

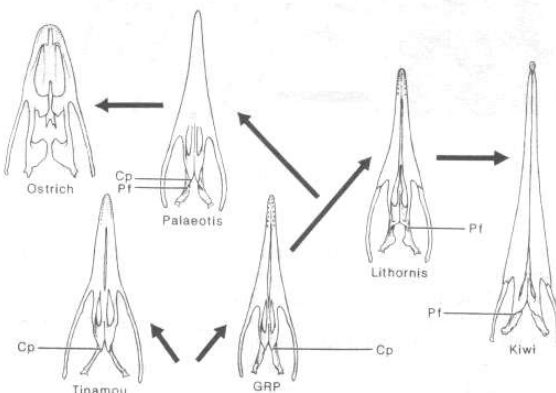
## Ostrich ancestors found in the Northern Hemisphere suggest new hypothesis of ratite origins

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Modern ratites (ostriches, rheas, cassowaries, emus, and kiwis) are flightless birds which have a palatal structure termed 'palaeognathous'<sup>1</sup> and are found on daughter-landmasses of the Mesozoic supercontinent Gondwanaland. It has been suggested<sup>2-4</sup> that a single flightless ancestor, widely distributed in Gondwanaland, gave rise to the various lineages of ratite birds. The temporal calibration of the DNA molecular clock is primarily based on the divergence of ratites, and depends on the validity of this hypothesis. Newly studied fossils suggest that the ancestors of ostriches are instead among a group of North American and European birds, the 'Lithornis-cohort', that had the potential of flight and from which the kiwis may have arisen separately.

The *Lithornis*-cohort of fossils is a group of hen-sized, palaeognathous carinates which had the potential of flight and are found in Palaeocene and Eocene deposits in North America and Europe<sup>5</sup>. The group includes *Lithornis*, *Paracathartes* and a genus I will refer to here as the 'Green River palaeognath' ('GRP'). They are the closest relatives of the ratite birds known to have had the capacity for flight, closer than the palaeognathous tinamous (*Tinamidae*), the extant sister group of ratites<sup>1,2,4,6</sup>. *Palaeotis weigelti* was a crane-sized, flightless palaeognathous ostrich from the Middle Eocene of Germany, whose ancestry may be traced to the *Lithornis*-cohort. *Lithornis*<sup>7</sup>, *Paracathartes*<sup>8</sup> and *Palaeotis*<sup>9</sup> were originally described from isolated, fragmentary remains and were mistaken for neognathous birds. Newly available, essentially complete skeletons that include the palatal bones (Fig. 1) now show unequivocally that these were palaeognathous birds. *Palaeotis* should not be confused with the incomplete fossils comprising the Asian family *Ergilornithidae* that have been suggested as ancestors of



**Fig. 1** Grades of evolution in the palatal complex of bones in the fossil and extant palaeognathous birds: tinamou (*Tinamus*, drawn from Smithsonian specimen USNM 345738); 'Green River palaeognath' (drawn from USNM 336103); *Lithornis* (drawn from USNM 391983; agrees with *Paracathartes*, USNM 391984); *Palaeotis* (drawn from HLMD Me 7530); kiwi (drawn from USNM 19025) and ostrich (drawn from USNM 224852), not to scale. The branching pattern does not necessarily represent the correct phylogenetic relationships of the fossil taxa but the monophyly of the ostrich and kiwi and the sister group relationship of tinamou is supported by molecular data<sup>6</sup>. Cp, caudal process of the palatine; Pf, pterygoid fossa.

ostriches<sup>10,11</sup>. *Ergilornithids* were not palaeognathous birds.

The monophyletic origin of the *Lithornis*-cohort can be shown on the basis of shared derived characters (Fig. 2, character suite 2), all of which are absent in tinamous. Cranial (Fig. 1) and histological characters (Fig. 3) that characterize the living ratites evolved step by step in the phylogeny of the *Lithornis*-cohort. The large pterygoid fossa with no palatine process first appeared in clade 3, and the longitudinal pattern of bone osteons was replaced by the transverse pattern in clade 4 (Fig. 2). A higher-taxonomic group, comprised of the *Lithornis*-cohort, would thus be paraphyletic. That is, it does not include all of its evolutionary derivatives (the ratites), which have secondarily lost some of the distinguishing flight-related characters of the *Lithornis*-cohort.

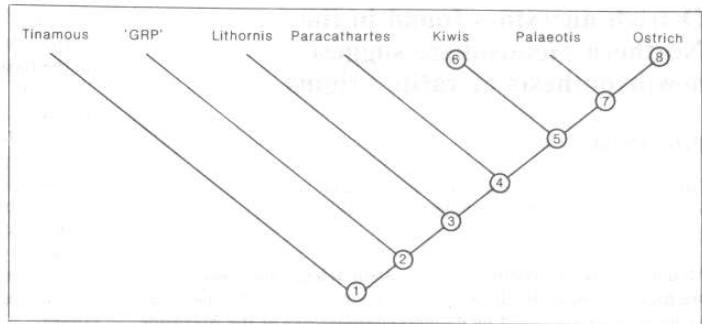
An important element in the elucidation of ratite phylogeny is the fossil *Palaeotis*. Two skeletons of *Palaeotis weigelti* (specimen GM 4362, Geiseltalmuseum, Martin-Luther University, Halle a. Saale, GDR and specimen HLMD Me 7530, Hessisches Landesmuseum, Darmstadt, FRG) reveal all the characters that together define ratite birds<sup>1,2,6</sup>. Derived characters that further distinguish *Palaeotis* as an ostrich (family *Struthionidae*) are listed (Fig. 2, legend, character suite 7). Characters that are derived at the level of the *Lithornis*-cohort (Fig. 2, character suite 2) and primitively retained by *Palaeotis*, but not found in other birds, show that ostriches evolved from this group. Only *Palaeotis* and members of the *Lithornis*-cohort have palates with a caudal process of the palatine and a pterygoid fossa (Fig. 1), although both characters are not found together in *Lithornis*, *Paracathartes*, or the 'GRP'. *Palaeotis* forms an important link between the *Lithornis*-cohort and ostriches because all these characters are absent in large ratites, having been secondarily lost by all but kiwis.

Thus, ostriches were not only present in the Northern Hemisphere, but they may have evolved there long after the breakup of Gondwanaland. If so, then ostriches emigrated from Europe to Africa some time during the early or middle Tertiary, a dispersal route for which there are independent data for other taxa<sup>12</sup>. The hypothesis of ratite origins in Gondwanaland relies on the same route of dispersal, but in the opposite direction, to account for the presence of the recently extinct ostriches of Asia<sup>2,13</sup>. The absence of the *Lithornis*-cohort in early Tertiary deposits of the Southern Hemisphere does not conclusively prove that these birds lived only in the Northern Hemisphere at that time, but their absence there is conspicuous since *Lithornis* has been collected in relative abundance in the Northern Hemisphere for more than two centuries.

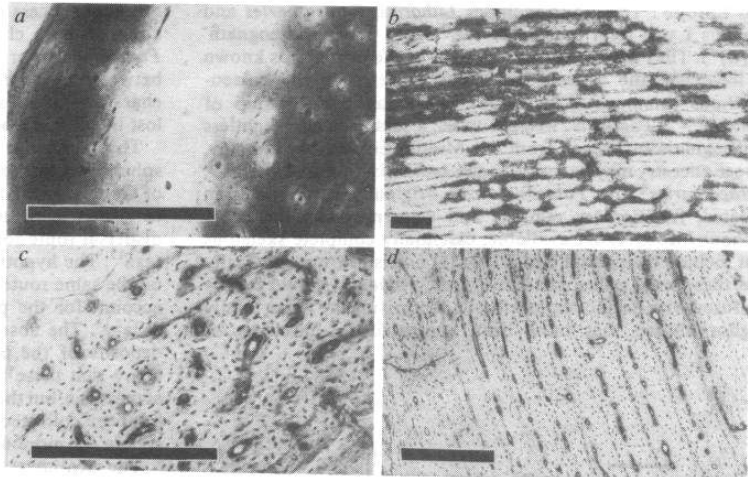
The vicariance biogeography hypothesis of ratite distribution requires that populations of flightless ratites were isolated as the result of geotectonic events and that the birds' own powers of dispersal were minimal. However, this hypothesis does not explain the occurrence of kiwis (*Apterygidae*) in New Zealand. Sibley and Ahlquist<sup>4</sup> could not reconcile the early (Cretaceous) divergence of the New Zealand plate from Gondwanaland with the relatively late (Eocene) divergence of kiwis from other ratite birds, based on DNA hybridization data. The fossils discussed here suggest that kiwis could have evolved directly from a palaeognath that flew to New Zealand and lost its power of flight independently of other ratite birds. Of the ratites, only kiwis retain primitive characters that are uniquely derived in the *Lithornis*-cohort (Fig. 1; Fig. 2, character suites 2 and 3), suggesting a relatively close relationship.

The far reaching implications of this study lie with the temporal calibration of the DNA hybridization molecular clock. Sibley and Ahlquist<sup>4</sup> postulated that the divergence of ostrich DNA from rhea DNA was initiated by, and therefore could be dated by, the spreading of the Atlantic seafloor. They have since<sup>14</sup> applied this calibration to a variety of other avian and mammalian taxa. With the simplicity of the vicariance biogeography hypothesis of ratite origins now challenged, one cannot accept this part of the calibration of the DNA molecular clock without at least some degree of scepticism. I have else-

**Fig. 2** Cladogram of some taxa of palaeognathous birds of unequal rank. Ratites without direct bearing to this discussion are omitted. Character suites are presumed to be apomorphic for all clades above 1. The caudal process of palatine is convergently absent in *Lithornis*, *Paracathartes* and Kiwis (not shown in cladogram). Character suites are: (1) palate palaeognathous, caudal process of palatine bone present, pterygoid narrow, vomer articulates with premaxillae, rhamphothecal grooves present, internarial septum small, splenial extends near to or forms part of mandibular symphysis, bill narrow, cervical vertebrae stout, ilioischadic foramen open-ended, femur gracile, primary osteons of tibiotarsus predominantly oriented longitudinally, tibiotarsus with large lateral cnemial crest and well differentiated medial and lateral condyles, tarsometatarsus with pronounced, spherical intercotylar eminence, four toes present; (2) internarial septum large, pterygoid broad, quadrate fits into V-shaped notch in mandible, buttressed from behind by retroarticular process of mandible, scapula with styloid acromion, tarsometatarsus with large interosseous foramen, deeply concave anterior face and deeply excavated origin of extensor digiti IV brevis muscle; (3) pterygoid fossa present, vomer does not articulate with premaxillae; (4) primary osteons of tibiotarsus predominantly oriented transversely; (5) scapulocoracoid fused and sternum unkeeled, humerus long and spindly, with pronounced internal tuberosity and without pneumatic foramen, antebrachium short; (6) bill elongate, eyes reduced, tarsometatarsus without concave anterior face and excavated origin of extensor digiti IV brevis muscle, interosseous foramen small; (7) scapulocoracoid with large glenoid, acromion and acrocoracoid process, carpometacarpus with accessory foramina between each of the metacarpal bones, ilioischadic foramen elongate, femur short, tarsometatarsus long, hallux absent (condition of quadrate mandible articulation unknown); and (8) pterygoid fossa absent, caudal process of palatine bone absent, V-shaped notch in mandible for quadrate absent, bill broad, cervical vertebrae elongate, femur short and robust, tibiotarsus with pronounced anterior cnemial crest and undifferentiated medial and lateral condyles, tarsometatarsus without spherical intercotylar eminence, concave anterior face and excavated origin of extensor digiti IV brevis muscle, interosseous foramen small and only two trochleae present.



**Fig. 3** Bright field photomicrographs of transverse lapidary thin sections through the same level (distal metaphysis) of a, tinamou (*Rhynchotus*, Princeton University PU 728); b, ratite (*Rhea*, specimen unnumbered); c, *Lithornis* (USNM 290554); and d, *Paracathartes* (USNM 361407), showing histological character states used in Fig. 2. Vascular canals appear as thin dark lines, spots, or circles on a light background of inorganic bone. Large dark regions are more opaque regions of bone, in which vascular canals may appear as light spots. Scale, 0.3 mm. The patterns formed by primary osteons are characteristically different in the leg bones of palaeognathous birds (tinamou and ratites) and neognathous birds (all other birds)<sup>16,17</sup>. The primary osteons in the tibiotarsus of *Lithornis* are predominantly parallel to the longitudinal axis of the bone, as in the tibiotarsus of the palaeognathous tinamou but unlike ratites and neognathous birds. Primary osteons in the tibiotarsus of *Paracathartes* are predominantly arranged in concentric rings that lie in the transverse plane of the bone, as in the tibiotarsus of ratites but unlike the tinamou and neognathous birds. Although the patterns of primary osteons could be evolved separately by unrelated birds, no correlation has been found between the pattern of primary osteons and flightlessness, ontogeny, or overall size among neognathous birds<sup>18</sup>.



where<sup>15</sup> discussed problems with the four other data used to calibrate the DNA molecular clock.

I thank A. J. Charig for his comments on this manuscript and D. Baird, J. Becker, D. P. Domning, A. Elzanowski, P. D. Gingerich, H. Haubold, A. E. Houde, W. v. Koenigswald, S. L. Olson, A. de Ricqlès, G. Stanton and R. L. Zusi for their assistance. This work was supported by the A. Wetmore Memorial Fund of the American Ornithologists Union, A. Wet-

more Memorial Fund of the Smithsonian Institution, F. M. Chapman Memorial Fund of the American Museum of Natural History, Museum of Paleontology of the University of Michigan, National Science Foundation Dissertation Grant (BSR 8313209), Sigma Xi, Smithsonian Predoctoral Fellowship and National Institutes General Medical Sciences Grant (GM07803) to L. V. Leak of Howard University.

Received 23 January; accepted 18 September 1986.

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