

THE EVOLUTION OF RATITES

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THE EVOLUTION OF RATITES

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SYNOPSIS

Adequate knowledge of the structure of *Archaeopteryx* now enables a comparison to be made between it and the Carinates. In the latter the structure of the wing, the tail, and the cerebellum can be shown to be adaptations to flight. Since these same adaptations are found in Ratites, they would be inexplicable unless the Ratites were descended from flying birds. The palate of the Ratites is not primitive but neotenous, and represents an early stage through which the palate of many Carinates passes during development. Other neotenous features of the Ratites are the plumage and the persistence of sutures between the bones of the skull.

INTRODUCTION

In the first edition of the *Origin of Species* (1859, p. 134) Darwin wrote: "As Professor Owen has remarked, there is no greater anomaly of nature than a bird that cannot fly; yet there are several in this state." There was a touch of irony in making this quotation, for as is well known, Owen's views on evolution were uncertain and equivocal, and the very existence of flightless birds was inescapable evidence of descent with modification from the "archetype" of birds. Darwin himself continued: "We may believe that the progenitor of the ostrich genus had habits like those of the bustard, and that, as the size and weight of its body were increased during successive generations, its legs were used more, and its wings less, until they became incapable of flight."

A few years later, in his treatise on *The Anatomy of Vertebrates* (1866, 2, 12.) Owen put forward the view that the Cursores or Ratites were not "a natural order; some of its exponents have demonstrably closer affinities to other groups of which they are wingless members." Further on (*loc. cit.*: 43), Owen referred to the Ratites as "those birds in which the power of flight is abrogated". For a man who did not believe unreservedly in evolution, this was about as near as he could get to the view that the Ratites are descended from flying birds, and he even supplied the explanation of such a descent (*loc. cit.*: 12): "by the arrested development of the wings unfitting them for flight".

The view of the degenerate nature of the Ratites has been supported by M. Fürbringer (1888), T. J. Parker (1892), W. P. Pycraft (1901), R. Broom (1906), J. E. Duerden (1920), E. Stresemann (1927-34), W. K. Gregory (1935), and many others; and it might have been thought that the evolution of flightless birds from flying birds was generally accepted. Nevertheless the hypothesis has been put forward that the structure of the Ratites is in many respects so primitive that they must have

branched off from the main stem of bird evolution before the power of flight was acquired. B. Lindsay (1885), R. S. Wray (1887), A. C. Chandler (1916) and J. C. Ewart (1921) are of this opinion, but the foremost exponent of this view has been P. R. Lowe (1928, 1935), with whom M. Friant (1945, 1946) has expressed agreement.

It has been known for a long time that the Ratites show a number of characters which have been considered as primitive. Among these is the palate, on which T. H. Huxley (1867) based a system of classification of the birds in which the dromaeognathous type, characteristic of the Ratites, was regarded as the most primitive. Pycraft (1900, 1901) who extended Huxley's observations, summed up (1901: 343) the situation as he saw it in the words: "The contention that the Struthious (Palaeognathine) palate is of a more ancient type than the Neognathine is admitted by all." The term palaeognathine or palaeognathous is equivalent to dromaeognathous, while neognathine or neognathous includes all the other categories of Huxley's classification.

This argument has been adopted by Lowe, in whose view the Ratites show "the primitive palate from which the neognathous palate characteristic of the modern or flying birds was obviously derived". To this Lowe has added six further arguments, all in support of his view that the ancestors of Ratites never flew. They are:

1. The "primitive" disposition of the muscles.
2. The fact that "all the feathers borne by the adult ostrich or by any other struthious form whether they are situated on the wing, or body generally, are nothing more than down, or modified down," and being juvenile structures are he thinks therefore ancestral and primitive.
3. The absence of the rudiment of the clavicle in the embryo of the ostrich, which, in his view, is proof that the ostrich descended from ancestors which had lost the clavicle, and therefore not from flying birds in which the clavicle is preserved.
4. The persistence of the sutures in the skull of the ostrich, in which it resembles the condition of the ancestral reptiles and differs from that of flying birds in which the bones of the skull are firmly fused in the adult.
5. The obtuse angle subtended between the coracoid and the scapula, which resembles the condition of the ancestral reptiles and differs from that of flying birds where this angle is more or less acute.
6. The similarity between the bones of the hand of the ostrich and those of a dinosaur such as *Ornitholestes*.

With perfect logic, Lowe contended that if, as he believed, the Ratites were descended from birds which had never acquired the power of flight, then it must follow that *Archaeopteryx* could not have been in the line of ancestry of birds, but must have been an independent offshoot from the reptiles.

The detailed knowledge now available of the structure of *Archaeopteryx* (de Beer, 1954b) can be used to test this hypothesis. Two related problems are involved: the evolution from reptiles of birds in general, and the evolution of Ratites in particular. These problems can be solved by finding the answers to the following three questions:

1. Is *Archaeopteryx* on the line of evolution from reptiles to birds?
2. Are there any characters by which modern flying birds differ from *Archaeopteryx* which can be attributed with certainty to adaption to active flight?
3. Are these characters also shown by the Ratites?

ARCHAEOPTERYX AND THE ANCESTRY OF BIRDS

If *Archaeopteryx* was the product of an independent line of evolution from the reptiles, unrelated to the stock which gave rise to birds, it then becomes necessary to believe that the feathers of *Archaeopteryx* and the feathers of all other birds were independently evolved. The identical details of structure which the feathers show involve the quill, the vane formed of barbs, held together and parallel with one another and yet capable of being torn apart, the proportions between the vane and the quill and between the proximal and distal portions of the vane. In all these respects, the structure of the feather in *Archaeopteryx* and in modern flying birds is so exactly identical that it is impossible to believe that they were independently evolved.

But this is not all. In addition to the feathers themselves, there is the manner in which they are arranged on the wing, the differentiation between larger feathers or remiges and smaller feathers or coverts, and the further differentiation of the remiges into primaries, borne on the wrist-joint and hand, and secondaries borne on the forearm. Here again the conditions are identical in *Archaeopteryx* and in modern flying birds. It follows that the view that *Archaeopteryx* is not related to the modern birds is completely untenable.

Granting that *Archaeopteryx* represents an example of an early stage in the evolution of feathered organisms away from the reptiles, it may still be asked whether *Archaeopteryx* is ancestral to modern birds. The remarkable mosaic of reptilian and avian characters that *Archaeopteryx* shows has been discussed elsewhere (de Beer, 1954a). The conclusion to be drawn is that *Archaeopteryx* is a *rara avis* among fossils in that it is possible to say that nothing is known, either by way of structures which it possesses or does not possess, or of the time-relations of its occurrence, which might disqualify it from being regarded as a true ancestor of modern birds. As G. G. Simpson (1936: 92) has said, "every difference between *Archaeopteryx* . . . on one side and true reptiles of possible ancestral type, especially the Pseudosuchia, on the other, is definitely in the direction of true birds".

If, as H. Steiner (1918, 1956) believes, *Archaeopteryx* was aquitocubital, it would provide yet another proof that it was ancestral to modern birds.

CARINATES AND ADAPTATIONS TO FLIGHT

Accepting the fact that *Archaeopteryx* is a mile-stone on the road from reptiles to modern birds and represents the type of structure from which Carinates evolved, attention may be turned to the question whether any of the differences observable between *Archaeopteryx* and the modern flying birds or Carinates can with certainty be ascribed to adaptation to flight. That the flying bird is highly adapted to its

mode of life is a commonplace of biological expression, and in the case of some structures it is easy to prove it. Attention will here be confined to the carpometacarpus, the pygostyle, and the cerebellum. The keel on the sternum is deliberately omitted from the discussion since its absence in the Ratites is the basis of their diagnosis, and the question at issue is whether this absence is primitive or specialized.

The carpometacarpus is the product of fusion between the distal carpals and the three metacarpals, the 2nd and 3rd of which are fused again at their distal extremities. The result is a structure providing a light and resilient yet firm basis for the attachment of the primary remiges. It is absolutely characteristic of modern birds and found nowhere else.

In *Archaeopteryx* the forelimb skeleton consists of proximal carpals, the radiale and ulnare which remain more or less separate, distal carpals fused together and to the base of the third metacarpal, and separate and independent 1st and 2nd metacarpals. *Archaeopteryx* was unable to do much more than glide, and as Dr. H. W. Parker has remarked to me, the air-pressure on the feathers of its wings must have been lower than in an actively flying bird with the same ratio of wing-area to mass, because *Archaeopteryx* was unable to maintain itself in the air continuously against the pull of gravity. The carpometacarpus of the Carinate is without doubt an adaptation to flight by enabling the wing to exert and withstand greater pressure.

There is one further feature of the wing of Carinates that calls for notice, and that is the presence of a small number of feathers attached to the first digit of the hand, forming a "bastard wing". These few feathers add nothing to the weight-bearing power of the wing, yet they perform a function of capital importance in flight for they serve like the slotted wing of a modern aircraft to maintain a slip-stream of air and prevent stalling. The "bastard wing" is a beautiful adaptation to flight.

In *Archaeopteryx* the tail is very long, as long as the rest of the body, and its skeleton consists of 20 elongated separate vertebrae, to each of the hinder 15 of which correspond a pair of rectrices, quill-feathers, which form an oblong and elongated air-resisting surface. In Carinates the tail is very short, consisting of about a dozen flattened vertebrae, the hindmost half-dozen or so of which are fused together, giving rise to a pygostyle. The rectrices, to the number of a dozen pairs, are disposed transversely. A masterly analysis and comparison of the conditions in the tail of *Archaeopteryx* and Carinates has been given by H. Steiner (1938).

It has been pointed out by J. Maynard Smith (1952) that the structure of the most primitive flying animals is one that imparts aerodynamic stability. That is to say that they are of a shape such that when in "flight" through the air, they are able to maintain the direction of their progress without muscular intervention and compensatory movements. In other words, such animals are gliders, and the structure of the skeleton, wings, and tail of *Archaeopteryx* is just such as would have enabled it to glide with stability, but not fly actively. The perfection of the power to fly has involved the development of the ability to perform mechanically unstable flight-movements, such as rapid pitching, yawing, and banking, for which a reduction of the long axis of the animal is essential. The pygostyle of the Carinates is without doubt an adaptation to flight.

The cerebellum of *Archaeopteryx* is best characterized negatively by saying that it is small and does not overlap forwards over the midbrain. In other words, the brain of *Archaeopteryx* is similar to that of reptiles. In Carinates, on the other hand, the cerebellum is so large that it expands forwards as a median and unpaired structure over the dorsal surface of the midbrain, which it presses downwards, and so the cerebellum comes into contact with the hinder part of the cerebral hemisphere. The result is that the cerebellum of Carinates hides the optic lobes, whereas the latter structures are plainly visible in *Archaeopteryx*.

The cerebellum has been defined by Sherrington as the head-ganglion of the proprioceptive system. As L. Edinger (1912: 300) has shown in *Columba*, among the most important sources of impulses conducted to the cerebellum are the organs of balance in the semi-circular canals of the ear, which respond not only to changes in static conditions, but also to changes in the dynamic conditions of the organism caused by alterations in speed and direction of motion. In the case of Carinates, as flying birds the possibilities of direction of motion are greatly increased by the introduction of the vertical dimension. At the same time, the performance of flight requires high speed of adjustment and compensatory movements, not only in actual flight but in landing on small objects. As J. Z. Young (1950: 455) has said, there is reason to think that the large size of the cerebellum in flying birds is connected with the precise control of movement in all planes of space during flight.

The view that the cerebellum of Carinates is an adaptation to flight is confirmed by the conditions in the pterosaurs. There, as T. Edinger (1941: 678) has shown, there is "a cerebellum thrust forward above the midbrain to adjoin the forebrain as in birds; obviously this is one of the characters distinguishing all pterosauria from the other reptiles". There can be no doubt that the parallel development and large size of the cerebellum in pterosaurs and in birds, by which they both differ from all non-pterosaurian reptiles, are due to the same cause: adaptation to flight.

Having now established that the carpometacarpus, the "bastard wing", the pygostyle, and the large size of the cerebellum of Carinates are adaptations to flight, attention may be turned to the conditions in Ratites in respect of these structures.

ADAPTATIONS TO FLIGHT IN RATITES

The skeleton of the wing of Ratites is built on identically the same plan as that of the Carinates. B. W. Tucker (1938a: 224) has stressed the similarity not only in the points of fusion between the various elements which go to make up the carpometacarpus in both Carinates and Ratites, but also subtle points, such as the curvatures of the 2nd and 3rd metacarpals and the expansion of the basal phalanx of the 3rd digit.

H. Steiner (1949: 367) has studied the wings of Carinates and Ratites by means of X-rays and concludes that it "lässt sich ohne jeden Zweifel feststellen, dass genau die gleichen Eigentümlichkeiten zu beachten sind. Ausgehend von irgend einem Carinatenflügel kann ausserdem über den Flügel von *Rhea* und *Struthio* bis zu jenem von *Casuarius* eine zunehmende Verkümmderung verfolgt werden, welche über die Zustände, wie sie bei *Dromaeus* und *Apteryx* angetroffen werden, bis zur vollständigen

Reduktion des Flügels bei den ausgestorbenen Riesenstraussen *Aepyornis* und *Dinornis* geführt hat".

There can be no doubt that the skeleton of the wing in the Ratites shows features associated with adaptation to flight which are explicable only on the view that they were inherited from ancestors which flew.

The skeleton of the tail in Ratites has been studied by W. Marshall (1873) and referred to by W. K. Gregory (1935), but otherwise has not attracted much attention. It is composed of a varying small number of vertebrae which in some forms decrease in size caudally and taper out. But in the ostrich there is a structure composed of the fusion of the terminal vertebrae which undoubtedly constitutes a pygostyle. It is shown in Pl. 5 in comparison with a Carinate pygostyle. Since this structure in Carinates is certainly associated with the power of flight, its presence in a Ratite is inexplicable unless the ancestors of Ratites also flew. This has also been pointed out by Gregory.

The cerebellum of birds has been subject to an exhaustive study by S. Ingvar (1918), the results of which show that the large size of the cerebellum in Carinates is matched by a similar large size in Ratites. Not only does the cerebellum of the ostrich, for instance, project forwards over the dorsal surface of the mid-brain towards the cerebral hemisphere, but it shows the same *arbor vitae* structure as the cerebellum of a Carinate when seen in sagittal section. In Plate 6 are shown the brain of *Archaeopteryx* in side view, and sagittal sections through the brains of *Rhea* and *Tringa*. It is clear that the structure of the cerebellum is the same in the Ratites as in the Carinates; and if its structure in the latter is an adaptation to flight, its structure in the former is inexplicable unless the Ratites were descended from flying birds.

On all three counts, the evidence is conclusive that the Ratites must have evolved from flying birds. It remains now to consider a few further points which receive ready explanation on this view, and to refute the grounds on which Lowe thought that the Ratites were primitively flightless.

It has been shown above that the skeleton of the wing of the Ratites bears evidence of adaptation to flight. It may be added that in one form, the *Rhea*, there is still to be seen a trace of the differentiation between primary and secondary remiges, as shown in Plate 7. This distinction, which already exists in *Archaeopteryx* would be meaningless unless the *Rhea's* ancestors had been capable of flight. Even more remarkable is the presence in the *Rhea* of feathers on the 1st digit forming a "bastard wing", an adaptation evolved in Carinates which results in the maintenance of the slip-stream in flight.

The curious phenomenon of diastataxy or aquintocubitalism, the absence of the 5th secondary remex from the row of flight feathers in the wing, has long been a puzzle. Its most probable explanation has been provided by H. Steiner (1918) who has shown in a brilliant and exhaustive series of studies that it is associated with the peculiar method of folding the wing, the ulnar flexure, adopted by birds. When a bird folds its wings, the hand is moved sideways relatively to the forearm through an angle of almost 180°. The development of this new type of movement affected the feather-rudiments in the skin at the point of flexure and dislocated them in such a way that the rudiment which would have given rise to the 5th secondary remex is

displaced, and, instead, develops into the 5th major covert, leaving a gap in the series of secondaries. Steiner has shown conclusively that in the Carinates the aquitocubital condition is primitive, and that the presence of the 5th secondary remex, which is found sporadically in some members of nearly all groups of birds, is due to a secondary readjustment. Be that as it may, it is clear that the phenomenon of aquitocubitalism is intimately associated with the structure and arrangement of the remiges in a flying wing. It is therefore remarkable that a vestige of the aquitocubital condition is found in the wing of the young *Apteryx* (Steiner 1918 : 434) which thereby is shown to possess a structure characteristic of primitive Carinates and which could not have been independently evolved. Professor Steiner has kindly informed me that he has evidence that other Ratites also are aquitocubital.

Further, there is another line of evidence relating to the loss of the power of flight of *Apteryx*. R. Broom (1947 : 49) has ingeniously shown that as New Zealand has had no land connexions with any other continent since early Jurassic times, and as the centre of evolution of birds exemplified by *Archaeopteryx* was situated in the Palaeartic continent in middle Jurassic times, the ancestors of *Apteryx* could not have reached New Zealand unless they flew thither.

THE NEOTENY OF RATITES

Reverting now to the reasons on which Lowe sought to base the view that the Ratites were primitive birds whose ancestors had never flown, one : the similarity between the hand of the ostrich and that of the dinosaur, has been dismissed as invalid. Tucker (1938b) has shown that such resemblances as there are between them are only superficial and without significance. Another : the angle between the coracoid and the scapula, can be shown to be due to the reduction of the length of the pectoral muscles in the Ratites ; for it is the lengthening of the coracoid in the Carinates which is responsible for the acuteness of the angle between the coracoid and the scapula ; and the length of the coracoid may be regarded as an adaptation to flight since it is associated with the lengthening of the pectoral muscles.

Whether the disposition of the muscles in the Ratites is "primitive", as Lowe has contended, is a matter for argument ; but what is no matter for argument is the explanation of the presence in the Ratites of nestling-down, permanent sutures between the bones of the skull, and the dromaeognathous structure of the palate. All these are demonstrably the result of neoteny or the secondary retention of features which were juvenile in the ancestors of the Ratites.

To begin with the feathers. It is well known that the down-feathers, nestling-down or neossoptyles, are nothing but the fluffed-out distal ends of the rudiments of the adult feathers or teleoptyles. In Carinates, particularly those in which the young are nidifugous and have a "chick" stage, the nestling-down is well developed, and it owes its fluffiness to the fact that the barbs have no hooks and therefore the feathers form no vanes. This nestling-down is subsequently discarded when the adult feathers or teleoptyles take the place of their former distal extremities the neossoptyles. That the Ratites are neotenous in retaining their "ostrich feathers" or nestling-down throughout life is admitted by Lowe himself (1935 : 420) : "So far

as their feather covering is concerned the Struthionines are big, overgrown chicks. They are the "Peter Pans" of the avian world. They have never grown up."

The same phenomenon of neoteny is responsible for the retention of the sutures between the bones of the skull in the ostrich. In the Carinates, the sutures between the bones are present in the young stages, but they are obliterated in the adult skull, which is a structure of great solidity, in all probability adapted to the necessity for withstanding the mechanical stresses consequent upon active flight. In retaining the sutures between the bones of the skull the ostrich, having lost the power of flight, shows a secondary return to the juvenile condition of the ancestral flying bird, and, of course, the ancestral reptile.

The inclusion of the dromaeognathous or palaeognathous palate among the neoteny features of the Ratites, with the implication that it is the result of a secondary retention of an ancestral juvenile condition, may appear surprising in view of the selection of this very structure by T. H. Huxley as the basis for his classification of birds, and his view that the dromaeognathous type was primitive. Nevertheless, the evidence is quite clear, as W. P. Pycraft (1900, 1901) has shown, although he did not realize its significance. The so-called palaeognathous palate is an arrested stage in the development of the neognathous palate. Precisely the same conclusion was reached by S. McDowell (1948) on other grounds, namely the impossibility of giving a definition of the palaeognathous palate applicable to all Ratites and tinamus and excluding all Carinates (except tinamus) because of its great variation.

The essential feature of Huxley's dromaeognathous and Pycraft's paleognathous palate is the fact that the pterygoids extend forwards and make contact with the hinder ends of the prevomers, while the palatines lie further to the side. In Huxley's schizognathous and aegithognathous types, or Pycraft's neognathous palates, the usual condition in the adult is that the pterygoids do not make contact with the prevomers, but are separated from them by the palatines with which the pterygoids make a joint. But Pycraft's remarkable discovery, to which insufficient attention has been paid, was that in the development of many "neognathous" birds the palate passes through a "palaeognathous" stage in which the pterygoids actually or nearly come into contact with the prevomers; but the anterior ends of the pterygoids then become detached from the remainder of these bones, and, instead, become attached to the hinder ends of the palatines, where they give rise to the so-called "mesopterygoid" elements of W. K. Parker (1875, 1876, 1877, 1879), and the "hemipterygoid" of Pycraft. Between the detached anterior portion and the remainder of the pterygoid a joint is formed. This is why in the adults of these birds the pterygoid seems not to reach the prevomer, whereas morphologically, in fact, it does or almost does reach it. The hemipterygoid in various Carinates is shown in Plates 8 and 9 for comparison with the conditions in Ratites.

For those, if there be any, who still believe in the theory of recapitulation, it would no doubt be tempting to say that the neognathous palate "recapitulates" in its development the condition of the palaeognathous palate which would therefore be ancestral. But in view of the overwhelming evidence that the Ratites are secondarily descended from flying birds, the fact that the Ratites already show

neoteny in two other features, the plumage and the bones of the skull, and the probability, from A. Kleinschmidt's (1951) reconstruction, that the palate of *Archaeopteryx* was neognathous (schizognathous), it is impossible to believe that in their palates the Ratites are primitive. The palaeognathous type of palate must therefore be neotenous. This means a complete reversal of the hitherto generally held view of the palate of birds and necessitates the conclusion that the so-called neognathous palate is primitive.

The primitive nature of the neognathous palate in birds is probably connected with the phenomenon of kinesis. J. Versluys (1910) has shown that the mesokinetic condition in Carinates, where the quadrate and pterygoid bones are capable of a certain amount of movement and sliding, and there is a joint between the pterygoid and palatine whereby the upper jaw can be moved on a hinge at the level of the lacrimal bones and raised relatively to the brain-case, is only intelligible if the birds were evolved from reptiles in which a similar though less extensive power of movement was possible: the condition which he has called metakinetic. According to him (1910: 244) even *Archaeopteryx* had a kinetic skull capable of movement, although it still possesses a preorbital bar separating the preorbital fossa from the orbit, and a suborbital bar. But in the Ratites the power of movement has been reduced; the quadrate has a broad connexion with the pterygoid, the latter has equally broad connections with the palatines and the prevomer, and there is no movable joint between the pterygoid and the hemipterygoid because these two elements have not become separated. It must be concluded therefore that with the loss of flight, general increase in size, and acquisition of different feeding habits, the Ratites have lost the Carinates' power of movement of the upper jaw, by retaining the juvenile condition of the palate before any joint is formed. I am greatly indebted to Dr. W. C. Osman Hill for informing me that even in the kiwi, which is the smallest of the Ratites, there is no mobile joint at the base of the upper jaw; and that in the cassowary the only very slight mobility in the upper jaw is at a point far forward, just behind the nostrils.

Further, there is a curious point in the distribution of the palaeognathous type of palate among the birds. It is found not only in Ratites, but also in the tinamus, which are Carinates with a well-developed keel on the sternum and good power of flight. This fact in itself is sufficient to indicate that the Ratites have lost the power of flight, for it could hardly be contended that the tinamus have evolved flight from a flightless Ratite condition.

As for the argument that the absence of any rudiment of the clavicle in the ostrich implies that it was evolved from ancestors which lacked the clavicle (and, by implication, could not fly), it is another example of the fallacies to which the theory of recapitulation leads by its assertion that early embryonic stages of development must represent early ancestral stages in evolution. Modern birds lack even the rudiments of teeth, but teeth are present in *Archaeopteryx*, *Hesperornis*, and *Ichthyornis*. The absence of tooth rudiments in modern birds no more excludes *Archaeopteryx* from their ancestry than the absence of limb-rudiments in snakes indicates that their ancestors were limbless.

Finally, the embryonic development of the emu, studied by H. Steiner (1936)

and H. Lutz (1942), shows that the structure and organization of the Ratite embryo is so similar to the Carinate that it can only be interpreted on the view that Ratites have evolved from flying birds.

CONCLUSIONS

On all these grounds, therefore, there can be no doubt that Owen was correct in regarding the Ratites as birds which have "abrogated" the power of flight. It is possible to go further and to say that they have degenerated from a Carinate condition. Whether the Ratites represent a natural group or whether they are an assemblage of forms which have independently followed parallel lines of evolution consequent on the loss of flight is a further problem for ornithologists to solve.

In view of the incontrovertible evidence from the structure of the wing, the pygostyle, and the cerebellum, that the Ratites have degenerated from flying birds, any attempt to explain the persistent juvenile characters of the Ratites (nestling-down, skull-sutures, and palate) as phylogenetically primitive is doomed to failure; and the Ratites must be regarded as providing one of the most telling exposures of the fallacy of the theory of recapitulation.

I am glad to acknowledge the help of my colleagues in the Bird Room of the British Museum (Natural History), Mr. J. D. Macdonald and Miss P. A. Lawford, of Dr. W. E. Swinton of the Department of Geology, and of Mr. J. V. Brown, Senior Photographer.

SUMMARY

Now that the anatomy of *Archaeopteryx* is adequately known, it is possible to make a rigorous analysis of the characters of the Ratites in the light of the conditions shown by primitive birds. The structure of the wing, tail, and brain in Carinates shows advances on *Archaeopteryx* which are undoubtedly adaptations to flight. The presence of the same features in Ratites proves that they are descended from flying birds. The condition of the plumage, the sutures between the bones of the skull, and the disposition of the bones of the palate in Ratites, all show secondary retention of characters which are juvenile in Carinates, and are evidence of neoteny in the Ratites.

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EXPLANATION OF PLATES

PLATE 5

(1) Right side view of the pygostyle in a Carinate, *Leptoptilos crumeniferus* (Marabou Stork) and (2), in a Ratite, *Struthio camelus*, showing the similarity of structure. (ap), the anterior portion showing the elements of a distinct vertebra; (pp) posterior portion composed of fused vertebrae.

PLATE 6

(1) The brain as seen in right-side view in *Archaeopteryx lithographica*. (2) sagittal section of the brain in a Carinate, *Tringa ocropus* (Green Sandpiper), and (3) in a Ratite, *Rhea americana*. (ce), cerebellum; (ch), cerebral hemisphere; (ol), optic lobes.

PLATE 7

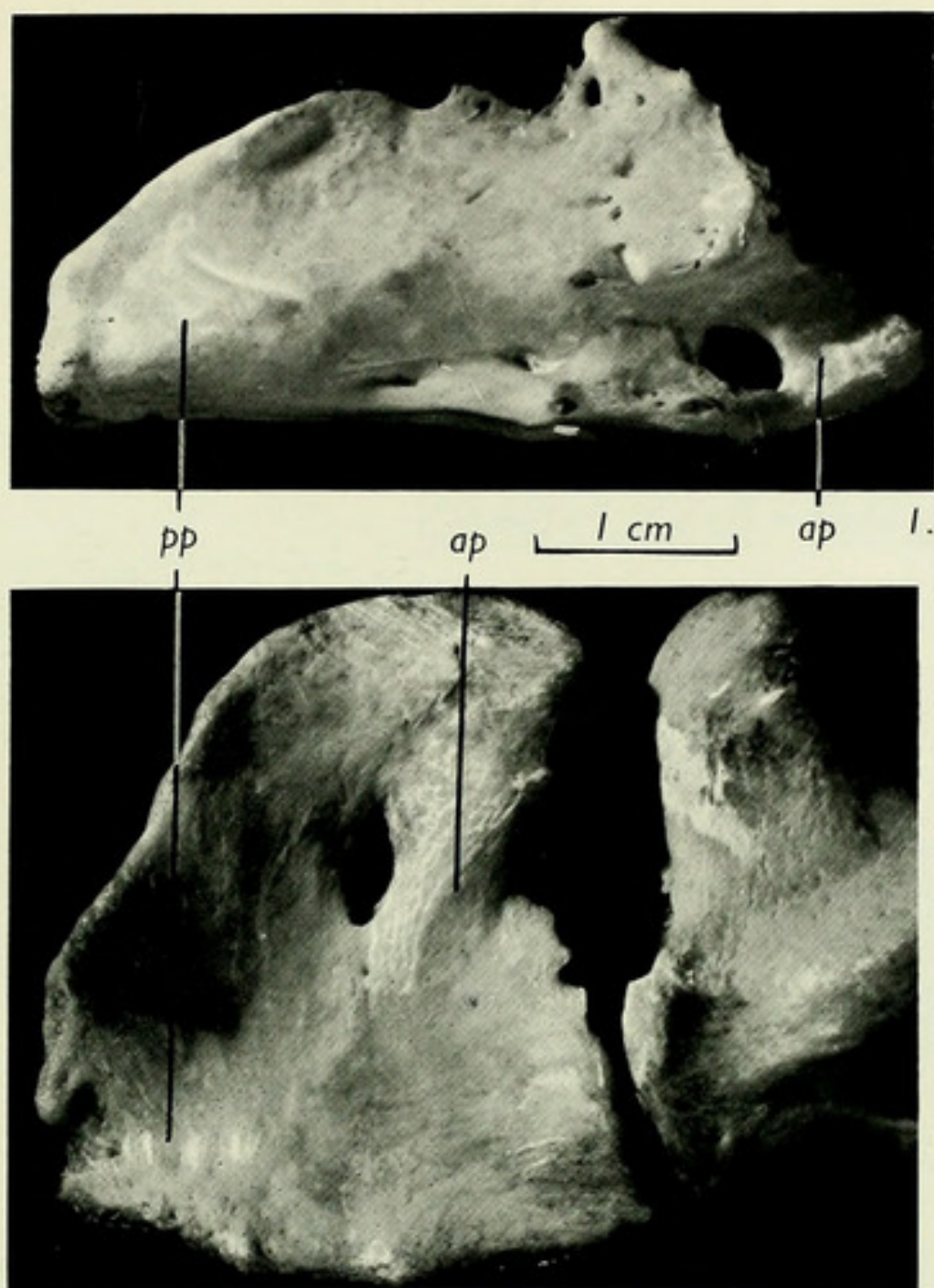
The arrangement of the feathers on the wing of a young Ratite, *Rhea americana*, showing the differentiation between primary and secondary remiges, bastard wing, and wing-coverts.

PLATE 8

(1) Ventral view of the structure of the palate in the Carinate *Pygocelis papus* (Gentoo penguin) nestling; (2) in the Carinate *Anthropoides paradisea* (blue crane); and (3) in the Ratite *Dromiceus novae-hollandiae* (emu). (hpt), hemipterygoid; (pa), palatine; (pt) pterygoid; (pr), prevomer; (qu), quadrate.

PLATE 9

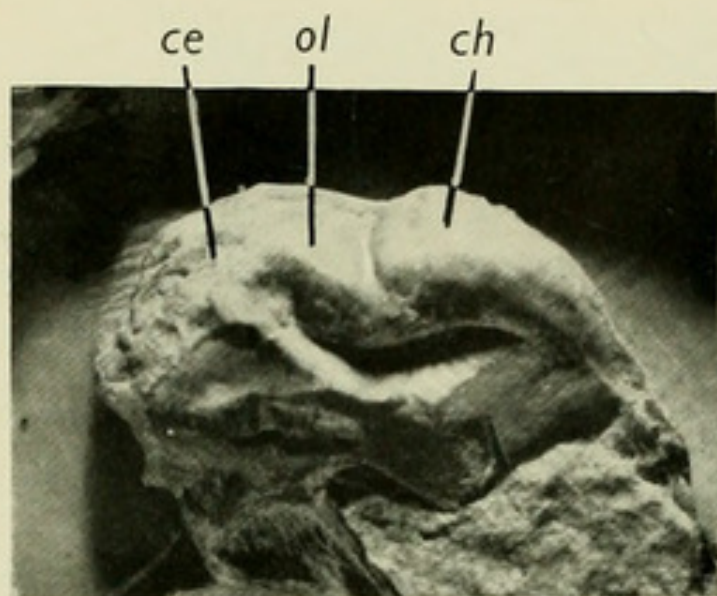
(1) The structure of the palate as seen in left-side view in *Corvus frugilegus* (rook) young; (2), *Megalaema virens* (Himalayan barbet). (hpt), hemipterygoid; (ju), jugal; (pa), palatine; (pt), pterygoid; (pr), prevomer; (qu), quadrate.



2.

PLATE 5

(1) Right side view of the pygostyle in a Carinate, *Leptoptilos crumeniferus* (Marabou Stork), and (2), in a Ratite, *Struthio camelus*, showing the similarity of structure. (ap), the anterior portion showing the elements of a distinct vertebra; (pp) posterior portion composed of fused vertebrae.

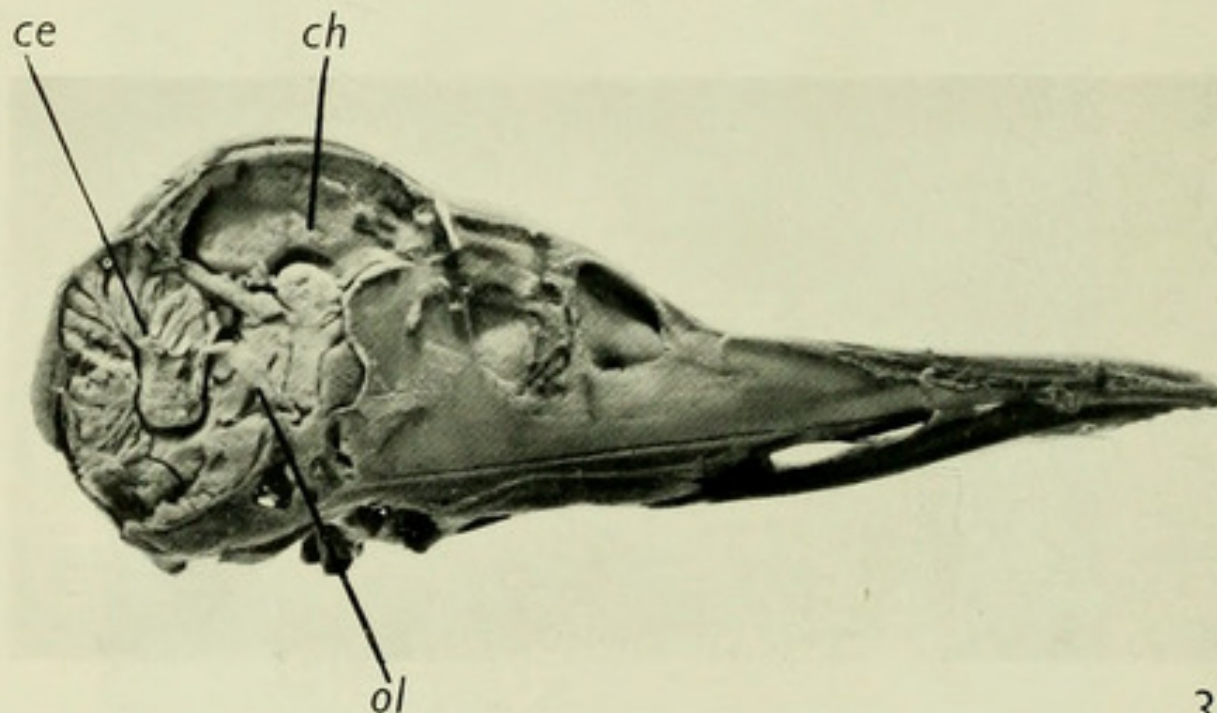


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1 cm



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3.

PLATE 6

(1) The brain as seen in right-side view in *Archaeopteryx lithographica*. (2) sagittal section of the brain in a Carinate, *Tringa ocropus* (Green Sandpiper), and (3) in a Ratite, *Rhea americana*. (ce), cerebellum; (ch), cerebral hemisphere; (ol), optic lobes.



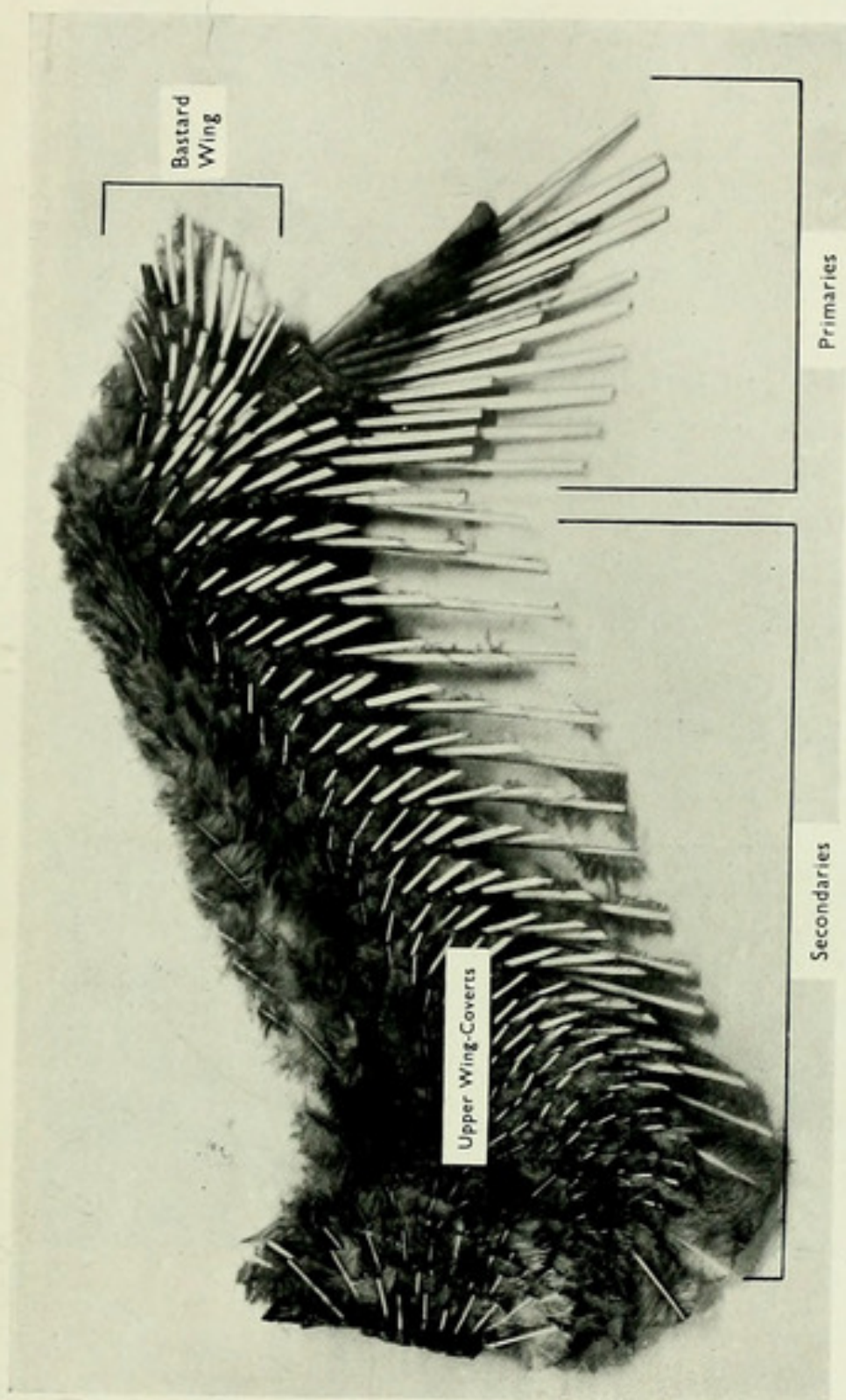


PLATE 7

The arrangement of the feathers on the wing of a young Ratite, *Rhea americana*, showing the differentiation between primary and secondary remiges, bastard wing, and wing-coverts.

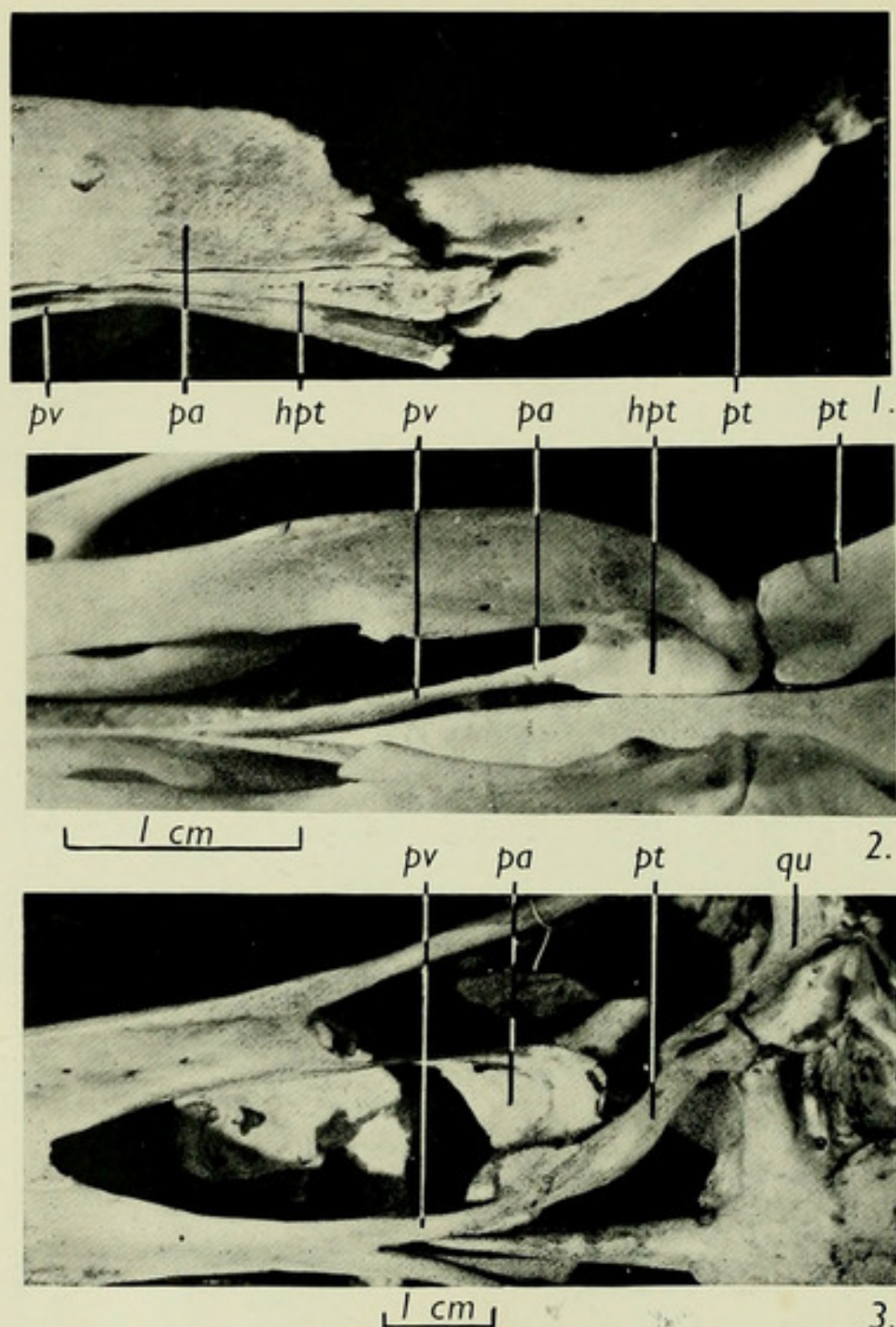


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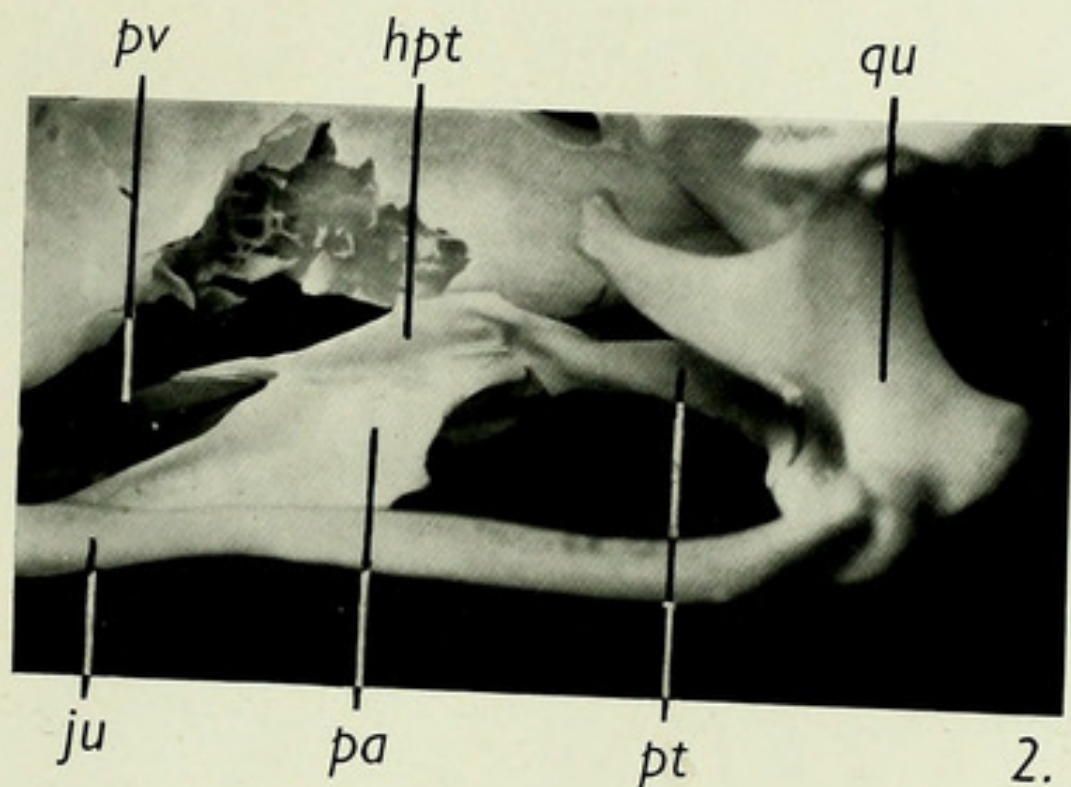
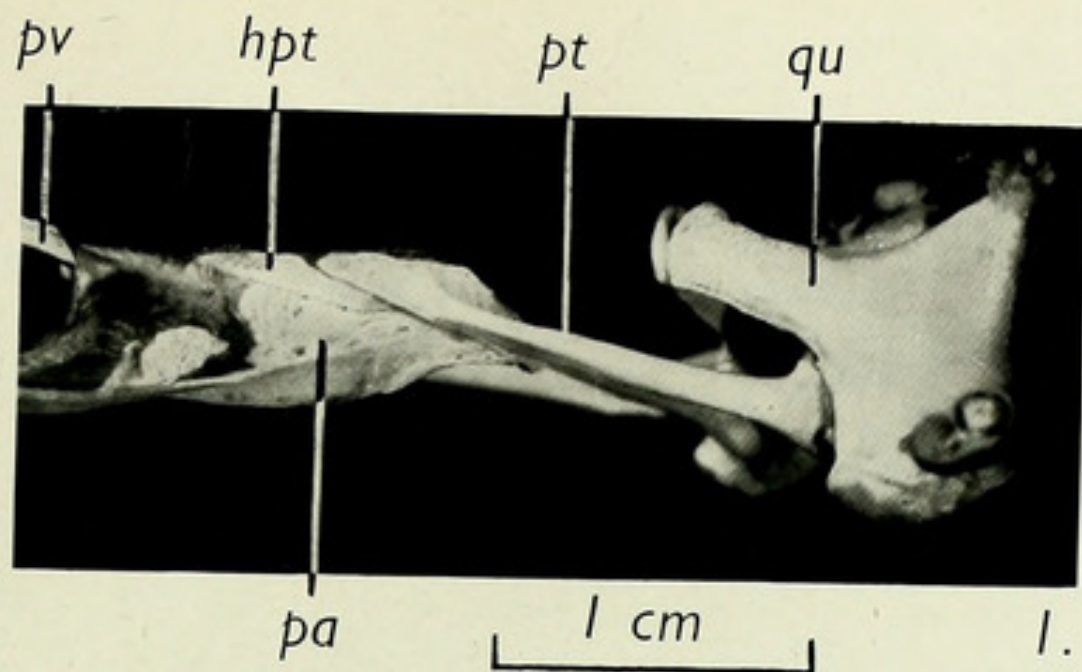


PLATE 9

(1) The structure of the palate as seen in left-side view in *Corvus frugilegus* (rook) young;
 (2), *Megalaema virens* (Himalayan barbet). (hpt), hemipterygoid; (ju), jugal; (pa), palatine;
 (pt), pterygoid; (pr), prevomer; (qu), quadrate.





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