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the **TIMETREE** *of* **LIFE**

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Birds (Aves)

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Abstract

Living birds (~9500 species) are grouped into 20–28 orders, comprising the Subclass Neornithes of the Class Aves. With few exceptions, molecular phylogenetic analyses have supported two morphological divisions within Neornithes, Paleognathae (ratites and tinamous) and Neognathae (all other living birds). Within Neognathae, there is universal support for the recognition of two superorders: Galloanserae (landfowl and waterfowl) and Neoaves (all other neognath orders). The neornithine timetree shows a Paleognathae–Neognathae split at ~120 million years ago (Ma) and the Galloanserae–Neoaves split at ~105 Ma, both possibly related to continental breakup.

Living birds are grouped in the Subclass Neornithes, and currently divided into three Superorders: the Paleognathae (ratites and tinamous), Galloanserae (waterfowl and gamefowl), and Neoaves (all other birds; Fig. 1). Based on morphological classification, Neornithes and archaic birds are grouped together in the Class Aves, a subgroup of theropod dinosaurs. The evolution of archaic avians to neornithine birds shows progressive loss of teeth, reduction in tail length, and modification of feathers and limbs for powered flight. These combined characteristics are not yet seen in the oldest lineage of birds, *Archaeopteryx*. However, several nonmodern birds also displayed remarkable flight adaptations, particularly the Cretaceous enantiornithines. Between 9000 and 10,000 living species of birds have been described, and they have been placed in 20–28 orders (1, 2). Here, the relationships and divergence times of the three superorders of living birds are reviewed.

Until recently, the classification of neornithine birds pioneered by Huxley (3) and expanded by Fürbringer (4) has followed the arrangement proposed by Wetmore (5). This classification is still reflected in published bird guides today. In it, species were placed in two major groups: Paleognathae (ratites and tinamous) and

Neognathae (all other orders). These two major divisions reflected differences in jaw morphology and flight capabilities (3). Paleognaths have primitive jaws reminiscent of non-avian theropods, while neognaths possess modern jaws with adaptations reflecting diverse feeding modes and postcranial modifications related to lifestyle and mode of locomotion.

Early molecular phylogenies based on immunological (6) and DNA–DNA hybridization (7) distances supported the grouping of paleognath birds, but they did not support the classical definition of Neognathae. Instead of finding penguins, loons, and grebes to be among the earliest diverging neognaths, those molecular studies identified the waterfowl (Anseriformes) and gamefowl (Galliformes) as closest relatives and forming a group (Galloanserae) separate from other neognaths (Neoaves). However, the position of Galloanserae with respect to Neoaves and Paleognathae was not yet firmly established.

DNA sequence studies over the last decade have addressed the relationships of avian orders and definition of superorders. Initial studies using small subsets of taxa gave conflicting results. An analysis of some short sequences of a nuclear gene (*α-crystallin*) in five species joined Galliformes and Anseriformes, with a paleognath (tinamou) basal (8). However, initial analyses of complete mitochondrial genomes in a small selection of avian



Fig. 1 A Rock Pigeon (*Columba livia*). Credit: M. Peck.

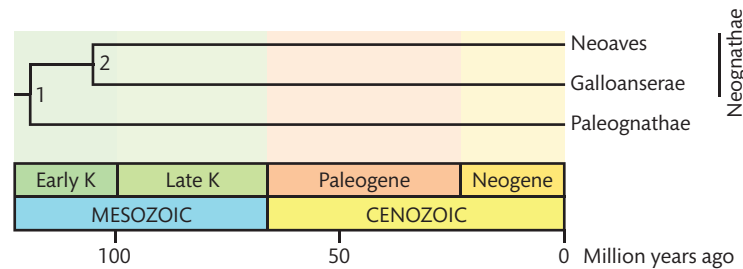


Fig. 2 A timetree of bird superorders. Divergence time estimates are from Table 1. Abbreviation: K (Cretaceous).

orders surprisingly placed songbirds (Passeriformes) in a basal position among living birds, with ratites nested within Neognathae (9–11).

Studies using longer sequences from nuclear genes and greater taxonomic coverage (12, 13) provided the strongest support yet for the three superordinal groupings initially defined by immunological distances (6). Galloanserae was found to be the closest relative of Neoaves, together forming Neognathae. Subsequent studies based on one or several nuclear genes (14–19) and mitochondrial genomes (20–25) continued to support this superordinal arrangement, now reflected in taxonomic updates (26).

A variety of studies have estimated divergence times among neornithine orders, in particular those covering the early history of modern birds. Based on 19 clock-like nuclear genes, the average divergence time between chicken, goose, Ostrich, and pigeon was estimated at 97 ± 12 million years ago (Ma), with mitochondrial DNA estimates ranging between 68 and 131 Ma (27). Subsequently, a quartet-dating study (28) on the *12S rRNA* and *c-mos* genes from several orders pushed the average neognath–paleognath split deeper into the Cretaceous (135 Ma), and supported Cretaceous ordinal origins as well. Analyses of complete mitochondrial genomes and broad taxon sampling yielded mid-Cretaceous time estimates for the Paleognathae–Neognathae split (120–110 Ma) and the Galloanserae–Neoaves split (100 Ma) (21, 23). Other mitochondrial studies have used a Bayesian approach and minimum constraints instead of fixed calibration points, which yielded divergence times that were on average 20 Myr older (22, 25).

These early divergence time estimates do not have direct support from the neornithine fossil record. However, the presence of derived waterbird fossils (23, 29, 30) from the latest Cretaceous (66 Ma) and the Paleocene (62–55 Ma) implicate Cretaceous ages for the deepest nodes on the neornithine timetree.

The first study that estimated superordinal divergence times with complete ordinal representation used a concatenated nonprotein-coding portion of the mitochondrial genome (two rRNAs, three tRNAs) and a lineage-specific method (31). Those time estimates agreed closely with estimates reported in two of three mitochondrial DNA studies (21, 23) (Table 1). The only neornithine timetree based on multiple nuclear genes (18) and comprehensive ordinal sampling supported a similar divergence time for the Galloanserae–Neoaves split (95 Ma). In summary, the neornithine timetree (Fig. 2) shows mid-Cretaceous diversification of superorders, which is indirectly supported by fossil evidence (18, 23, 29, 30) and is consistent with continental breakup and paleogeography (27, 32).

Acknowledgments

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Table 1. Divergence times (Ma) and their confidence/credibility intervals (CI) among birds (Aves).

Timetree		Estimates													
Node	Time	Ref. (18)		Ref. (21)		Ref. (22)		Ref. (23)		Ref. (24)		Ref. (25)		Ref. (29)	
		Time	CI	Time	CI	Time	CI	Time	CI	Time	CI	Time	CI	Time	CI
1	119.0	-		111.0	125-96	139	154-126	110.6	125-96	101	133.2	149-115	119.0	129-108	
2	105.0	95.0		99.0	112-87	122	135-110	99.1	112-87	90.0	126.0	140-112	104.0	110-99	

Note: Node times in the timetree represent the mean of time estimates from different studies. Divergence times were estimated from an analysis of ribosomal mitochondrial genes (29), protein-coding mitochondrial genes (25), complete mitochondrial genomes (21-24), and five nuclear genes (18).

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