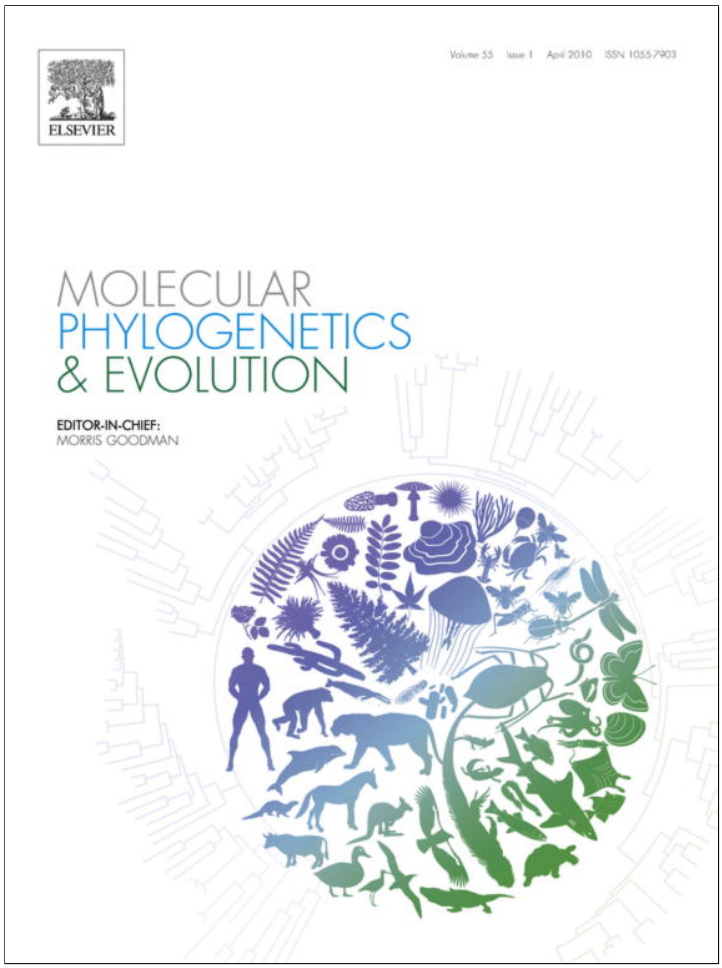

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Letter to the Editor

Response to Mayr and Manegold

Mayr and Manegold find the literature review in our recent article (Braun and Huddleston, 2009) inappropriate. We will address their specific concerns below, but we first note that propriety is a subjective concept; what may seem inappropriate to some may be deemed entirely appropriate by others. We stand by the literature review in our article as a fair representation of the state of knowledge when it was written, while accepting the fact that opinions will often vary on what the state of knowledge actually is.

We also note that, regardless of propriety, our review of the literature was reasonably extensive. The References section of Braun and Huddleston (2009) contains 101 entries. By comparison, the 21 regular articles in one recent issue of *Molecular Phylogenetics and Evolution* (vol. 53(2), Nov. 2009) have an average of 65 references (range = 20–114). Only two have more than 101.

Mayr and Manegold find it ironic that the only higher-level clade supported by our data was first proposed on the basis of morphological characters. We find this neither ironic nor entirely true. Because molecular data are relatively new in systematics, it is often the case that clades found in a molecular tree have been previously proposed based on morphological or other evidence. Indeed, in some cases, all possible relationships between the relevant taxa have been previously proposed. The larger question then is: Of the possible relationships, which is the correct one? This must be decided by accumulation of evidence.

To our knowledge, Mayr (2002) was the first to propose a sister group relationship between Aegothelidae and Apodiformes in a peer-reviewed publication. However, the first evidence of this relationship published in a format widely available to the ornithological community was provided by Braun and Huddleston (2001), when we described a four codon (12 bp) insertion in the c-*myc* gene linking these two taxa. Frankly, though, we are less interested in when a clade was first proposed than when sufficient evidence has been marshalled to make its acceptance inevitable for most biologists. This, of course, may be a matter of opinion. In the present case, evidence for this relationship accumulated between 2001 and 2006 (e.g., Mayr et al., 2003; Cracraft et al., 2004; Ericson et al., 2006). We personally consider the published evidence to have become quite strong only when Barrowclough et al. (2006) published their careful analyses of RAG-1 data and specifically excluded base compositional artifacts.

Mayr and Manegold object to our description of the Aegothelidae–Apodiformes clade as a "novel association", but this again is a matter of opinion. By all accounts, this relationship is a surprising one, and has been considered a legitimate possibility for less than ten years. In a field as old and active as avian systematics, that makes it novel to us.

Mayr and Manegold decry our suggestion that the grouping of Nyctibiidae with Steatornithidae "deserves further scrutiny" without mentioning morphological evidence for a grouping of Nyctibiidae with Caprimulgidae (Cracraft, 1981; Mayr, 2002). Our purpose here was simply to point out the present day biogeographical affinities of these taxa. We had no intention to review the literature on the possible relationships of these groups, which we consider unresolved by the available evidence. Mayr and Manegold themselves fail to mention the equally strong evidence for a grouping of Caprimulgidae with Podargidae provided by Barrowclough et al. (2006).

Mayr and Manegold fault us for not fully exploring the 12-bp c-*myc* insertion that links Aegothelidae and Apodiformes in our Introduction section and not citing them and their collaborators in this regard. In fact, we do mention the previous evidence for this relationship in both the Abstract and Introduction, and cite their most relevant paper (Mayr et al., 2003). The 12-bp insertion is explored in our Results section under *Phylogenetic Utility of Introns, UTRs and Indels*, because it is homoplasious within birds, and we are making the point that homoplasy in indels is rare and can often be explained by well known molecular processes (in this case, tandem duplication of a mildly repetitive element). We further show that the homoplasious12-bp insertion in barbets is phylogenetically nested in a way that suggests it occurred independently. Mayr et al. (2003) only mention these insertions in their Materials and Methods and never suggest that they support an Aegothelidae/Apodiformes clade. Mayr (2008) lists this insertion as an apomorphy for Aegothelidae/Apodiformes but does not discuss its homoplasy. We revisit the phylogenetic significance of this four codon insertion in the Discussion, where we again credit Mayr et al. (2003).

Mayr and Manegold find our citations of Peters (1940) and Tripepi et al. (2006) "somewhat eclectic". In fact, we cited these and other "seminal" works at the specific suggestion of an anonymous reviewer, who was clearly knowledgeable on caprimulgiform systematics. The fact that Tripepi et al. (2006) dealt with spermatid ultrastructure was a happy coincidence.

Mayr and Manegold accuse us of "completely ignoring" the fossil record, but we cite six papers dealing primarily with fossils (Collins, 1976; Mourer-Chauviré, 1982, 1987a; Olson, 1987; Peters, 1991; James, 2005). Our reference to Mourer-Chauviré (1987a) was an error; we intended to cite Mourer-Chauviré (1987b). Mayr and Manegold are also unhappy with our regard for the insight of Collins (1976). Collins did discuss the similarity of the humeri of Aegialornithidae and caprimulgids but apparently did not examine *Aegotheles*. Mayr himself later wrote that "Aegialornithidae ... closely resemble the recent Caprimulgidae and Aegothelidae in their osteology..." (Mayr, 2002, p. 84). Actually, the formal proposal of Collins (1976, p. 126) was to "... place the Aegialornithidae as a family within the Caprimulgiformes, possibly allied to the Caprimulgidae." He further stated that "... the possibility exists that the Aegialornithidae are representatives of a caprimulgiform lineage that later gave rise to the swifts..." and that a "caprimulgiform–apodiform relationship should be reviewed further when additional fossil elements are found that can definitely be assigned to the Aegialornithidae" (Collins, 1976, pp. 126–127). In the light of a now well-supported Aegothelidae/

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Apodiformes clade, that proposal seems quite plausible today. It was clearly "prescient" in 1976, whether one believes that fossil Aegialornithidae represent that particular lineage or not.

Mayr and Manegold dispute our statement that "the finding that Aegothelidae is the sister group of Apodiformes suggests that the diurnal swifts and hummingbirds...may be derived from a nocturnal ancestor", but they either misunderstand this sentence or fail to grasp the principle of parsimony. If the sister group of a diurnal group is diurnal, parsimony compels us, in the absence of other information, to suppose that the most recent common ancestor was diurnal. If the sister group of a diurnal group is nocturnal, we must similarly suppose that the common ancestor was either diurnal or nocturnal. That suggests the ancestor may have been nocturnal. Their point that one should actually infer a nocturnal ancestor only if it can be shown that Apodiformes has two or more successive nocturnal sister taxa is exactly the point we make at the end of the same paragraph. Their overriding concern seems to be that we did not cite them (and ourselves) in this paragraph for having discussed these points previously (Mayr, 2002; Mayr and Manegold, 2002; Cracraft et al., 2004; Hackett et al., 2008). But this is not rocket science; the same intriguing possibilities would be immediately apparent to any competent evolutionary biologist reading Collins (1976).

Mayr and Manegold note that many issues raised in our Discussion are also addressed in a forthcoming study by one of them (Mayr, in press). We have not seen that study, so cannot comment on it. They end by highlighting our "praise of molecular data" and taking comfort in the fact that "studies of morphological and molecular data apparently can lead to strikingly similar conclusions". While this statement is of course true, we find no similar solace in it; it is unfortunately also true that studies of morphological and molecular data can lead to strikingly different conclusions.

The Aegothelidae/Apodiformes clade discussed here is actually a very good case in point. Working with one of the largest morphological data sets ever collected for birds, Livezey and Zusi (2007) found strong parsimony bootstrap support for a monophyletic Caprimulgiformes, including Aegothelidae, sister to a monophyletic Apodiformes, contradicting Mayr (2002), ourselves (Braun and Huddleston, 2001, 2009) and a host of others. Of course, we believe that Livezey and Zusi (2007) are wrong. Mayr (2008) criticized two of Livezey and Zusi's five apomorphies for the relevant node, and we pointed out that the difference may be due to a rooting issue (Braun and Huddleston, 2009).

Still, how can such a large dataset, collected and analysed by two well-respected avian morphologists, be strongly at odds with both previous morphological analyses and a large and consistent body of molecular evidence? One reason is the subjectivity inherent in the collection and analysis of morphological data. It is often hard to completely avoid making subjective decisions in morphological systematics at three levels – choice of characters, definition of characters and scoring of characters – and this difficulty increases as the number of characters increases (e.g., Scotland et al., 2003). As long as this is true, it will be possible for perfectly reasonable morphologists to look at the same features of the same taxa and come to different conclusions about their relationships.

Molecular data are far from perfect, and there are many unsolved challenges in their analysis. But working with molecular data is inherently more objective at each of the levels mentioned above, and this is one reason for their success.

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