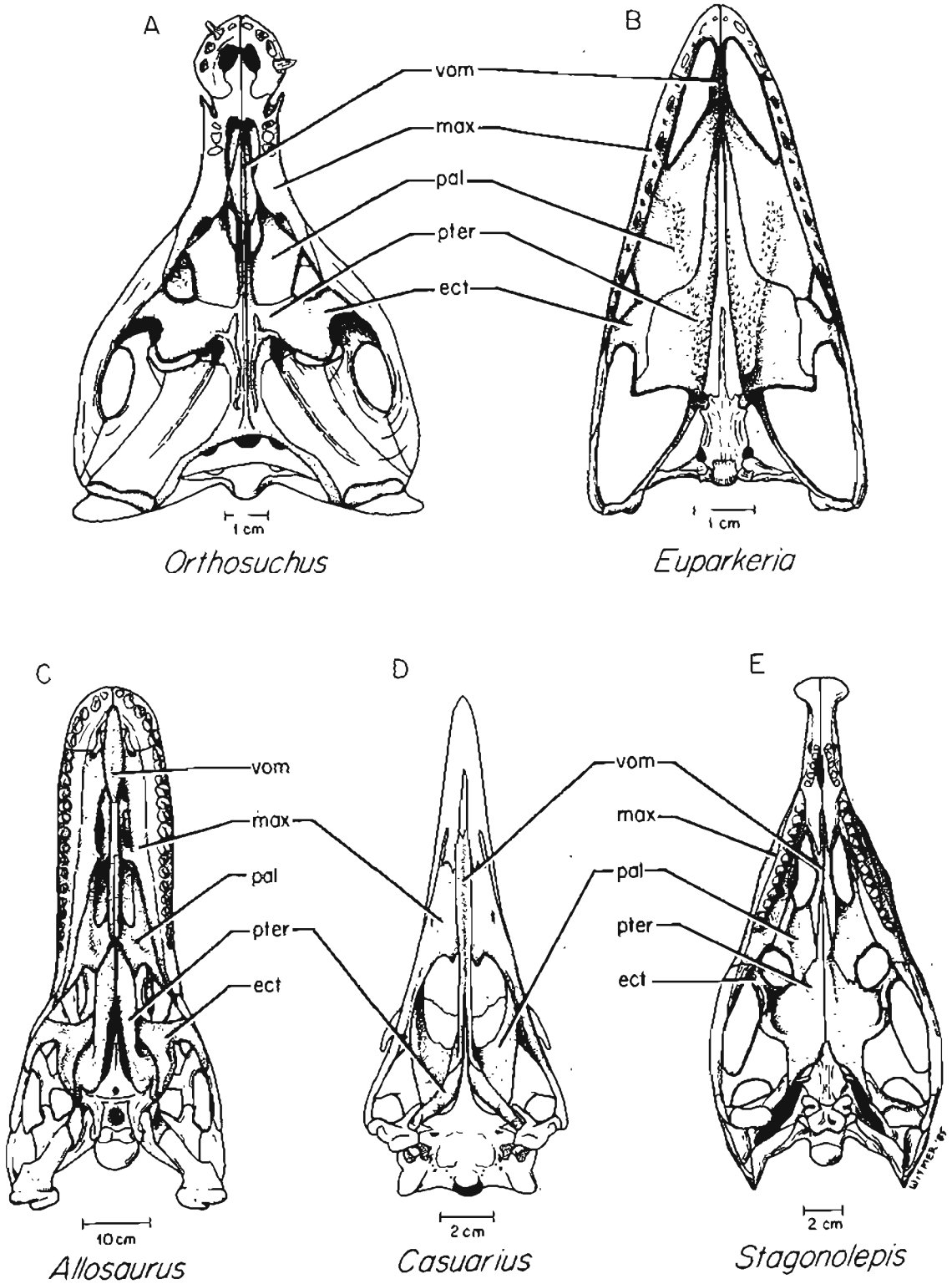
It is probably safe to assume that certain features common to all fossil archosaurs may be ancestral for birds, regardless of which specific group may be more closely related to birds. We therefore have compared the palates of theropod dinosaurs (e.g., *Allosaurus*, fig. 1C), Triassic crocodiles (e.g., *Orthosuchus*, fig. 1A), and also "thecodonts" (e.g., *Euparkeria*, fig. 1B and *Stagonolepsis*, fig. 1E). The palatal features shared by these taxa may be, at least in part, symplesiomorphies of a clade including birds. Below are listed some of these shared features.

1. CONTACT OF THE PTERYGOID AND VOMER : A vomeropterygoid articulation is the rule not only in archosaurs but in almost all tetrapods. This primitive relationship is very conservative as indicated by the elongate vomerine ramus of the pterygoid in forms with short vomers (e.g., *Euparkeria*, fig. 1 B) and the elongate pterygoid ramus of the vomer in forms with short pterygoids (e.g., *Casuarius*, fig. 1 D).

2. PTERYGOIDS AND VOMERS EXCLUDE THE PALATINES FROM THE MIDLINE : Anterior to the interpterygoid vacuities the pterygoids and vomers form a median bony floor to the palate which by necessity prevents the palatines from contacting each other. Primitively in amniotes the palatines are widely separated, but in archosaurs they often approach, but very rarely contact, each other.

3. ELONGATE PTERYGOIDS : In non-avian archosaurs the vomerine rami of the pterygoids are elongate and extend well past the orbits anteriorly. In *Proterosuchus* (Cruickshank, 1972), the earliest well-known archosaur, the pterygoids are extensive elements with a length approximately 60 % that of the skull as a whole ; in *Euparkeria*, (fig. 1B) they are even larger, running about two-thirds the length of the skull (Ewer, 1965).

4. PALATINES CONTACT THE MAXILLAE BUT NOT THE PREMAXILLAE: The typical archosaurian condition is for the palatine bone to contact the pterygoid (and often vomer) posteriorly and medially and the maxilla anteriorly and laterally. The palatine is usually separated from the premaxilla by the vomer and sometimes the maxilla. In a few occasions the palatine contacts the premaxilla as in some (but not all) phytosaurs (Case, 1929) and pterosaurs (Wellnhofer, 1978).


A
B
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1 cm
Orthosuchus
Euparkeria
C
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10 cm
2 cm
2 cm
Allosaurus
Casuarius
Stagonolepis

5. VOMERS CONTACT PREMAXILLAE : Contact of the vomer to the premaxilla is primitive for tetrapods as a whole, as well as for archosaurs. This relationship is maintained in most taxa, but in those forms exhibiting development of a secondary or "false" palate the premaxillovomerine articulation is lost. For example, in crocodiles the formation of a tubular secondary palate has severed this contact, even in the earliest stages (e.g., *Orthosuchus*, fig. 1A). Likewise, in some theropods with a secondary palate (e.g., *Oviraptor*, Osmolska, 1976 ; *Gallimimus*, Osmolka, *et al.*, 1972), the primitive situation has been modified.

6. PRESENCE OF ECTOPTERYGOIDS : Ectopterygoids are found in all non-avian archosaurs with no known exceptions.

7. PALATAL BONES ARTICULATE BY IMMOVABLE SUTURES : The bones of the palate of non-avian archosaurs generally articulate by long sutures with little if any relative movement between bones. This does not necessarily preclude cranial kinesis ; in fact, kinesis has been suggested at one time or another (with varying success) for almost all archosaurian taxa.

8. PRESENCE OF BASIPTERYGOID PROCESSES : Basipterygoid processes are present in all non-avian archosaurs and form the articulation between the braincase and palate. The pterygoid bones articulate with these processes toward the posterior end of the bone.

Two additional characters may be ancestral for birds, not because they are found within archosaurs as a whole, but because of their presence in the two leading candidates for a close relationship to birds, crocodiles and theropod dinosaurs.

9. PALATAL PROCESSES OF THE MAXILLAE FORM ANTERIOR TO THE INTERNAL NARES THUS ENCLOSING A FALSE OR SECONDARY PALATE : Within *Vertebrata*, eusuchian crocodiles have the most highly derived secondary palate, in which the choanae are fully within the pterygoids. Early crocodylomorphs (e.g., *Orthosuchus*, fig. 1A), however, have only the beginnings of this system, and the internal nares are posterior to the maxilla. Various, but not all, theropods have some development of a secondary palate. As mentioned, in the caenagnathid *Oviraptor* and the ornithomimid *Gallimimus* the choanae are posterior to the palatal processes of the maxillae. This is also the condition in the carnosaurs *Allosaurus* (fig. 1C ; Madsen, 1976) and *Tyrannosaurus* (Osborn, 1912 ; SDSM 12047). This, however, apparently was not the situation in the deinonychosaurs, the dinosaurs postulated by Ostrom (1976) and Padian (1982) to be closest to birds. Ostrom (1969, fig. 5) reconstructed *Deinonychus* without palatal processes of the maxillae.

10. PRESENCE OF A MAXILLARY AIR SINUS : The maxillae of theropod dinosaurs are characterized by the development of sinuses and chambers within the bone. Their position suggests that these maxillary sinuses were formed by diverticula from the nasal cavity. Crocodilians also have diverticula from the nasal cavity pneumatizing the maxillary bones. The phylogenetic level at which these maxillary sinuses arose is uncertain, and at least one group of "thecodonts", the rauisuchians (e.g., *Postosuchus*, Chatterjee, 1985) have some development of maxillary sinuses.

Fig. 1 – **Palatal views of the skulls of A, *Orthosuchus sternbergi*, a Triassic crocodilian ; B, *Euparkeria capensis*, a Triassic thecodont ; C, *Allosaurus fragilis*, a Jurassic theropod dinosaur ; D, *Casuarius casuarius*, a Recent cassowary ; and E, *Stagonolepis robertsoni*, a Triassic aetosaur.** Abbreviations : **ect**, ectopterygoid ; **max**, maxilla ; **pal**, palatine ; **pter**, pterygoid ; **vom**, vomer. (Redrawn from A Nash, 1975 ; B Ewer, 1965 ; C Madsen, 1976 ; E Walker, 1964).

Fig. 1 – **Face inférieure des crânes A, d'*Orthosuchus sternbergi*, un crocodile triasique ; B, d'*Euparkeria capensis*, un «thécodonte» triasique ; C, d'*Allosaurus fragilis*, un dinosaure théropode jurassique ; D, de *Casuarius casuarius*, un casoar récent ; et E, de *Stagonolepis robertsoni*, un aétosaure triasique.** Abréviations : **ect**, ectoptérygoïde ; **max**, maxillaire ; **pal**, palatin ; **pter**, ptérygoïde ; **vom**, vomer. (D'après A Nash, 1975 ; B Ewer, 1965 ; C Madsen, 1976 ; E Walker, 1964).

III. THE PRIMITIVE PALATAL FEATURES OF MODERN BIRDS

Table I presents the distribution of these primitive characters within modern birds which are here divided into the two superorders *"Palaeognathae"* and *Neognathae*. To briefly summarize, palaeognaths show many of the primitive features, while neognaths are relatively specialized. The taxon name *«Palaeognathae»* is placed in quotes because it is not demonstrably monophyletic.

A. *"PALAEOGNATHAE"*

Traditionally, the evolution of the palate of birds has been thought to proceed from the "dromaeognathous" (Huxley, 1867) or "palaeognathous" (Pycraft, 1900) palate characteristic of ratites and tinamous to the "neognathous" palate characteristic of non-tinamiform carinates. In other words, the palaeognathous palate is primitive. It is probably best to avoid the typological constructs of "palaeognathous palate'" and "neognathous palate" when discussing primitive - derived sequences. As McDowell (1948) has correctly pointed out, there is no archetypical definition of these terms that applies to all morphologies. Instead, it is better to consider specific features of a palate and decide if those features are primitive or derived. In other words, "palaeognathous palate" is not a taxonomic character. The terms palaeognath and neognath are useful, however, but should be restricted to taxon names, for examples : *«Palaeognathae»* and *Neognathae*. Pycraft (1900) erected the *Palaeognathae* to include the ratites and tinamous, replacing Huxley's (1867) *Dromaeognathae* which included only tinamous. Pycraft (1900) explicitly considered his *Palaeognathae* polyphyletic and implied their paraphyly. The *Palaeognathae* remained a superorder of birds in avian systematics (e.g., Wetmore, 1930, 1940) until McDowell (1948) questioned its naturalness. Later classifications (e.g., Wetmore, 1951 ; Mayr and Amadon, 1951) omitted the *Palaeognathae/Neognathae* dichotomy. In 1974, Cracraft resurrected the *Palaeognathae* as a monophy-

Table 1

PRIMITIVE PALATAL CHARACTERS	*AR*	*GO*	*HE*	PA	NE
1. Contact of vomer & pterygoid	?	yes	no	yes	var.
2. Pter. & vom. exclude pal. from midline	?	yes	yes	yes	no
3. Pterygoids elongate	yes?	yes?	no	no	no
4. Pal. contact max. but not premax.	?	yes?	yes	yes	no
5. Vomers contact premaxillae	yes?	?	no	yes	no
6. Ectopterygoids present	no?	no	no	no	no
7. Palatal bones joined by immovable sutures	?	yes?	no?	yes	no
8. Basipterygoid processes present	?	?	no?	yes	var.
9. Palatal proc. max. form false palate	yes	yes	yes	yes	yes
10. Maxillary sinus present	yes	yes	yes	yes	yes

AR = *Archaeopteryx* *GO* = *Gobipteryx* *HE* = *Hesperornis* PA = "Palaeognathae"
NE = Neognathae var. = variable

Table 1 – **Distribution of primitive palatal characters (determined by outgroup comparison with non-avian archosaurs) over five avian taxa.**

Tabl. 1 – **Distribution des caractères primitifs du palais (déterminés par comparaison extra-groupe avec les archosaures non-aviens) pour cinq taxons aviens.**

letic taxon (his Order Palaeognathiformes) on the basis of three characters (one of which was the "palaeognathous palate"). As Olson (1985) correctly noted, all three characters are primitive and as such cannot be used as synapomorphies. The status of this group will not be rigorously assessed here. See Olson (1985) for a discussion of the problem of the "palaeognathous" birds. Claims that the palate of ratites and tinamous can be derived through paedomorphosis from a neognath (e.g., de Beer, 1956 and many others), although feasible, remain unsubstantiated. The ratites and tinamous form a useful phenetic cluster and we will use the terms *"Palaeognathae"* and palaeognath provisionally with no implications of monophyly. Despite the amount of research already invested in this problem, more work is warranted.

As Table 1 indicates, palaeognaths exhibit a large number of primitive palatal characters. Some of these features, for example characters 1, 2, 4, 5, 7, and 8 were among those cited by Bock (1963) as defining the ratite palate. There are, of course, exceptions. For example, *Struthio* lacks a vomeropterygoid contact (character 1), but this has been considered as a specialization by essentially all workers. Also, in tinamous the palatine often contacts the premaxilla (character 4). Palaeognaths are not uniformly primitive, however. In all modern birds the pterygoids are drastically shortened relative to non-avian archosaurs (character 3) and do not extend past (or even approach) the anterior margin of the orbit. Likewise, no modern bird is known to have an ectopterygoid (character 6). We do not accept McDowell's (1978) homology of the reptilian ectopterygoid with the avian os lachrymopalatinum for reasons that will be discussed in another paper.

B. *NEOGNATHAE*

Based on this analysis the *Neognathae* form a monophyletic unit. They exhibit the primitive characters of a secondary palate formed by palatal processes of the maxilla (character 7; these processes, the "maxillopalatines", are reduced in some lineages) and the presence of maxillary sinuses (character 8). Character 1, the vomeropterygoid articulation, is scored as variable because in most neognaths the embryonic pterygoid segments (i.e. splits), with the anterior portion fusing to the palatine and the posterior portion remaining free and articulating with the anterior portion by a joint (Pycraft, 1900, 1901). Thus in neognaths the plesiomorphic vomeropterygoid articulation present in the embryo is obscured in the adult by pterygoid segmentation. This itself is a synapomorphy of neognath birds, and Balouet (1982) considered virtually all other features of neognaths a consequence of pterygoid segmentation. Some neognath lineages suppress segmentation and as such show an apparent reversal to the primitive condition.

C. SUMMARY

Thus, palaeognaths exhibit many palatal plesiomorphies based on outgroup comparison with non-avian archosaurs. All modern birds share the derived characters of shortened pterygoids (character 3) and loss of the ectopterygoids (character 6). Neognaths exhibit the following synapomorphies : pterygoid segmentation (character 1), palatines not excluded from the midline (character 2), palatines contact the premaxilla (character 4), the vomer not contacting the premaxilla (character 5), and formation of an intrapterygoid joint (character 7).

IV. MESOZOIC BIRDS

A. *ARCHAEOPTERYX*

Archaeopteryx lithographica from the Upper Jurassic Solnhofen limestone of Bavaria, West Germany is the oldest known bird and has generated an immense literature (see Ostrom, 1976 for a review). Five skeletal specimens of this most reptilian of all birds have been discovered thus far, but only three include cranial material.

1. The London skull

The skull of the "London" specimen consists of an intact braincase (described by Whetstone, 1983) with a possible skull bone nearby on the main slab and, on the counterslab, scattered skull bones including the left premaxilla, a fragment of the right maxilla, both nasals, a lacrimal, and an unidentified cranial element. The London specimen, therefore, supplies little useful information on the palate

2. The Berlin skull

Likewise, the "Berlin" *Archaeopteryx* is of little help in reconstructing the palate. The skull is poorly preserved and crushed flat. Only general features can be discerned, such as the size and shape of the skull, orbit, antorbital fenestra, and external nares. Few if any sutures can be identified with confidence. The hyoid is surprisingly well preserved. Even Heilmann (1926), who drew a famous, if imaginative reconstruction of *Archaeopteryx*, did not attempt to reconstruct a ventral view from this specimen. A palatal reconstruction was provided, however, by Kleinschmidt (1951) who considered the Berlin specimen to be neognathous and schizognathous (*sensu* Huxley, 1867). There is no evidence for Kleinschmidt's reconstruction, a fact that has been recognized by most workers (e.g., Simonetta, 1960; Gingerich, 1973). Nevertheless, some investigators, seeking any available evidence for an apomorphic palaeognathous palate (e.g., de Beer, 1956 ; Cracraft, 1974), have cited Kleinschmidt.

3. The Eichstätt skull

Although study of the London and Berlin specimens of *Archaeopteryx* yields little in the way of palatal data, the most recently described specimen, the "Eichstätt" specimen, is of some use in this regard. The palate of the Eichstätt skull is viewed dorsolaterally through the orbit, antorbital fenestra, and perhaps external nares. As with the other specimens, the skull is crushed flat. Elements from the left ramus of the lower jaw are mingled with the palatal bones, and the sclerotic plates cover crucial areas. Due to this obscured view and two-dimensional presentation, little can be said with absolute certainty. Many of the uncertainties probably could be resolved by study of the other side of the skull. Preparation of the reverse of the main slab is warranted.

a. Quadrate. Of the hypothetical palatal elements, only two can be identified with some degree of confidence. One of these is the right quadrate (fig. 2, Q). Although relatively well-preserved posteriorly, the anterior margin of the bone is indistinct and somewhat difficult to trace. It seems clear, however, that a typically avian "orbital process of the quadrate" was not developed in *Archaeopteryx*.

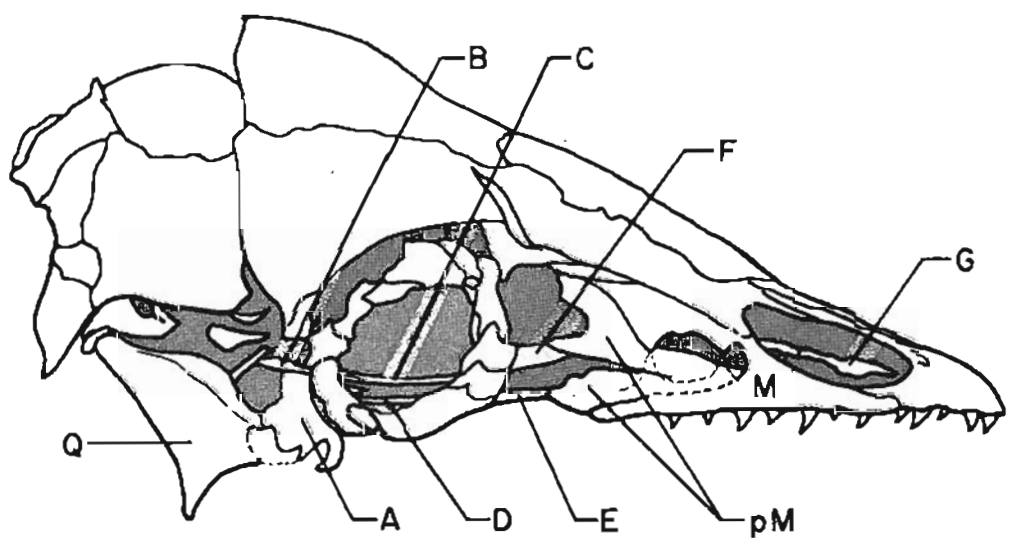


Fig. 2 – **Skull of Eichstätt specimen of *Archaeopteryx* in right lateral view.** Lower jaw bones have not been drawn. Abbreviations : **M**, maxilla ; **pM**, palatal process of maxilla ; **Q**, quadrate ; **A-G** are possible palatal elements and are discussed in the text.

Fig. 2 – **Face latérale droite du crâne du spécimen d'*Archaeopteryx* d'Eichstätt.** Les os de la mâchoire inférieure n'ont pas été dessinés. Abréviations : **M**, maxillaire ; **pM**, processus palatal du maxillaire ; **Q**, carré ; **A-G** sont de possibles éléments du palais décrits dans le texte.

b. Maxilla. The other identifiable elements are the palatal processes of the maxillae (fig. 2, pM) which are viewed through the antorbital fenestra (as in modern birds). These are the "maxillopalatines" of previous students of the Eichstätt specimen (Wellnhofer, 1974 ; Whetstone, 1983 ; Martin, 1983b). Both left and right palatal processes are present although only the right maxilla is fully exposed. The palatal processes are clearly separate posteriorly and may be anteriorly as well, but this area is poorly preserved. The posterior margin of the right palatal process is somewhat damaged, but the same area of the left process seems relatively complete ; it is emarginated posteriorly and overlies a portion of the left dentary (not shown in fig. 2). The unidentified cranial bone found near the lacrimal on the London counterslab and photographed by de Beer (1954, plate IX, fig. 5) shows some of the features of the palatal processes of the maxillae of the Eichstätt specimen, such as similar relative size and the u-shaped emargination.

The right maxilla of the Eichstätt specimen also shows evidence of the presence of a maxillary sinus. Wellnhofer (1974) correctly identified the dorsally situated nasal process of the maxilla. Whetstone (1983) reinterpreted the structure as a mesethmoid, but it seems to be a part of the maxilla. Ventrally from this nasal process descend two or perhaps three fragmentary bony struts that if complete would have contacted the labial or palatal process. Wellnhofer (1974) considered these struts to partition off subsidiary antorbital fenestrae. These excavations of the maxillae within the antorbital fenestra are indicative of maxillary sinuses, again probably associated with diverticula of the nasal cavity.

Of some relevance here are paired fragments of bone located immediately anterior to the lacrimal on the counterslab. Wellnhofer (1974, fig. 5c) labeled these hook-like structures as "uncinata". The os uncinatum *(ossiculum lachrymopalatinum)* in modern birds is a small secondary ossification between the lacrimal and palatine (Jollie, 1957). Wellnhofer was tentative in this assigment, and it seems likely that these bones are maxillary fragments. They lie at the posterior ends of the palatal processes of the maxillae. In life these bones may have been attached to the medial portion of the palatal processes and been oriented more or less vertically. They probably were associated with the maxillary sinuses just as the homologous structures are in modern birds and in *Hesperornis.*

c. Other possible palatal bones. Other candidates for palatal elements are much more equivocal. Figure 2 shows seven lettered elements : A) a squarish element anterior to the quadrate, posterior to the sclerotic plates, and bearing an apparent hook ; B) a rod of bone dorsal to A and seemingly continuous with C ; C) a medially grooved rod passing through the orbit ; D) a rod of bone very similar to C and apparently continuous with E; E) a short rod either contacting or passing ventral to the right palatal process of the maxilla within the antorbital fossa ; F) a larger bone contacting the left palatal process of the maxilla ; and G) a poorly preserved bit of bone within the external nares.

Structure A has been considered to be an ectopterygoid by all previous workers, although this was questioned by Martin (1983b). Its identification as an ectopterygoid is based primarily on the basis of a "hook-like" process, which is characteristic of the ectopterygoids of many non-avian archosaurs. There is a distinct possibility that this element indeed represents an ectopterygoid. *Archaeopteryx* would be then the only known bird to possess an ectopterygoid.

It is equally possible if not probable, however, that no bird, including *Archaeopteryx*, possesses an ectopterygoid. Structure A is more posterior (behind the orbit) than is the ectopterygoid of most non-avian archosaurs, which is directly ventral or anterior to the orbit. Structure A also appears to contact (or at least is in close proximity to) the quadrate. These are features of pterygoids. The "ectopterygoid hook" is also oriented more or less vertically rather than horizontally.The jugal, with which an ectopterygoid would articulate, is exposed in medial view on the Eichstätt counterslab ; we could find no unequivocal evidence for an articulation on the jugal for the "hook" of structure A. Furthermore, it also seems possible that its description as a hook may be inaccurate. This hook may be nothing more that the exposed rim of a transverse structure buried in matrix. If so, the "hook" may be the lateral portion of the pterygoid flange. Thus, by its structure, posterior position, and contact with the quadrate it seems more likely that the body of structure A is the quadrate ramus of the pterygoid and the "hook" is the lateral margin of the pterygoid flange.

Structure B is a thin rod of bone that is flattened dorsally and is located just above structure A on the slab. It is probably continuous with structure C under the sclerotic plates and will be considered as part of C. Structures B and C and structures D and E are very similar in morphology, being elongate, thin rods of bone running longitudinally through the skull, and are probably left and right elements of a paired bone. Wellnhofer (1974) identified the bones as paired elements but considered C and D to be pterygoids and E and F to be palatines. We think that structure F is not the left bone of E. Whetstone (1983) labelled C, D, and E as "?" and F as "Dn?" (dentary).

B-C and D-E could be a number of things. These bones may not be palatal at all but may be hyoid elements ; recall the well-preserved hyoid elements of very similar morphology found on the Berlin *Archaeopteryx*. Alternatively, these bones may be palatines ; *Hesperornis* has elongate, thin palatines that run from short pterygoids (perhaps comparable to structure A) to the maxilla (E appears to contact the maxilla). Considering the many primitive features of *Archaeopteryx*, however, it seems possible that B-C and D-E, like A, are part of the pterygoids. Thus, B-C and D-E would be the elongate vomerine rami of the pterygoid (elongate pterygoids are primitive).

Structure F was considered perhaps to be a dentary fragment by Whetstone (1983) but the left dentary is already reliably accounted for. On the other hand, Wellnhofer's (1974) identification of F as a left palatine seems reasonable. It would pass from the pterygoid (perhaps represented by C with which it would articulate under the sclerotic ring) to the palatal process of the maxilla. The right palatine would be missing according to our appraisal.

Structure G is a poorly preserved scrap of bone within the external nares. Whetstone (1983) could not identify it and Wellnhofer (1974) identified it as possibly a maxillary fragment or the vomer. This bone cannot be identified on the basis of structure but only on the basis of position. Positionally, Wellnhofer's second guess of vomer seems most likely. Recall that in palaeognaths and non-avian archosaurs the vomer contacts the premaxilla. Bone G could be interpreted as having this relationship. Whether or not it represents the anterior fusion of the paired vomers or if the vomers remain separate is not addressable due to the preservation. If the vomers (perhaps G) contacted the pterygoids (perhaps B-C and D-E) as in the primitive situation, then it would have to be ventral to the palatal processes of the maxillae (which is also primitive).

4. Summary

The palate of *Archaeopteryx* is still far too poorly known to attempt reconstruction. Table 1 shows a summary of these results. Little is known for sure. Palatal processes of the maxillae (character 9) and maxillary sinuses (character 10), however, seem to have been present in the oldest known bird. The identification of Wellnhofer's ectopterygoid (structure A) as the posterior portion of the pterygoid implies that no bird would be known to have an ectopterygoid. Finally, if B-C and D-E are the anterior portions of the pterygoids then the primitive feature of elongate pterygoids (character 3) would obtain.

B. *GOBIPTERYX*

1. Relationships

Recently it has become apparent that *Archaeopteryx*, while not directly ancestral to any modern birds, may represent the earliest member of a group of birds that is now totally extinct. This group is the Subclass *Sauriurae* and is composed of four orders : The Archaeopterygiformes, the Alexornithiformes, the Enantiornithiformes, and the Gobipterygiformes. See Martin (1983b) for a discussion of the *Sauriurae*.

Having discussed the palate of *Archaeopteryx*, it is with some interest that we turn to its possible relative *Gobipteryx minuta*. *Gobipteryx* was a terrestrial bird that lived in Mongolia during the Late Cretaceous and has been described in a series of papers by A. Elzanowski (1974, 1976, 1977). It is the only Mesozoic bird known to lack teeth. Palatal material of *Gobipteryx* is preserved and was in fact the basis of Elzanowski's original taxonomic placement. The palate of *Gobipteryx* shows many of the features of the ratites, and Elzanowski (1974) considered it to be a member of the *Palaeognathae*. As discussed above, however, many of these features are probably ancestral. With the description of morphologically similar birds from the Cretaceous of South America (Walker, 1981) - - - the enantiornithines - - - Elzanowski (pers. comm.) agrees that the affinites of *Gobipteryx* are with this group and not with the ratites and tinamous.

Elzanowski (1981) described some embryonic birds and considered them probably to be specimens of *Gobipteryx*. These specimens are extremely interesting but contribute little to our knowledge of the palate of this bird. There are two adult skulls of *Gobipteryx*. See Elzanowski (1977) for detailed description of these skulls. Below is a discussion of the features of these skulls pertinent to the subject of palatal plesiomorphies.

2. The holotype skull

The holotype skull (ZPAL MgR-I/12) is very poorly preserved and interpretation of the palate is extremely difficult. Elzanowski (1977) identified various elements of the palate of this specimen,

but the skull is so distorted that we can neither confirm nor deny his assignments. The right quadrate, however, is relatively well preserved and shows some distinct similarities to that of *Archaeopteryx*. The right mandibular ramus is comparatively intact and is useful for determining palatal length.

3. The second skull

The other skull (ZPAL MgR-I/32) is better preserved but lacks the posterior portion of the palate. The right side of the palate is relatively intact and *in situ* but the left side is quite distorted. Palatal elements that can be clearly observed are pterygoid fragments (of which both sides are present), the vomers, the right palatine, and the palatal process of the left maxilla. As figure 3a shows, the right pterygoid contacts the right vomerine ramus and prevents the right palatine from approaching the midline. Again, these are primitive features.

The palatal process of the maxilla is preserved on the left side. It is the typical flat plate of bone anterior to the internal naris and thus forms a secondary palate. Elzanowski (1977) identified an "indistinct maxillopalatine-palatine suture". We cannot confirm the presence of such a suture, but the palatine must have articulated with the palatal process of the maxilla. In left lateral view (fig. 3b) can be seen a dorsoposteriorly directed process of the palatal process of the left maxilla. Elzanowski (1977) considered this process homologous to the nasal process of the maxilla which in some recent ratites does not contact the maxillary process of the nasal and is correlated with ratite-grade rhynchokinesis ; thus, he postulated rhynchokinesis for *Gobipteryx*. While possible, this homology is not certain and the study of the kinetics of the skull of *Gobipteryx* should await better material. It is clear, however, that the process in question represents the anterodorsal border of the maxillary sinus. Matrix fills the sinus laterally but it is likely that the sinus was of the typical form, being a cup-shaped structure that was concave laterally.

We could not identify ectopterygoids for *Gobipteryx*.

4. Summary

A reconstruction of the palate of *Gobipteryx* (fig. 3c) shows that the skull of this bird is still very poorly known. Among the few certain features are that a vomeropterygoid articulation existed and it separated the palatines. Also, there was a false palate formed by the palatal processes of the maxillae. The palatines passed from the pterygoids to the maxillae ; the palatal processes of the premaxillae are not preserved and it is unknown whether or not they would have contacted the palatines or the vomers. Elzanowski (1977) suggested that the vomers were fused anteriorly. We cannot confirm this fusion but it is possible.

Perhaps the most interesting feature of the palate of *Gobipteryx* is the reconstructed length of the pterygoids. Elzanowski (1977) reconstructed the pterygoids as rather elongate bones. While the posterior area of the palate is not preserved, based on the positions of preserved elements and, more importantly, the length of the palate determined from the lower jaw, Elzanowski's pterygoid length seems reasonable.

As table 1 indicates, *Gobipteryx* shows many of the primitive features exhibited by palaeognaths and apparently shows the additional primitive feature of elongate (or at least not shortened) pterygoids.

C. HESPERORNITHIFORMES

1. The cranial material

Unfortunately, the state of the fossil material of *Archaeopteryx* and *Gobipteryx* prevents us from making detailed descriptions of palatal elements and from reconstructing the palate as a whole. This is not the case for the Late Cretaceous foot-propelled diving birds *Hesperornis* and *Parahesperornis*. Three relatively complete skulls are known. The Yale skull (YPM 1206) of *Hesperornis regalis* is that described by O.C. Marsh in 1875 and especially in his 1880 monograph "Odontornithes". This skull is essentially complete although crushed and damaged is some areas. In 1894, a smaller hesperornithiform bird was collected by H.T. Martin and was briefly described by Lucas (1903). This specimen, although badly crushed, fortunately preserves many of the articulations (the other skulls are more disarticulated). This smaller hesperornithiform was described by Martin (1984) and is the holotype specimen of *Parahesperornis alexi* (KUVP 2287). Perhaps the best skull of a hesperornithiform bird was discovered by M. and C. Bonner in 1981. This skull (KUVP 71012) is a nearly complete, disarticulated, and, with the exception of the braincase, nearly undistorted specimen of *Hesperornis regalis*. Discovery of this specimen permits us to describe in detail the cranial morphology of this important group of birds. It also allows us to reconstruct the palate, evaluate previous reconstructions, and examine cranial kinesis. We have described

together with P. Bühler the cranial kinesis of the hesperornithiform skull and this topic will be discussed elsewhere. Bühler (this volume) presents some of our results.

In addition to these three relatively complete skulls are portions of other skulls. Another Yale skull (YPM 1207) includes only a few cranial fragments (which provide no data that cannot be gained from the better specimens) and also the posterior portion of the braincase which, being relatively undistorted, is very useful. Hesperornithiform remains of another individual are housed in the Smithsonian Institution (USNM 4978) and comprise various cranial and mandibular elements including the premaxilla and a lacrimal. This material was briefly described by Lucas (1903).

2. Previous reconstructions

For Mesozoic birds (even Tertiary birds for that matter) this is a considerable amount of cranial material. But despite the presence of adequate material, few palatal reconstructions have been attempted. In 'Odontornithes", Marsh did not attempt to reconstruct a ventral view even though he had all of the palatal elements. Marsh's apparent confusion about the palate is reflected in his misidentification of the vomers as palatines and palatines as vomers. Lucas (1903) was the first to notice the mistake and suggested that (p. 547) "the bone heretofore supposed to be a palatine may, perhaps, be the vomer."

Two workers, however, accepted Marsh's identification of the palatal bones but disagreed with its supposed «struthious» affinities and, following Thompson (1890), instead postulated relationships with loons *(Gaviidae)*. These workers (Shufeldt, 1915 ; Heilmann, 1926) also offered the first reconstructions of the palate of *Hesperornis* (although neither had studied the actual fossils). Shufeldt's (1915) ventral view is essentially that of a loon. He considered the "vomers" to be fused anteriorly and reconstructed a fully neognathous palate. Heilmann (1926) stayed closer to Marsh's drawings, retained the unfused "vomers", and arrived at a distinctly less modern interpretation ; however, he could not accept the very short pterygoids and restored a more modern pterygoid length.

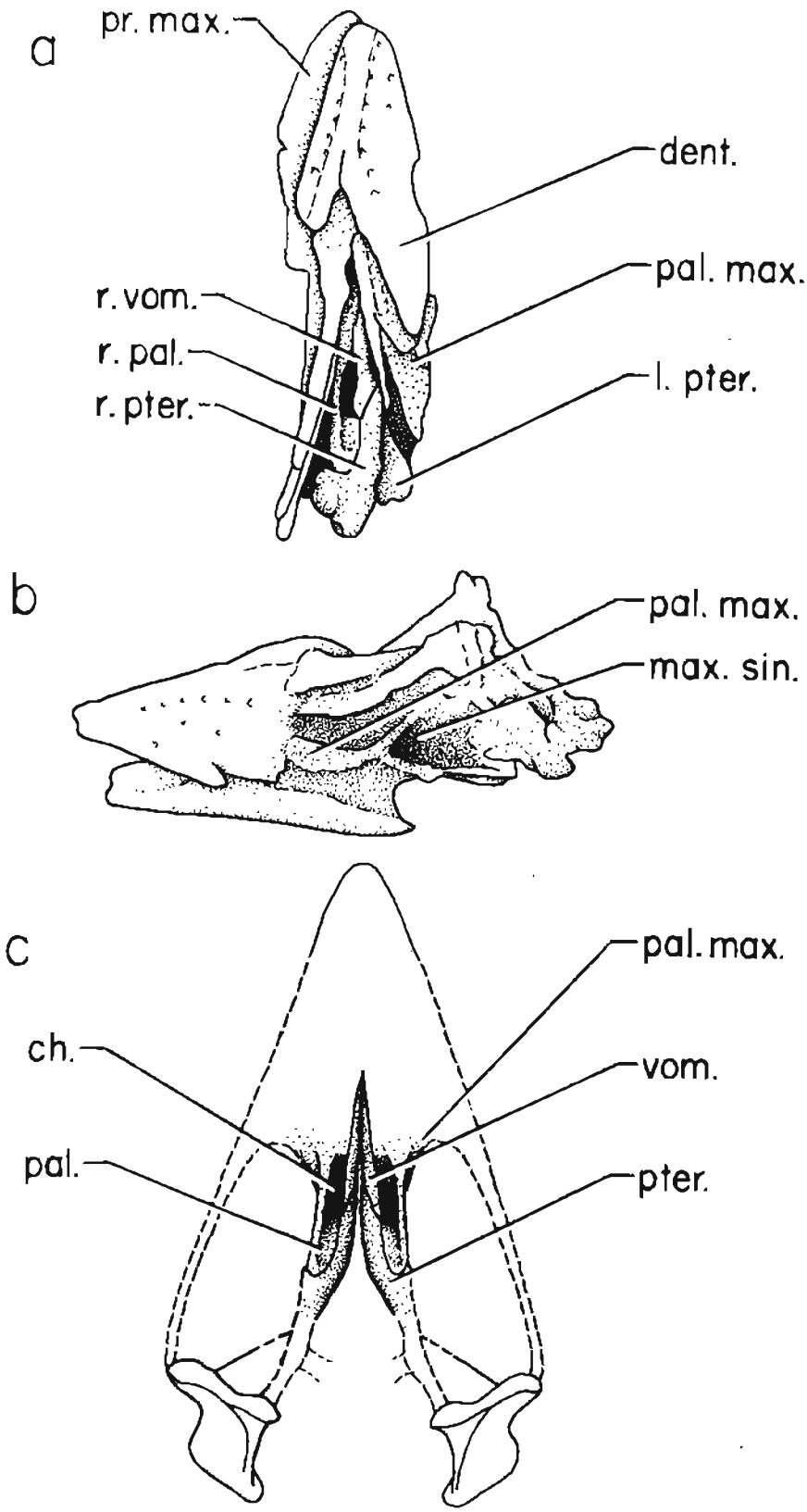
Philip Gingerich (1973) re-examined the Marsh material and, as had Lucas, correctly identified the vomer and palatine. He also provided the first reconstruction of the palate of *Hesperornis* based on study of the actual material. His reconstruction is reasonably accurate in most general features although we are able to correct a number of mistakes due to the discovery of the new skull. Gingerich claimed (1973, 1976) that the palate of *Hesperornis* is "palaeognathous" and thus the «palaeognathous palate" is primitive. While we would generally agree with the latter statement, the former statement is inaccurate. As is discussed below, the hesperornithiform palate shows some of the primitive characters found in palaeognaths but it also shows some characters that must be considered derived.

3. Reconstruction of the palate of *Hesperornis*

Figure 4 presents a new reconstruction of *Hesperornis regalis* based primarily on the new material. What follows is a general discussion of the palatal elements and their relative positional relationships as a means of testing our hypotheses of character polarity. A detailed description of the hesperornithiform palate will be presented by us in a later contribution. To preview the major features depicted in figure 4, *Hesperornis* is characterized by : 1) rather modern-looking quadrates ; 2) short, very complex pterygoids ; 3) long, slender, and simple palatines ; 4) complex, long, and unfused (i.e., separate) vomers that do not articulate with the pterygoids ; 5) maxillae that despite the presence of teeth are quite modern ; and 6) an edentulous premaxilla that totally lacks palatal processes.

Fig. 3 – *Gobipteryx minuta* ELZANOWSKI (ZPAL MgR-I/32) in **a**, ventral view ; **b**, left lateral view ; and **c**, reconstructed in ventral view. Abbreviations : **ch.**, choana ; **dent.**, dentary ; **l.**, left ; **max. sin.**, maxillary air sinus ; **pal. max.**, palatal process of maxilla ; **pr. max.**, premaxilla ; **r.**, right ; others as in fig. 1. (Redrawn from Elżanowski, 1977).

Fig. 3 – *Gobipteryx minuta* ELZANOWSKI (ZPAL MgR-I/32). **a**, face ventrale ; **b**, face latérale gauche ; **c**, reconstitution en vue ventrale. Abréviations : **ch.**, choane, **dent.**, dentaire ; **l.**, gauche ; **max. sin.**, sinus maxillaire pneumatique ; **pal. max.**, processus palatal du maxillaire ; **pr. max.**, prémaxillaire ; **r.**, droite ; voir fig. 1 pour les autres abréviations. (D'après Elżanowski, 1977).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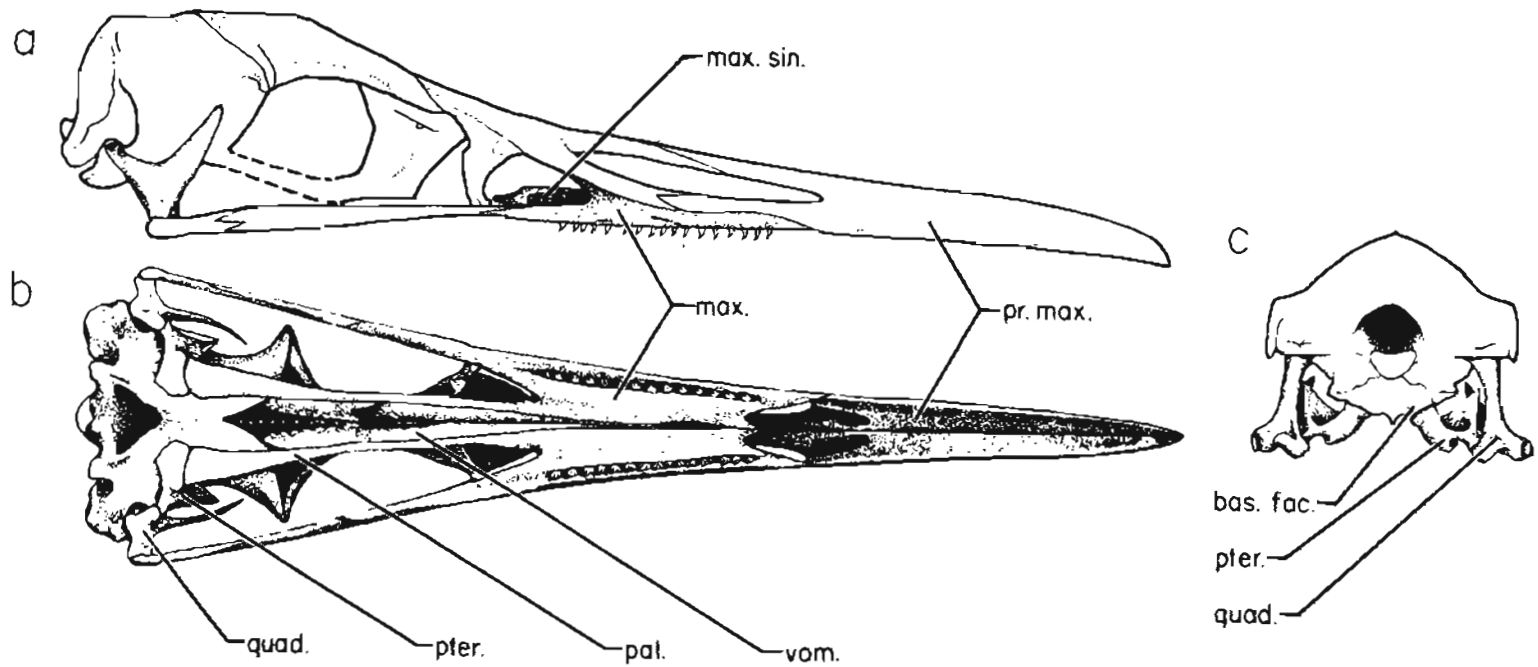

Fig. 4 – **Reconstruction of *Hesperornis regalis*** in **a**, right lateral view ; **b**, ventral view ; and **c**, posterior view. Abbreviations : **bas. fac.**, basicranial facets ; **quad.**, quadrate ; others as in fig. 1.

Fig. 4 – **Reconstitution d'*Hesperornis regalis*.** **a**, face latérale droite ; **b**, face ventrale ; **c**, face postérieure. Abréviations : **bas. fac.**, facettes basicrâniales ; **quad.**, carré ; voir fig. 1 pour les autres abréviations.

a. Quadrates. The quadrates of hesperornithiforms are of quite modern aspect. They possess a typical quadratojugal cup and, as figure 4a shows, a rather elongate orbital process. There is no noticeable development of a pterygoid condyle. Also lacking are pneumatic foramina, which is not too suprising for obligate diving birds. The two dorsal capitula are undivided as in most modern palaeognaths, yet, as in all modern birds (including palaeognaths), the dorsal capitula articulate with both braincase and squamosal.

b. Pterygoids and basicranial articulation. The pterygoids of hesperornithids (fig. 4b, c) are very complex and very different from those of any archosaur, including birds. The bones are very short and articulate with the quadrates, palatines, and braincase, but not the vomers. A major feature of the pterygoid is a vertically-situated triangular dorsal wing which may be homologous with the quadrate ramus of the pterygoid of non-avian archosaurs. Gingerich (1976) provided a photograph (his fig. 3) of the left quadrate and pterygoid of *Parahesperornis* in which the posterior edge of the dorsal wing articulated along its entire length with the quadrate's orbital process. The fit, one must admit, is remarkable, but when an attempt was made to articulate the bones of the palate we found that this cannot be correct - - - the palatines protruded from the palate at an impossible angle ! Instead, the dorsal wing cannot articulate with the quadrate's orbital process but in fact must be somewhat medial to it (fig. 4 b, c). The quadrate articulation itself is saddle-shaped and at the posteroventral apex of the dorsal wing.

The pterygoid's articulation with the braincase is very unusual and consists of a medially projecting process with a distinct facet. The generic differences between the two hesperornithids is apparent in this feature : in *Parahesperornis* the facet is at roughly a right angle to the dorsal wing while in *Hesperornis* (fig. 4 c) the facet is directed more dorsally and forms an acute angle with the dorsal wing. The braincase has rather elliptical facets to receive these processes from the pterygoid. These structures have been called "basipterygoid processes" by all previous workers, and in fact Gingerich (1973) cited "strong basipterygoid processes" as among the features indicating a "palaeognathous palate" in *Hesperornis*. Homology of all "basipterygoid processes" is by no means certain (McDowell, 1978), and Bock (1963) used the term "basitemporal process" instead. Our analysis has considered basipterygoid processes perhaps to be primitive features of Recent palaeognaths. In ratites and tinamous (and many neognaths) the basipterygoid processes project strongly from the braincase and articulate with mere facets on the pterygoids. As Figure 4c shows, the reverse is true in hesperornithiforms : the pterygoids have projecting processes and the braincase mere facets. Thus, we suggest the more noncommital term "basicranial facets" which emphasizes the uncertain homology.

The pterygoid articulates with the palatine by means of a dorsoventrally oblique groove on the anterolateral face of the pterygoid. This groove is rather deep in KUVP 71012. It is not clear whether or not the pterygopalatine articulation was the primitive immovable suture of palaeognaths and non-avian archosaurs. Some relative movement may have been possible. If it were a diarthrotic joint, however, and hence kinematically active, it is a little difficult to understand precisely how it functioned.

One feature that is clear is that the pterygoids did not contact the vomers. This may seem a little surprising in a toothed Mesozoic bird, as a vomeropterygoid articulation must be considered primitive, but probably is merely another manifestation of the aberrancy of the hesperornithiform palate.

c. Palatines. The palatines (fig. 4 b) of hesperornithiform birds show primitive connections : they articulate with pterygoids posteriorly and maxillae anteriorly. The palatines, however, were extremely simple and slender bones, especially anteriorly. These are certainly not the stout bones characteristic of other archosaurs. It seems likely that the palatines were braced dorsally by a hook-like process of the vomer.

d. Maxillae. The maxillary bone of hesperornithiforms is a complex bone, but despite the presence of teeth, it is surprisingly modern in some important respects. The maxilla is preserved in both the new University of Kansas specimen (KUVP 71012) and the Yale University specimen (YPM 1206) of *Hesperornis regalis*. As figures 4 a and b show there is an elongate, dorsoventrally flattened jugal process ; a broad, platelike palatal process to which the vomer articulated ; and a posteromedial process to receive the palatine and vomer and bearing the maxillary sinus. Ventrally (fig. 4 b), there is an elongate lateral groove in which the teeth were implanted. This groove is oblique such that the teeth did not point directly down, but were inclined laterally. There is another lateral maxillary groove on the dorsal surface of the bone. This groove receives the subnarial processes of the premaxilla and nasal (fig. 4 a). Although Gingerich (1973, 1976) related this groove to a peculiar form of kinesis (maxillokinesis), it is present in modern birds such as penguins, loons, and certain ratites in which no maxillokinesis occurs and is, therefore, probably a primitive character for birds at some level.

The maxillary sinus (fig. 4 a) is preserved in both the Kansas and Yale specimens. As in many modern birds it is a cup-shaped structure that is concave laterally, vertically oriented, and drawn out posteriorly into a pointed process. The maxillary sinuses are obscured by the vomers and palatines in ventral view but can be seen (again as in modern birds) laterally through the antorbital fenestra. Thus, despite their being toothed, the maxillae of *Hesperornis* show most of the features of modern avian maxillae.

*e. **Vomers.*** On the other hand, the vomers are perhaps the most unusual element of the hesperornithiform palate, which probably accounts for Marsh's (1880) misidentification. The vomers were unfused, did not contact the pterygoids, and clasped the parasphenoid rostrum and mesethmoid somewhat dorsally to the rest of the palate. Five hesperornithid vomers are known : both left and right vomers from the Kansas and Yale skulls of *Hesperornis* and the left vomer of *Parahesperornis*.

Anteriorly the bone is elongate and somewhat triangular in cross-section with articulations for the maxilla and probably the vomer of the other side. It is broader posteriorly with certainly one and perhaps another articular surface dorsally for the mesethmoid and parasphenoid rostrum. A curious feature is a pronounced "hook" arising from approximately the middle of the bone's length and projecting ventrolaterally. The tip of this hook is flattened and may represent an articulation. As alluded to previously, we think it likely that this hook may have braced the slender palatine dorsally as the latter passed ventrally from pterygoid to maxilla. In all five examples the hook is separated from the body of the vomer by a suture or crack. This may indicate that it is not a primary vomerine ossification but may in fact be a secondary ossification of connective tissue, an occurrence that is common in modern birds.

*f. **Premaxilla.*** The premaxilla (fig. 4 a) is like that of modern birds in some respects (e.g., it lacks teeth and has the typical subnarial and dorsal processes) but is unique in the lack of palatal processes. All modern birds have palatal processes of the premaxilla even if they are very reduced (e.g., loons) or lost in the adult (e.g., *Struthio,* see Webb, 1957). It is not clear whether this feature is primitive for birds or uniquely derived in hesperornithiforms.

*g. **Ectopterygoids.*** Hesperornithid birds lacked ectopterygoids. In none of the existing material does a bone of characteristic size or shape present itself - - -even in the very complete and disarticulated new specimen. Likewise, we now have an accurate view of the individual elements and there appears to be no place to articulate an ectopterygoid on the chance that it was not preserved in the existing specimens.

4. Summary.

As table 1 shows, hesperornithiforms show a marked departure. Some primitive characters are retained, such as the palatal processes of the maxillae (character 9), maxillary sinuses (character 10), lateral positions of the palatines (character 2), and the contacts of the palatines (character 4). There are however, a number of derived characters, such as the failure of the pterygoids to contact the vomers (character 1) perhaps due to the loss of the vomerine ramus, which would account for the very short pterygoids (character 3). Likewise, the vomers do not contact the premaxilla (character 5) perhaps due to the lack (loss ?) of the premaxilla's palatal processes. Also, the morphology of the palatal elements, especially the pterygoids, vomers, and palatines, indicates the highly apomorphic nature of the hesperornithiform palate.

Gingerich's (1973, 1976) claims of "palaeognathy" for *Hesperornis* are demonstrably inaccurate. Balouet (1982), however, considered the hesperornithiform palate to be neognathous and thus *Hesperornis* should be included within the *Neognathae*. He interpreted short pterygoids, loss of the vomeropterygoid articulation, and palatines articulating to the anterior portion of the pterygoid to be due to the pterygoid segmentation synapomorphic of neognaths. There is, however, absolutely no evidence of neognath pterygoid segmentation in hesperornithiforms. There is no identifiable anteropterygoid segment (the diagnostic feature of pterygoid segmentation). The palatal elements also lack the morphology and connections of neognath birds. Such attempts to force hesperornithiforms into existing typologies are counterproductive. It seems clear that the observed features are derivable from those here considered to be ancestral for birds and that it is impossible to derive the palate of any modern bird from such a set of structures.

V. CONCLUSIONS AND SUMMARY

The palates of birds often have been thought to be separated by a broad morphological gap from those of reptiles. Indeed, at first glance the differences between the palates of a sparrow and a lizard or recent crocodile are irreconcilable. Perhaps it was for this reason that McDowell (1978) suggested that the avian palatal elements have been misidentified for all these years. Our study offers no support for McDowell's hypotheses. On the contrary, the avian palate agrees quite well with that of archosaurian reptiles.

Comparisons with these non-avian archosaurs are essential to an understanding of the evolution of the avian palate, and hence we have concentrated on features that are possibly ancestral for birds. Cladistic analyses generally focus on the identification of uniquely derived characters ; however, a rigorous attempt at determining what is primitive must precede such analyses. We have thus performed outgroup analysis using all archosaurs and especially the two leading contenders for sister-group status, theropod dinosaurs and crocodiles, as outgroups. We have tested these polarities by looking at the palates of the oldest known birds.

What features, then, may have been ancestral for birds ? From our analysis two features are certainly ancestral : palatal processes of the maxillae forming a secondary or false palate and the presence of a maxillary air sinus. These features are found in crocodiles, theropods, all the Mesozoic birds studied, and all modern birds (with minor exceptions).

Other features are very likely to have been present in the first birds. A vomeropterygoid contact must be considered primitive for birds. This is the situation in virtually all archosaurs and palaeognaths, and is part of the ontogeny of all modern birds even if some (most neognaths) obscure this pattern as adults. Likewise, having the palatines excluded from the midline by the pterygoid and vomer is found in archosaurs, *Gobipteryx*, *Hesperornis*, and palaeognaths (*Archaeopteryx* is unclear on this point) ; neognaths are derived in their sagittal contact of the palatines. Lack of significant relative movement within the palatal skeleton is probably also primitive due to the presence of immovable sutures joining the bones in non-avian archosaurs, *Gobipteryx*, and palaeognaths (*Archaeopteryx* is equivocal). This does not imply akinesis because palaeognaths are rhynchokinetic. The pterygopalatine articulation in hesperornithids is unusual and may have been mobile. Neognaths have well-defined pterygopalatine or intrapterygoid diarthroses (which are lost in some forms). The palatine contacts are also likely to be primitive. Palatines passing from pterygoids to maxillae but not premaxillae are characteristic of most archosaurs, probably *Gobipteryx*, *Hesperornis*, palaeognaths, and perhaps *Archaeopteryx* as well ; neognaths exhibit a premaxilla-palatine articulation as a derived feature probably associated with the palatal bending zone.

Some characters may be primitive but the evidence is open to other interpretations. Basipterygoid processes are prominent features of archosaur palates and some very similar structures are found in palaeognaths and some neognaths. But, as mentioned, the homologies have been questioned, *Hesperornis* lacks unequivocal basipterygoid processes, and both *Archaeopteryx* and *Gobipteryx* are unknown in this area.

Although all archosaurs have ectopterygoids, it seems likely that no known bird can be described as having them. *Archaeopteryx* is the only candidate, but the element in question (fig. 2, A) compares better with a pterygoid than with an ectopterygoid. Thus loss of the ectopterygoid would be a synapomorphy for an avian clade excluding other archosaurs but would be, of course, a symplesiomorphy within this clade.

Pterygoid length is an important feature. Non-avian archosaurs have elongate vomerine rami of the pterygoids. This also appears to have been the case with *Archaeopteryx* and *Gobipteryx*, and thus elongate pterygoids are primitive. Hesperornithids and all modern birds, however, have shortened pterygoids. The drastic shortening of avian pterygoids may have been a functional prerequisite of avian cranial kinesis ; it was perhaps the shaping force of the palate, resulting in the very long vomers of palaeognaths and the segmented pterygoids of neognaths. Due to the aberrant morphology of hesperornithid pterygoids, it is unclear whether or not the pterygoid-shortening is homologous in hesperornithids and modern birds.

In summary, avian palates are not as dissimilar to archosaurian palates as previously thought. In fact many of the observed features are primitive retentions. Knowledge of these plesiomorphies permits systematics analysis showing, for example, that neognath birds are relatively specialized while ratites and tinamous exhibit many primitive characters. Additionally, this knowledge is enlightening regarding the diversity of morphology, as in the almost bizarre morphology of *Hesperornis*. It also permits us to make reasonable interpretations of poorly preserved fossils, such as those of *Archaeopteryx* and *Gobipteryx*.

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