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 Pfannenstiel-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" of "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.
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*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.

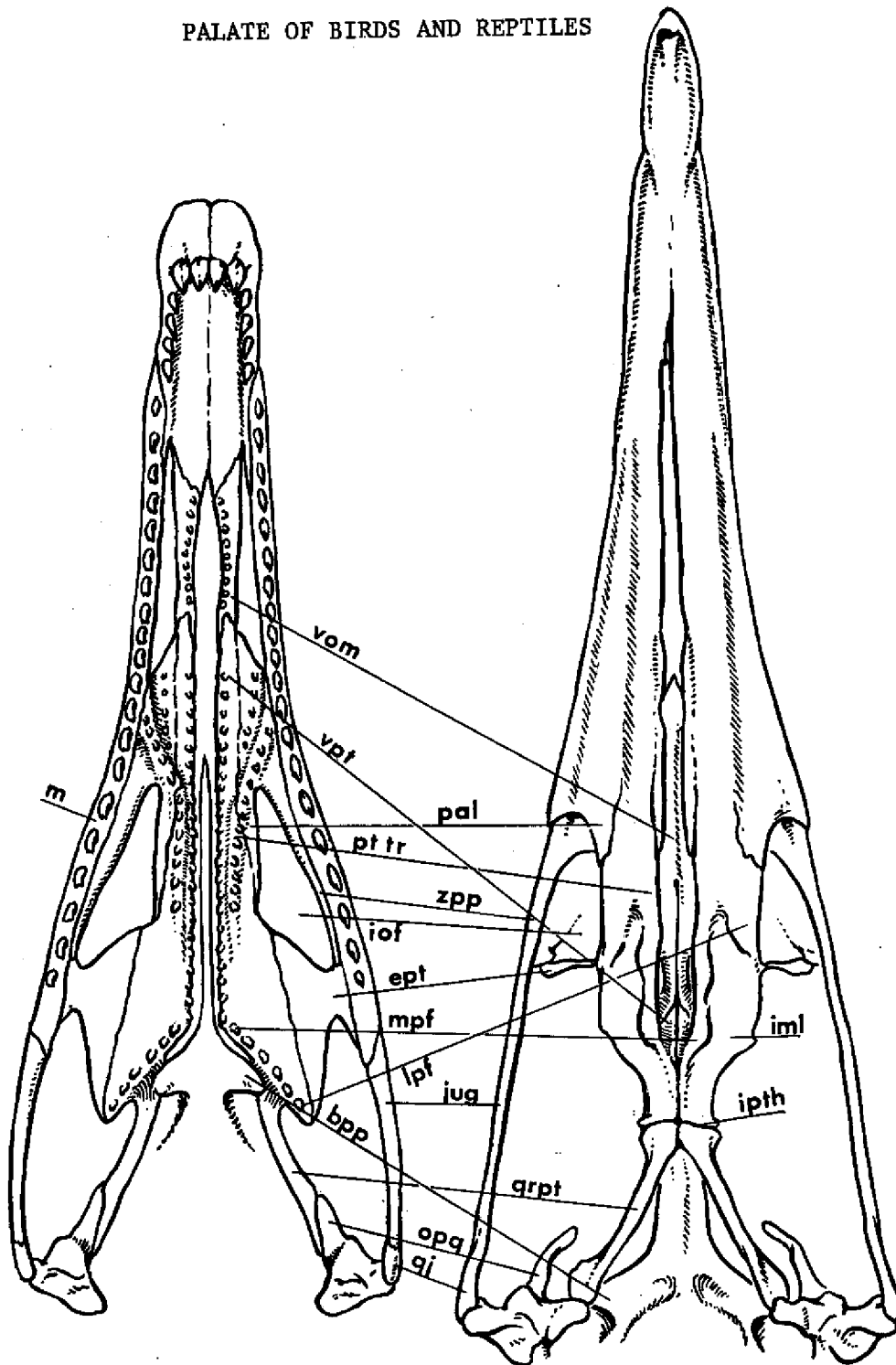Storrs L. Olson, Smithsonian Institution, Washington, DC 20560

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 Archo-
sauria 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 spec-
ialisations.

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 develop-
ment 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
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Figure 1 (to right). Homologies here proposed for palatal struc-
tures between (on left) the primitive thecodont archosaur Protero-
suchus (after Cruickshank) and (on right) a modern bird, Diomedea.
Abbreciations: bpp, true basipterygoid process, formed from basi-
trabecular 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 rep-
tiles; jug, jugal bone (fused to adjacent bones in birds); lpf,
lateral end of pterygoid flange; m, maxilla (lost in modern birds);
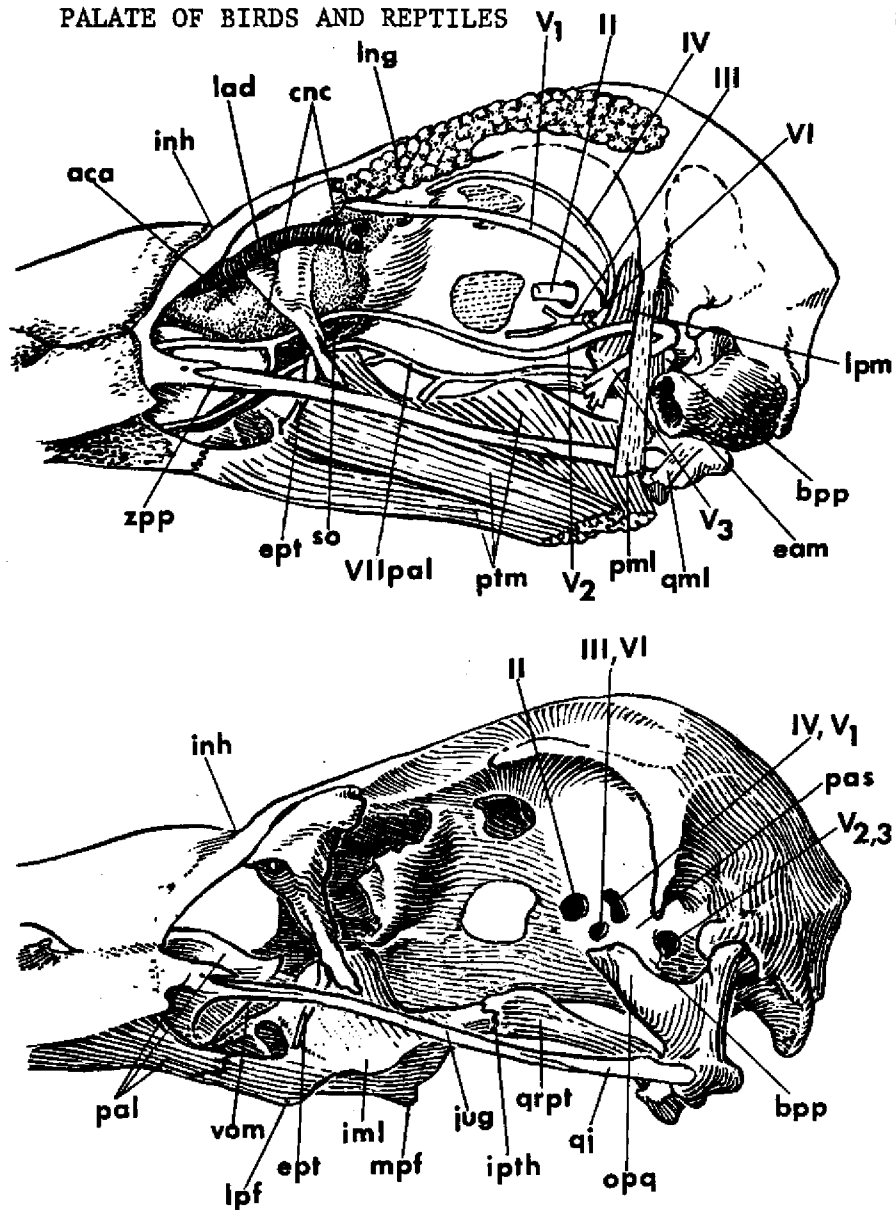mpf, medial end of pterygoid flange; opf, orbital process of quad-

rate bone; pal, palatine bone ("maxillopalatine" of birds); pttr,
middle pterygoid tooth row of Proterosuchus, represented in Dio-
medea by the edge of the nasopharyngial duct opening; qj, quadrato-
jugal 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 ptery-
goid 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 "paleo-
gnathous" 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 de-
finitive 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 artic-
ulation as the homologue of the reptilian palatine-pterygoid con-
tact. This presents difficulties. The palatine of reptiles is
closely associated with the choanal region of the olfactory cap-
sule and develops in the region of the primary choana; in the
embryo crocodilian (de Beer, 1937, The development of the verte-
brate skull, Oxford, Clarendon Press) the palatine starts develop-
ment 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
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Figure 2 (to right) Lateral view of the palatal region of a modern
bird, Diomedea; upper figure showing some associated soft struc-
tures; 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 squamatan and testud-
inate reptiles); bpp, true basipterygoid process, formed from
basitrabecular process of chondrocranium with addition of para-
sphenoid 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 ab-
ducens nerves; iml, intermuscular lamina of pre-pterygoid ("pala-
tine" of other authors); inh, intranasal (cranio-facial) hinge;
ipth, intra-pterygoid hinge; IV, trochlear nerve; IV, V_1, foramen
for trochlear and profundus nerves; jug, jugal bone; lad, lachrymal
duct; lng, lateral nasal gland; lpf, lateral end of pterygoid
flange; lpm, levator pterygoideus muscle; mpf, medial end of ptery-
goid 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-man-
dibular ligament; qrpt, post-pterygoid, homologous to the quad-
rate ramus of the pterygoid of reptiles ("pterygoid bone" of other
authors); so, ostium of orbitorostral air sinus; V_1, profundus
(ethmoidal or ophthalmic) ramus of trigeminal nerve; $V_{2,3}$, for-
amen for maxillary and mandibular rami of trigeminal nerve; V_3,
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)

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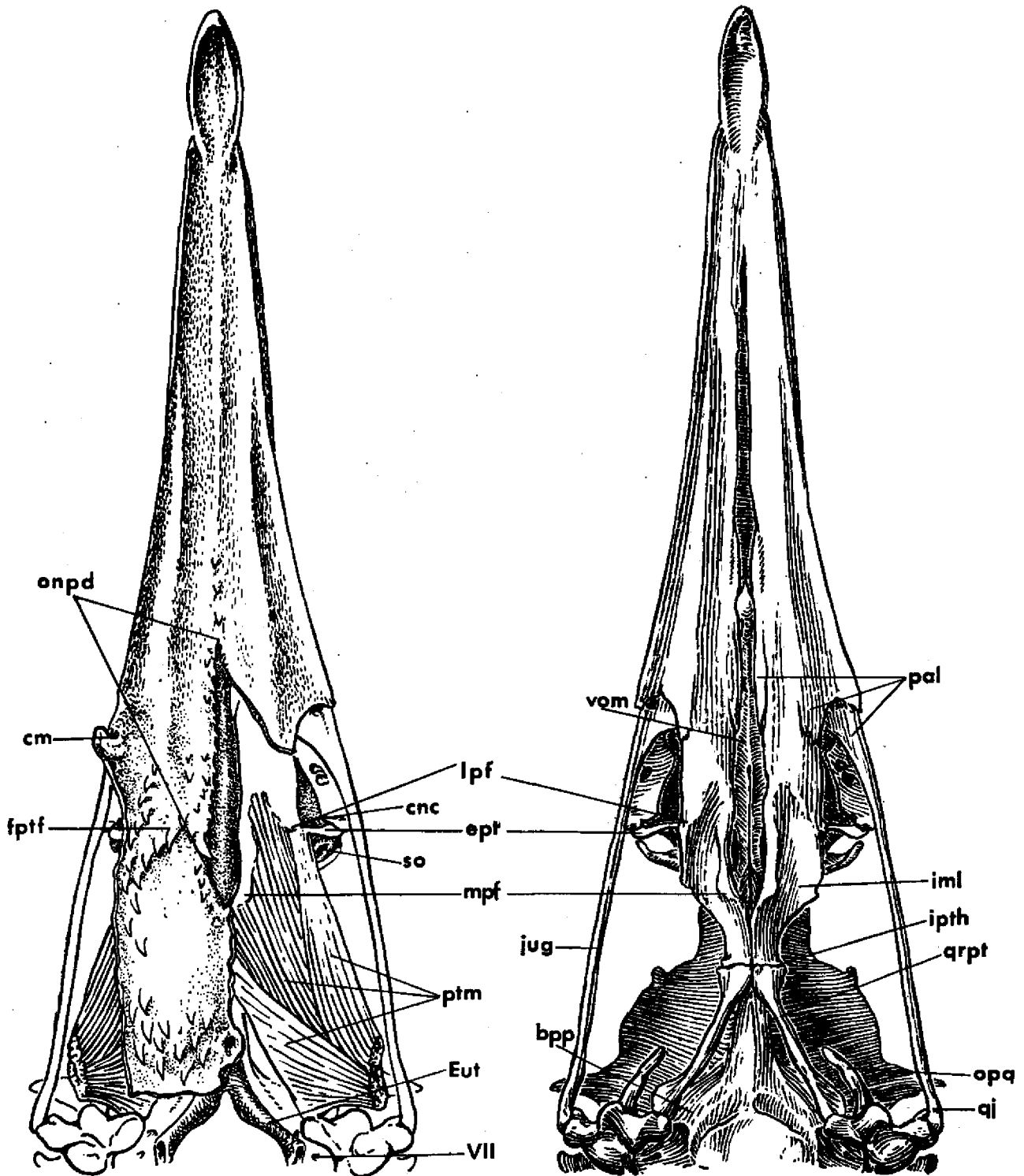
of other authors); ptm, pterygoideus muscle; qj, quadratojugal
bone; qrpt, postpterygoid ("pterygoid bone" of other authors),
homologous to the quadrate ramus of the pterygoid of reptiles;
so, ostium of orbitorostral air sinus; VII, foramen for facial
nerve; vom, vomer.

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 por-
tion 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
Trigeminus-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 for-
ward 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
otherkind 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 postpterygoid 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 Dro-
maeidae 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 ptery-
goids, 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
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*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 robit 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 re-
presented 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 com-
pleted 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 ecto-
pterygoid.)

   (A further aside: The palate of Proterosuchus is of consid-
erable 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 fric-
tional 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 postero-
lateral 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
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upper jaw that bore teeth (see Gingerich, 1976, Smithsonian Contri-
butions 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 yeild the palate of
such a bird as <u>Diomedea</u> or <u>Gallus</u>; converting the denticulated
crests into bony shelves meeting on the midline would form the
ductus nasopharyngeus of Crocodilia. The pterygoid flange of
<u>Proterosuchus</u> 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 <u>Diomedea</u> and <u>Gallus</u>. The lateral papilla row of
<u>Diomedea</u>, <u>Gallus</u>, <u>Mesoenas</u>, etc. seems to be represented in <u>Pro-
terosuchus</u> 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 pro-
cess of lizards and <u>Sphaenodon</u>. In reptiles, the main component
of the basipterygoid process is the basitrabecular process, aris-
ing 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 develop-
ment, 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 basi-
trabecular 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 en-
closed 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 <u>it</u> <u>does</u> <u>not</u> <u>articulate</u> <u>with</u> <u>the</u> <u>pterygoid</u> <u>bone</u>. 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 quad-
rate, receiving the insertion of the levator pterygoideus muscu-
lature. 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 man-
dibular branches of the trigeminal nerve, defined dorsally by a
notch for the passage of the stapedial artery and vena capitis
lateralis (or the rete mirabile formed by these two vessels) be-
tween 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 (charac-
teristic 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
thecarotid artery (more anteriorly, the palatine nerve accompanies
thepalatine branch of the carotid when the cerebral carotid sepa-
rates 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 ex-
cavation 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 pos-
sible that "basipterygoid processes" have originated several times
within Aves. The presence of a cartilaginous core in the "basi-
pterygoid 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 conse-
quences 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 "zygo-
matic" 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 inter-
preted 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 al-
ready 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 illus-
tration 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 obser-
vations.

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 prim-
itive palate probably not dissimilar to that of the archosaurian
group ancestral to birds, whatever that group may have been, al-
though 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 in-
formation on dinosaurian osteology.