



OXFORD
BIOLOGY



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

edited by **S. BLAIR HEDGES** *and* **SUDHIR KUMAR**
foreword by James D. Watson

Advanced birds (Neoaves)

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Abstract

Neoaves, the largest superorder of living birds (Neornithes), consists of 16–24 orders and ~9000 species. Although recent progress has been made, available molecular data continue to show remarkable lack of phylogenetic resolution and the basal splits within Neoaves are still uncertain. The neoavian timetree shows an initial divergence at ~95 million years ago (Ma) followed by Cretaceous (87–75 Ma) diversification of southern hemispheric orders and younger times for northern and aquatic orders (Paleogene, 65–30 Ma). The time-tree thus implicates possible roles for continental breakup (Cretaceous) and climate (Paleogene) in the diversification of advanced birds.

Neoavian birds are included in the Subclass Neornithes, and most broadly can be defined as those orders with advanced flight capabilities. Such birds include the arboreal songbirds, cuckoos, parrots, and woodpeckers, the nocturnal owls and nightjars, aerial fliers such as swifts and hummingbirds, as well as several other distinct lineages including pigeons, raptors, shorebirds, wading birds, and marine birds (Fig. 1). Excluded from Neoaves are the primitive flightless paleognath landbirds (ratites), the primitive paleognath and neognath volant landbirds (tinamous and landfowl), and primitive neognath waterbirds (waterfowl). Approximately 9000 living species of Neoaves have been described and placed in 16–24 orders.

Traditionally, neognath orders with limited aerial flight capability (penguins, loons, grebes) were thought to be primitive and placed ahead of other bird orders in classifications (1–3). The unit Neoaves was first described from molecular data from the 1970s and 1980s (4, 5), and its monophyly continued to gain support from DNA sequence data (6–11). Although initial complete mitochondrial genome data supported neoavian paraphyly with passerines as the earliest diverging modern birds,

this result is now considered an artifact of limited taxon sampling (7, 15). Phylogenetic resolution among the main divergences within Neoaves continues to remain a major hurdle (10), with most neoavian orders appearing to have diverged in close succession. This “neoavian comb” (10) on the one hand has been interpreted as evidence for a real (hard) polytomy among most, if not all, neoavian orders (12), indicating a rapid evolutionary radiation. Others have maintained that additional taxonomic and nucleotide sampling will provide added resolution (10).

At present, three molecular studies (7, 13, 14) exist that have included a combination of both complete neoavian ordinal sampling and nuclear gene sequencing. Two of these studies were based on nuclear gene



Fig. 1 A Great Blue Heron (*Ardea herodias*), Order Ciconiiformes, from Canada. Credit: M. Peck.

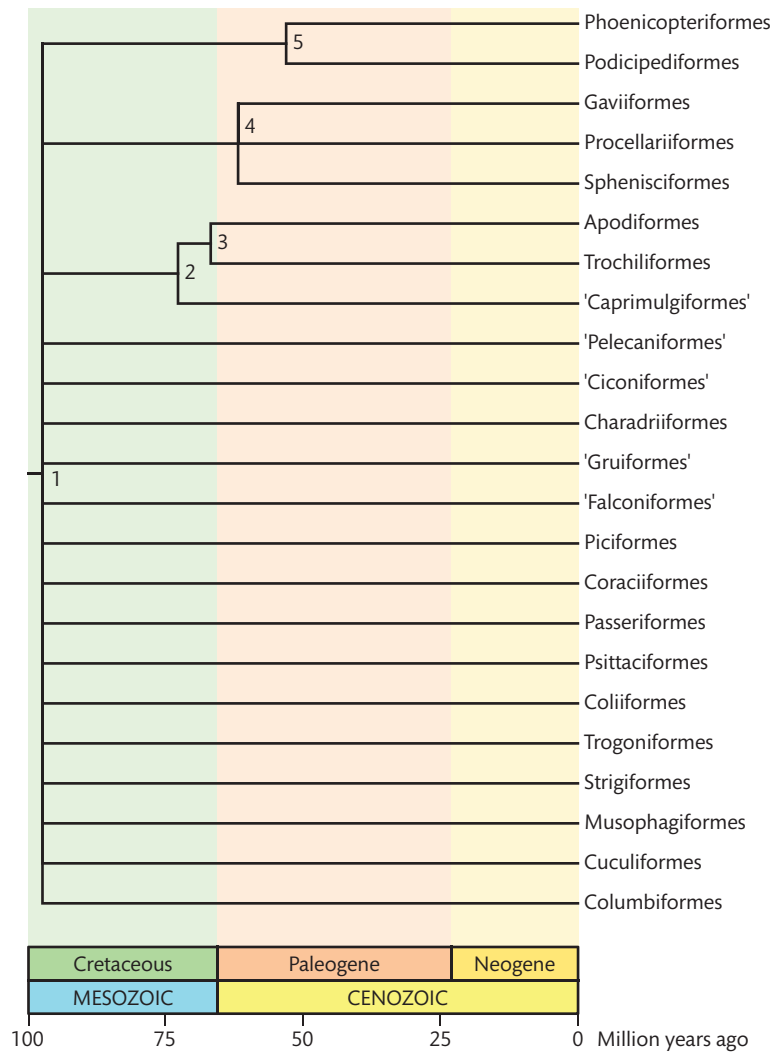


Fig. 2 A timetree of advanced birds (Neoaves). Divergence times are from Table 1.

sequences of single genes (*18S rRNA* or *beta-fibrinogen* intron) with or without additional mitochondrial DNA sequences. Both studies differed considerably in phylogenetic resolution among neoavian orders. The study larger in nucleotide sampling (7) showed limited resolution across Neoaves. Instead, the second study (14) based on intron seven of the *beta-fibrinogen* gene was more extensive in taxon sampling and claimed support for a broad division within neoavian birds, that are between two newly defined groups, Metaves and Coronaves. Several traditional orders were broken up by this new classification, which suggested a provocative scenario for convergent evolution in morphology and ecology across many extant bird orders. For example, Metaves included some

enigmatic gruiform families while the better-known gruiform cranes and rails were placed in Coronaves. The enigmatic Hoatzin was allocated to Metaves, while their supposed cuculiform and musophagiform relatives were placed in Coronaves, also clustering among several waterbird orders. Finally, the peleciform tropicbirds were placed with flamingos, grebes, sandgrouse, swifts, hummingbirds, and caprimulgiform birds in Metaves while other peleciforms, shorebirds, and owls were allocated to Coronaves.

The most recent nuclear study (13) was based on five nuclear genes and extensive taxon sampling across every order. These new sequence data combined with the published *beta-fibrinogen* sequences also supported

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

Timetree		Estimates												
Node	Time	Ref. (13)	Ref. (18)		Ref. (20)		Ref. (21)		Ref. (23)		Ref. (24)		Ref. (25)	
		Time	Time	CI	Time	CI	Time	CI	Time	CI	Time	CI	Time	CI
1	97.3	95	-	-	118.5	132-105	77	83-72	103.8	111-97	89.3	108-70	100	123-83
2	72.7	62	-	-	-	-	67	69-65	-	-	-	-	89	112-73
3	66.7	45	-	-	80.5	100-61	61	63-60	67.9	73-63	75.7	91-60	70	88-55
4	61.8	58	71.1	76-66	-	-	-	-	41.2	44-38	-	-	77	97-67
5	53.0	31	-	-	52	70-30	-	-	-	-	-	-	76	96-61

Note: Node times in the timetree represent the mean of time estimates from different studies. Divergence times were obtained from an analysis of ribosomal mitochondrial genes (24), partial (20), or complete (16, 18, 19) mitochondrial genomes, two nuclear introns (21), five nuclear genes (13, 25), or DNA-DNA hybridization distances (23).

the distinction between Metaves and Coronaves, but only when the fibrinogen sequence data were included. Expanded mitochondrial studies (15–20), and nuclear studies (21) based on incomplete sampling among neoavian orders also fail to show support for Metaves or Coronaves. Thus, these studies exemplify the current status of neoavian molecular systematics. Molecular sequence studies (including expanded mitochondrial gene studies, 15–20) have been unable to provide solid support for the resolution of major ordinal groupings within Neoaves. Nonetheless, there has been consensus support for a grouping of flamingos (Ciconiiformes, Phoenicopteridae) and grebes (Podicipediformes, Podicipedidae) (10, 11, 13, 19, 20, 22); for joining hummingbirds (Trochiliformes) with swifts (Apodiformes) and imbedding this grouping within a paraphyletic Caprimulgiformes (10, 13, 20, 21) and for joining penguins (Sphenisciformes), tubenosed birds (Procellariiformes), and loons (Gaviiformes) together (5, 10, 13, 22, 23).

A variety of studies have estimated divergence times among neoavian orders (Table 1). The first study that estimated divergence times from a complete ordinal data set used a concatenated nonprotein-coding portion of the mitochondrial genome (2 rRNAs, 3 tRNAs) and a lineage-specific method (24). The timing of the neoavian divergences agreed closely with that reported in two of three mitogenomic studies (16, 18). This study also confirmed a rapid Cretaceous radiation involving the origination of all neoavian orders starting at 90 Ma. Application of the same calibration method on a taxonomically much larger DNA–DNA hybridization data set suggested a rapid diversification of Gondwanan orders (85–75 Ma) following the origin of Neoaves (104 Ma), but

younger ages for Laurasian orders (75–60 Ma), and the entirely Paleogene origin (55–30 Ma) of several traditional waterbird orders (23).

A second timetree (13) of Neoaves based on multiple (five) nuclear genes and comprehensive ordinal sampling was constrained on several nodes internal to Neoaves and used two separate rate-smoothing methods. Results from one of the smoothing approaches (penalized likelihood) agreed well with previous timing results. An alternative timetree was presented that showed considerably younger origination times for neognath orders, and this timetree was preferred because of the better agreement with the fossil record. However, others have used the same and additional data to argue for older Cretaceous ages of many neoavian groups and pointed to an average age of 110 Ma for the first divergence among extant Neoaves (20, 25). Resolution of which of the two timetrees is more accurate is essential to understanding the evolutionary tempo and mode of Neoaves. One timetree scenario (Fig. 2) shows consistency across all molecular data sets in mid-Cretaceous ordinal origination and superordinal diversification. It correlates well with the timing of Gondwanan biogeography, which has direct fossil support for Cretaceous origination of galloanserine orders and superordinal diversification, but it also imposes considerable fossil gaps for many lineages. The second scenario shows better consistency between nuclear DNA sequence and fossil divergence times and suggests that neoavian orders originated rapidly and diversified in the Paleogene.

Similar discrepancy exists in the available time estimates for the origin of Caprimulgiformes, Apodiformes, Procellariiformes, and Podicipediformes (Table 1). It is

yet unclear whether any of these orders originated in the Cretaceous or Paleogene. A case in point concerns the origin of Apodiformes, which was based on six time estimates from mtrRNA, mtDNA, nuclear exons, and nuclear introns. While BEAST and PATHd8, respectively, provide the maximum (81 Ma) and minimum (45 Ma) estimates for Apodiformes, all confidence/credibility intervals (CI) overlap with the Cretaceous–Paleogene boundary. Without consistency in calibration, gene sampling and timing methodology, the source of the varying time estimates among studies remains as yet unclear. Resolution will likely come from additional nuclear gene sequences, and more Cretaceous and Paleocene fossil material.

Acknowledgments

Support was provided by Netherlands Organization for Scientific Research (NWO) and the Eppy foundation.

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