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Waterfowl and gamefowl (Galloanserae)

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Abstract

The Galloanserae is a monophyletic group containing 442 species and 129 genera of Anseriformes (waterfowl) and Galliformes (gamefowl). The close relationship of these two orders and their placement as the closest relative of Neoaves are well supported. Molecular time estimates and the fossil record place the radiation of living Galloanserae in the late Cretaceous (~90 million years ago, Ma) and the radiation of modern genera and species in the Cenozoic (66–0 Ma). The basal split within Galloanserae is coincident with the breakup of Gondwana, and later diversification occurred following subsequent dispersal to other continental masses in the Eocene (56–34 Ma).

Galloanserae is an ancient clade of birds including the Orders Anseriformes (waterfowl; Fig. 1) and Galliformes (gamefowl). Waterfowl are strong flyers, and most members are also good swimmers. There are about 48 extant genera and 161 species distributed in four families (1). The Family Anhimidae includes three species of South American screamers, named after loud calls emitted when threatened. The monotypic Anseranatidae includes the Australian Magpie Goose, which is unusual among waterfowl because it is the least aquatic species, has partial molt of flight feathers and copulates on land instead of water. The Family Dendrocygnidae groups all eight species of tropical and subtropical whistling ducks in only one genus. Whistling ducks have long necks and legs, and longer hind toes than most ducks. Unlike other families in the order, the Anatidae is more diverse, with 45 genera and about 150 species of geese and swans (Subfamily Anserinae) and true ducks (Subfamily Anatinae). They have fully webbed feet and a worldwide distribution. The family can be divided in two subfamilies: Anserinae (geese and swans) and Anatinae (true ducks).

The Order Galliformes is more diverse than Anseriformes. There are about 281 species and 81 genera of gamefowl (1). Galliformes is classified into five families. The Megapodiidae includes 21 species of megapodes distributed in six genera found in the Australasian region. The family includes the scrub fowl, brush-turkeys, and Mallee Fowl, also known collectively as mound-builders because of their habit of burying their eggs under mounds of decaying vegetation. The Cracidae is a Neotropical group of 10 genera and about 50 species of forest-dwelling birds, including curassows, guans, and chachalacas. Cracids have blunt wings and long broad tails, and may have brightly colored ceres, dewlaps, horns, brown, gray or black plumage, and some have bright red or blue bills and legs. Numididae includes four genera and six species of guineafowl found in sub-Saharan Africa. Guineafowl have most of the head and neck unfeathered, brightly colored wattles, combs or crest, and a large bill. The Family Odontophoridae harbors about 32 species of new world quails, which are medium-sized birds, with short, powerful wings, “toothed” bill, and lack of tarsal spurs. The remaining members of the Galliformes are placed in the Family Phasianidae, which is the most diverse within Galliformes. It includes chicken, grouse, partridges,



Fig. 1 A Mute Swan (*Cygnus olor*), Family Anatidae, from Lake Ontario, Toronto. Credit: S. L. Pereira.

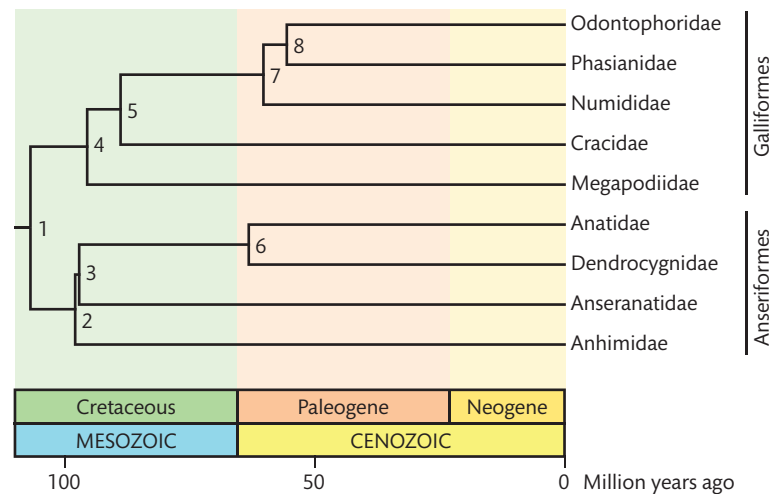


Fig. 2 A timetree of waterfowl and gamefowl (Galloanserae). Divergence times are shown in Table 1.

pheasants, and turkeys. In general, phasianid birds are medium-sized to large birds, with short, rounded wings, short toes with blunt claws, and raised hallux. Many subdivisions within the Phasianidae have been proposed, with some subfamilies sometimes considered as separate families (e.g., turkeys and grouse placed in the Families Meleagrididae and Tetraonidae, respectively). Although a Cenozoic origin for Galloanserae has been long hypothesized (e.g., 2), based on fragmentary and incomplete specimens, definitive evidence was found only recently (3). *Vegavis iaii*, the oldest known anseriform fossil from the Maastrichtian stage of the late Cretaceous, is closely related to the lineage of ducks and geese. This finding implies that modern anseriform families, and hence their closest living relative, the Galliformes, were already independent lineages in the late Cretaceous (3). Other fossils of extinct lineages with phylogenetic affinities to extant Galloanserae are known from the Eocene, and modern genera from both orders only show up in the fossil record in the Neogene (23–0 Ma) (2, 3). Here, the systematic and phylogenetic relationships of Galloanserae are reviewed briefly, and estimates of the divergence times for major lineages of Anseriformes and Galliformes derived from molecular data are summarized (Fig. 2).

The first suggestion of a close relationship between Anseriformes and Galliformes can be dated back to about 140 years ago (4), and constantly reaffirmed since then by phylogenetic analyses of nonmolecular (e.g., 5, 6) and molecular data (e.g., 7–9). Despite sporadic disputes (e.g., 10), an analysis of 2954 morphological characters scored across 150 extant birds provided compelling evidence

for the monophyly of Galloanserae and indicated that Neoaves is its closest relative (11). This analysis identified nine derived morphological characters supporting Galloanserae as a natural (monophyletic) group (11).

Morphological (6, 11, 12) and molecular data (9, 13) have provided strong evidence for family relationships within Anseriformes, placing Anhimidae as the closest relative of Anseranatidae and the remaining families, Anatidae and Dendrocygnidae as each other's closest relative (Fig. 2). Despite considerable effort to establish the phylogenetic relationships for some groups, such as geese and swans (14) and some ducks (15–17), based on molecular and nonmolecular characters, phylogenetic relationships at the tribal and generic levels are yet not fully resolved within the Subfamily Anatinae (12, 13, 15, 18). This is likely due to insufficient character sampling, leading to poor overall resolution across tribes and genera.

The phylogenetic relationships of Galliformes have received considerably more attention than Anseriformes. It is widely accepted that Megapodiidae is the closest relative of all galliform families, followed by Cracidae (11, 19–21). This contrasts with earlier results from DNA–DNA hybridization studies that placed Cracidae and Megapodiidae as reciprocally monophyletic groups (the Craciformes), which in turn were considered the closest relative of remaining galliform families (22). Additionally, there is considerable debate whether Odontophoridae or Numididae is closest to Phasianidae (reviewed in 11, 19, 20). Combined analyses of morphological and behavioral data and DNA sequences (19), or

Table 1. Molecular time estimates (Ma) and their confidence/credibility intervals (CI) among waterfowl and gamefowl (Galloanserae).

Timetree		Estimates								
Node	Time	Ref. (8)		Ref. (19)		Ref. (27)		Ref. (35)		Ref. (41)
		Time	CI	Time	CI	Time	CI	Time	CI	
1	106.9	101.0	113–92	–	–	105.0	135–84	114.6	130–97	–
2	97.9	–	–	–	–	91.0	119–72	104.7	121–86	–
3	97.2	92.1	103–82	–	–	–	–	102.3	119–83	–
4	95.4	86.6	96–79	107.0	122–91	95.6	112–77	103.1	120–85	84.9
5	88.8	–	–	92.8	107–79	88.5	113–71	95.9	114–78	77.8
6	63.2	–	–	–	–	–	–	63.2	84–43	–
7	59.8	52.4	59–48	60.2	71–53	64.1	85–53	72	90–53	50.3
8	62.4	–	–	55.5	66–50	68.8	92–55	66.1	85–48	59.3

Note: Node times in the timetree represent the mean of time estimates from different studies. Data analyzed were complete mitochondrial genomes (8), partial mitochondrial sequences (21, 35, 41), and combined analysis of nuclear and mitochondrial genes (19).

separate analyses of morphological (20) or molecular (23) data, however, seem to point out to a closer relationship between Odontophoridae and Phasianidae (Fig. 2). Additionally, the phylogenetic relationships within Phasianidae are still unsettled (19). Many phylogenetic hypotheses at the genus and species level have also been proposed for many groups, including megapodes (24), cracids (25–27), grouse (28, 29), and some clades within Phasianidae (28, 30–32). In general, the phylogenetic hypotheses based on DNA sequences have provided stronger support than analyses using morphological data for relationships within Anseriformes (12, 13) and Galliformes (19–21, 33), regardless of the taxonomic level under scrutiny.

The molecular time estimates within Galloanserae are largely congruent among most studies (8, 19, 21, 34, 35), with appreciable overlap in age uncertainties measured by credible or confidence intervals (Table 1). Estimates suggesting a post-Cretaceous radiation of Galloanserae families have been obtained in three studies that used a single calibration point to calibrate the molecular clock (33, 36, 37), and in a fourth study (38) that used some inappropriate fossil constraints (34), and imposed a maximum age for the root of the timetree (i.e., split between Paleognathae from other birds, including Galloanserae) at 95 Ma, without considering published molecular estimates for an earlier age (e.g., 8, 34, 39).

On the other hand, molecular time estimates derived from complete or partial sequences of the mitochondrial genome using multiple fossil constraints and a Bayesian

approach that accounts for uncertainties in both phylogenetics and fossil constraints (8, 21, 35) have placed the split between Anseriformes and Galliformes at the end of the early Cretaceous (Fig. 1). Similar conclusions have been reached using nuclear genes evolving at a constant rate among vertebrates (39, 40) and DNA–DNA hybridization studies (22). The fossil record supports the molecular time estimates (3).

The radiation of living Anseriformes is dated at ~97 Ma (or earlier according to a DNA–DNA hybridization study; 36), with the split of Anhimidae from other Anseriformes. The split of Anseranatidae from other anseriforms also occurred early in the history of Anseriformes around the same time (Table 1). The only divergence time available for the split between Dendrocygnidae and Anatidae based on DNA–DNA hybridization (36) places their split at 63.2 Ma.

Based on mitochondrial genomes and multiple fossil constraints, the radiation of extant Galliformes is contemporaneous with that of crown Anseriformes, and was placed at ~95 Ma (Table 1) with the separation of the Megapodiidae from the other families (Fig. 2). However, estimates based on DNA–DNA hybridization (36) and combined analysis of mitochondrial and nuclear DNA sequences (27), both using single-point calibrations for the molecular clock, suggest a much younger date (76–59 Ma). The split between Cracidae and the remaining Galliformes occurred at ~88 Ma, also before the Mesozoic–Cenozoic transition. The molecular time estimates for Numididae and Odontophoridae are

incongruent across studies (Table 1). As pointed out earlier, the placement of Odontophoridae and Numididae relative to Phasianidae has been contentious (19, 20, 41). Strong support for the close relationship between Odontophoridae and Phasianidae has been achieved only recently with increased character and taxonomic sampling (11, 19). Hence, we have chosen time estimates for nodes 7 and 8 (Fig. 2) from ref. (19). Some studies have shown that the radiation of galliform genera occurred mostly during the Eocene and Oligocene, and speciation occurred mostly in the Miocene to Pleistocene (25–27, 30, 42).

The radiation of living Anseriformes and Galliformes as estimated from molecular data (Table 1) and supported by some fossil evidence (3) is consistent with a vicariant mode of diversification due to the breakup of Gondwana during the Mesozoic (251–66 Ma), and continental drift throughout the Cenozoic (66–0 Ma). The first two cladogenic events within both orders isolated the South American and Australian waterfowl and gamefowl from their relatives now found in other Gondwanan and Laurasian landmasses. Dispersal to these other landmasses likely started during the Eocene (56–34 Ma) (19, 21), and favored the diversification of dispersing lineages as they colonized new continents and adapted to new ecological niches throughout the Cenozoic.

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