Reports

Paleognathous Carinate Birds from the Early Tertiary of North America

Abstract. *Fossils newly discovered in the Paleocene and early Eocene of western North America document some of the oldest birds known from nearly complete skeletons. These were medium-sized carinates with powers of sustained flight but which had a paleognathous palate like that of the flightless ostrich-like birds and the tinamous. The fossils provide additional evidence that the paleognathous palate is probably primitive and therefore should not be cited as a derived character state to define the ostrich-like birds as a monophyletic group.*

The single most contested issue in avian evolution continues to be the question of the affinities of the large flightless ratites (ostriches, rheas, emus, cassowaries, elephant birds, and moas) and their presumed relatives the kiwis and tinamous. Whether these represent a natural, monophyletic group or a paraphyletic or polyphyletic assemblage of primitive or neotenic taxa has been the subject of controversy (*1*). This diverse collection of birds has historically been associated by the distinctive configuration of the palatal bones, first noted by Huxley (*2*) and later referred to as the paleognathous palate (*3*) in the belief that it represented a primitive condition. More recently, proponents of ratite monophyly have argued that the paleognathous palate represents a specialized condition derived from the neognathous palate of typical birds (*4, 5*). The question has remained unresolved, however, partly because of the dearth of fossil evidence bearing on either position.

Hitherto, there have been no pre-Quaternary birds that have been shown to be unequivocally paleognathous (*6*). We have recently obtained fossils of medium-sized, volant, carinate birds from the Paleocene and Eocene of North America, the shells of which unquestionably had all of the definitive characters of the paleognathous palate. Individual bones and associated portions of skeletons of at least two individuals have been recovered from late Paleocene limestone concretions in the Fort Union Formation in Montana. Another specimen, from shales of the early Eocene Green River Formation in Wyoming (see cover), of a very similar species consists of a skull and mandible with the first nine cervical vertebrae. With the exception of the Late Cretaceous toothed diving bird *Hesperornis*, these are the oldest birds known from a nearly complete representation of the skeleton including the palate.

The fossil skulls (Fig. 1) meet all the criteria collectively accepted as diagnostic of the paleognathous palate and the rhynchokinetic skull (*4*): (i) the vomer is long, extending from the premaxillae, with which it appears to be unfused, to the pterygoids, with which it is definitely fused; (ii) the palatines are continuous with the pterygoids and no suture is visible between them; (iii) there are pronounced processes on the basisphenoid rostrum (the so-called basipterygoid or basitemporal processes) that articulate extensively with the caudal extremity of the pterygoid; (iv) the pterygoquadrate articulation is extensive and complex and includes a large portion of the orbital process of the quadrate; (v) the zygomatic process is large and closely applied to the lateral surface of the quadrate; (vi) the lateral nasal bar is unfused ventrally and appears to have been capable of sliding over a groove in the palatine process of the maxilla; and (vii) the nasal septum is very extensive and continuous with the orbital septum.

Lack of fusion in the cranial bones is marked. The frontals and parietals meet but do not ankylose (Fig. 1), the premaxillae apparently are not fused to the nasals, and the splenial is large and free. This lack of fusion is not the result of immaturity, however, as the surface of the bone in these specimens is not porous, and in cross section the bone is double-layered—both conditions being typical of adult birds. The frontals and parietals are not merely unfused, but actually form an articulating joint, as may also be true of certain Hesperornithiformes (*7*) and as has been postulated for *Archaeopteryx* (*8*).

The postcranial skeleton (Fig. 2) is superficially more similar to that of many neognathous birds than to any modern paleognaths, including the volant tinamous. The relatively short sternum has a well-developed carina, and the truncate posterior margin is unnotched, quite unlike the long, deeply notched sternum of the tinamous. The wing is superficially similar to that of many raptorial birds (hawks and owls), and the fossil birds may be assumed to have had considerably greater powers of sustained flight than tinamous. Isolated portions of the

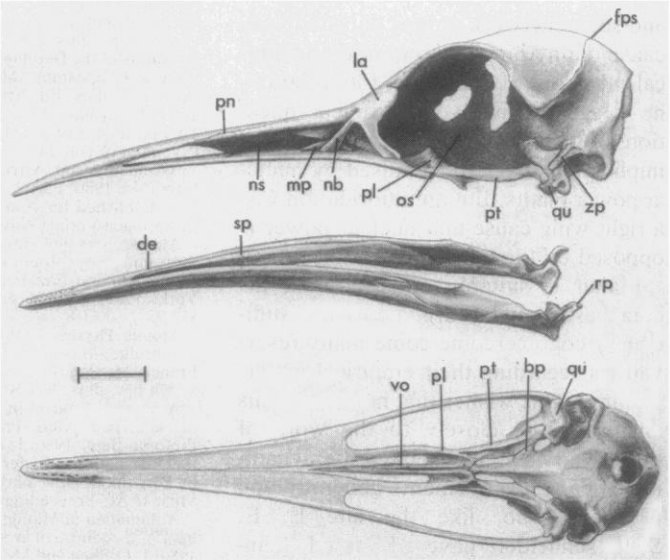

Fig. 1. Lateral view of skull and mandible (top) and ventral view of skull (bottom) of an early Tertiary paleognathous bird; composite reconstruction based mainly on a skull from the Green River Formation of Wyoming, with details of the ventral view supplied from a specimen from the Paleocene of Montana. Abbreviations: *bp*, "basipterygoid process"; *de*, dentary; *fps*, frontoparietal suture; *la*, lacrimal (prefrontal); *mp*, palatine process of maxilla; *nb*, lateral bar of nasal bone; *ns*, nasal septum; *os*, orbital septum; *pl*, palatine; *pn*, premaxillo-nasal suture; *pt*, pterygoid; *qu*, quadrate; *rp*, retroarticular process of mandible; *sp*, splenial; *vo*, vomer; and *zp*, zygomatic process. Scale, 1 cm. [Modified from a drawing by J. Gurche]

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skeleton of these birds could probably be assigned to various modern orders. The near impossibility of diagnosing taxa of Paleogene birds on the basis of single ends of limb bones has already been emphasized (*9*) and is even more conclusively demonstrated by the fossils discussed here.

The occurrence of these birds early in the Tertiary, their reptilian-like splenial bone, the possession of an articulating frontoparietal joint, the overall lack of fusion of cranial elements, and the very generalized nature of the postcranial skeleton are sufficient to suggest that these birds, and the paleognathous palate as well, are primitive. This is supported by the existence of at least some of the features of the paleognathous palate in the early ontogeny of some neognathous birds (*10, 11*).

The palatine and pterygoid of neognathous birds have been hypothesized to be homologous with the anterior and posterior portions of the reptilian pterygoid, with the "intrapterygoid joint" being a derived character of neognathous birds (*12*). If so, this would provide further evidence that the paleognathous palate is primitive, as the intrapterygoid joint is lacking and the configuration is thus like that of the reptilian pterygoid.

If the paleognathous palate is primitive, then it cannot be used as evidence for monophyly of the ratites and tinamous. The argument that the paleognathous palate evolved from the neognathous palate (*4*) was predicated largely on the unrelated fact that ratites evolved from volant ancestors (*10*), for which reason the ratites, and consequently their palate, were considered to be "derived." The volant Tertiary paleognaths suggest the opposite evolutionary sequence. The assumption of a monophyletic origin of the ratites and tinamous from a neognathous ancestor requires a pre-Cenozoic radiation of these birds in Gondwanaland, as postulated by Cracraft (*13*). However, the occurrence of paleognathous birds in the Paleocene and Eocene of North America does not agree well with the tectonic and temporal constraints of this zoogeographical hypothesis.

The new fossil birds reported here are probably remnants of what may have been a diverse radiation of paleognathous carinates that preceded, and were possibly ancestral to, the later radiation of neognathous birds. Tinamous and ratites may have descended independently from various families or orders within this radiation of paleognaths, or some of the ratites may have evolved secondarily from neognathous birds through neoteny. A monophyletic origin of the ratites and tinamous is far from being an established fact, and the evidence suggesting that they are paraphyletic or polyphyletic (*14*) now deserves serious consideration and evaluation. A conclusive resolution of the problem will have to depend largely on new fossil evidence and more original anatomical and embryological studies of living taxa, rather than additional reinterpretations of the same data that have been brought to bear on the question in the past.

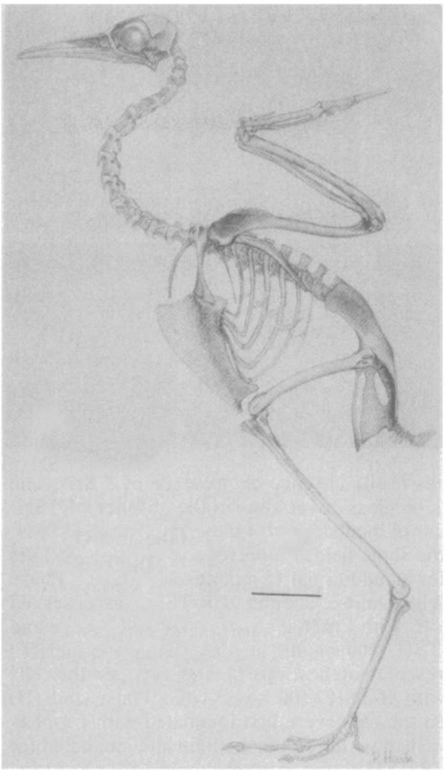

Fig. 2. Reconstructed skeleton of a volant, early Tertiary paleognathous bird based mainly on fossils from the Paleocene of Montana. Scale, 4 cm.

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Adenosine 3′,5′-Monophosphate Modulates Thyrotropin Receptor Clustering and Thyrotropin Activity in Culture

Abstract. *A biologically active rhodamine conjugate of thyrotropin binds at 4°C to diffusely distributed membrane thyrotropin receptors which patch and become endocytosed into thyroid cells in a temperature-sensitive process. When the cells are first incubated with 8-bromo-cyclic adenosine monophosphate at 37°C, the conjugate also binds to clustered receptors at 4°C. Furthermore, 8-bromo-cyclic adenosine monophosphate reduces the amount of adenosine 3′,5′-monophosphate (cyclic AMP) induced by thyrotropin. Hence, increased intracellular cyclic AMP induces receptor patching and reduces the concentration of cyclic AMP normally induced by thyrotropin. This suggests that cyclic AMP acts both as the second messenger of thyrotropin and also as the regulator of the level of thyrotropin receptors.*

Normal function of the thyroid gland is regulated by the pituitary through the hormone thyrotropin (TSH). This hormone binds to specific receptors on the membrane of thyroid cells and induces a variety of biological responses (*1–3*). Furthermore, TSH activates a thyroid adenylate cyclase and many of its responses are mimicked by analogs of adenosine 3′,5′-monophosphate (cyclic AMP). Therefore, it is generally accepted that TSH response is regulated by the concentration of cyclic AMP (*4, 5*). Since increased intracellular cyclic AMP, mediated by either TSH (*6*) or by other hormones (*7, 8*), desensitizes the thyroid adenylate cyclase (E.C. 4.6.1.1), this could serve as a feedback mecha-

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