

NEOTENY AND THE EVOLUTION OF THE RATITES

The origin of the large flightless birds and whether they are descended from flying ancestors have long been debatable questions. (1) (2)

Nothing has been found in the fossil record which might indicate the nature of ratite phylogeny; although Wetmore (3) has painted a vivid picture of an "ostrichlike form" *Eleutherornis helveticus* Schaub (1941) which was named on the basis of a "fairly well preserved pelvis" from the Eocene of Switzerland. This bird, which lived perhaps 50 million years ago, is said to have had "affinities with the carinate groups, while being at the same time of unquestioned ratite stock." Wetmore regards it as "a link that decides the long debate on the ancestry of the struthious birds, since it indicates clearly that these flightless groups of modern times have come from flying ancestors . . ."

The opposite view was strongly presented by the late P. R. Lowe in a series of papers between the years 1928 and 1944, and he claimed that his morphological studies proved the 'primitiveness' of the characters of present-day Ratites which he described as 'dinosaurian'. The features which Lowe regarded as primitive included, among others, the sternum, the sternal callosities, wing, cranial sutures which persist at least until senescence, fluffy downlike feathers without barbules in the adult, and the form of the palate. This last-named structure is often quoted in connection with the higher classification of birds. It has been used to define the Ratites as a separate group, the super-order Palaeognathae, but as pointed out in the recent work of McDowell (1948) and Hofer (1949) the "palaeognathous" palate is undefinable, and it is possible to recognise at least four well-defined palatal types among the Ratites.

Lowe described the Struthious birds as "surviving relics" and was of the opinion that their evolution towards flight "was permanently retarded or compromised by some factor or other millions of years ago *before* flight had been evolved" in birds. At the present time the concensus of zoologists is that Lowe's suggestions are not acceptable. The question is taken up by Sir Gavin de Beer (1956), who considers that, now that the anatomy of the fossil toothed-bird *Archaeopteryx* is adequately known, a rigorous analysis of the characters of the Ratites in the light of conditions shown by primitive birds indicates that they are birds which have "abrogated" the power of flight. Indeed, the unavoidable conclusion is that they have degenerated from flying birds, while

(1) The Evolution of Ratites, by Sir Gavin de Beer, F.R.S. 1956. *Bull. Brit. Mus. (N.H.) Zool.*, 4, ii, p. 57-70, pl. 5-9.

(2) The word Ratite is used in a vernacular sense only, nowadays, for what must be regarded as a polyphyletic group composed of the following orders: Struthionidae, Apterygidae, Casuariidae, Rheidae, and Crypturidae; some would combine the last two which are South American. The Ratites are also referred to by various authors as "Struthionids," or "Palaeognathae".

(3) Wetmore, A. 1950. Presidential Address. The Xth Internat. Ornith. Congress. Uppsala.

still retaining a number of structural features in common with flying birds or Carinates and which are intimately connected with the requirements of active flight. Among these are the fused condition of the wing bones in the carpal region to form a very characteristic avian structure (the carpometacarpus), the short tail and pygostyle, the ala spuria or 'bastard wing' (in *Rhea*), and an enlarged cerebellum. It now seems certain that the large cerebellum in Carinates is connected with the need for a proper means of controlling equilibration and flight. A similar development of this part of the brain occurred in the Mesozoic flying reptiles or Pterodactyls, where are found many analogies in structure with birds, but independently derived. In *Archaeopteryx*, on the other hand, the cerebellum was small and there is good reason to believe that it was not an active flier, although it possessed feathers exactly identical to those of Carinates. For one thing, the forelimb or wing skeleton differed markedly from that of all flying birds, and could not have exerted or withstood the pressures connected with active flight. The tail was very long, as long as the rest of the body, with 20 elongated vertebrae, and 15 pairs of rectrices, one pair to each of the hinder vertebrae, and arranged to form a palm-like tail. Doubtless, *Archaeopteryx* could do little more than glide, and if we regard this primitive Jurassic bird as the type of structure from which Carinates evolved, then many of the characters in which the last-named differ from it must be attributed to adaption to active flight. In *Rhea*, where the wing is well-developed, the young show differentiation of primary and secondary remiges as well as wing coverts and a 'bastard wing' (see de Beer, plate 7). This last-named structure is formed by the attachment of a small number of feathers to the "first" digit of the "hand" and seeing that in Carinates it has the sole purpose of maintaining the slipstream during flight, its presence in *Rhea* would appear to be highly significant.

The occurrence of vestiges of diastataxy or aquitocubitalism in young *Apteryx* and other Ratites may be further evidence that their ancestors were not cursorial. Diastataxy is a condition, found in a large majority of flying birds, in which the fifth cubital (i.e. fifth secondary attached to the ulna) is absent, although the corresponding major covert is present. It is supposed to be

connected with the peculiar method of folding the wing in flying birds, and is a primitive condition. The presence of the fifth cubital in some birds, such as cuckoos, is a secondary readjustment. In many ways the course of Ratite morphogenesis is so similar to the Carinate that it would be inexplicable unless they were descended from flying birds.

At one time the belief was firmly held that the presence of large flightless birds in the continents of the southern hemisphere was evidence of a much greater extent of these land masses in the geologic past, or at least of former land bridges or connections. It is now recognised that the large flightless birds are not very closely related, and that the forms confined to the various regions may have arisen independently. It is unnecessary, therefore, to postulate former land connections to explain their distribution, and the theory has been finally disposed of, for the benefit of geologists, by Prof. E. Mayr (1944). However, the presence of moas and kiwis in New Zealand still requires proper explanation. Geologists maintain that New Zealand has had no land connections with any continent since early Jurassic times (perhaps 150 million years ago), which would mean that the ancestors of the apterygious forms must have flown there. This is a question which lends itself to speculation. Recently there have been hints, from various quarters, that the land surfaces of the unstable Pacific regions were once more extensive than they are at present, in which case it is unnecessary and even a little misleading to mention the present isolation of New Zealand in connection with Ratite evolution as was done by Broom (1947).

According to Dr. de Beer the "primitive features" of the Ratites are, in fact, persistent juvenile characters whose presence can be explained by a process known as neoteny. Neoteny is said to occur when the adult animal bears features so that it resembles the young form of its ancestors. It is now considered that this process may have played an important part in the evolution of many species, including Man. The classic example of neoteny is the North American Tiger Salamander *Amblystoma tigrinum*, which in one part of its range (the United States) is a lung-breather and spends much of its time on land. In Mexico, this same species (but known as the Axolotl) usually becomes sexually mature and breeds in the large-

headed, gill-breathing larval stage; metamorphosis can be induced by feeding on the hormone thyroxin. The axolotl is only partially neotenus, but there are other newt-like forms (e.g. *Proteus*) in which the condition is permanent. Neoteny, which is believed to be under genetic control, can be defined as precocious development of the reproductive organs accompanied by a relative reduction in the speed of bodily growth. Usually it is not limited to one specific feature, neotenic structures in external form perhaps accompanying others not so easily observed. Neoteny has been described as a phenomenon which offers a means of escape from extinction for animals highly specialised in the adult condition, providing, of course, the young stages are less or differently adapted and possess a gene complex which will sooner or later affect the rates of different developmental processes.

In the Ratites the possession of downlike feathers, persistent cranial sutures, and a type of palate formation associated with a reduced mobility of the upper jaw, are structures which in Carinates are temporary and embryonic or juvenile, and therefore the struthious birds can be regarded as "gigantic neotenus chickens." Such a view is in direct contradiction of the now discarded "Theory of Recapitulation" which has been attributed to Haeckel (1866) but was in fact propounded more than half a century before. This so-called "law" stated in effect that the developmental history of the individual repeats the evolutionary history of the species. As pointed out by Dobzhansky (1955) the "law" does contain an important "kernel of truth," but if followed literally

then many so-called evolutionary sequences deduced from comparative morphology are false and should be read in the opposite direction.

Dr. de Beer's welcome contribution to the problem of bird origins is a re-affirmation of his belief in the importance of neoteny and pedomorphosis as major evolutionary processes and one which he has consistently held for many years. Much of the evidence is purely circumstantial and it might be objected that the validity of the conclusions reached is open to question pending the discovery of more fossils. Wetmore, as a result of the finding of the Eocene fossil *Eleutherornis helveticus*) is satisfied that the struthious birds have come from flying ancestors and Craigie (1936, 1940), working on the cerebral cortex of birds, found nothing to indicate that they had an origin distinct from Carinates. The principle of neoteny suggests that the evolutionary changes which gave rise to the Ratites were retrogressive in character but associated with adaption to a particular mode of life.

Although the superficial resemblances between the largest forms are strong there seems to be little doubt that here is an excellent example of convergent evolution and the various orders are not closely related, except through ancestral groups which may have possessed genetic constitutions with similar potentialities for change. Edinger (1942), after a general survey of living and fossil giant animals, has made the interesting suggestion that large size, plumage characters and other peculiarities in the Ratites may be the result of pituitary disturbances.—
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