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Swifts, treeswifts, and hummingbirds (Apodiformes)

Joseph W. Brown^{a,*} and David P. Mindell^{a,b}

^aDepartment of Ecology and Evolutionary Biology & University of Michigan Museum of Zoology, 1109 Geddes Road, University of Michigan, Ann Arbor, MI 48109-1079, USA; ^bCurrent address: California Academy of Sciences, 55 Concourse Drive Golden Gate Park, San Francisco, CA 94118, USA

*To whom correspondence should be addressed (josephwb@umich.edu)

Abstract

Swifts, treeswifts, and hummingbirds constitute the Order Apodiformes (~451 species) in the avian Superorder Neoaves. The monophyletic status of this traditional avian order has been unequivocally established from genetic, morphological, and combined analyses. The apodiform timetree shows that living apodiforms originated in the late Cretaceous, ~72 million years ago (Ma) with the divergence of hummingbird and swift lineages, followed much later by the divergence (34 Ma) of swifts and treeswifts.

The neoavian Order Apodiformes is classified into three reciprocally monophyletic families (1): Apodidae (swifts, ~100 species; cosmopolitan), Hemiprocnidae (treeswifts, four species; Asia and Australasia), and the speciose Trochilidae (hummingbirds, ~347 species; North and South America). The order is characterized by small birds with strong flight muscles which are used in energetic flight, and have, as the name suggests, diminutive feet with limited function (Fig. 1). Although all apodiforms are insectivorous, hummingbirds are predominantly nectivorous (supplementing their diets with insect prey), and consequently constitute a major pollination vector for many neotropical plants (2). Here, the relationships and divergence times of the families of Apodiformes are reviewed.

In the Superorder Neoaves, where the monophyletic status of most traditional multifamily orders has been questioned, Apodiformes has been a refreshing bastion of taxonomic stability. Despite striking superficial morphological, ecological, and behavioral similarities between the acrobatic swifts and swallows (Family

Hirundinidae, Order Passeriformes), and between the nectivorous hummingbirds and sunbirds (Family Nectariniidae, Order Passeriformes), the monophyletic status of Apodiformes has been well supported in all of the major avian classifications since before Fürbringer (3). A comprehensive historical review of taxonomic treatments is available (4). Recent morphological (5, 6), genetic (4, 7–12), and combined (13, 14) studies have supported the apodiform clade. Although a classification based on large DNA–DNA hybridization distances (4) promoted hummingbirds and swifts to the rank of closely related orders (“Trochiliformes” and “Apodiformes,” respectively), the proposed revision does not influence evolutionary interpretations.

One of the most robustly supported novel findings in recent systematic ornithology is a close relationship between the nocturnal owlet-nightjars (Family Aegothelidae, Order Caprimulgiformes) and the traditional Apodiformes. Originally proposed on the basis of osteological characters (15), this relationship has since been supported in analyses of individual (12, 14)



Fig. 1 A Black-crested Coquette (*Lophornis helenae*), Family Trochilidae, from Arenal Observatory Lodge, Costa Rica. Credit: S. Hinshaw.

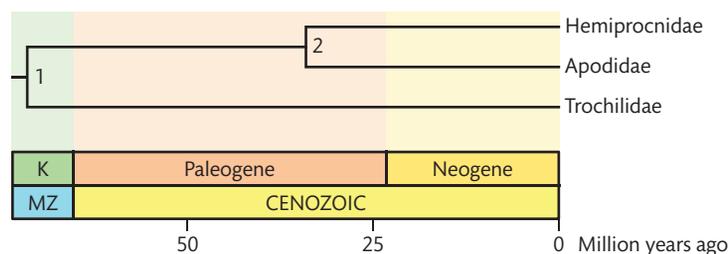


Fig. 2 A timetree of swifts, treeswifts, and hummingbirds (Apodiformes). Divergence times are shown in Table 1. *Abbreviations:* MZ (Mesozoic) and K (Cretaceous).

and combined (7, 8, 13) nuclear genes, phylogenetically informative indels (12, 14), additional morphological traits (13) (but see 5), and analyses of combined morphological and molecular data (13, 14). So compelling is this evidence that a name has been proposed for the node uniting these taxa, identified as the clade “Daedalornithes” (16). It is as yet unknown whether a grouping of all traditional caprimulgiform and apodiform taxa constitutes a monophyletic clade.

DNA evidence tends to support a late Cretaceous origin of apodiform taxa. Several molecular studies have explicitly estimated divergence times for Apodiformes (Table 1), but most have sampled only from Apodidae and Trochilidae (Fig. 2). Analyses of mitochondrial (mt) DNA (17) and published DNA–DNA hybridization data (4) yielded estimates of ~68 and 84 Ma for this split, respectively, with a mean estimate of about 76 Ma (17). An extensive consideration of alternative dating methodologies and tree topologies on a matrix of 5 kb of mtDNA and 135 avian taxa yielded different divergence time estimates for this node: ancestor-descendant rate smoothing, 77–75 Ma; closest-relative rate smoothing, 70–54 Ma; Bayesian autocorrelated model of rate evolution, 77–63 Ma; overdispersed clock, 56 Ma; Bayesian non-autocorrelated model of rate evolution with unfixed topology, 81 Ma (18) (Table 1).

Only two studies have yet estimated divergence times for all families belonging to “Daedalornithes” (Table 1), and both analyzed the same five nuclear genes for a broad sampling of neoavian taxa. The first study (8) employed a fixed-age calibration for the hummingbird–swift split at 47.5 Ma while primarily using a closest-relative rate smoothing method. The results, and those produced from an ancestor-descendant rate smoothing method, are the youngest yet reported date estimates for these nodes from genetic data, but are consistent with a macroevolutionary model, derived from the fossil record, of an explosive diversification of birds following the K–T boundary (19).

Those relatively young dates were affected by the fixed-age constraint placed on the origin of Trochilidae. A reanalysis (20) of these data, using the same topology but a Bayesian model of autocorrelated rate evolution and an improved set of fossil calibrations, yielded considerably older divergence time estimates, consistent with those from previous molecular studies (Fig. 2). These results refute the explosive model, and instead support apodiform diversification in the late Cretaceous, with the divergence of swifts and hummingbirds at around 70 Ma, and swifts and treeswifts at 42 Ma.

A challenge that has beset the ornithological community for the past decade is the markedly different macroevolutionary scenarios that are separately but strongly supported by the fossil record and molecular genetic data (21). Apodiform taxa seem to pose a particular problem, because their characteristic diminutive stature likely reduces fossilization potential. Fossil gap analysis (22) has nevertheless been used to attempt to construct confidence intervals on the origin of this order, and supports the classical Cenozoic view. However, this method assumes that fossils are uniformly recovered through time since the origin of the taxon. The use of alternative fossil recovery curves has been shown to lead to different scenarios, including ones consistent with most molecular genetic timelines (23).

In summary, we presently have an incomplete understanding of the evolutionary history of Apodiformes. However, the history of this taxon is likely to prove complex, as fossils of a modern-type hummingbird, today restricted to the New World, have recently been found in Europe (24).

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Table 1. Divergence times (Ma) and their confidence/credibility intervals (CI) among swifts, treeswifts, and hummingbirds (Apodiformes).

Timetree		Estimates						
Node	Time	Ref. (8)	Ref. (17)		Ref. (18)		Ref. (20)	
		Time	Time	CI	Time	CI	Time	CI
1	71.5	-	75.7	91-60	69.1	84-55	69.8	89-55
2	34.0	25.7	-	-	-	-	42.2	57-31

Note: Node times in the timetree represent the mean of time estimates. When multiple time estimates were available from the same study, then the mean of reported times and CIs is used as the representative estimate. The estimate from ref. (17) represents an average derived from a molecular clock analysis of several mtDNA genes, and genome-wide DNA-DNA hybridization data (4) assuming a rate of 3.92 $\Delta^{\circ}\text{C}$ per Ma. The estimate presented from ref. (8) is derived from an analysis of five nuclear genes using two different rate-smoothing dating methods: closest-relative smoothing and ancestor-descendant smoothing (the divergence for Node 1 was fixed at 47.5 Ma). Ref. (20) reports a reanalysis of the data from ref. (8) using the same tree topology, but improved fossil calibrations and a dating method that employs a Bayesian autocorrelated model of rate evolution. Ref. (18) 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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