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THE BONY PALATE OF BIRDS. PART I  
THE PALAEOGNATHAE

BY SAM MCDOWELL

THIS is the first in a series of papers in which the author intends to describe the osteology of the known birds with the end in mind of throwing more light on their higher systematics. I have chosen as my first topic the bony palate because of the stress laid upon this part of the avian skeleton from Cornay to the present in the classification of birds.

## ACKNOWLEDGMENTS

The author is deeply indebted to Dr. Ernst Mayr of the American Museum of Natural History for his generous encouragement and wise advice; to Dr. George Gaylord Simpson, Curator of Fossil Mammals and Birds of the same institution, for his invaluable suggestions and commentaries on the preliminary draft of this paper; to Mr. R. deSchauensee and Mr. James Bond of the Academy of Natural Sciences of Philadelphia for generously allowing the author the use of the Academy's skeletal material; to Messrs. Charles O'Brien and Alexander Seidel of the American Museum of Natural History for their valuable aid and for allowing the author the use of skeletal material in the American Museum's bird collection; to M. Charles Lambertson, of the Academie Malagache, for supplying me with references on the Malagasy ratites; and to Dr. J. T. Zimmer, Editor

of the Auk, for his patience in bearing with the author's spelling and stenography.

#### CLASSIFICATION OF THE PALAEOGNATHAE

The first zoologist to distinguish the large flightless birds from the remainder of the Aves was Merrem, who characterized a special group, Ratitae, on the basis of a keelless sternum, a large number of lumbar vertebrae, and parallel iliac bones. This group included *Struthio*, *Dromaeus*, *Casuaris*, and *Rhea*; *Apteryx* was apparently not classified, and the tinamous were placed in the contrasting group, Carinatae, characterized by keeled sternum, fewer lumbar, and divergent ilia.

Huxley's classification was essentially similar. *Rhea*, *Struthio*, *Casuaris* and *Dromaeus*, and *Apteryx* were included in the Superorder Ratitae, and the tinamous were placed in the Carinatae, though considered very near the ratites on the basis of the palatal characters and placed at the bottom of the Carinate list. (Huxley, 1867).

The work of Parker, Newton, and others, particularly Andrews and Milne-Edwards, did not change this classification except by including the extinct families Dinornithidae and Aepyornithidae in the Ratitae, these families apparently unknown to Huxley.

Garrod and Forbes regarded the ratites as a natural group, but placed them in the same group as the gallinaceous birds, rather than as a separate superorder.

Max Fürbringer (1888), however, argued that the ratites were a polyphyletic group. The ostriches (*Struthio*) he placed in one 'order' (Fürbringer's orders in reality correspond to superorders; what are generally termed orders were called by Fürbringer 'gens'), the Struthionithes, *Rhea* in an 'order' Rheornithes, *Casuaris* and *Dromaeus* in an 'order' Hippalectryornithes, and both the Apterygidae and Tinamidae in an 'order' Alectorornithes with the gallinaceous birds. Fürbringer based his conclusions on a detailed study of the muscular, nervous, and skeletal systems of the trunk and limbs, as well as a study of the fossil record.

Dissenters, however, particularly Gadow (1891), attempted to refute Fürbringer and reassert the naturalness of the ratite group on the basis of the similarity of the bony palate among the ratites. Gadow also employed certain visceral characters. He placed *Struthio*, *Rhea*, *Apteryx*, *Casuaris*, *Dromaeus*, the Dinornithidae, and Aepyornithidae, as well as the Phororhaci, Diatrymae, and Gastornithes, in a superorder Ratitae, the tinamous being placed as an order Crypturi in the Carinatae, next to the Galliformes.

Beddard (1898) did not distinguish superorders of Ornithurae, but

placed all the ratite palaeognaths in one order Struthioness, and the Tinamidae in an order Tinami, stating a close relationship between the two groups in the text, and basing his conclusion on the similarity of palatal structure.

Pycraft (1901), after a study of the osteology, myology, pterylography, and reproductive system of the ratites and tinamous, classed them together in a superorder Palaeognathae, placing the remainder of the ornithurine birds in a superorder Neognathae. Again the point used to establish naturalness of the ratite-tinamou group was the structure of the palate. The palaeognathous birds have the palatine and pterygoid bones articulated by squamous suture, while the neognathous forms are supposed to have the articulation by ball-and-socket joint.

The classification of Pycraft is the one most generally in use today, being the basis of such well-known classifications as that of Wetmore in use by the American Ornithologists' Union.

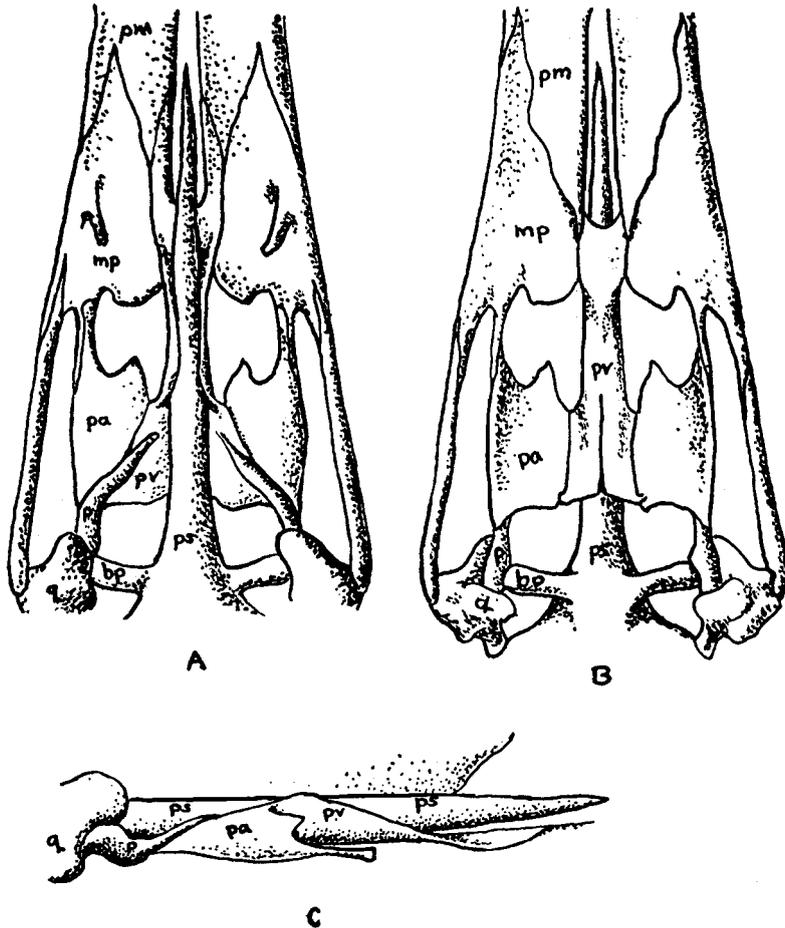
One notable exception is that of Stresemann (1927). He makes no superorders of Neornithes (Ornithurae), but places the palaeognathae in the orders Struthioness, Rheae, Casuarii, Aepyornithes, Apteryges (including Dinornithidae), and Crypturi, all these orders being placed next to one another at the beginning of the classification, immediately preceding the Galli. G. M. Allen (1925) follows a similar scheme.

Percy Lowe has advanced a theory that the Tinamidae are close to the stem-form of the flying birds, while the ratites diverged from the avian stem at a time when the power of flight had not yet been attained but the fore-limbs had become rather wing-like. This theory would necessitate believing that birds had at some stage of evolution sacrificed the use of their anterior limbs in order to acquire flight at a considerably later date, a teleology not acceptable to post-Lamarckian students of evolution. Lowe's theory may be discounted both on these theoretical grounds and on the basis of Fürbringer's study of the wing-musculature of birds.

It seems obvious from the foregoing account that forming a decision on the relationship of the ratites and the tinamous to one another and to the remainder of the birds requires a critical study of the bony palate. It does not seem amiss, therefore, to redescribe the palatal structure of the so-called palaeognaths in some detail.

#### RHEIDAE

The pterygoid articulates with the quadrate by an extensive ankylosis extending the length of the inferior surface of the orbital wing of the quadrate, and bears a small dorsal lip to receive the basipterygoid process on its quadrate foot. The bone is roughly cylindrical in form and S-shaped in the vertical plane, ascending along



TEXT-FIG. 1.—PALATE OF *RHEA* [RHEIDAE]

A. Dorsal view; B. Ventral view; C. Lateral view. mp = maxillopalatine; p = pterygoid; pa = palatine; pm = premaxillary; ps = parasphenoid; pv = prevomer; bp = basipterygoid process; q = quadrate.

the orbital wing of the quadrate, descending for its short free portion, then ascending again as a long finger-like process running along the dorsal side of the palatine on the latter's mesial margin, then curving inward to contact and ankylose with the dorsal surface of the posterior fork of the prevomer. The pterygoid and palatine are ankylosed where in contact. The pterygoids are separated from the parasphenoid and from one another by the prevomer.

The palatines are in the form of flat bony plates, only the shafts and mesial portions of the external laminae being developed. The latter is sometimes fenestrate. The internal border of the mesial plate sutures with the prevomer and underlaps the external portion of the posterior prevomerine fork. The palatine shaft is very short

and the maxillary runs back along its external side for some distance. From the anterior border of the mesial portion of the external lamina a triangular plate-like projection juts forth into the choana. The palatine shafts articulate by suture and overlap with the lateral portions of the maxillopalatines and do not extend forward beyond them. The palatine shafts are well separated from the mid-line, being much nearer to the jugal bar than to the prevomer. The outer border of the palatine runs straight from its pterygoid articulation to its maxillopalatine articulation, without outbowing or development of a posterolateral process.

The prevomer is very large and broad, without ventral carina. It is divided into two forks posteriorly by a longitudinal slit about a third the length of the mid-line of the bone. The forks are broad and truncated posteriorly, and closely appressed to one another. They lie wholly ventral to the parasphenoid and do not include it between them. The anterior extremity of the prevomer is also forked, the forks separated by a deep, broad, rounded notch, so that the anterior extremity of the bone is U-shaped. These forks are rather long and pointed, but almost completely underlapped by the palatal processes of the premaxillaries. The prevomer is closely appressed to the parasphenoid, and its sides are curled up to form ascending processes which embrace the sides of the parasphenoid, extending slightly dorsal to it to contact the mesethmoid. These ascending processes are very low and obtuse triangles with the obtuse angle dorsal. Other than the basiptyergoid processes, these ascending processes are the only contact the palate makes with the cranium proper.

The maxillopalatines are very low and flat plates, sometimes fenestrate, which extend inward to abut against the sides of the anterior part of the prevomer, and forward to overlap the posterior portion of the palatal processes of the premaxillaries. The palatines articulate with the posterior portion of the external third of the maxillopalatines, and a portion of the maxillopalatine runs down the external side of the palatine shaft.

The palatine processes of the premaxillary bones extend back to underlap the anterior forks of the prevomer. They are far separated from the palatines by the wide prevomerine extensions of the maxillopalatines.

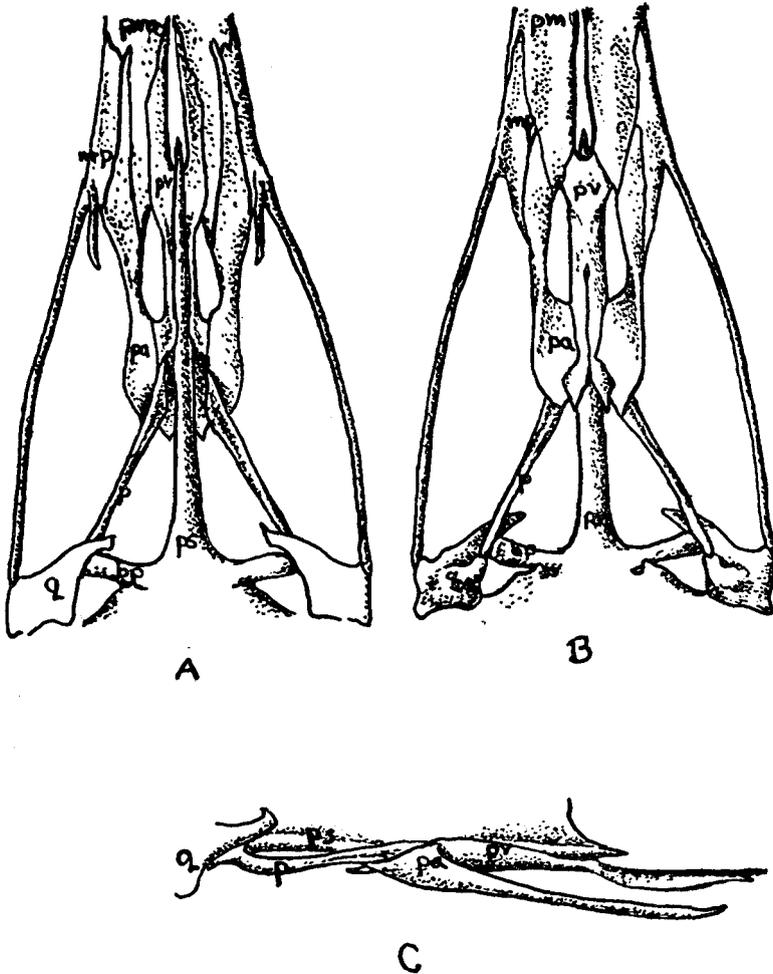
The basiptyergoid processes arise from the base of the parasphenoid. They are long and almost transverse to the axis of the skull. The parasphenoid rostrum is long, extending well anterior to the mid-line of the prevomer. In *Rhea* it also exceeds in forward extent the anterior prevomerine furcation, but not in *Pterocnemis*.

#### TINAMIDAE

The palate is remarkably similar in basic pattern to that of the Rheidae, but there are certain differences in detail.

The pterygoid is much longer, straighter, and more slender, and vertically compressed rather than cylindrical; its foot does not extend far up the ventral border of the orbital wing of the quadrate and presents to the quadrate a small lip extending dorsal to the origin of the shaft; the relations of the pterygoid with the palatine and prevomer are as in *Rhea*.

The palatine differs in not underlapping so much of the posterior portion of the prevomer and anterior portion of the pterygoid; it does not underlap more than the extreme anterior portion of the pterygoid, and occasionally does not completely conceal the pterygoid-prevomer contact. The palatines are much nearer to the mid-line of the skull than in *Rhea*, the shafts being much farther from the jugal bar than from the parasphenoid and prevomer, instead of the reverse; the mesial plate of the external lamina is therefore narrower. There is no anterior free projection of the



TEXT-FIG. 2.—PALATE OF *RHYNCHOTUS* [TINAMIDAE]

A. Dorsal view; B. Ventral view; C. Lateral view. mp = maxillopalatine; p = pterygoid; pa = palatine; pm = premaxillary; pv = prevomer; ps = parasphenoid; q = quadrate; bp = basipterygoid process.

mesial plate. The external border of the palatine is more convex and bulging than in *Rhea*, owing to the greater narrowness of the bone posteriorly, causing the posterior outline to dip inward. The relation of the palatine to the maxillopalatine is as in *Rhea*, but the process of the maxillopalatine extending down the outer surface of the palatine shaft is much narrower. The palatine shaft is much longer and narrower than in *Rhea*. Unlike *Rhea*, the palatal process of the premaxillary extends back to come into contact with the mesial border of the anterior extremity of the palatine shaft.

The prevomer is essentially as in *Rhea*, but the posterior furcation is much deeper,

extending almost half the length of the bone; these forks are more pointed than in *Rhea* and less flared-out laterally, the prevomer being narrower posteriorly than in *Rhea*. The anterior furcation is exactly as in *Rhea*, except that the forks extend anterior to the level of the tip of the parasphenoid (as in *Pterocnemia*). Other than these few points, there are no differences in the prevomer between the two groups.

Unlike *Rhea*, the maxillopalatine is not produced mesiad to the palatine articulation, and does not come into contact with the prevomer. Other than this the maxillopalatines are the same in both groups.

The difference in the palatal process of the premaxillary has been discussed above.

The parasphenoid and basipterygoid processes are as in *Rhea*, save that the basipterygoid processes are more depressed and flattened.

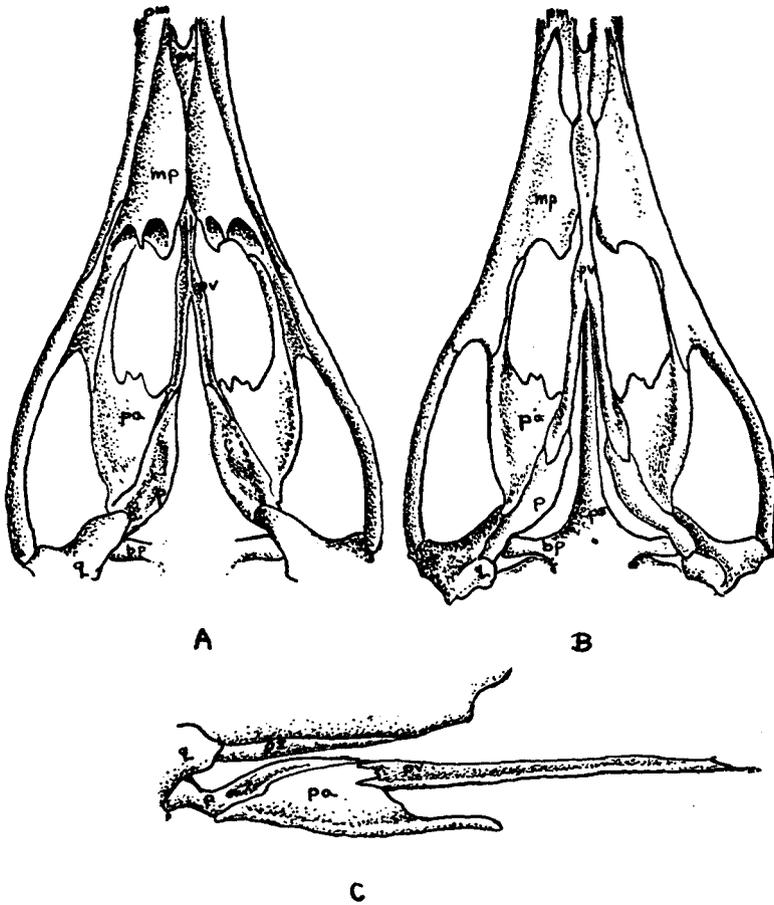
In general, the palate is longer and narrower in the Tinamidae than in the Rheidae, and most differences may be attributed to this difference in proportions. It is well to point out, however, that the maxillopalatine and palatine are never fenestrated in the Tinamidae.

#### CASUARIIDÆ

The pterygoid is inflated and excavated above. The quadrate foot sutures along the anterior face of the quadrate and part of the ventral margin of the orbital wing of the latter. The palatine sutures along the main portion of the lateral border of the pterygoid. The short, free (posteriormost) portion of the pterygoid is cylindrical and descending in the vertical plane. The pterygoid articulates with the basipterygoid at its extreme posterior extremity. It lies beneath the level of the parasphenoid, as does the rest of the palate, the palate being completely free of the brain-case except for the basipterygoid contacts. The portion of the pterygoid in contact with the palatine is transversely dilated, the pterygoid having the shape of a transverse ellipse.

The palatine, as before mentioned, sutures along the lateral border of the greater part of the pterygoid, as well as the posterior portion of the lateral border of the prevomer. The bone is formed entirely of the rather short shaft and the mesial plate of the external lamina. The mesial border of the shaft grades evenly into the anterior border of the mesial plate. The external lamina, of which the shaft forms the lateral margin, is directed downward and outward. From the anterior margin of the mesial plate a more or less triangular process juts forward freely. The shaft is inserted on the maxillopalatine. The latter runs back along the entire length of the lateral border of the anterior half of the palatine, not as a process free of the jugal process of the maxillary, but as a mesiad extension of it, separated by only a very shallow posterior notch. The outer border of the palatine is convex, since it dips inward toward the pterygoid posteriorly. The palatines are well separated from the midline of the skull, the shafts lying much nearer the jugal bar than the parasphenoid and prevomer. The palatine is in contact with only the lateral surfaces of the pterygoid and prevomer, and neither underlaps nor overlaps either bone.

The prevomer is the longest among birds. It lies wholly ventral to the parasphenoid and has no ascending processes, although there are low vertical crests on the dorsal surfaces of the posterior forks. There is no ventral carina, the ventral surface of the anterior portion of the bone being, in fact, concave. The bone is very deeply forked posteriorly by a long and narrow longitudinal fissure, which extends anteriorly to, or almost to, the mid-point of the bone. The posterior forks are perfectly straight, undilated, and separate from one another. These forks underlap the anterior extremities of the pterygoids and ankylose with them. The lateral margins of their



TEXT-FIG. 3.—PALATE OF *CASUARIUS* [CASUARIIDAE]

A. Dorsal view; B. Ventral view; C. Lateral view. mp = maxillopalatine; p = pterygoid; pv = prevomer; pa = palatine; ps = parasphenoid; pm = premaxillary; q = quadrate; bp = basipterygoid process.

posterior extremities suture with the mesial plates of the palatines. Just anterior to the posterior furcation the prevomer is quite narrow. It then broadens anteriorly and at its extreme anterior extremity is slightly forked by a rounded median notch, but the arms of the furcation are quite short. At the junction of the two posterior forks their dorsal carinae fuse to form a single longitudinal dorsal carina which gradually slopes into the flat dorsal surface of the anterior third of the undivided part of the bone. The prevomer is everywhere rather narrow.

The maxillopalatines in their relation to the palatines have already been described. Anteriorly to the palatine articulation the maxillopalatines extend mesiad to contact the sides of the prevomer, and farther forward extend mesially to contact one another dorsal to the prevomer. The maxillopalatines have, in addition to the flat palatine

lamina, a dorsal arched lamina which joins the ventral palatine lamina at its margins, except the posterior. The maxillopalatines thus have the form of hollow cones with their openings posterior.

The palatal processes of the premaxillaries extend back not only to underlap the anterior forks of the prevomer, but to underlap the sides of the anterior half of the undivided portion of that bone as well. They are well separated from the palatines.

As stressed before, the parasphenoid lies wholly dorsal to the plane of the palate, and does not enter into the palate, a departure from the condition of the other 'palaeognaths' except *Dromaeus*. It is likewise shorter than in the remaining 'palaeognaths,' its tip being on the level of the descending process of the lacrymal, behind the level of the posterior point of furcation of the prevomer. The tip of the parasphenoid is pointed and closely appressed to the ventral border of the mesethmoid, which exceeds it in anterior extent. From the base of the parasphenoid arise the cylindrical basipterygoid processes, which extend laterad to articulate with the posterior (quadrate) extremities of the pterygoids.

#### DROMAIDAE

The palate is similar in most respects to that of *Casuarius*, but its shorter and broader proportions have induced certain differences.

The pterygoid does not come into contact with the palatine, although the mesial border of that bone is produced back parallel to the lateral border of the pterygoid. The pterygoid is flattened, depressed, and dilated as in *Casuarius*, but is not excavated above. The relation of the pterygoid to the prevomer is as in *Casuarius*, except that the pterygoid is produced anteriorly to run along the mesial surface of the entire posterior fork of the prevomer. The ankylosis between the pterygoid and prevomer is even stronger than in *Casuarius*.

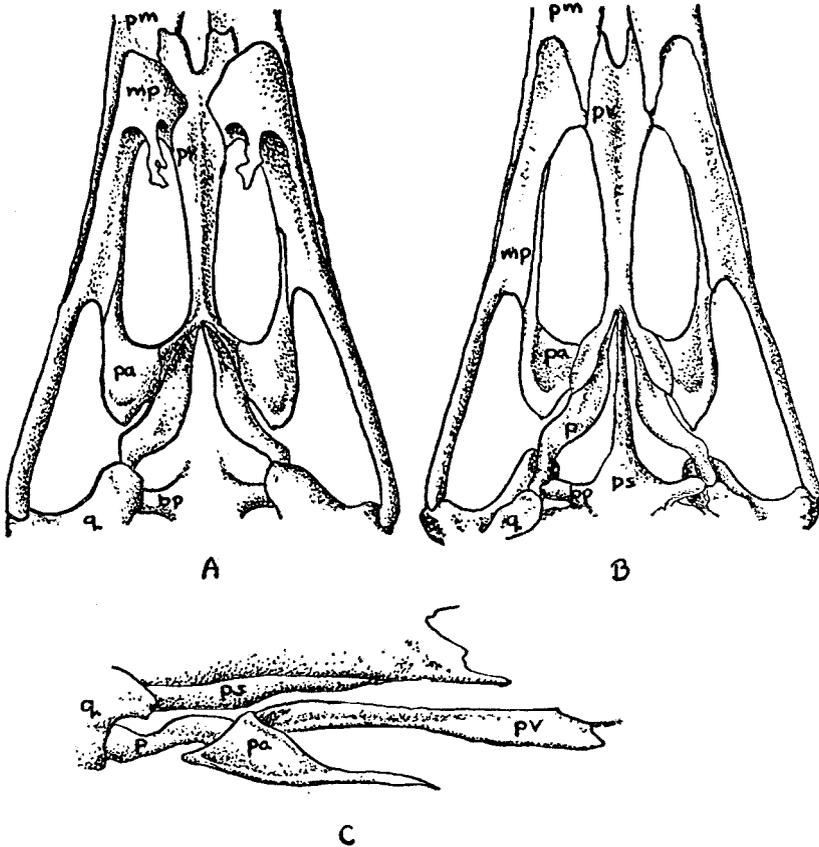
The palatine is very similar to that of *Casuarius*, but presents the following differences. The posterior portion of the mesial surface is produced back along the lateral side of the greater portion of the pterygoid, but instead of being in sutural contact, is separated from the pterygoid by a fissure of moderate breadth. The mesial plate is shorter and broader, and lacks the anterior triangular projection of *Casuarius*. Other than these peculiarities, the bone is similar to that of *Casuarius*.

Correlated with the broader and shorter skull, the prevomer of *Dromaeus* is shorter and broader than that of *Casuarius*. The posterior forks are shorter and more broadly separated than those of *Casuarius*, so that the fissure separating them becomes a triangular notch. This notch extends forward for only a fourth of the length of the prevomer, rather than a half. As in *Casuarius*, the prevomer is narrowest just anterior to the posterior furcation, but broadens anteriorly much more rapidly. Except for these particulars the bone is much the same in both genera.

The maxillopalatines are much as in *Casuarius*, except the anterior cones formed by the dorsal arched laminae are much shorter and blunter, more pocket- than cone-shaped. As in *Casuarius*, the anterior portions of the maxillopalatines overlap the prevomer, but in *Dromaeus* they do not contact one another, a consequence of the broader prevomer.

The palatine processes of the premaxillary are as in *Casuarius*, but almost completely underlap the prevomer-maxillopalatine contact.

The parasphenoid and basipterygoid processes are as in *Casuarius*, except that the median process (rostrum) of the parasphenoid is longer, reaching anterior to the level of the descending process of the lacrymal, about to the mid-point of the prevomer. In addition, this median shaft is keeled and compressed beneath.



TEXT-FIG. 4.—PALATE OF *DROMAEUS* [DROMAEIDAE]

A. Dorsal view; B. Ventral view; C. Lateral view. mp = maxillopalatine; pm = premaxillary; pv = prevomer; pa = palatine; p = pterygoid; q = quadrate; ps = parasphenoid; bp = basiptyergoid process.

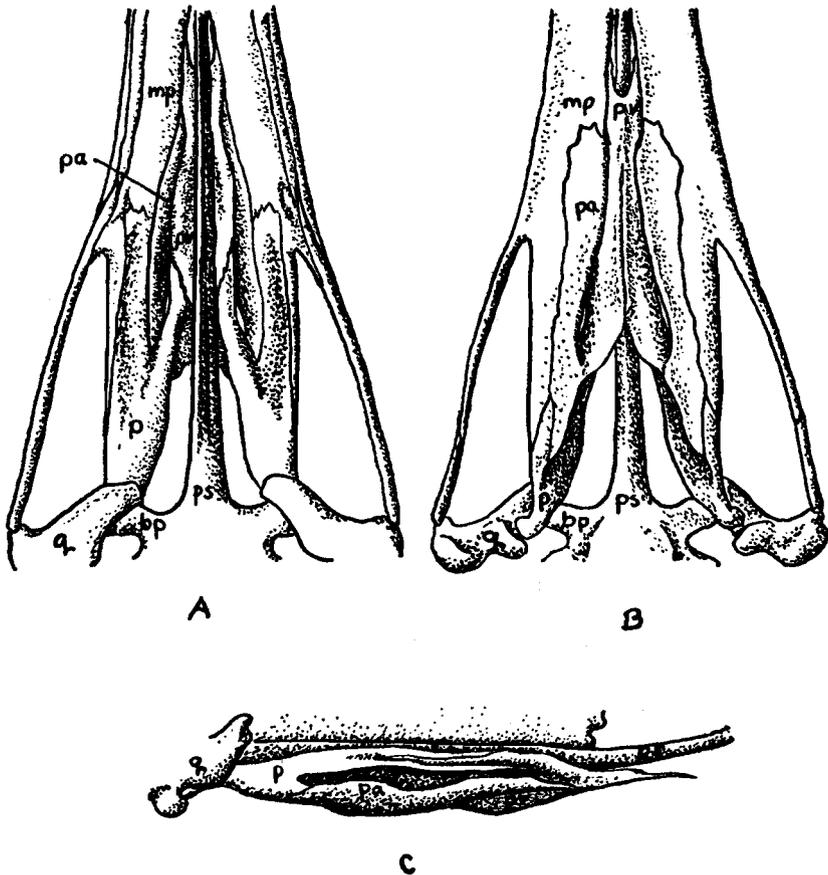
DROMORNITHIDAE

The palate of this fossil group has not as yet been discovered. However, the great similarity of known bones to those of the Casuariidae and Dromaeidae makes it seem likely that the palate was of similar construction as well. The known mandible (that of *Genyornis*), however, is very strong and heavy. Therefore, we may expect that the palate of this family was considerably sturdier than in the extant families, in consequence of the greater strain from the *Musculi pterygoideales*.

APTERYGIDAE

The pterygoid is unique among birds in being forked anteriorly. The outer tine runs along the dorsal surface of the posterior process of the maxillopalatine and the dorsolateral surface of the palatine. The inner fork runs along the dorsal surface of

the prevomer and comes into contact with the parasphenoid. This inner tine is about as long as the unforked basal portion of the pterygoid, while the outer is slightly longer. The pterygoid in general is broad, depressed, and concave ventrally. The lateral border of the unforked portion and of the lateral fork is bent downward and inward to suture with the lateral border of the palatine, except for the extreme anterior portion of the latter. The pterygoid, therefore, is in the form of a curled lamina forked anteriorly. The anterior extremity of the lateral tine of the pterygoid is posterior to the anterior extremity of the palatine, being about on a level with the descending process of the nasal. The mesial tine is also deflected and inflected to suture with the lateral border of the prevomer. Anteriorly, however, the entire ventral surface of the prevomerine (mesial) tine is applied to the dorsal surface of the



TEXT-FIG. 5.—PALATE OF *APTERYX* [APTERYGIDÆ]

A. Dorsal view; B. Ventral view; C. Lateral view. mp = maxillopalatine; p = pterygoid; pa = palatine; ps = parasphenoid; pv = prevomer; q = quadrate; bp = basipterygoid process.

prevomer and fused with it. Posteriorly the pterygoid is developed into a transverse circular tongue which fits into a corresponding slot on the ventral surface of the base of the orbital wing of the quadrate. In addition, the lateral border of the pterygoid is in contact with the mesial surface of the orbital wing of the quadrate.

The palatines likewise are of unique shape among birds. They are simple flat laminae, apparently homologous with the external laminae of other birds. But rather than extending downward and outward, they extend downward and very strongly inward, so that the mesial palatal margin of *Apteryx* corresponds to the lateral palatal margins of other birds, and vice versa. The outer border of the palatine of *Apteryx* is sutured for all its length, except the posteriormost extremity, to the posterior process of the maxillopalatine. This process lies external to, and conceals the inflexed lateral border of, the pterygoid, which also sutures with all but the anteriormost extremity of the lateral border of the palatine. The anterior portion of the mesial border of the palatine rests on the ventral surface of the prevomer, so that the combined prevomer and anterior palatine extremities form a sort of false palate, forcing the narrow choanae well back. The middle third of the mesial border of the palatine is concave, but immediately posterior to the middle third the mesial border extends inward as a triangular salient to fuse with the posterior extremity of the prevomer. The anterior extremities of the palatines are sutured with the maxillopalatines and are not contacted by the premaxillaries.

The prevomer is of moderate length but very broad. For its posterior two-thirds it is divided into two forks by a longitudinal sagittal fissure, but, except for the posterior fifth of the bone, the forks are very closely approximated to one another, with their mesial margins turned downward, so that a shallow ventral carina is formed. This carina is carried forward by a blunt ridge onto the solid portion of the bone. The posterior extremities of the forks (about one-fifth the length of the bone) diverge rather strongly from one another, and are truncate distally, fusing with the palatine as above described. Anteriorly the prevomer is shallowly forked, the tines being short and narrow, and appressed to the mesial borders of the maxillopalatines. They are not in contact with the premaxillary. The anterior two-thirds of the prevomer is separated from the posterior one-third by a constriction of the bone forming a neck. Similarly, a neck separates the anterior one-third from the posterior two-thirds, so that the prevomer is divided into three subequal parts. The posterior segment is broadest, the middle segment less broad, while the anterior segment is rather narrow. The lateral border of the posterior two segments of the prevomer is sutured to the deflected outer border of the mesial pterygoid fork, and the entire ventral surface of the mesial pterygoid tine is appressed to the dorsal surface of the middle segment of the prevomer. The lateral borders of the two posterior segments of the prevomer are bent up and thickened to embrace the parasphenoid. The contact of the dorsal surface of the middle segment of the prevomer with the parasphenoid brings the mesial tine of the pterygoid into contact with the parasphenoid as well.

The maxillopalatines are simple flat plates without dorsal laminae. They extend inward to abut against the sides of the anterior segment of the prevomer and are separated by the latter from the parasphenoid in some specimens. The maxillopalatine sutures with the anterior extremity of the palatine, and sends back a strong posterior process which lies external to the lateral pterygoid tine, and sutures along almost the entire lateral margin of the palatine, being excluded from the posterior extremity of the latter by the pterygoid.

The premaxillary has well-developed palatal processes, but these do not extend

backward to the level of the palatine and prevomer, being confined to the ventral surface of the rostrum.

The parasphenoid is compressed and keeled ventrally. It is closely applied to, and embraced by, the prevomer and contacted by the mesial pterygoid tine, but not by the palatine. The parasphenoid is sometimes contacted by the maxillopalatine. It is continued far anterior to the prevomer, curving upward anteriorly. It continues far anterior to the mesethmoid. The basiptyergoid processes are broad and depressed plates arising from the base of the parasphenoid and extending to the posterior extremities of the pterygoids.

#### DINORNITHIDAE

The author has been unable to examine any palatal material of this family, since of the many moa skulls in the American Museum of Natural History, not one retains the fragile bones of the palate. I have been forced to rely, therefore, on the description and lithograph given by Parker (1895). Unfortunately, Parker does not make reference to certain characters here deemed critical.

From Parker's illustration, the palatines are somewhat intermediate between those of the tinamids (and primitive neognaths) and those of *Apteryx*; they are roughly vertical in plane, with the ventral border slightly lateral to the dorsal border posteriorly. Posteriorly the dorsal palatine border sutures with the lateral border of the prevomer, as in all birds except *Apteryx* and *Struthio*. The unforked pterygoid apparently overlaps the prevomerine-palatine suture, ankylosing with both bones. This is suggestive of *Apteryx*, having similar relations to the forked homologous bone of the latter, but with the tines appressed to one another (a consequence of the apposition of the prevomer and palatine) and either fused to one another or not yet separated. This condition is superficially like that found in the Rheidae and Tinamidae, but in these the pterygoid overlaps the prevomer, then curves backward and outward to overlap the palatine; moreover, the pterygoid of the moas is plate-like, as in *Apteryx*, rather than cylindrical or compressed. The prevomer is very deeply divided sagittally, or even paired, as in *Apteryx*. The prevomer, according to Parker, embraces the parasphenoid and runs forward, overlapping the maxillopalatines to contact the premaxillary. (Overlapping of the maxillopalatines by the prevomer is unique among palaeognaths and suggests numerous neognaths, such as the Passeriformes and some Procellariiformes). From Parker's illustration, the maxillopalatines, though coming very close to the mid-line of the skull, are not produced abruptly mesiad to the palatine, and the premaxillary does not contact the palatine. All this is as in *Apteryx*. There is no false palate in the moas; hence the peculiarities of the palatine found in *Apteryx* are not so much in evidence.

Parker believed the palate of the Dinornithidae most nearly resembles that of the Apterygidae. Beddard (1898), however, believed that *Rhea* shows the closest similarity. Most of the similarities between the Rheidae and Dinornithidae seem to be merely primitive avian characters; however, without direct study of material, the author would not like to take a definite position.

#### AEPYORNITHIDAE

As in the case of the *Dinornithidae*, the author has been unable to examine material of this fossil family, owing to the absence of any skulls of this group from the collections of the American Museum of Natural History. I have relied, therefore, on the account of the palate of *Aepyornis hildebrandti* given by Lambertson (1930). Lambertson's account is not altogether clear on some points here deemed essential (e. g.,

whether or not the pterygoid is furcate) and his illustration is a photograph in which it is difficult to determine sutures and which does not show a dorsal view of the anterior part of the palate. With these reservations, I attempt a secondary description based on Lambertson's work.

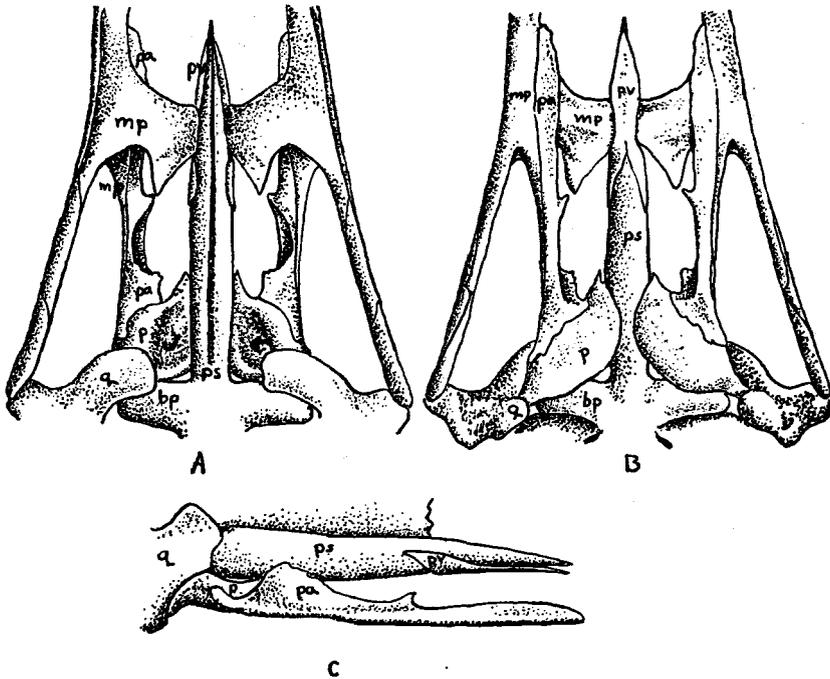
The basipterygoid processes are very broad, apparently similar to those of *Apteryx* in shape and relations, to judge from the figure (plate vi). Lambertson notes that the parasphenoid is very short for a 'ratite' (he makes no mention of having compared the emu or the cassowary) and much compressed. The pterygoid is concave ventrally and broadened. Anteriorly it is fused to the posterior extremities of the prevomer. Lambertson also states (p. 155) 'en avant de la caverne dont on vient de parler, la ptérygoïde est à peu près horizontal et se termine en une pointe triangulaire qui s'insinue entre le palatin et le maxillaire.' This is borne out by rather ambiguous suggestions of sutures in corresponding positions in his illustration. Although we cannot be certain, it appears from this that the pterygoid of *Aepyornis* is forked anteriorly as in *Apteryx*, the tines apparently having approximately the same relations, except that the furcation occurs at the posterior extremity of the bone. In general shape the bone appears to be similar in the two genera. The palatine, to judge from the illustration, is of the simple, highly inflected lamina type seen in *Apteryx* and does not seem to differ in any notable way, save that it does not contact the prevomer at any point (no false palate being formed) and joins the pterygoid at the extreme posterior extremity of the latter. In these points it resembles *Struthio*. Little can be determined from Lambertson's account and illustration about the prevomer, except that it is shallowly forked posteriorly, each tine fusing with the anterior extremity of the pterygoid of the same side, and that it is not carinate ventrally. I can determine nothing about its anterior extremity. Lambertson states that it is fused with the parasphenoid, a remarkable character. The posterior extremity of the prevomer apparently slightly underlaps the anterior extremity of the pterygoid. The maxillopalatine apparently sends back a process which runs along the entire dorsal border of the palatine, except where separated by the lateral tine of the pterygoid, to join the posterior extremity of the pterygoid. The sutures of the anterior palate cannot be made out from Lambertson's figure, but apparently the palatal process of the premaxillary broadly contacts both the prevomer and the palatine. The anterior palate seems unusually complete, forming a solid and continuous wall of bone anterior to the chaonae. Altogether, the posterior palate is very similar to that of *Struthio*, except that the prevomer contacts the pterygoid (in *Struthio* a ligament hints at a similar connection) and the pterygoid apparently has an outer prong as in *Apteryx*; but the anterior palate and parasphenoid seem to be as different as could be imagined.

#### EREMOPEZIDAE

The fossil fragments ascribed to the Aepyornithidae from the continent of Africa are, on the whole, very poorly known. No palates have yet been discovered. *Eremopezus*, known from a tibiotarsus, shows no particular resemblance to the Aepyornithidae, and in many characters (*e. g.*, the deep intercondylar groove) is quite different and more nearly resembles *Struthio*. Nothing as yet can be said of the relationships of this group.

#### STRUTHIONIDAE

The pterygoids are reminiscent of *Casuaris*. Their posteriormost extremities are cylindrical and decurved from the greater part of the bone. The posterior



TEXT-FIG. 6.—PALATE OF *STRUTHIO* [STRUTHIONIDÆ]

A. Dorsal view; B. Ventral view; C. Lateral view. mp = maxillopalatine process; p = palatine; pa = palatine; ps = parasphenoid; pv = prevomer; bp = basipterygoid process; q = quadrate.

extremity sutures with the anterior face of the condyle of the quadrate and the ventral portion of the anterior margin of the orbital wing of the quadrate. Anterior to the very short posteriormost cylindrical portion of the bone, the pterygoid is dilated into a broad ellipse, the maximum breadth being about half the length of the bone. This ellipse is excavated above, with the outer wall of the excavation much stronger than the inner. The palatine sutures along the middle third of the lateral border of the pterygoid, but does not underlap it. The anterior half of the mesial border of the pterygoid lies against the parasphenoid, or may lie below it, the pterygoid being capable of some movement in the vertical plane. The mesial borders of the pterygoids are only moderately separated from one another, the pterygoids being less broadly separated than in other 'Palaeognathae.' The anterior extremities of the pterygoids are pointed. The pterygoid is well separated from the prevomer, but a tough ligament connects the anterior extremity of the pterygoid with the posterior extremity of the prevomer. This ligament may represent the posterior portion of the latter.

The palatines differ from those of other palaeognaths in possessing both internal and external laminae, although the internal lamina is slight. The internal lamina is in the form of a rather narrow horizontal shelf jutting off from the mesial surface of the palatine shaft. It is broadest anteriorly, where it forms the main part of the bone and underlaps the maxillopalatine and fuses with it. At about the mid-point

of the palatine the internal lamina develops a triangular spine which projects forward and mesially to be connected by ligament with the posterior spine of the dorsal lamina of the maxillopalatine (as in *Anseres*). The external lamina is represented entirely by the mesial plate, which rises almost vertically from the shaft and contacts neither prevomers nor parasphenoid. It is much reduced, being confined to the posterior half of the bone. It originates at the dorsal surface of the mesial triangular process of the internal lamina and runs back along the lateral border of the shaft. Posteriorly the palatine broadens out to suture with the middle third of the outer border of the pterygoid. The relation of the palatine to the maxillopalatine is complex, since the maxillopalatine has two laminae, a dorsal and a ventral, as in *Casuaris* and *Dromaeus*. The ventral lamina is flat and runs along the outer edge of the palatine for most of the length of the latter. The dorsal lamina of the maxillopalatine is arched and convex dorsally and runs mesially to unite again with the ventral lamina. Against the ventral surface of the united ventral and dorsal laminae is fused the dorsal surface of the internal lamina of the palatine. In addition, the dorsal lamina of the maxillopalatine, which extends mesially to articulate with the prevomer, sends back from its posterior margin a triangular plate, the apex of which articulates by ligament with the apex of the triangular mesial process of the internal palatine lamina, as above described. The palatine makes no contact with the prevomer. The anterior extremity of the palatine projects freely a short distance anterior to the maxillopalatine (*Struthio c. australis*) or is delimited anteriorly by the anterior margin of the maxillopalatine (*S. c. camelus*). The lateral margin of the palatine is straight. The palatine does not touch the premaxillary and is broadly separated from its fellow.

The prevomer is short, forked behind, and pointed anteriorly. It contacts neither pterygoid nor palatine, owing to its extreme anterior position on the parasphenoid, the prevomer being much shorter than in remaining palaeognaths. It is applied closely to the parasphenoid. For its anterior two-thirds it is applied to the ventral surface of the parasphenoid and is simple, pointed, and flat. The posterior third, however, is furcated by a broad triangular notch, the tines extending halfway up the sides of the parasphenoid to embrace it. The maxillopalatines make squamous suture with the middle third of the sides of the prevomer (just anterior to the sides of prevomerine forks) and slightly overlap, as in some *Apteryx*, the prevomer to make contact with the parasphenoid. The prevomer extends forward, tapering to a point, approximately to the tip of the parasphenoid, but may exceed or fall short of it. It is not approached by the premaxillaries.

The relations of the maxillopalatine to the palatine have been described above. As mentioned above, the maxillopalatine is of a bilaminar type, as in *Casuaris* and *Dromaeus* (and *Anseres*). Unlike these genera, however, the two laminae, in uniting together, do not make a pocket or cone extending forward to the anterior extremity of the maxillopalatine, but form only a short fossa, the anterior portion of the maxillary being a flat lamina. As above mentioned, the maxillopalatines extend mesiad to contact the prevomer and the parasphenoid.

The premaxillaries are entirely devoid of palatal processes, and do not at all enter into the formation of the palate or contact any of its bones.

The parasphenoid and basiptyergoid processes are much stouter than in other birds. The parasphenoid is very stout, rounded below, and constricted just anterior to the basiptyergoid processes. It is pointed terminally and far exceeds the mesethmoid in anterior extent, though this is concealed in the adult by ossification of the internarial membrane. The parasphenoid is in contact with the pterygoid and

prevomer, but not the palatine. It is contacted by the maxillopalatine as described above. The basipterygoid processes arise at the base of the sagittal parasphenoid spike, and extend laterad and normal to the parasphenoid to contact the posterior thirds of the pterygoids; they are very broad and stout and elliptical in cross-section, being somewhat depressed.

#### INTERRELATIONSHIPS

The families herein described (Struthionidae, Rheidae, Casuariidae, Dromornithidae, Dromaeidae, Aepyornithidae, Eremopezidae, Dinornithidae, Apterygidae, and Tinamidae) have, since Pycraft (1901), been considered as closely related and constituting a special superorder of Neornithes, the Palaeognathae characterized by possessing a 'dromaeognathous' palate. It is the author's contention that the palate cannot be used to define such a superorder of birds, and, indeed, seems rather to separate the Palaeognathae into several groups.

##### I. THE IMPOSSIBILITY OF DEFINING THE PALAEOGNATHOUS PALATE

The standard definition of the palaeognathous or dromaeognathous palate is that of Huxley (1867) as a palate in which the posterior extremity of the prevomer is produced back to receive the anterior extremity of the pterygoid and posterior extremity of the palatine, separating both these bones from the parasphenoid. This definition will do very well for *Rhea* and the Tinamidae, but is quite inadequate for the entire group for these reasons:

1. As Beddard (1898: 139) points out, *Struthio* would be excluded by this definition, since the prevomer is not in contact with the pterygoid, which touches the parasphenoid. In *Apteryx*, also, the pterygoid contacts the parasphenoid. In the Struthionidae, Apterygidae and Aepyornithidae the posterior extremity of the palatine does not contact the prevomer.

2. Some neognaths, such as *Anhima* and the Anseres, have pterygoids which are only narrowly separated from the prevomer, rendering the distinction trivial.

3. In many neognaths the palate is suspended beneath the parasphenoid rostrum, so that neither the pterygoid nor palatine contacts it. Examples are such well-known birds as the common fowl and duck. The same condition exists in *Casuaris* and *Dromaeus*.

Huxley also states that the prevomer is large in dromaeognathous birds. The prevomer of *Struthio* cannot be called large by any standard, while several neognaths, such as *Diomedea* have relatively larger prevomers than do *Apteryx* or the Tinamidae.

The backward position of the basipterygoid processes, the third

point of Huxley's definition, can be matched by the Musophagidae and Turnicidae among the Neognathae.

Pycraft (1901) was, in fact, forced to reduce his definition of the palaeognathous palate to a palate in which the pterygoid and palatine articulated by squamous suture, the Neognathae supposedly having an articulation by ball-and-socket. This definition, also, falls short for these reasons:

1. In *Dromaeus* there is no contact at all between the palatine and the pterygoid.

2. Numerous Neognathae have a squamous sutural articulation between the pterygoid and palatine. Examples are the Galli, Anhimae, Anseres, and Sagittarioidae.

3. The details of this squamous suture are quite different in the various groups of the Palaeognathae, and therefore, real similarity must be considered dubious (*see* below).

The writer has had no more success than Huxley or Pycraft in finding characters to define the dromaeognathous or palaeognathous palate. He must conclude, therefore, that the palaeognathous palate is undefinable.

## II. THE DIVERSITY OF THE PALAEOGNATHOUS PALATE

The author feels, however, after consideration of the morphological data assembled above, that the families of Palaeognathae may all be assigned to four well-defined palatal types, with a possible fifth type for *Aepyornis*, of which the palate is imperfectly understood. These types are:

1. The Tinamiform type: The prevomer is large, its halves imperfectly fused, the bone being deeply furcate before and behind; it embraces the parasphenoid, the palate thus being bound to the braincase. The palatines lack internal laminae; their ventral borders lie far lateral to their dorsal borders. There is no false palate. The posterior portion of the dorsal border of the palatine slightly underlaps and fuses with the lateral border of the posterior extremity of the prevomer. The pterygoid overlaps and sutures squamously with the prevomer, then curves backward and outward to overlap and ankylose with the posterior extremity of the palatine; it is cylindrical or compressed and slender, the maxillopalatine is unilaminar. The premaxillary has a strong palatal process.

Rheidae (Pliocene to Recent of South America); Tinamidae (Pliocene to Recent of Central and South America).

2. The Casuariiform type: The prevomer is long, but rather narrow, its halves imperfectly fused, the bone being shallowly furcate anteriorly.

only, rather deeply furcate posteriorly. The entire palate, including the prevomer, lies wholly ventral to the parasphenoid, not contacting it, and is free of the brain-case, except at the basiptyergoid facets. The palatines lack internal laminae, their ventral margins lying well lateral to their dorsal margins, and do not contact the prevomer except at the posterior extremity. There is no false palate. The pterygoid is simple and transversely plate-like, its anterior extremity ankylosed to the posterior extremity of the prevomer, there thus being formed an arch. To the lateral surface of this arch the mesial border of the posterior part of the palatine fuses. The pterygoid contacts neither parasphenoid nor maxillopalatine. The premaxillary has a strong palatal process underlapping the anterior extremity of the prevomer. The maxillopalatine is bilaminar. The parasphenoid is reduced.

Dromaeidae (Pleistocene to Recent of Australia); Casuariidae (Pleistocene to Recent of Australian region). Almost undoubtedly also Dromornithidae (Pleistocene of Australia).

3. The Struthioniform type: The prevomer is much reduced by loss of its posterior half. Its halves are well fused, the bone being pointed anteriorly and rather shallowly furcate posteriorly. It is nowhere in contact with the pterygoid or palatine, but embraces the parasphenoid. The palatines have narrow internal laminae, giving them an L-shaped cross-section. The ventral border of the palatine is lateral to the dorsal border. There is no false palate. The palatine sutures along the lateral border of the pterygoid and its anterior extremity extends to or beyond the anterior margin of the maxillopalatine. The maxillopalatine is bilaminar. The pterygoid is simple and plate-like, its anterior extremity contacting the parasphenoid. The pterygoid contacts neither prevomer nor maxillopalatine. The premaxillary has no palatal processes. The parasphenoid is long and stout.

Struthionidae (Pliocene to Pleistocene of Europe, Asia, and Africa; Recent of Africa and western Asia). Possibly, also, Eremopezidae (Eocene to Oligocene of Africa).

4. The Apterygiform type: The prevomer is rather large, its halves imperfectly fused, the bone being shallowly furcate (? as to Aepyornithidae) anteriorly, and deeply furcate posteriorly, or even paired. The prevomer embraces the parasphenoid, binding the palate to the skull. The palatines lack internal laminae, *but are decidedly inverted, their ventral borders being beneath or mesial to their dorsal borders.* The palatine sutures with the lateral margin of the pterygoid. The pterygoid is plate-like, and forked (Apterygidae, Aepyornithidae [?]) or simple (Dinornithidae). It ankyloses with the dorsolateral border

of the posterior extremity of the prevomer. The pterygoid thus contacts the palatine and the prevomer simultaneously (or, in those forms in which the pterygoid and palatine parts of the pterygoid are separated from one another by a fissure, separately), rather than contacting the prevomer first, then contacting the palatine more posteriorly, as in the Tinamiform type. Maxillopalatines unilaminated. The premaxillary has a strong palatal process. In all but the Dinornithidae the maxillopalatine contacts the pterygoid.

Apterygidae (Pleistocene of Australia; Pleistocene to recent of New Zealand). Dinornithidae (Pleistocene of New Zealand). ?Aepyornithidae (Pleistocene of Madagascar).

There are two possible explanations of this diversity:

1. The so-called palaeognaths are truly closely related, but the palate has become so variable as to lose significance in determining affinities (Hypothesis of unity).
2. The Palaeognathae are not a natural group (Hypothesis of disunity).

Let us examine these hypotheses.

### III. THE HYPOTHESIS OF UNITY

If we are to believe that the palate is variable to such an extent that we cannot use it to define the Palaeognathae, then we are faced by a dilemma, for it is on the very basis of the palate that the Palaeognathae have been separated from the Neognathae and held to be homogeneous. To accept the hypothesis of unity of the Palaeognathae requires that we invalidate the definition of the group offered at present. Until other criteria are offered, therefore, we must, in duty to scientific doubt, deny the unity of the Palaeognathae.

### IV. THE HYPOTHESIS OF DISUNITY

Accepting the refutation of the hypothesis of unity, we must accept the validity of the present alternative. We may further consider the possible explanations of disunity.

1. The families of palaeognaths have evolved from a common ancestor along at least four main phylogenetic lines, these lines having become as distinct from one another morphologically in regard to the palate as from the Neognathae (Hypothesis of common ancestry).
2. The families of palaeognaths have descended from several very distinct ancestors (united, of course, at the common Neornithic stem) (Hypothesis of archaic diversity).
3. The families of palaeognaths have descended from groups of

Neognathae, acquiring a secondarily primitive palate (Hypothesis of reversal).

Hypotheses 1 and 2 imply that the palates of the palaeognaths are in truth primitive; that is, the path of morphological change has followed the path of genetic evolution. Hypothesis 3 assumes that morphological change has at some point reversed itself and become negatively, rather than positively, correlated with genetic evolution. Let us consider this latter possibility.

#### V. THE HYPOTHESIS OF REVERSAL

There is some evidence to indicate at least the possibility of truth of this hypothesis.

1. The similarity of the palate of the Rheidae to that of the Tinamidae is also borne out by similarities in the nasals, lacrymals, calvarium, costal processes, hypotarsus, sculpture of leg-bones, coiling of gut, etc. This resemblance is so great, in fact, that close phylogenetic relationship seems unavoidable. Now, for many reasons, such as wing-like form of the anterior limb, myology of the anterior limb, the philosophical reasons given in the discussion of Lowe in the historical account, etc., it seems fairly definite that the ratite forms have evolved from flying forms, and, therefore, that *Rhea* is evolved from the Tinamidae, rather than the reverse. But the palate of *Rhea* is more 'primitive' than that of the Tinamidae in several respects: (a) the palatines are more broadly separated; (b) the pterygoid is shorter; (c) the palatine does not contact the premaxillary; (d) the prevomer is broader. Here we apparently have an example of evolution proceeding from a less to a more primitive condition of palate. Since it has apparently happened here, can we not say it may possibly have occurred in other palaeognaths?

2. There are numerous examples in zoology of neoteny having worked morphological reversals. Examples are the Sphenisci, where neoteny has produced a less fused, and therefore more reptilian, tarsometatarsus (*see* Simpson, 1946), and the Urodela, where several morphologically primitive forms were shown (*see* Noble, 1931) to be neotenic forms of several distinct families (Hynobiidae, Amblystomidae, and Salamandridae), whereas they had previously been placed in one group, the 'Perennibranchiata.' Now, there are several indications of neoteny in the skulls of the 'Palaeognathae,' in addition to the numerous indications of neoteny in the wings and pelvis (as the failure of the ilium and ischium to coössify posteriorly). Examples of neoteny in the skulls of 'palaeognaths' are:

a. The failure of the anterior bony nares to close behind and

become separate from the preorbital fossa. This cannot be looked upon merely as a retained reptilian character, for in Archaeopterygidae (Heilmann, 1926) the nares and the preorbital fossa are separated by a buttress of bone formed from the maxillary and nasal and premaxillary. In the Pseudosuchia, which Heilmann gives us good reason to regard as ancestral to the Aves, the same condition exists, as shown by published figures (*see* Heilmann, 1926; Broom, 1913; von Huene, 1920; Broili and Schroeder, 1934-1937, pt. 5). We can only regard this as retention in the adult of an embryonic character (neoteny).

b. Failure of the cranial sutures to close, at least until senescence.

c. The tendency for the eustachian canals to remain open or partly open inferiorly, most obvious in the Apterygidae and Aepyornithidae.

We must not forget that neoteny is usually not limited to a specific organ. Thus, neotenic persistence of gills in the 'perennibranchs' is accompanied by neotenic skull-characters and muscular characters, and neoteny in the tarsometatarsus of the Sphenisci is accompanied by late obliteration of the cranial sutures. We may, therefore, expect that the neoteny of the wings of the ratites might affect the palate.

Neoteny might easily explain such a palatal characteristic as the imperfect fusion of the halves of the prevomer. Pycraft, in the 'Infancy of Animals,' states that neognaths go through a *Dromaesus*-like stage of development in respect to the prevomerine-ptyergoid contact, the difference being produced by fusion of the hemipterygoid (the connecting piece) to the palatine. If this is true, then neoteny could also explain the pterygoid-prevomer contact, the heart of Pycraft's definition of the 'Palaeognathae.'

3. Although all the 'palaeognaths' show some characters which appear primitive, there is no particular agreement among the various groups as to exactly which 'primitive' characters are exhibited. We may consider the so-called primitive characters of the 'palaeognaths':

a. A large prevomer. We may first doubt the primitiveness of this feature, since in none of the Archaeosauria can the prevomer be considered relatively large, while in such primitive pseudosuchians as *Chasmosaurus* (*see* Broili and Schroeder, 1934-1937, pt. 5) the prevomer is quite small. Secondly we may point out that the prevomer of such neognaths as *Diomedea* and *Puffinus* is large, while the Passeriformes have the prevomer of broad and flat form as in the 'palaeognaths.' Thirdly, the prevomer of *Struthio* is not large.

b. Furcation of the pterygoid. This is a character seen in such

Pseudosuchia as *Ornithosuchus* (see illustration in Heilmann, 1926). It is found in *Apteryx* and *Aepyornis* but not in other birds. Even here it may be explained by adaptation (see below).

c. Imperfect fusion of halves of prevomer. Reptilian, but see discussion above. This character is not shown by *Struthio* to any greater extent than by numerous neognaths, such as Pici and Charadrii.

d. Articulation of palatine with lateral border of pterygoid, rather than with ventral surface of anterior extremity of latter. Reptilian, but not indicated in Tinamidae or Rheidae.

e. Pterygoid plate-like in form. Possibly reptilian, but not indicated in Tinamidae or Rheidae, and approached by such Neognathae as recent Spheniscidae, but not by ancient Spheniscidae (see Simpson, 1946).

f. Pterygoid contacting prevomer. Reptilian, but see discussion above. Not seen in *Struthio*.

g. Long parasphenoid. Doubtfully reptilian. Not so in *Casuaris*, *Dromaeus*, or *Aepyornis*. The parasphenoid is rather long in such neognaths as *Phalacrocorax*.

The author has not been able to find one primitive palatal character common to the 'palaeognathous' forms and not also found in Neognathae. He finds himself unable to believe, therefore, that this group represents a uniform primitive avian stock. Moreover, since no one of the four palaeognathous types enumerated above seems more primitive than any other, he finds it hard to believe these stocks represent successive offshoots from the primitive avian stem.

4. It occasionally happens that typical neornithic birds will show individual mutations of a 'palaeognathous' nature. An example is Lowe's discovery of a hummingbird skull in which the pterygoid fused to the prevomer. Other such cases are known (see note in Oliver, 1945). Picidae also frequently approach this condition. This would seem to indicate that neognaths have in their genotypes potentialities for the 'palaeognathous' palate.

5. The variation between individuals in palatal structure among Palaeognathae may indicate that palatal characters of the families are fairly recently acquired and not yet stabilized. Examples are the variability of fenestration of the palatine and maxillopalatine in the Rheidae, the variability as to parasphenoid-maxillopalatine contact in the Apterygidae. Pycraft (1901) has defined the subspecies of *Struthio camelus* by differences in the structure of the palate.

6. Although these large-boned birds inhabiting arid regions might be expected to be the most easily fossilized birds, and are, in fact very

frequent (for birds) in Pleistocene deposits, not one family definitely known to possess a 'palaeognathous' palate is known from pre-Pliocene deposits. Yet such brittle-boned forest forms as Passeres are represented in the Eocene by such genera as *Laurillardia* and *Palaeogithalus*. This leads one to be somewhat dubious of the antiquity of the 'Palaeognathae.'

It must be remembered, however, that definitely neognathous forms with neotenic wings, such as *Strigops* and *Didus*, show typically neognathous palates. This need not cause us to deny validity to the reversal hypothesis for there is no reason why all neoteny should affect the palate, any more than that all neoteny should not do so. If the dodo had undergone serious palatal changes, it is possible that its neognathous affinities would not have been realized, and it would be considered to bear the same relation to the Columbæ that the Tinamidae are considered to bear to the Galli. (The author is indebted to Dr. Ernst Mayr for the suggestion of possible reversion in the Palaeognathae.)

#### VI. POSSIBILITIES OF ADAPTATION

Certain of the features of the 'palaeognathous' palate may also be explained by adaptation and convergence. An example is the false palate of *Apteryx*. *Apteryx* is highly specialized as an helminthophagous form, the specialization including a very elongate beak with the nostrils terminal, thus forming a sensitive probe. Now, the mammalian genus most nearly paralleling *Apteryx* in habits is *Myrmecophaga*, and here again we see great extension of the false palate, which is longer in this latter genus than in any other mammal. This in itself hints that false palate-formation is coördinated with insectivorous habits. A possible explanation is that the internal nares are brought back into closer fit with the glottis, the greater respiratory efficiency thus achieved perhaps compensating for the greater difficulty in drawing a column of air through the beak, which has been greatly lengthened for the helminthophagous method of feeding. The furcate pterygoid of *Apteryx* seems to the author to be another adaptation correlated with the false palate, rather than a real resemblance to *Ornithosuchus*. The false palate of the kiwi is formed by a strong inversion of the palatines. Unless the axis of rotation of the palatine had passed along the dorsal border of the bone, which it has not, the inward rotation of the normally lateral ventral border would produce an outward rotation of the dorsal border. This outward rotation of the dorsal border of the palatine has separated the portion of the pterygoid which runs along it from the portion of the pterygoid which

runs along the outer border of the prevomer. In *Aepyornis*, although there is no false palate, the palatine is rotated as in *Apteryx*, and the pterygoid is likewise furcate. The Dinornithidae, which in most palatal characters, as well as in structure of the rest of the skeleton, resemble *Apteryx*, have very short beaks and no false palate, and therefore the pterygoid is simple.

As to the solid connection of the pterygoid with the palatine found in this group, this modification seems to be coördinated with the fact that this group lacks the cranio-facial hinge found in numerous neognaths, particularly in Psittaci. In hinge-faced birds the pterygoid acts as a connecting bolt between the quadrate, which initiates the forward push, and the palatine, which conveys this push to the rostrum. Now, since the quadratic foot of the pterygoid moves in a circle around a centre which is the squamosal-quadrate articulation, it has an upward movement ( $y$ ):

$$y = \sqrt{r^2 - x^2}$$

where  $r$  (the radius) is the distance from the pterygoid-quadrate articulation to the squamosal-quadrate articulation, and  $x$  is the horizontal movement of the pterygoid-quadrate articulation. The palatine, however, is almost incapable of movement in the vertical ( $y$ ) direction, and thus the pterygoid must be able to rotate vertically around the palatine articulation if it is to maintain connection with both palatine and quadrate while the mechanism is in motion. The hinge-faced birds always have a loose and mobile articulation between pterygoid and palatine. The 'palaeognaths,' however, are, with the exception of *Apteryx* and the tinamous, grazing birds, requiring a solidly fixed upper mandible, so that a strong pinching action may be exerted at the tip, while the tinamous feed to some extent on roots and require a similarly strong pinching power. *Apteryx* frequently uses the bill as a crutch and requires a stable upper mandible. Hence we find that the palate has been locked in place by ankylosis of the pterygoid and palatine, while the pterygoid-quadrate articulation has been soldered together not only by the firm union of these bones, but by the posterior position of the basipterygoid processes, which come to bear directly on the pterygoid-quadrate articulation. Thus three characters of the palaeognathous palate may be explained adaptively, and hence are open to suspicion of convergence. In neognaths which lack the cranio-facial hinge, such as *Sagittarius*, the pterygoid-palatine articulation is usually strong and palaeognath-like.

The large ratites (*Rhea*, *Struthio*, *Casuaris*, and *Dromaeus*) have specialized toward the enlargement of the gape, probably to facilitate

the swallowing whole of large objects. (The propensities of the ostrich in this direction are proverbial.) Dr. George G. Simpson, who has had considerable experience with *Rhea*, informs me that this bird is quite proficient as a fly-catcher, and enlargement of the gape in this genus may be correlated with this. This broadening of the mouth may be responsible for such characters as the broadened prevomer and wide separation of the palatines. In the Tinamidae, where the mouth is not broadened, the palatines are not widely separated and the prevomer is not particularly broad.

In conjunction with the enlargement of the mouth in these birds, the tongue has become much reduced, so as not to obstruct the pharyngeal passage. This has resulted in a lower, flatter, less arched palate, owing to reduction of lingual pressure. In the Procellariiformes, among Neognathae, the tongue is similarly reduced and the palatines lie low in the skull, among some Hydrobatoidea below the level of the jugal arch.

The larger ratites lay relatively thick-shelled eggs, apparently a specialization required of birds which lay conspicuous eggs on the ground, usually in unprotected places. Dr. Simpson has suggested to me, quite rightly, that the great weight of the incubating father is at least partly responsible for this thickness of egg-shell. This thick shell must present a serious problem to the chick attempting to peck its way out. This pecking must jar the palate considerably and require considerable force to be conveyed along it. This may account for the sturdier and more massive form of the bones of the palate in the ratites than in the Neognathae. The tinamous have thin-shelled eggs and their palatal bones are thin and no stronger than in the average neognath.

#### VII. THE HYPOTHESES OF COMMON ANCESTRY AND OF ARCHAIC DIVERSITY

We have presented what evidence there is for believing that the palates of the 'Palaeognathae' are not primitive, but either neotenic reversals or adaptive developments. We may now consider the possibility that the palatal patterns exhibited by these birds are, in truth, primitive. Assuming this, we again have a choice between believing: (1) that the four main types outlined above are independent of one another down to the basic Neornithic stem; or that (2) the four main lines come from a common ancestor in turn derived from some other neornithic (ornithurine) group. The author feels the morphology of the palate of known forms is inconclusive in making this choice. No one of the four groups here defined seems any more like one of the others or like the Neognathae than do the rest. Only on palaeonto-

logical evidence not as yet presented to us could the affinities with one another of these four lines be judged from the palate alone. Since palaeontology has up to now failed us, we must rely on morphology of other systems. But here we seem to be presented with equally inconclusive evidence. The pelvis of the Rheidae is as different as could be imagined from that of the Tinamidae, while the rest of the anatomy of the two groups is strikingly similar. Similar difficulties beset us with other systems.

But although we cannot as yet determine the affinities of these lines with one another, we can make some statements concerning phylogeny within the particular lines:

*Tinamiform line:* As discussed above under the section v, the Tinamidae appear to be the basal stock. The Rheidae seem to be a fairly late offshoot, modified in a ratite direction. Of the tinamous, *Tinamus* itself seems the most rhea-like in having a pterygoid very much like that of an immature *Rhea*, being more sigmoid and cylindrical than in the rest of the Tinamidae. Of the rheas, *Pterocnemia* is more like the tinamous than is *Rhea* in that the anterior forks of the prevomer extend anterior to the tip of the parasphenoid.

*Casuariiform line:* In those characters in which *Dromaeus* differs from *Casuaris*, such as separation of pterygoid and palatine, keeling of the parasphenoid, etc., it seems to depart more from the usual avian pattern and appears to be more specialized. Although the Casuariidae are too specialized to be directly ancestral to the Dromaeidae, they appear to be nearer to the common ancestry than does the emu. This is also borne out by the morphology of the rest of the system, as in the myology of the thigh, the Garrodian formula being ABXY for *Casuaris*, BXY for *Dromaeus*. The exact affinities of the Dromornithidae are uncertain, though possibly more with the emu than with the cassowary.

*Apterygiform line:* *Apteryx*, in its false palate, furcate pterygoid, elongate palate and rostrum in which the premaxillary fails to reach the prevomer, etc., seems more specialized than the Dinornithidae, and probably represents a diminutive, helminthophagous modification of that group. On the basis of shape of beak, presence of hallux, and shape of sternum, *Anomalapteryx* seems the moa nearest to the Apterygidae. Without more information on the palate of the Aepyornithidae I hesitate to make any statement concerning their affinities. It is with some doubt that I include the family in this group.

*Struthioniform line:* Only one family is referred here.

## VIII. SYSTEMATIC CONCLUSIONS

As will appear from the account above, all theories concerning the affinities of these birds seem largely conjectural. On morphological grounds alone we can say merely that the Palaeognathae cannot be defined, but that there are four main lines. What the affinities of these lines are to one another and to the Neognathae we cannot definitely know until fossil evidence is unearthed. We may make certain systematic conclusions, however. Whether we consider the 'palaeognaths' as reversals from a neognath stock or stocks, or whether we consider them as truly primitive birds, the evidence for considering them closely related seems inadequate, and rather speaks against such affinity. Therefore, until other evidence for close phylogenetic relationship is produced, it seems best to the author that the 'superorder Palaeognathae' of present definition be dropped from classifications of birds. We have a choice, I believe, between either dropping all superordinal classification of the Neornithes (except possibly the Odontognathae) or making the four 'palaeognathous' lines here defined each a superorder, co-ranking with the Neognathae. Since there is a definite possibility, however, that these lines may have arisen from the Neognathae, it seems to the author that a definite violation of truth might be committed by the latter procedure, while a needless complication of classification seems almost certain. It seems best, therefore, that the first method be applied, and the orders of birds hitherto placed in a superorder Palaeognathae be placed in the Neornithes without separation from the birds hitherto called 'Neognathae.'

It would also seem wise to simplify the classification of this group by the merging of certain orders which seem, on the basis of palatal pattern, to be closely related. Thus:

Order Tinamiformes to include the Rheidae in addition to the tinamous, thus eliminating the order 'Rheiformes' from the list.

Order Apterygiformes to include the Apterygidae, Dinornithidae, and (tentatively) the Aepyornithidae, thus eliminating from the list the orders Dinornithiformes and Aepyornithiformes.

Orders Casuariiformes and Struthioniformes to stand as at present.

Family Eremopezidae to be considered as *familia incertae sedis*.

## SUMMARY

1. The history of classification of the Palaeognathae is briefly outlined.

2. The palates (where known) of the Palaeognathae are described, and those of the living forms figured.

3. It is shown that the 'palaeognathous' palate is not susceptible to definition.
4. It is further shown that the so-called 'palaeognathous' type of palate includes four distinct morphological types.
5. Possible explanations of this diversity are considered, particularly those of neotenic and adaptive reversal.
6. It is concluded that the superorders Palaeognathae and Neognathae should be merged, and that the orders Rheiformes and Tinamiformes be combined, the orders Apterygiformes, Dinornithiformes, and Aepyornithiformes likewise combined, and the Struthioniformes and Casuariiformes be allowed to stand as before, thus reducing the 'palaeognathous' assemblage to four orders, each one equivalent to one of the four morphological palatal types here distinguished.

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## NOTES ON TWO SPECIES OF CALLIPHORIDAE (DIPTERA) PARASITIZING NESTLING BIRDS

BY JOHN L. GEORGE AND ROBERT T. MITCHELL

IN the course of studies on the effect of feeding DDT-killed insect larvae to nestling birds, some incidental information was gathered on Calliphorid parasites of the nestlings. The work was done at Lake Clear Junction, N. Y., during June and July, 1946.

The authors are indebted to Mr. Phillip Dowden, Division of Forest Insects, Bureau of Entomology and Plant Quarantine, who reared the flies, and also to Mr. Curtis Sabrosky of the United States National Museum and Mr. David Hall for their determinations of the adult specimens.

Larvae of *Apaulina metallica* (Townsend) were found feeding on nestlings in one nest, each, of Hermit Thrush, Chipping Sparrow, Song Sparrow and Redstart. The larvae were present in moderate numbers, varying from two to six per nest, except in the case of the Redstart, in which thirty maggots were found.

The single nestling in the Redstart nest was, on July 5, an active and apparently healthy bird that, as is normal, readily consumed the