

Homology Mapping of the Primitive Archosaurian Reptile Palate on the Palate of Birds*

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ABSTRACT: The bone called "palatine" in birds, along with the bone called "pterygoid", together represent the homologue of the reptilian pterygoid. The reptilian pterygoid has become divided by a hinge in birds as part of increased kinesis, just as the nasal bone has been divided into two bones by a hinge in many birds, as part of this same kinesis. In some birds (Phasiani, Anseres) there is a single division of the pterygoid, associated with Pfannenstiell-kinesis (primarily transverse rotation of the quadrate to broaden the gape), but most birds follow this division of the pterygoid with a second division after the nestling stage, this second division being associated with Versluys-kinesis (primarily longitudinal rotation of the quadrate, lifting the upper jaw when the lower jaw is depressed). The true homologue of the palatine in birds is the "maxillo-palatine" or "maxillary bone". Modern birds have probably lost the true maxillary bone in the process of losing teeth. The parasphenoidal process called "basipterygoid process" in modern birds is not the homologue of the reptilian basipterygoid process (formed from the basitrabecular process with a ventral investment of parasphenoid); the true basipterygoid process is present in birds, however, as a vertical lamina between the orbital and tympanic cavities, usually forming the lateral wall of a presphenoid air sinus. Because the dermal pterygoid of birds has become almost entirely free of (and ventral to) the endochondral palato-quadrate arcade ("orbital process of the quadrate"), the true basipterygoid process does not approach the pterygoid, but may (e.g. Spheniscidae) make a glancing contact with the orbital process of the quadrate. The pila antotica spuria is a morphologically extracranial supporting strut for the part of the cranial wall giving origin to the levator pterygoideus muscle and is only one of several extracranial struts in this region that support the levator origin and define foramina for the oculomotor, abducens, trochlear, and various trigeminal nerves that do not correspond to the primary (dural) foramina for these nerves. It is possible that the pattern and contents of these foramina could be of taxonomic value in birds.

*This communication is part of an unsolicited, handwritten letter I received from Sam McDowell in November 1976, with instructions to use any of the ideas contained therein as I saw fit. Having subsequently been impressed with the fact that much of systematic ornithology is based on unsubstantiated traditions, I realized McDowell's hypothesis, that the avian homologues of the elements of the reptilian palate were misidentified, to have a better than average chance of being correct. I have therefore submitted the pertinent portions of the text of McDowell's letter as received, with illustrations supplied later by McDowell, in the expectation that if nothing else, avian anatomists will be forced to produce a more rigorous justification for the nomenclature now in use for the avian palate than presently exists.

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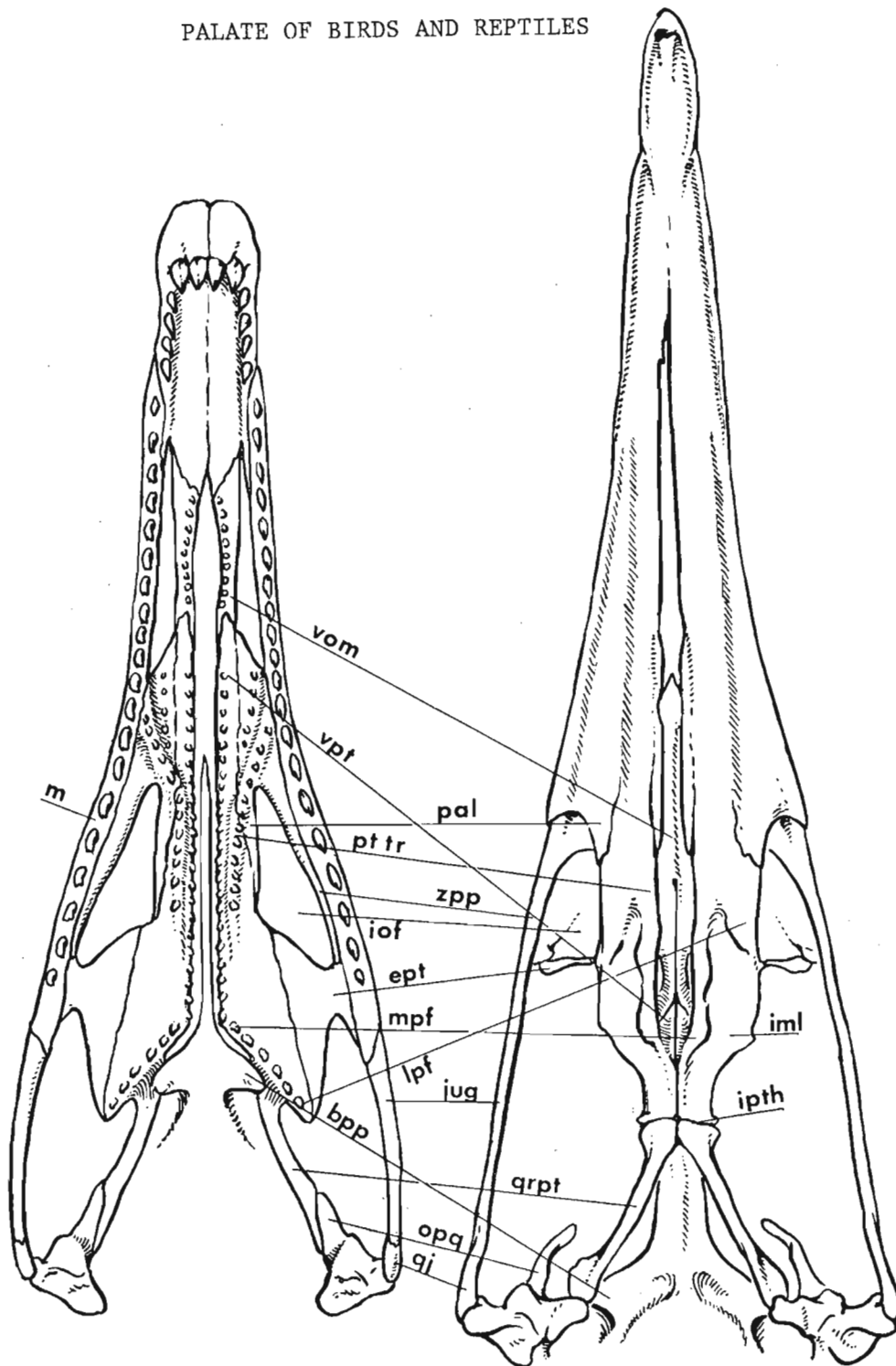
At the time when Huxley, Kitchen Parker, Pycraft et al. were forming the traditions for labelling parts of the bird skull, little was known of the details of skull structure of fossil Archosauria or even of Crocodilia; the relationships of skeletal elements, bony protruberences, foramina and cavities to soft structures was largely unknown; and no attempt was made to catalogue which points on an archosaurian skull must enlarge, which must be reduced, and which remain the same in a gradual transformation into the skull of a bird. The names of various structures of the bird skull (e. g. basipterygoid process, palatine bone, maxillopalatine process) reflect this period of imprecision.

As more knowledge of the development of the vertebrate skull and of the skull structure of earlier archosaurs accumulated, no attempt was made to bring the naming of bird skull structures into conformity with that of reptiles. This has no serious consequences for most comparisons of birds with other birds, but it does confuse comparison of birds with reptiles and thus makes difficult the determination of what characters in birds are primitive (i.e., retentions of reptilian features) and what characters are specialisations.

The braincase and palate of early archosaurs was remarkably similar in details to that of lizards, except for the lack of a Squamatan peculiarity (separation of the vomer from the pterygoid by the palatine), and the contents of the cranial foramina, canals, and grooves can be inferred from those of lizards with at least as much confidence as the contents of the cranial foramina of a dog skull can be inferred from dissection of the head of a cat. This is important, because the only living (and dissectable) archosaurian reptiles, the Crocodilia, have departed more from the primitive archosaurian pattern in attachment of the palate to the braincase than have birds, and less is known about development of the crocodilian head. Sphaenodon [J.E. Gray's original spelling] is even better for interpreting the skull of early fossil archosaurs, but adds very little that cannot be learned from lizards.

The usual naming of bones in the palate of birds suggests a most remarkable transformation from the reptiles: the pterygoid flange and most of the muscles originating on the pterygoid of reptiles have been transferred to the palatine bone. I believe the "palatine" of birds is merely the anterior portion of the reptilian pterygoid, separated from the posterior part of the pterygoid by a new joint that has developed in the waist of the pterygoids, just behind the pterygoid flanges (Figure 1). The

 Figure 1 (to right). Homologies here proposed for palatal structures between (on left) the primitive thecodont archosaur Proterosuchus (after Cruickshank) and (on right) a modern bird, Diomedea. Abbreviations: bpp, true basipterygoid process, formed from basitrabecular process of chondrocranium with parasphenoid addition; ept, ectopterygoid ("os lachrymopalatinum" or "os uncinatum" of Diomedea); iml, intermuscular lamina of pterygoid (pre-pterygoid) of birds, without homologue in Proterosuchus; iof, infraorbital fenestra; ipth, intra-pterygoid hinge, without homologue in reptiles; jug, jugal bone (fused to adjacent bones in birds); lpf, lateral end of pterygoid flange; m, maxilla (lost in modern birds); mpf, medial end of pterygoid flange; opf, orbital process of quad-



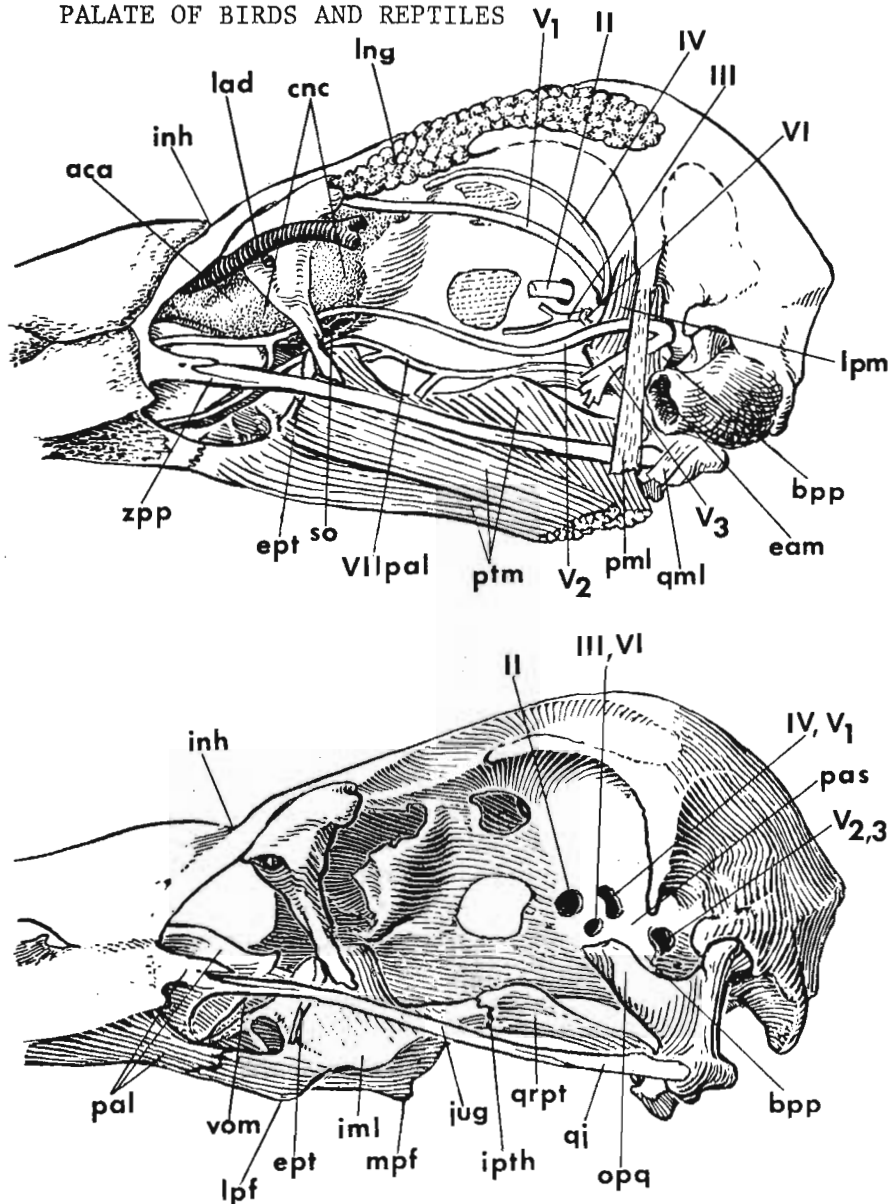
rate bone; pal, palatine bone ("maxillopalatine" of birds); pttr, middle pterygoid tooth row of Proterosuchus, represented in Dio-medea by the edge of the nasopharyngeal duct opening; qj, quadratojugal bone (fused to jugal in birds); qrpt, quadrate ramus of pterygoid bone (post-pterygoid of birds, "pterygoid bone" of birds according to other authors); vom, vomer (separate in Proterosuchus, but partially fused to its fellow in birds and most archosaurs); vpt, vomerine process of pterygoid; zpp, zygomatic process of palatine, forming lateral border of infraorbital fenestra in Proterosuchus, fused to jugal in birds.

"palatine"-pterygoid joint of birds is functionally linked to the Versluys-kinesis [I shall explain this term below] of the skull that elevates the upper beak when the lower end of the quadrate and palate slide forwards in opening the mouth. The other major joint involved in Versluys-kinesis is across the nasal bones. In most birds, the nasal hinge involves only an histological change in the bone, a transverse zone of fibrous and elastic bone across the nasals; but in parrots, boobies, and some other birds, the nasal bone becomes completely divided into anterior and posterior parts by joint capsule. I suggest that the reptilian pterygoid has been similarly divided into anterior and posterior portions by a joint capsule in birds (the fusion of "palatine" and pterygoid in some birds, such as the hawfinch, is probably secondary).

Even conventional ornithology accepts this for the majority of birds. Pycraft showed (most succinctly in *Journal of the Linnean Society, London, Zoology*, vol. 28: pp. 343-357, pls. 31, 32) that the definitive "palatine"-pterygoid joint of most "Neognathae" lies entirely within the pterygoid of the nestling and the anterior end of the nestling pterygoid is thus cut off as a "hemipterygoid" to fuse with the palatine. In Anatidae and (according to Pycraft) Phasiani this does not occur, and Pycraft interpreted the "paleognathous" or "dromeognathous" palate as a consequence of either fusion of the hemipterygoid with the vomer (a later interpretation) or failure of the pterygoid to segment into hemipterygoid and definitive pterygoid. Jollie (1957, *Journal of Morphology*, vol. 100, pp. 389-436) showed that in Phasiani (at least *Gallus*) the condition is not as in Anatidae; rather, the "pterygoid" has its anterior ("hemipterygoid") portion separated off at the inception of ossification from the rest of the pterygoid and is fused from the beginning to the "palatine".

Pycraft interpreted the nestling "palatine"-pterygoid articulation as the homologue of the reptilian palatine-pterygoid contact. This presents difficulties. The palatine of reptiles is closely associated with the choanal region of the olfactory capsule and develops in the region of the primary choana; in the embryo crocodilian (de Beer, 1937, The development of the vertebrate skull, Oxford, Clarendon Press) the palatine starts development far anterior to the developing pterygoid and the two bones subsequently grow towards each other. In birds, the "palatine" is in contact with the "pterygoid" from the beginning but lies entirely behind the cartilaginous olfactory capsule and primary choanae (Figures 2, 3); it forms the lateral margins of a median

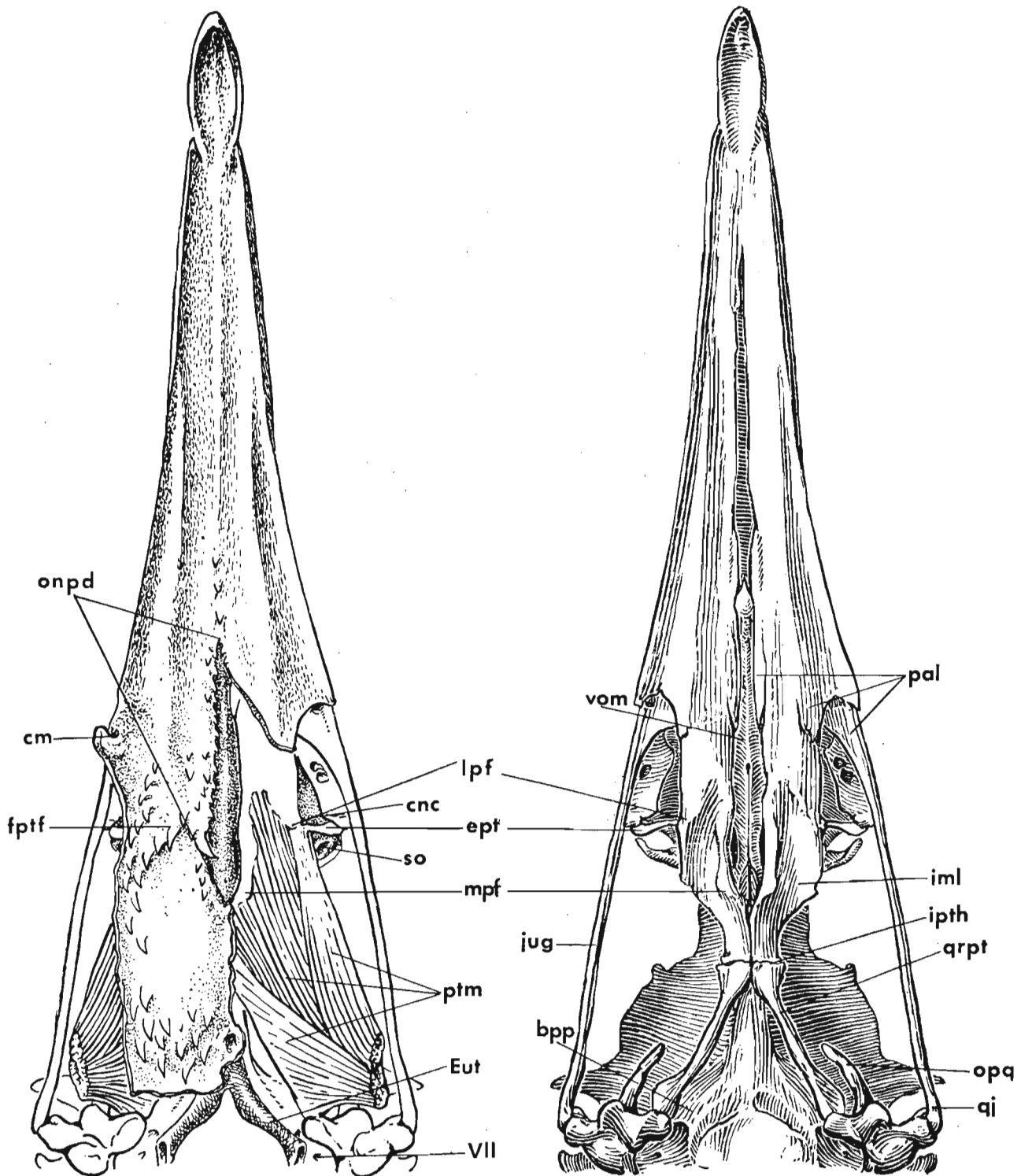
 Figure 2 (to right) Lateral view of the palatal region of a modern bird, *Diomedea*; upper figure showing some associated soft structures; lower figure showing ossifications. Abbreviations: aca, aditus conchae avium, the concavity on the outer surface of the nasal capsule corresponding to a convexity within the capsule (probably not homologous to the concha of squamates and testudinate reptiles); bpp, true basipterygoid process, formed from basitrabecular process of chondrocranium with addition of parasphenoid wing, dorsal to palatine ramus of facial nerve; cnc, cartilaginous nasal capsule; eam, external auditory meatus; ept, ectopterygoid ("os lachrymopalatinum," "os uncinatus"); II, optic



nerve (upper figure) or foramen for optic nerve (lower figure); III, oculomotor nerve; III, VI, foramen for oculomotor and abducens nerves; iml, intermuscular lamina of pre-ptyergoid ("palatine" of other authors); inh, intranasal (cranio-facial) hinge; ipth, intra-ptyergoid hinge; IV, trochlear nerve; IV, V₁, foramen for trochlear and profundus nerves; jug, jugal bone; lad, lacrimal duct; lng, lateral nasal gland; lpf, lateral end of pterygoid flange; lpm, levator pterygoideus muscle; mpf, medial end of pterygoid flange; opq, orbital process of quadrate bone; pal, palatine bone ("maxillopalatine" of other authors); pas, pila antotica spuria; pml, ligament from postorbital process to mandible; ptm, pterygoideus muscle, qj, quadratojugal bone; qml, quadrato-mandibular ligament; qrpt, post-ptyergoid, homologous to the quadrate ramus of the pterygoid of reptiles ("ptyergoid bone" of other authors); so, ostium of orbitorostral air sinus; V₁, profundus (ethmoidal or ophthalmic) ramus of trigeminal nerve; V_{2,3}, foramen for maxillary and mandibular rami of trigeminal nerve; V₃, mandibular ramus of trigeminal nerve; VI, abducens nerve; VII_{pal}, palatine (Vidian) ramus of facial nerve; vom, vomer; zpp, zygomatic process of palatine ("zygomatic process of maxilla" of other authors).

fossa, into which the primary choanae open, but without any supporting cartilages of the olfactory capsule; this median fossa seems clearly homologous to the interpterygoid vacuity of lizards and Sphaenodon and the embryo of crocodilians, but has become converted into a ductus nasopharyngeus by folds of oral mucosa that grow medially beneath it (the ductus nasopharyngeus of crocodilians develops in precisely this way, except that the folds of oral mucosa contain shelves of the pterygoid bones that meet and form a suture beneath the interpterygoid vacuity, with the vomer completing the roof). In reptiles, the palatine is normally free of muscle attachments (snakes have developed an attachment to the levator pterygoideus or Constrictor I dorsalis complex through modification of the levator bulbi muscle into a retractor palatini et pterygoideus); in birds, most of the pterygoideus component of the adductor mandibulae originates from the lateral edge of the "palatine," yet the fibres of the muscle do not seem different in orientation to the pterygoideus fibres originating on the lateral edge of the pterygoid in lizards and Sphaenodon. In primitive reptiles, from Captorhinomorpha to lizards, the pharyngeal surface of the pterygoid (that is, the surface of the pterygoid immediately deep to the oral mucosa) is expanded just anterior to the basipterygoid articulation to form a pterygoid flange, primitively bearing a transverse row of small palatal teeth. So constant is this pterygoid flange that Romer has used it as a key character for distinguishing Permo-Carboniferous reptiles from contemporary amphibians. It is even retained in most mammals, as the hamular process of the pterygoid, and may be large and heavy (e.g. Sphaenodon and Crocodilia) or reduced to a small tubercle (e.g. snakes, where it may be lost). The one thing that has not been observed in any reptile is the transfer of this process to the palatine bone. In most birds there is a "posterolateral process of the palatine" that agrees well with the pterygoid flange of reptiles but, following standard homologies of the bones, seems to be on the wrong bone. It should be noted that in many birds (Charadriiformes, Procellariiformes are conspicuous examples), there are two posterolateral angles of the "palatine." The outer process is enveloped on both its dorsolateral and ventromedial surfaces by the pterygoideus muscle and seems to be purely an "intermuscular crest"; but the inner posterolateral process (generally oriented almost vertically, to form a spout-like orifice for the posterior opening of the ductus nasopharyngeus)

Figure 3 (to right) Ventral view of the palate of a modern bird, Diomedea; figure on left showing some soft structures (the oral mucosa removed on the reader's right); figure on right showing ossifications. Abbreviations: bpp, true basipterygoid process, formed from basitrabecular process of chondrocranium, with parasphenoid addition; cm, corner of mouth; cnc, cartilaginous nasal capsule; ept, ectopterygoid ("os uncinatum," "os lachrymopalatinum"); Eut, Eustachian tube; fptf, fold of pharyngeal mucosa at region of pterygoid flange; iml, intermuscular lamina of prepterygoid ("palatine" of other authors); ipth, intra-pterygoid hinge; jug, jugal bone; lateral end of pterygoid flange; mpf, medial end of pterygoid flange; onpd, orifice of nasopharyngeal duct; opq, orbital process of quadrate; pal, palatine bone ("maxillopalatine"



of other authors); ptm, pterygoideus muscle; qj, quadratojugal bone; qrpt, postpterygoid ("pterygoid bone" of other authors), homologous to the quadrate ramus of the pterygoid of reptiles; so, ostium of orbitorostral air sinus; VII, foramen for facial nerve; vom, vomer.

has oral mucosa on its ventromedial surface and pterygoideus musculature on its dorsolateral surface, thus agreeing with the reptilian pterygoid flange. All of these difficulties disappear if we interpret the "palatine" bone of birds as the anterior portion of the reptilian pterygoid. Thus, the "palatine"-pterygoid articulation of even nestling birds would be a new structure, rather than a reptilian heritage. Lakjer (1926, Studien über die Trigemini-versorgte Kaumuskulatur der Sauropsiden, Copenhagen, C.A. Reitzel) has figured and described the pterygoideus muscles of a number of birds, including Crypturus (Tinamidae) which does not differ from the "neognaths" in this respect.

If both the natal and definitive intra-pterygoid joints are new structures, why should a nestling bird form the neomorphic hinge twice? I believe that each kind of intra-pterygoid hinge is useful to a kind of cranial kinesis, but that many nestlings change the kind of cranial kinesis in the transition from broad-mouthed, short-billed nestling to narrow-mouthed, long-billed adult. In most adult birds, the major cranial kinesis is of the type intensively studied and reported on by Versluys, involving rotation of elements in the sagittal and parasagittal planes. The main result of this, which I call Versluys-kinesis, is forward movement of the palate when the mouth opens, pivoting the premaxillary region upward (rotation around cranio-facial hinge within the nasals) and pivoting the pre-pterygoid (which moves with the premaxilla) upward relative to the post-pterygoid. The other kind of kinesis involves outward rotation of the quadrato-articular joints, broadening the gape. This kind of kinesis, with rotation of elements in transverse planes, was ably described for anthracosaurs by Max Pfannenstiel and I call it Pfannenstiel-kinesis; it may involve rotation (as seen from directly in front or behind) of the post-pterygoid from a downward-and-outward slant to a nearly horizontal position, and a longitudinally oriented, rather than a transversely oriented, intrapterygoid hinge is necessary. In at least some birds that retain Pfannenstiel-kinesis throughout life (Anatidae, Anhimidae, Tinamidae, Rhea) the anterior ("hemipterygoid") end of the post-pterygoid is a cylindrical peg resting on a nearly flat dorsal surface of the pre-pterygoid, an articulation that would seem to allow enough rolling action to allow adjustment of the angle of the post-pterygoid. However in Tinamidae, Rheidae, Casuariidae and Dromaeidae the main hinge line for this action is probably the longitudinal vomer-pterygoid contact, and in Anatidae rotation of the pre-pterygoids around a median axis seems important.

If the "palatines" of birds are really part of the pterygoids, where are the homologues of the reptilian palatines? The bones that best fit the positional relations of reptilian palatines are the "maxillopalatines" of birds: they lie along the lateral borders of the primary choanae and are intimately associated with the cartilages of the choanal region (Figure 2). I am not sure whether this homology implies that the maxilla of birds is compound, or that birds lost the maxilla (probably in the process of losing teeth*) and the "maxilla" of birds is the

*This becomes an alluring proposition when it is realized that in Hesperornis the maxilla was free and was the only bone in the

palatine. The "maxillo-palatine" is built around an air-sinus that occupies the anteroventral part of the orbit and the ant-orbital region. It is attractive to believe the characteristic antorbital fenestra of early archosaurs was for this sinus (a diverticulum of the olfactory capsule), but this is untestable because the archosaurians with an antorbital fenestra are all extinct, just as it is difficult to prove the homology of the sinus of birds with the posterior diverticulum of the olfactory capsule of the living Alligatoridae "hintere laterale Nebenhöhle" of Bertau (1935, Zeitschr. Anat. Entwickl., vol. 104, pp. 168-202).

(It should be noted that comparisons within the Aves would be more to the point if the parts of the "maxillo-palatine" were distinguished. In Rhea and Tinamidae, the palatine bone is represented almost entirely by the lamina forming the ventrolateral flooring of the sinus and lying along the ventrolateral surface of the pterygoid ["palatine"], concealing the anterior end of the pterygoid from ventral view; in Phasiani, only the laminae dorsomedial to the sinus are developed, and the entire length of the pterygoid is exposed ventrally. In Diomedea, both laminae are well developed and the ventrolateral lamina, extending along the lateral margin of the pterygoid and also along the jugal arch, with a suborbital fenestra (closed by membrane) between these two branches; the posterior margin of the suborbital fenestra is completed by a transverse rod of bone ("os uncinatum" or "os lachrymo-palatinum") that lies at the anterior extremity of the origin of the pterygoideus and seems to have a few pterygoideus fibres on its medial end (Figures 2, 3); these positional relations suggest that the "os uncinatum" is the homologue of the ectopterygoid of such a thecodont as Proterosuchus (see Cruickshank, pp. 89-119 in Studies in vertebrate evolution, K.A. Joysey and T.S. Kemp, Eds., 1972. Winchester Press, New York); the enormous orbit of birds would explain the apparent forward displacement of the ectopterygoid.)

(A further aside: The palate of Proterosuchus is of considerable interest because this is one of the few archosaurians to have retained palatal teeth, in the form of rows of denticles too small to have had any cutting action, but presumably aiding frictional hold on the prey. Just what happened to the palatal teeth in archosaurs is a mystery, but a possibility worth exploring is that they were replaced by cornified papillae of the oral mucosa, such as are present in many birds. I go far beyond my evidence in this, but if we accept homology between papilla-rows of some birds and the denticle rows of Proterosuchus, some interesting similarities of pattern emerge. The median row of denticles of Proterosuchus, running along the vomers and pterygoids bordering the interpterygoid vacuity, is probably absent in birds, since it would lie in the ductus nasopharyngeus. In Proterosuchus there is a middle denticle row, forming a raised crest from the posterolateral corner of the choana backward to the medial corner of the pterygoid flange. The region between the two middle denticle rows of Proterosuchus would correspond closely to the ductus nasopharyngeus

 upper jaw that bore teeth (see Gingerich, 1976, Smithsonian Contributions to Paleobiology, no. 27, pp. 23-33). S.L.O.

of Aves and Crocodilia; strengthening of the crest and replacement of the denticles by cornified papillae would yield the palate of such a bird as Diomedea or Gallus; converting the denticulated crests into bony shelves meeting on the midline would form the ductus nasopharyngeus of Crocodilia. The pterygoid flange of Proterosuchus bears a series of teeth that I would homologise with the long cornified papillae on the posterior edge of the triangular flap of oral mucosa bordering the ductus nasopharyngeus of such birds as Diomedea and Gallus. The lateral papilla row of Diomedea, Gallus, Mesoenas, etc. seems to be represented in Proterosuchus by a row of teeth just lateral to the middle denticle row on the pterygoid.

The "basipterygoid process" of birds most definitely does not correspond to the major component of the basipterygoid process of lizards and Sphaenodon. In reptiles, the main component of the basipterygoid process is the basitrabecular process, arising in cartilage (usually as a separate "polar cartilage") and soon fusing to the trabecular cartilage at its mesial end while its lateral end articulates with the medial face of the anterior process of the quadrate cartilage, approximately opposite the base of the ascending (epipterygoid) process of the quadrate cartilage; in most lizards the cartilage connecting the base of the epipterygoid with the quadrate disappears early in development, so that these two endochondral components of the pterygoid cartilage are connected only by the dermal bone (pterygoid) that develops around the ventral edge of the quadrate cartilage; the levator pterygoideus musculature is transferred in its insertion to the (dermal) pterygoid bone. The palatine branch of the facial nerve and palatine artery pass ventral to the base of the basitrabecular process and the basitrabecular process forms the anterior rim of the enormous Eustachian tube orifice in most lizards.

In addition to this endochondral component, the basipterygoid process of reptiles has a dermal component, formed from a lateral extension of the parasphenoid; since this parasphenoid component develops just deep to the oral mucosa, it lies ventral to the palatine artery and palatine nerve and these structures are enclosed between the parasphenoid and basitrabecular process in a canal ("Vidian canal" or "parabasal canal").

The embryos of all birds studied, even those said not to have basipterygoid processes, have large basitrabecular processes. The basitrabecular process of birds agrees with that of Crocodilia (and differs from that of other living vertebrates) in having a posteroventral lobe, the infrapolar process, that extends backward, lateral and ventral to the carotid artery and Eustachian tube, to join the ventral plate of the chondrocranium, thus enclosing the carotid in a canal and nearly or quite enclosing the Eustachian tube. The basitrabecular process of birds persists in the adult, but it does not articulate with the pterygoid bone. Birds are peculiar (but approached by snakes in some details) in having the dermal pterygoid bone dissociated from the quadrate cartilage, except for a short articulation (but in a few birds, such as Ciconiidae, I have found a rather elongate pterygoid-quadrate contact) and the anterior process of the quadrate cartilage, with

which the basitrabecular process would be expected to articulate, extends freely into the orbit as the orbital process of the quadrate, receiving the insertion of the levator pterygoideus musculature. The basitrabecular process forms a sharp-edged vertical crest defining the middle ear cavity from the orbital region, just behind or just below the foramen for the maxillary and mandibular branches of the trigeminal nerve, defined dorsally by a notch for the passage of the stapedia artery and vena capitis lateralis (or the rete mirabile formed by these two vessels) between middle ear and orbit, and defined ventrally by the canal (or canals) for the carotid artery and Eustachian tube. The lateral walls of the carotid and Eustachian canals are formed from the infrapolar process, essentially an extension of the basitrabecular process, and in some birds (e.g. Gallus) the outer wall of the carotid canal may meet the metotic process (characteristic of Crocodilia and all birds except Phaethon, forming a posterior wall for the middle ear cavity and anchoring the posterior edge of the tympanic membrane). The palatine branch of the facial nerve runs ventral to this crest, generally in the same canal as the carotid artery (more anteriorly, the palatine nerve accompanies the palatine branch of the carotid when the cerebral carotid separates to enter the pituitary fossa of the braincase). The position of this crest is thus quite typical of a basitrabecular process, but its form is not, partly because it has no articular surface for the orbital wing of the quadrate (although it may touch that process without a formed articulation, as in Spheniscidae), and partly because the process has been hollowed out from behind by a pneumatic diverticulum from the middle ear. This pneumatic excavation makes the basitrabecular process appear to be no more than the lateral rim of the presphenoid air sinus opening.

The tubercles or facets on the parasphenoid of various birds, called basipterygoid processes in the taxonomic literature, are ventral to the palatine branch of the facial nerve and have no homology with the basitrabecular process of reptiles, as realised by Kesteven (1942, Proceedings of the Linnean Society of New South Wales, vol. 67, pp. 213-237). Perhaps they are homologous with the parasphenoid component of the reptilian basipterygoid process, but dissociated from the basitrabecular process (just as the dermal pterygoid has become dissociated from the anterior process of the quadrate cartilage). However, I know nothing that could be cited as evidence for even this reptilian homology and it is quite possible that "basipterygoid processes" have originated several times within Aves. The presence of a cartilaginous core in the "basipterygoid process" of some birds, such as Dromaeus (Kesteven, op. cit.) that cannot be matched in position in the chondrocranium of reptiles suggests that the avian structure is a neomorph, at least in some avian groups.

The peculiarities of the bird palate have functional consequences in the formation of the braincase. The area of origin of the levator pterygoideus lies on the anterolateral surface of the braincase, near the root of the horizontal "postorbital" or "zygomatic" process, apparently formed partly by the pro-otic and partly by the laterosphenoid bones. The entire stress and strain of skull

kinesis must come to bear on this region, and the area of origin of the levator pterygoideus complex is braced by a vertical strut that extends downward behind the profundus (V_1) branch of the trigeminal and anterior to the maxillary (V_2) nerve; this strut, the pila antotica spuria, does not lie in the same plane as the primary braincase wall (defined by the dura mater), but distinctly more laterally, so that in the embryo the cranial wall may be duplicated in this region. If I have interpreted a dried skull correctly, at least Sula has the cranial wall duplicated in the adult, with a true pila antotica, pierced by the abducens (as usual in reptiles) and deep to the Gasserian ganglion space, as well as the pila antotica spuria. Kesteven (op. cit.) reports a true pila antotica in the embryo of Phalacrocorax, undoubtedly a relative of Sula.

I suspect that the pila antotica spuria, as a superficial duplication of the cranial wall to brace the levator pterygoideus origin, may be more extensive, at least in some birds, than has been suspected by others. Bland Sutton argued (and was ultimately proven right by paleontology and embryology) that the alisphenoid region of the mammalian skull could not be part of the primary braincase wall because the nerves do not emerge from it in the same sequence in which they pierce the dura mater. A similar argument could be made for rear wall of the orbit of Diomedea. For D. immutabilis I find the following foramina, with their contents: 1) an anterior (midorbital) foramen for the optic nerve; 2) a foramen just behind and slightly ventral to the optic foramen, containing the oculomotor and abducens nerves; and 3) a foramen just behind and dorsal to the last, containing the trochlear and profundus (V_1) nerves. Not only is this grouping of the extrinsic eye muscle nerves out of sequence with emergence from the brain, but it is also unlike the grouping for Spheniscus embryo (Crompton 1953, Acta Zoologica, vol. 34, pp. 71-146), Gallus (Kitchen Parker, 1878, Encyclopaedia Britannica, 9th Ed., Edinburgh, Adam and Charles Black, vol. 3, pp. 699-728; ; pers. obs.), Anas embryo (de Beer and Barrington 1934, Philosophical Transactions of the Royal Society of London, ser. B, vol. 223, pp. 411-467) or any lizard I know. I do not guarantee anything, but I suspect that a study of the orbital cranial foramina, with contents determined by dissection, would yield useful taxonomic data.

Critical to this argument is the nature of the palate in the (fossil) toothed birds. Unfortunately, the palate of these fossils is insufficiently known to be used either in support or in refutation of the argument presented here.

Gingerich (in a preliminary note in 1973, Nature, vol. 243, pp. 70-73, and in 1976, S. L. Olson (Ed.), Smithsonian Contributions to Paleobiology, no. 27, pp. 23-33) has attempted to reconstruct the palate of Hesperornis from dissociated bones, mainly of Marsh's (Yale Peabody Museum) skeleton. The reconstruction presents a bird quite unlike any living form, and while it provides a number of points that could be used for supporting my own interpretation, it would be best to await discovery of an Hesperornis with the palate in natural articulation. Gingerich finds the "pterygoid" (by my interpretation, the post-pterygoid)

to be a short and essentially vertical lamina with a very long contact with nearly the entire orbital process of the quadrate. No living bird (including tinamous and "ratites") has such an extensive contact of the dermal pterygoid with the chondrocranial pterygoid process (i.e., the orbital process of the quadrate), and Hesperornis would seem to be reptilian in this feature--- but it should be remembered that the pterygoid and quadrate were not found in articulation.

The bone identified as the palatine by Gingerich is a long lamina without projecting flanges of any kind and totally unlike the palatine of any reptile or the "palatine" (my pre-pterygoid) of any bird. Although unusually long and without medial fusion, it is much more like the vomer of some modern birds (Marsh's original interpretation of Hesperornis); it could also be interpreted as a hyoid element, but Gingerich finds a peculiar S-shaped facet at the rear of this bone that can be matched by a facet on the anterior edge of the "pterygoid", making it likely that the element called palatine by Gingerich was in articulation with the "pterygoid".

The bone identified as the (paired and unfused) vomer by Gingerich is peculiar in shape, with three laminae, and unlike the vomer of any bird or reptile known to me. By Gingerich's restoration, it would be quite free at its posterior end from both the palatine and pterygoid (as in Struthio only among living birds, but the vomers of Struthio are fused and quite unlike the element of Hesperornis in form). Gingerich restores this element as close to the midline, in the belief it is a vomer, but believes it could not be closely bound to its fellow without interfering with jaw kinesis (this bone is not known in its natural position, but the Yale specimen indicates it was contact with the maxilla and in the general region of the nasals). If the "vomer" of Gingerich were restored in a more lateral position, it would not be dissimilar to the "maxillopalatine" (i.e., my palatine) of many modern birds. The maxilla of Hesperornis, on the other hand, has no resemblance to the "maxillopalatine" of any living bird; it is a longitudinal tooth-bearing element that appears adapted to sliding fore-and-aft.

If my own interpretation is followed, Hesperornis had already divided the pterygoid into pre-pterygoid and post-pterygoid, but the pre-pterygoid would be unknown at present; the palatine of Gingerich would be the vomer and the vomer of Gingerich would be the true palatine (i.e. "maxillopalatine").

What little is known about the palate of Archaeopteryx is summarised by Ostrom (1976, Biological Journal of the Linnean Society [of London], vol. 8, pp. 91-182) and is based entirely on what may be observed of the Eichstätt specimen in an oblique dorsolateral view through the orbit (where not obscured by the sclerotic ring) and antorbital fenestra. There is an element ("maxillopalatine") on the palatal surface medial to the toothed maxilla and separated from that bone, but whether by a suture or a fracture cannot be determined. The quadrate does not appear to have a narrow and elongated orbital process like that of other birds, but there is a vertically deep rectanguloid wing on the anterior edge of the quadrate, as in Thecodontia, Saurischia,

and Ornithischia. Anterior to this there is a rather broad and irregular lamina of bone (labelled ec by Wellnhofer, whose illustration is reproduced without comment by Ostrom); this might well be the pterygoid flange region of the pterygoid, and if so, a narrow longitudinal bar of bone extending back to the middle of the anterior wing of the quadrate, to be continued on that wing by a ridge sloping upward and backward, might well represent the posterior tail of the pterygoid. All that can be said is that nothing is known of the palate of Archaeopteryx that cannot be explained readily by the hypothesis presented here, but at least a dozen other hypotheses could be fitted as well to these observations.

In the illustration (Figure 1) showing the homologies here suggested between archosaurs and birds, I have chosen the very primitive thecodont Proterosuchus to illustrate an archosaur, mostly because it is one of the few early archosaurs for which the palate is well known, and partly because this seems a primitive palate probably not dissimilar to that of the archosaurian group ancestral to birds, whatever that group may have been, although the backward sweep of the lower end of the quadrate in Proterosuchus is less bird-like than is the corresponding region of most other archosaurs except for Crocodilia.

I have been unable to compare the palate of birds with that of, for example, early coelurosaurian Saurischia. Unfortunately, in a time when some students claim knowledge of the physiology and metabolism of dinosaurs, it is still impossible to get information on dinosaurian osteology.