the TIMETREE of LIFE

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Owls (Strigiformes)

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Abstract

Approximately 202 species of owls comprise the distinctive cosmopolitan neoavian Order Strigiformes. All morphological and genetic studies agree that the order is a natural group. Two families are recognized: Tytonidae (barn owls and bay owls) and Strigidae (typical owls). The strigiform timetree shows that these families are ancient, having diverged in the late Cretaceous 71 million years ago (Ma).

Owls (Order Strigiformes) are grouped into two cosmopolitan families: the species-rich Strigidae (typical owls, ~187 species; Fig. 1) and the relatively depauperate Tytonidae (barn owls and bay owls, ~15 species). Owls are broadly characterized by adaptations to predation (strong zygodactyl feet, raptorial bill and talons, and soft-fringed edges of some flight feathers enabling quiet flight) and adaptations to a predominantly nocturnal or crepuscular lifestyle (large eyes and highly developed auditory system, facilitated by feathers arranged in a distinctive "facial disc"). Here, we review the relationships and divergence times of the strigiform families.

Owls form a morphologically homogeneous group that is easily distinguishable from other avian orders. Since the earliest classifications there has been no question that owls form a natural group (1). Recent studies of DNA–DNA hybridization data (1), mitochondrial (mt) (2), nuclear (2–4), and combined (2) DNA sequences, and morphology (5–7) support the monophyletic status of this large avian order. Equally supported is the division of owls into two families, first identified ~160 years ago (8). In addition to the character data establishing monophyly of each family, karyological (9), allozyme (10), and mtDNA restriction fragment (11) data reveal a deep split between the two families. Bay owls (Genus *Phodilus*) are in some respects intermediate between Strigidae and the barn owls (Genus *Tyto*), which underlies early confusion of their taxonomic placement (1). However, recent results strongly support a close relationship between *Phodilus* and *Tyto* (2, 5, 9) and thus their placement in the Family Tytonidae.

Taxonomy below the family level is currently in a state of flux, partly because the same morphological regularity that clearly delineates groups at higher taxonomic levels hinders phylogenetic classification within the group itself. This is particularly problematic within the species-rich Family Strigidae, where a comprehensive phylogenetic analysis is long overdue. This is evident from the number of recognized strigid taxa, which increased by 57 species over an 8-year period (12, 13), and which is currently a matter of considerable speculation given recent rediscoveries of taxa previously thought to be extinct (14, 15). Furthermore, a seemingly steady stream of newly described species (16–21), aided in large part by vocalization data, have contributed to uncertainty in the breadth and phylogenetic classification of Strigidae.

Relationships of the owls to other avian orders is presently unclear. Historically, Strigiformes has been linked to either the nocturnal nightbirds (Order Caprimulgiformes) (1, 22, 23) or the diurnal raptors (Order Falconiformes) (5). Owls share several morphological characteristics that are separately mirrored in these two orders: the adaptations to a raptorial lifestyle (strong bill and feet) resemble those found in the falconiforms, whereas apparent adaptations to a nocturnal existence

Fig. 1 A Great Grey Owl (*Strix nebulosa*), Family Strigidae, from Coronado, Alberta. Credit: G. Court.
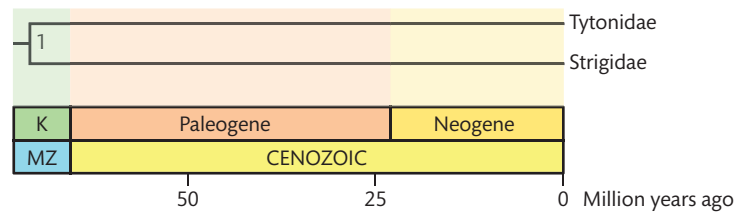
Fig. 2 The timetree of owls (Strigiformes). Divergence times are shown in Table 1. *Abbreviations*: MZ (Mesozoic) and K (Cretaceous).

(large eyes, and soft cryptic plumage used as camouflage from hunting diurnal raptors) are present in the caprimulgiforms. Although recent morphological studies tend to group owls with the diurnal raptors (*5, 24–26*) (forming the proposed Superorder "Falconimorphae"), molecular genetic studies fail to consistently group owls with any specific order (*1, 3, 4, 27, 28*). Nevertheless, recent nuclear DNA analyses decisively separate Caprimulgiformes from the two traditional raptorial orders with phylogenetically informative indels (*3*) and strong statistical support (*4, 29*). In summary, the morphological and molecular genetic data at hand prohibit uniting all three avian orders. In light of this, some of the defining characteristics of owls have clearly evolved convergently in other lineages, almost certainly with respect to Caprimulgiformes (*29*), and possibly with Falconiformes (*30*).

Several molecular studies focused on divergence time estimation in birds have included representatives from both strigiform families (Table 1). Early estimates for the timing of divergence between Tytonidae and Strigidae based on allozyme (*10*) and mtDNA restriction fragment (*11*) distances yielded similar early Oligocene estimates, 34 Ma and 30–28 Ma, respectively. However, time calibrations used in these two studies are suspect, and subsequent studies with broad species sampling tend to generate much older divergence time estimates. For example, although the age of this divergence was not estimated explicitly by Sibley and Ahlquist (*1*), the average rate of change in genome-wide DNA–DNA hybridization analyses was 4.5 million years per degree (centigrade) of DNA–DNA melting temperature lowered (*1*) suggests a much more ancient estimate of ~61 Ma.

Recent analyses of five nuclear genes for 87 taxa have generated a range of divergence time estimates when using alternative molecular clock methodologies (*4, 31*) (Table 1). Original analyses (*4*) of this data matrix using two different rate smoothing methods recovered dates that ranged from the mid-Eocene (40 Ma) to the late Cretaceous (66 Ma). A reanalysis of these data (*31*) using

a Bayesian modeling of rate evolution, together with improved fossil constraints, supported the Cretaceous (144–66 Ma) origin of the strigiform families, with the split dated at about 73 Ma (Fig. 2). A variety of analyses making different assumptions about how substitution rate variation evolves in a matrix of ~5 kb of mtDNA for 135 avian taxa (*27*) generally yielded internally congruent late Cretaceous average age estimates for this node: ancestor-descendant rate smoothing, 95–88 Ma; closest-relative rate smoothing, 89–79 Ma; Bayesian autocorrelated model of rate evolution, 87–82 Ma; overdispersed clock, 92 Ma; Bayesian non-autocorrelated model of rate evolution with unfixed topology, 84 Ma (Table 1).

Although the consensus across these most recent studies supports a late Cretaceous divergence of the two strigiform families, it is evident that the age of this node cannot yet be estimated precisely (Table 1). In a family as large as Strigidae, the sparse taxon sampling used in published dating analyses may have biased subsequent age estimates if the sampled taxa were not representative of their respective families, or if a significant node-density effect was present (*32*). In addition to the problem of sampling dissimilar species, differences between mt (*27*) and nuclear DNA (*31*) estimates may be a result of nucleotide substitution saturation in mtDNA sequences.

In contrast to dates inferred from DNA sequence data, fossil gap analysis (*33*) supports a Cenozoic (<66 Ma) origin for strigiforms. However, the assumption of randomly distributed fossils (uniformly recovered through time) is likely to be inappropriate, and a plausible alternative fossil recovery curve can be constructed that is more consistent with the molecular genetic timelines summarized here (*34*). Nevertheless, it remains to be seen how well more thoroughly sampled strigiform timetrees agree with the oldest known owl at ~58 Ma (*35*).

Acknowledgements

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

Timetree		Estimates						
Node	Time	Ref. (*4*)	Ref. (*10*)	Ref. (*11*)	Ref. (*27*)		Ref. (*31*)	
		Time	Time	Time	Time	CI	Time	CI
1	71.1	52.9	34.3	29	87.4	104–70	73.1	92–59

Note: Node times in the timetree represent the mean of time estimates for three studies (*4, 27, 31*), because of the considerable uncertainty in time calibrations in refs. (*10*) and (*11*). When multiple time estimates were available from the same study, then the mean of reported times and CIs is used as the representative estimate. In ref. (*10*), allozyme data are used with a calibration that one unit of Nei's *D* is equal to 23 Ma. The average result from ref. (*11*) is derived from mtDNA restriction enzyme data and assumes a sequence divergence rate of 2.0–2.2% per Ma. The estimate presented from ref. (*4*) is derived from an analysis of five nuclear genes using two different rate smoothing dating methods: closest-relative smoothing and ancestor-descendant smoothing. In ref. (*31*), data from ref. (*4*) are reanalyzed using the same tree topology, but with improved fossil calibrations and a Bayesian autocorrelated model of rate evolution. Ref. (*27*) constitutes an average estimate from analyses of ~5 kb of mtDNA under eight combinations of different dating methods (*n* = 5: ancestor-descendent rate smoothing, closest-relative rate smoothing, Bayesian autocorrelated model of rate evolution, overdispersed clock, and Bayesian non-autocorrelated model of rate evolution) and tree topologies (*n* = 3).

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