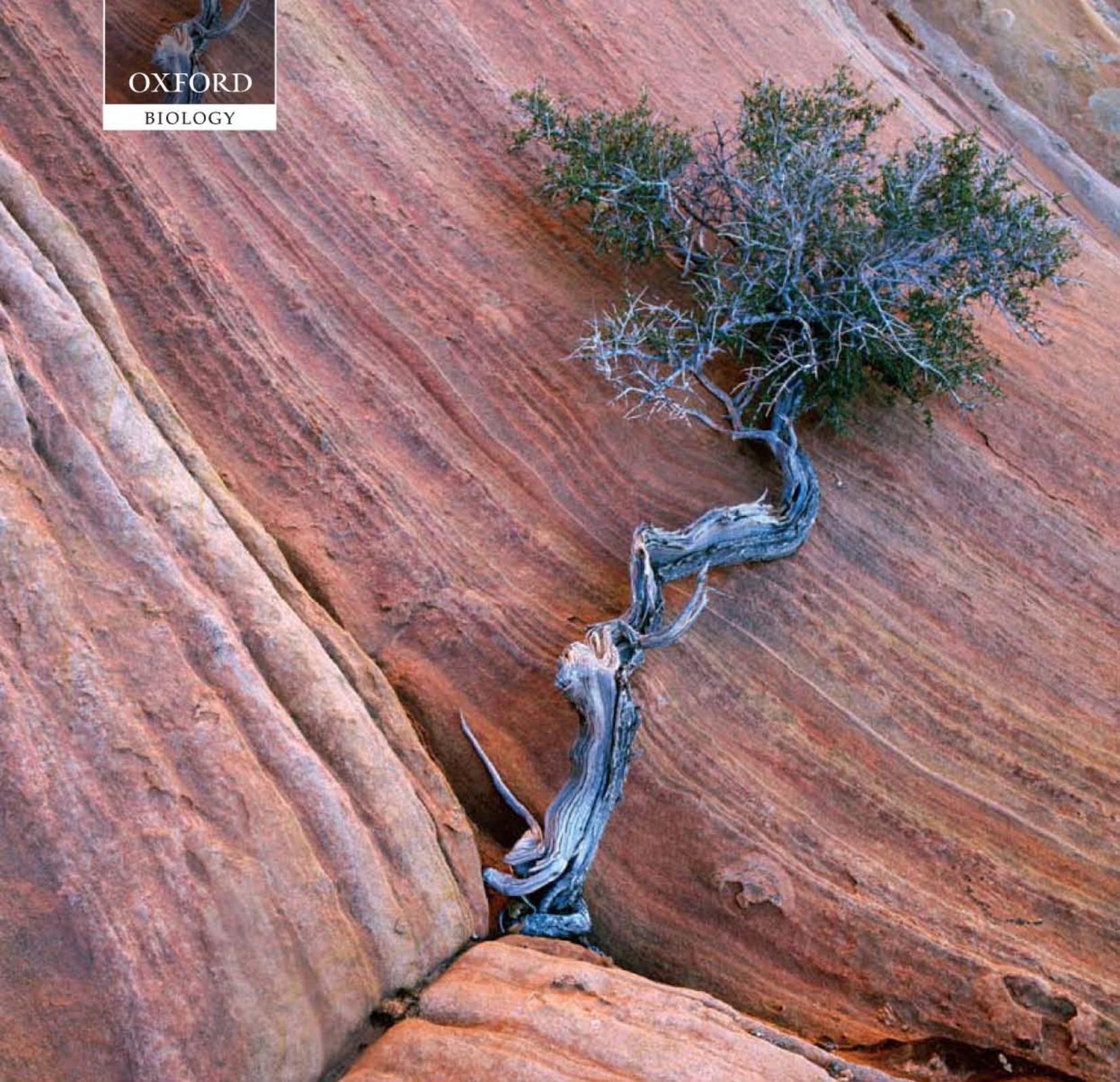


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# Ratites and tinamous (Paleognathae)

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## Abstract

The Paleognathae is a monophyletic clade containing ~32 species and 12 genera of ratites and 46 species and nine genera of tinamous. With the exception of nuclear genes, there is strong molecular and morphological support for the close relationship of ratites and tinamous. Molecular time estimates with multiple fossil calibrations indicate that all six families originated in the Cretaceous (146–66 million years ago, Ma). The radiation of modern genera and species occurred from the Oligocene–Miocene boundary (23 Ma) to the Pleistocene (1.8–0.012 Ma). The basal splits within the ratites are approximately coincident with the breakup of Gondwana, suggesting that the different lineages rafted on continental landmasses to their present locations.

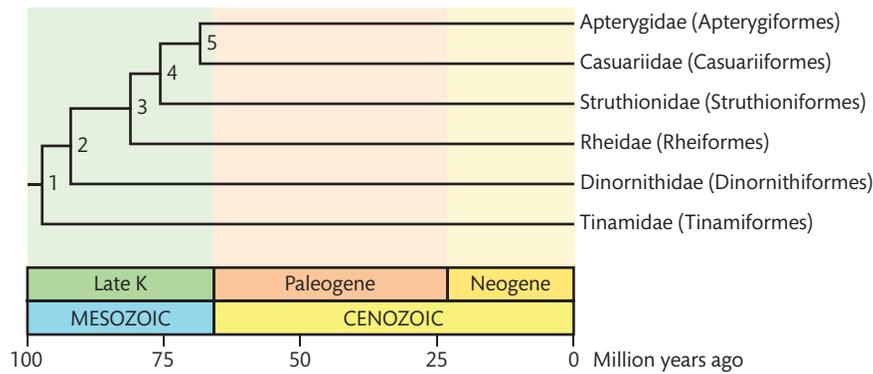
The Superorder Paleognathae consists of the flightless ratites and the volant tinamous. It is the closest relative of the remaining birds in the Superorder Neognathae. Ratites are named for their raft-like (ratis) sternum that lacks a keel, whereas the tinamous have a keeled sternum. Tinamous share with the ratites a complex bone structure in the roof of the mouth termed a paleognathous palate. The ratites include the Emu and four species of cassowaries in Australia and New Guinea (1), five species of kiwis (2) and possibly 14 extinct species of moas from New Zealand (3), two species of rheas from South America, the Ostrich (Fig. 1) now restricted to Africa but once more widely distributed across Europe and Asia, and five extinct species of elephant birds from Madagascar. Forty-six species of tinamous occur in South and Central America (1). Eight fossil species possessing a paleognathous palate occur from the late Paleocene (66–56 Ma) to the middle Eocene (~40 Ma) of the Northern Hemisphere (4). However, they appear to be a paraphyletic assemblage, and have been placed basal to

the ratites (5). Here, we review the phylogenetic relationships and divergence times of the extant clades of ratites, the extinct moas and the tinamous.

Longstanding debates about whether the paleognaths are monophyletic or polyphyletic were not settled until phylogenetic analyses were conducted on morphological characters (6–9), transferrins (10), chromosomes (11, 12),  $\alpha$ -crystallin A sequences (13, 14), DNA–DNA hybridization data (15, 16), and DNA sequences (e.g., 17–21). However, relationships among paleognaths are still not resolved, with a recent morphological tree based on 2954 characters placing kiwis (Apterygidae) as the closest relatives of the rest of the ratites (9), in agreement with other morphological studies using smaller data sets (6–8, 22). DNA sequence trees place kiwis in a derived clade with the Emu and Cassowaries (Casuariiformes) (19–21, 23, 24). The conflict between morphological and molecular



Fig. 1 An Ostrich (*Struthio camelus*), Family Struthionidae. Credit: J. Cracraft.



**Fig. 2** A timetree of ratites and tinamous (Paleognathae). Divergence times are shown in Table 1. *Abbreviation:* K (Cretaceous).

phylogenies lies in where to place the root of the tree (8). The extinct moas are not recovered as the closest relatives to kiwis (19, 20) in the molecular trees, contrary to the morphological trees where they are closest relatives. The rheas (Rheiformes) and ostrich (Struthioniformes) also exchange places in different molecular trees (8, 19, 20). Nuclear gene sequences often place tinamous (Tinamiformes) within the ratites (25), possibly due to stochastic sorting of gene lineages across short basal branches that prevent recovery of the species tree (26).

The Paleognathae timetree is based on the most recent analyses that include multiple fossil calibrations and allow for different rates of evolution in different branches of the tree (21, 27, 28) based on partial or complete mitochondrial genomes (Fig. 2). The basal split between ratites and tinamous is estimated to have occurred ~108 Ma. Moas diverged from the lineage leading to the other modern ratites ~95 Ma, followed by the rheas about 87 Ma, and ostrich 78 Ma. The Emu and cassowary lineage split from the kiwi lineage ~77 Ma, Emu and cassowaries diverged ~41 Ma, the rhea genera diverged about 14 Ma, and the moa and kiwi lineages diversified within the last 18–4 million years. Other estimates within Paleognathae have suggested more recent divergence times (18–31), but these were obtained using single anchor-points and methods of molecular dating that did not account for uncertainty in fossil ages or variable rates of molecular evolution.

With the possible exception of the Ostrich, which may have walked to Africa following the rafting of the India–Madagascar plate to Asia, ratite divergence times fit the vicariance biogeography hypothesis. These large flightless birds probably rafted to their current geographic locations on the landmasses resulting from the

fragmentation of the supercontinent Gondwana (21, 27). Early molecular dating studies that did not account properly for phylogenetic and fossil calibration uncertainties resulted in much younger divergence times (17, 18, 30, 31). This in turn led to the alternative hypothesis that flighted ancestors (e.g., lithornids) of crown-group taxa dispersed after the fragmentation of Gondwana (4) and that descendant lineages became secondarily flightless on separate landmasses in the southern hemisphere. New molecular dates (27, 28) based on multiple fossil anchor-points suggest instead that a single loss of flight in modern ratites in Gondwana is highly likely. The tinamous lineage probably originated in the South American portion of Gondwana and never dispersed beyond the Americas. Diversification of moas in New Zealand has been attributed to earth history events and global cooling that fragmented ranges and promoted allopatric divergence of lineages (3).

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**Table 1.** Divergence times (Ma) and credibility/confidence intervals (CI) among ratites and tinamous (Paleognathae).

Timetree		Estimates													
Node	Time	Ref. (18)		Ref. (19)		Ref. (20)		Ref. (21)		Ref. (27)		Ref. (28)		Ref. (29)	
		Time	CI	Time	CI	Time	CI	Time	CI	Time	CI	Time	CI	Time	CI
1	96.7	88.9	104–74	92.2	111–73	-	-	105.0	137–88	113	127–100	105.9	128–83	75.2	85–65
2	91.5	-	-	78.9	94–64	-	-	96.0	134–87	99.7	112–88	91.5	116–70	-	-
3	80.6	79.5	94–55	69.3	82–57	89.1	94–84	89.0	127–83	92.2	104–81	81.5	106–59	63.7	75–55
4	75.2	79.5	94–55	65.3	72–58	75.5	78–73	84.0	121–82	84.9	97–74	67.3	92–42	70.1	79–60
5	67.9	55.6	68–43	62.4	69–55	68	72–65	81.0	116–76	76.8	88–66	74.6	100–52	56.7	64–49

Note: Node times in the timetree represent the mean of time estimates from refs. (27, 29). Divergence times were estimated from analyses of complete mitochondrial genomes (19–21, 27, 28) and analysis of partial mitochondrial DNA sequences (18, 29).

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