



OXFORD
BIOLOGY



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

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

Cranes, rails, and allies (Gruiformes)

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Abstract

The cranes, rails, and allies (Order Gruiformes) form a morphologically eclectic group of bird families typified by poor species diversity and disjunct distributions. Molecular data indicate that Gruiformes is not a natural group, but that it includes an evolutionary clade of six “core gruiform” families (Suborder Grues) and a separate pair of closely related families (Suborder Eurypygae). The basal split of Grues into rail-like and crane-like lineages (Ralloidea and Gruoidea, respectively) occurred sometime near the Mesozoic–Cenozoic boundary (66 million years ago, Ma), possibly on the southern continents. Interfamilial diversification within each of the ralloids, gruoids, and Eurypygae occurred within the Paleogene (66–23 Ma).

The avian Order Gruiformes, as traditionally conceived, consists of as many as a dozen families of extant or recently extinct birds and nearly as many more families known only from fossils. The Family Gruidae is represented by 15 species of cranes, which are found worldwide except in Antarctica and South America. The nearly cosmopolitan Family Rallidae comprises some 135–142 species of rails, crakes, coots, moorhens, gallinules, and flufftails (1, 2). Cranes and rails comprise the genetically closely related and relatively morphologically homogeneous Suborder Grues (3), which in turn is divided into the stocky rail-like Superfamily Ralloidea (rails, finfoots, adzebills) and the lanky crane-like Superfamily Gruoidea (cranes, Limpkin, trumpeters). Ralloids and gruoids represent extremes along a continuum of size from 139 to 1524 mm in length (4). Most are drab somber birds of wetlands or aquatic habitats, although gallinules are colorful and many others have pigmented patches of skin on the head (Fig. 1).

The most primitive members of Grues prefer forested habitats, but a few live even in arid savannahs. Grues are typified by dense plumage, relatively long necks, large feet and/or long legs, wings of low aspect ratio, short tails, and insensitive bills of short to medium length, but most

of these features are subject to allometric scaling. Cranes are exceptional migrators. While most rails are generally more sedentary, they are nevertheless good dispersers. Many have secondarily evolved flightlessness after colonizing remote oceanic islands. Other members of the Grues are nonmigratory. They include the finfoots and sungrebe (Heliornithidae), with three species in as many genera that are distributed pantropically and disjunctly. Finfoots are foot-propelled swimmers of rivers and lakes. Their toes, like those of coots, are lobate rather than palmate. Adzebills (Aptornithidae) include two recently extinct species of flightless, turkey-sized, rail-like birds from New Zealand. Other extant Grues resemble small cranes or are morphologically intermediate between cranes and rails, and are exclusively neotropical. They include three species in one genus of forest-dwelling trumpeters (Psophiidae) and the monotypic Limpkin (Aramidae) of both forested and open wetlands. No fossils of reliably identifiable extant core gruiform families are known to predate the Oligocene, but crane- or rail-like fossils date to the early Eocene.

Many other extant families have been considered to be Gruiformes, including buttonquails, Australian Plains-wanderer, seriemas, mesites, and bustards. Most are monotypic or nearly so, are morphologically highly



Fig. 1 A Red-chested Flufftail (*Sarothrura rufa*), Family Rallidae. Photo credit: M. Ford.

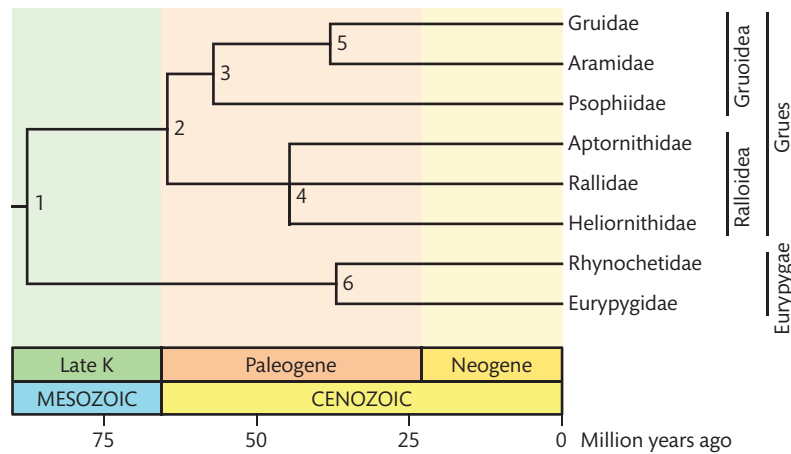


Fig. 2 A timetree of cranes, rails, and allies (Gruiformes). Only the monophyletic Suborders Grues and Eurypygae are included. Divergence times are shown in Table 1. *Abbreviation:* K (Cretaceous).

diverged from one another, and have restricted and often disjunct southern distributions. For example, the monotypic family pair of Kagu (Rhynochetidae) and Sunbittern (Eurypygidae) is endemic to New Caledonia and Amazonia, respectively. This has led some to hypothesize a pre-Cenozoic divergence for Gruiformes, while others have questioned its monophyly. This chapter reviews the relationships and divergence times of the families of Grues, and of Kagu and Sunbittern because they are believed by some to have close relationships to some members of Grues. Other putative members of the traditionally conceived Order Gruiformes are disregarded because their most recent divergences are among non-gruiform taxa.

Members of Gruiformes were first united on morphological gestalt in the mid-1800s (5), where they have remained in most morphology-based classifications until the present (1, 6, 7). Nevertheless, their monophyly has been questioned on the basis of morphological criteria (8, 9) and they have been the subject of few interfamilial or interordinal molecular genetic studies (3, 5, 10–22). The first attempts to address gruiform relationships using molecular genetic data were DNA hybridization trials (5, 10, 12, 21, 22) that neither included mesites nor incorporated a sufficient diversity of outgroups to test gruiform monophyly. Rather, where these were combined with non-gruiforms, the data were primarily intraordinal fitted to an interordinal supertree (5). Extraordinarily large DNA hybridization distances suggested that buttonquails were likely not Gruiformes (5), but their correct placement among shorebirds (Charadriiformes) was determined only later with multiple sequence data (14–16, 23, 24).

The Australian Plains-wanderer was first recognized as a member of Charadriiformes primarily on the basis of osteological characters (8). This conclusion has since been confirmed by numerous molecular studies (5, 14–16, 23, 24), but some morphologists argue that Gruiformes is paraphyletic to Charadriiformes (7).

There is irreconcilable disagreement between morphological and molecular studies about whether the remaining gruiforms are monophyletic. Analyses of small-subunit ribosomal mtDNA (12S) suggested that Kagu, Sunbittern, seriemas, bustards, buttonquails, and mesites were all more distant from the Grues clade than charadriiform and ciconiiform outgroups (13). Only two published molecular studies have sampled non-passerine neoavian families fairly comprehensively (14, 15). These, based on one and five nuclear loci, respectively, and another study combining mitochondrial and nuclear loci addressing Charadriiformes (16), strongly support a polyphyletic origin of Gruiformes. The only monophyletic groups among putative Gruiformes recovered by these studies are Kagu and Sunbittern within the proposed basal clade of Neoaves, Metaves, and among the families of Grues in the other proposed basal clade of Neoaves, Coronaves. In all, these studies found no fewer than six independent lineages of traditional Gruiformes even though the closest relatives of mesites, bustards, and seriemas remain poorly resolved. Grues alone were studied in greater detail with mitochondrial and three nuclear loci (3). Limpkin and cranes are the closest relatives and their group is in turn the closest relative of the trumpeters. Rails appear to be paraphyletic to both finfoots and adzebills, with flufftails (*Sarothrura*) closest

Table 1. Divergence times (Ma) and their confidence/credibility intervals (CI) among cranes, rails, and allies (Gruiformes).

Timetree		Estimates					
Node	Time	Ref. (3)		Ref. (15)(a)	Ref. (15)(b)	Ref. (31)	
		Time	CI	Time	Time	Time	CI
1	87.4	-	-	74.5	88.2	99.5	123–83
2	64.5	73.2	107–50	45.1	69.0	70.5	89–58
3	56.9	66.4	98–45	32.0	63.8	65.4	83–53
4	44.5	42.6	66–27	45.1	46.9	43.2	57–33
5	37.8	48.5	74–31	17.4	39.4	45.9	61–35
6	36.8	-	-	31.4	38.1	41	56–30

Note: Node times in the timetree represent the mean of time estimates from different studies. Three and five nuclear genes were analyzed using Multidivtime in refs. (3) and (31), respectively. In ref. (15), five nuclear genes were analyzed using (a) PATHd8 and (b) r8s programs.

to finfoots and adzebills the closest relatives of all other rails (Fig. 2).

Rates of molecular evolution are heterogeneous across all families of Grues and loci yet tested (3, 20, 22). A relaxed Bayesian clock was used in the Multidivtime program (25, 26) to estimate divergences within Grues based on intron 5 of *alcohol dehydrogenase-1* (*ADH-1*), intron 7 of *beta-fibrinogen* (*FGB*), and introns 3–5 and exons 3–4 of *glyceraldehyde-3-phosphate dehydrogenase* (*GAPD-H*), both with and without an upper bound set for the basal divergence of Gruidae at 25–20 Ma (3). Lower-bound calibrations internal to Gruidae were liberally construed from the fossil record (20, 22), and the lower bound on the Aramididae–Gruidae divergence was based on an Oligocene fossil (28 Ma) identified as a Limpkin (9). A fossil shorebird (23) was used as a lower-bound calibration external to Gruiformes, and analyses were conducted both with and without the constraints of internal and external upper bounds.

The basal divergence within Grues was estimated to be 51 Ma with upper bounds enforced in ref. (3). Without upper bounds, the Aramididae–Gruidae divergence was estimated at 48.5 Ma, the Psophiidae–Aramididae divergence at 66.4 Ma, the Heliornithidae–Rallidae divergence at 42.6 Ma, and the Gruoidea–Ralloidea divergence at 73.2 Ma (Table 1). Limited data (*12S* and *ADH-1* only) precluded the estimation of the Aptornithidae–Rallidae divergence, but it is bracketed by the Heliornithidae–Rallidae divergence (excluding *Sarothrura*).

Ericson *et al.* (15) estimated divergences across Neoaves using exon 3 of *c-myc* protooncogene (*c-myc*), *recombination activating gene-1* (*RAG1*), intron 2 of

myoglobin (*myo*), intron 7 of *FGB*, and introns 6–7 and exon 6 of *ornithine decarboxylase* (*ODC*). They fixed the age of the hummingbird–swift divergence at 47.5 Ma and used some 22 diverse fossils as minimum age constraints internal to Neoaves to calibrate their timetree. Two lower-bound constraints were internal to Grues, including a 14 Ma fossil sungrebe (27) and a 34–30 Ma fossil gruoid (28). Using PATHd8 (29) and penalized likelihood (PL) in the r8s program (30), respectively, they estimated the Aramididae–Gruidae divergence at 17.4 and 39.4 Ma, the Psophiidae–Aramididae divergence at 32.0 and 63.8 Ma, the Rallidae–Heliornithidae divergence at 45.1 and 46.9 Ma, the Gruoidea–Ralloidea divergence at 45.1 and 69.0 Ma, the Eurypygidae–Rhynochetidae divergence at 31.4 and 38.1 Ma, and the Eurypygiae–Grues (*vis á vis* Metaves–Coronaves) divergence at 74.5 and 88.2 Ma (Table 1).

Brown *et al.* (31) criticized Ericson *et al.*'s calibration as being generally too young, taking issue with the appropriateness of PATHd8 and some fossil calibrations; but see (32). They reanalyzed a modified DNA sequence alignment, using some alternative fossil calibrations and parametric Bayesian modeling of evolutionary rate in Multidivtime (25). They estimated the Aramididae–Gruidae divergence at 45.9 Ma, the Psophiidae–Aramididae divergence at 65.4 Ma, the Rallidae–Heliornithidae divergence at 43.2 Ma, the Gruoidea–Ralloidea divergence at 70.5 Ma, the Eurypygidae–Rhynochetidae divergence at 41.0 Ma, and the Eurypygiae–Grues divergence at 99.5 Ma (Table 1).

The traditionally conceived Order Gruiformes has been said to “exhibit strong Gondwanan distribution

patterns” (33) because its greatest familial diversity is in southern landmasses. Kagu, adzebills, and Sunbittern have occupied center stage, since the former two are flightless or nearly so. However, the notion that adzebills are the closest relatives of Kagu (1) is contradicted by all available molecular data (13). Ironically, adzebills were described as being a species of rail as early as 1866 (34). Constraints of divergence times of basal ralloids suggest that adzebills diverged from rails in the middle Eocene (more recently than 42.6 Ma). The familiar pattern of rail dispersal to oceanic refugia and their subsequent loss of flight renders the molecular hypothesis for the origin of adzebills biogeographically and evolutionarily plausible (13). Kagu and Sunbittern clearly are closest relatives, but their divergence occurred in the late Eocene (56–34 Ma) or early Oligocene (34–23 Ma). Fossils of Kagu-like or Sunbittern-like birds are well known from early to mid-Eocene deposits of North America and Europe (1, 35). Thus, the extant disjunct distribution of Kagu and Sunbittern simply may reflect the deterioration of tropical forests in the Northern Hemisphere during the Oligocene (36, 37).

The average of estimates (64.5 Ma) of the basal divergence of Grues is roughly coeval with the Cretaceous–Paleogene boundary, with estimates and errors ranging 107–45 Ma. The most primitive ralloids (i.e., flufftails, adzebills) are distributed in Africa, Madagascar, and New Zealand and the most primitive gruoids (i.e., trumpeters, Limpkin) are neotropical. Thus, the basal dichotomy of Grues may bear a Gondwanan signature. Alternatively, the generally forest-dwelling most primitive members of Grues may have retreated to southern tropical refugia in response to Oligocene global cooling. Indeed, fossils of basal gruoids are known from Oligocene (but not later) deposits of North America and Europe (9, 28). Interfamilial diversification within each of the ralloids and gruoids appears to have occurred in the early Paleogene (66–23 Ma), with considerable intercontinental dispersal by rails, finfoots, and cranes. The divergence of finfoots from flufftail rails and their Paleogene dispersal through Asia to the Americas is well-documented phylogeographically, by molecular time estimates, and by the fossil record (3, 27).

Acknowledgments

I thank C. L. Anderson, J. W. Brown, A. Cooper, P. G. P. Ericson, and M. G. Fain for assistance. This work was supported by the U.S. National Science Foundation.

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