

A higher-level taxonomy for hummingbirds

Jimmy A. McGuire · Christopher C. Witt ·
J. V. Remsen Jr · R. Dudley · Douglas L. Altshuler

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Abstract In the context of a recently published phylogenetic estimate for 151 hummingbird species, we provide an expanded informal taxonomy, as well as a formal phylogenetic taxonomy for Trochilidae that follows the precepts of the PhyloCode, but remains consistent with the hierarchical nomenclature of the Linnaean system. We compare the recently published phylogenetic hypothesis with those of prior higher-level and more taxonomically circumscribed phylogenetic studies. We recommend the recognition of nine new clade names under the PhyloCode, eight of which are consistent with tribes and one with a subfamily under the Linnaean system.

Keywords Phylogenetic taxonomy · PhyloCode · Phylogeny · Trochilidae

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J. A. McGuire (✉) · R. Dudley
Museum of Vertebrate Zoology and Department of Integrative
Biology, University of California, 3101 Valley Life Sciences
Building, Berkeley 94720-3160, USA
e-mail: mcguirej@berkeley.edu

C. C. Witt
Museum of Southwestern Biology and Department of Biology,
University of New Mexico, Albuquerque, NM 87131-0001, USA

J. V. Remsen Jr
LSU Museum of Natural Science, Louisiana State University,
119 Foster Hall, Baton Rouge, LA 70803, USA

D. L. Altshuler
Department of Biology, University of California, Riverside,
900 University Avenue, Riverside, CA 92521-0427, USA

Introduction

The taxonomy of hummingbirds presents special challenges for avian systematists. The low ratio of species to genera (~331 species in ~104 genera) and the large number of monotypic genera (~46) are symptomatic of the general difficulty of inferring higher-order relationships within this group, and it is therefore not surprising that the only taxa typically recognized above the genus level are the subfamilies Phaethornithinae and Trochilinae (the latter of which appears to be polyphyletic). We recently published a multilocus phylogenetic analysis of hummingbirds (McGuire et al. 2007), which represents the first intensively sampled (i.e., 151 species) phylogenetic analysis for this important avian model system. The McGuire et al. (2007) study was focused on methodological issues associated with data partitioning and on historical biogeography rather than on implications for classification and taxonomy. Consequently, we here take the opportunity to compare our phylogenetic findings with those of several prior hummingbird studies and to present informal and formal higher-level classifications for Trochilidae. The informal higher-level taxonomy for hummingbirds is a further expansion upon those of Bleiweiss et al. (1997) and Altshuler et al. (2004). The phylogenetic taxonomy formalizes the informal supergeneric treatment according to the precepts of the PhyloCode (2006), while providing sufficient flexibility to be interpreted in the context of the Linnaean system of nomenclature. The taxonomies established here reflect our growing understanding of hummingbird phylogenetic history and provide a convenient nomenclature for future comparative investigations focused on major clades of hummingbirds.

Phylogenetic framework

The phylogenetic study of McGuire et al. (2007) included 151 hummingbird species and 12 outgroup taxa. Redundant sampling for *Phaethornis longirostris* brought the total number of exemplars to 164. For most taxa, we obtained DNA sequences representing two mitochondrial genes (ND2 and ND4) and flanking tRNAs, as well as two nuclear introns, Adenylate Kinase intron 5 (AK1) and Beta Fibrinogen intron 7 (BFib). DNA sequence data were analyzed using Maximum Likelihood and Bayesian phylogenetic methods under a variety of partitioning regimes. We eventually settled on a 6-partition analysis as best-fitting for these data, which we determined using a decision-theoretic methodology. The topology of our preferred tree (Fig. 1; adapted from McGuire et al. 2007) provides the phylogenetic framework for the taxonomic discussion that follows.

As indicated by McGuire et al. (2007), our phylogeny is highly congruent with the two most recently published higher-level hummingbird phylogenetic studies, including the 26-taxon study of Bleiweiss et al. (1997), and the 75-taxon analysis of Altshuler et al. (2004). Furthermore, our new tree is largely consistent with an informal higher-level hummingbird taxonomy that includes, as major groupings,

the Hermits, Mangoes, Coquettes, Brilliants, Mountain Gems, Bees, and Emeralds (see Bleiweiss et al. 1997; Altshuler et al. 2004). Altshuler et al. (2004) and McGuire et al. (2007) noted, however, that the Bleiweiss et al. (1997) taxonomy cannot accommodate *Florisuga*, *Topaza*, and *Patagona*, and we comment further on these taxa below. Our new phylogenetic estimate (McGuire et al. 2007) can be further compared with more taxonomically circumscribed phylogenetic hypotheses for hermits (Bleiweiss et al. 1994, 2003; Hinkelmann and Schuchmann 1997; Gill and Gerwin 1989), *Heliodoxa* (Gerwin and Zink 1998), *Lampornis* (García-Moreno et al. 2006), and *Metallura* (García-Moreno et al. 1999). We consider these prior studies in the context of our expanded informal higher-level taxonomy for hummingbirds below.

An informal higher-level taxonomy for hummingbirds

Here, we provide a taxonomy for hummingbirds that further expands upon the informal groupings first proposed by Bleiweiss et al. (1997) and updated by Altshuler et al. (2004). In the discussion of each of these clades, we relate the phylogenetic findings of McGuire et al. (2007) to previous hypotheses of hummingbird relationships.

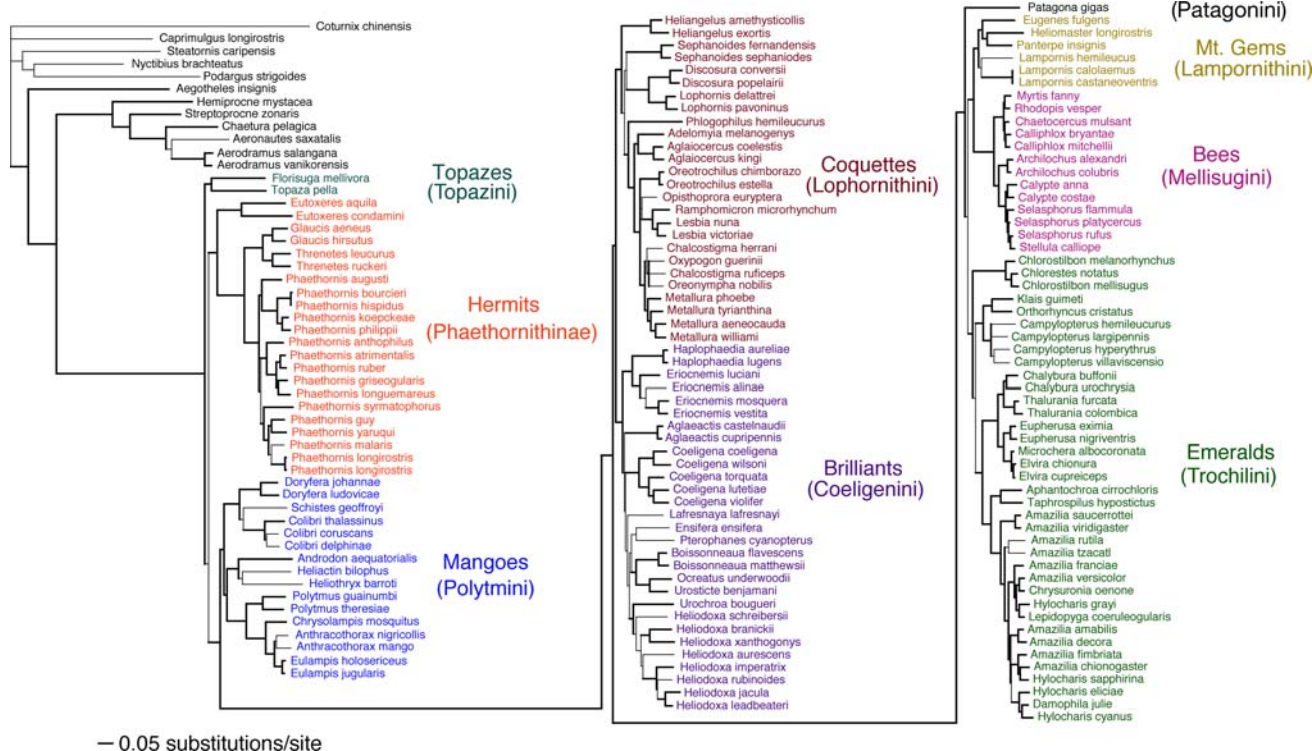


Fig. 1 Phylogenetic estimate for hummingbirds adapted from McGuire et al. (2007). Major clades are color-coded to reflect informal and formal higher-level taxonomic groupings. The original tree is based

on a partitioned Bayesian analysis of mitochondrial (ND2, ND4) and nuclear (AK1, BFib) sequence data for 151 ingroup taxa. *Thick branches* denote clades with posterior probabilities $\geq 95\%$

Topazes

We here designate a new informal clade name, “Topazes”, to accommodate *Florisuga* and *Topaza*. Unlike in our previous phylogenetic study (Altshuler et al. 2004), McGuire et al. (2007) found strong support for the monophyly of *Florisuga mellivora* and *Topaza pella*. More importantly, this clade is placed as the sister taxon of all other hummingbirds, albeit without strong support (posterior probability of 89%). This finding is of interest because the long-held view that the hermits are the sister taxon of all other hummingbirds has strongly influenced interpretations of hummingbird evolution. If *Florisuga* and *Topaza* together represent the sister taxon of all other hummingbirds, then this has important implications for hummingbird biogeography, as well as the evolution of important features such as vivid iridescent coloration, mating systems, and spacing systems. That said, we emphasize that the placement of these two genera as the sister taxon of all other hummingbirds requires further corroboration. Indeed, because *F. mellivora*, *T. pella*, and *T. pyra* have the Type 2 condition of the tensor patagii brevis wing musculature (Zusi and Bentz 1982), we think it is likely that these hummingbirds will ultimately prove to be the sister taxon of all non-hermits. Regardless, they are clearly only distantly related to the most proximate clades on the hummingbird tree, Hermits and Mangoes, and consequently should be designated their own informal group name. We proposed the name “Topazes” for want of a more appropriate descriptor.

Hermits

The informal term “Hermits” has long been used for a monophyletic assemblage, traditionally ranked as a subfamily, Phaethornithinae, that consists of the genera *Anopetia*, *Eutoxeres*, *Glaucis*, *Phaethornis*, *Ramphodon*, and *Threnetes*. Although McGuire et al. (2007) did not include *Anopetia* and *Ramphodon* in their study, these taxa are almost certainly members of the Hermits clade (see Bleiweiss et al. 2003 for a phylogenetic treatment of *Ramphodon*), and we continue to follow this usage here.

In several important respects, the relationships for hermits estimated by McGuire et al. (2007) are congruent with previous studies. For example, we find strong support for the monophyly of hermits as a major assemblage, as well as for the genera *Eutoxeres*, *Glaucis*, *Threnetes*, and *Phaethornis* (our study did not include the monotypic genera *Ramphodon* and *Anopetia*). Our findings of monophyly for hermits as a whole and for hermit genera, as well as our inferred intergeneric relationships, are congruent with most previous research (e.g., Bleiweiss et al. 1994, 2003; Hinkelmann and Schuchmann 1997; but see Gill and

Gerwin 1989 for a contradictory view of intergeneric relationships). Only two previous studies (Gill and Gerwin 1989; Hinkelmann and Schuchmann 1997) included relatively dense sampling of the most species-rich hermit genus, *Phaethornis*. Our tree is substantially congruent with the allozyme study of Gill and Gerwin (1989), especially with respect to the three monophyletic assemblages (their groups A, B, and C) highlighted in their discussion. Our tree is less congruent with the morphological study of Hinkelmann and Schuchmann (1997), albeit with less complete sampling in our study. For example, our findings agree with respect to monophyly of the small-bodied taxa formerly placed in a separate genus, *Pygmornis* (Pinto 1937), and treated by Hinkelmann and Schuchmann (1997) as a subgenus, but disagree both with respect to its internal relationships and its phylogenetic position relative to other *Phaethornis* species [we find “*Pygmornis*” to be nested within a larger *Phaethornis* assemblage, whereas Hinkelmann and Schuchmann (1997) found it to be the sister taxon of all remaining *Phaethornis*]. Furthermore, although our studies agree with respect to monophyly of three small sets of species (*P. koepckeae* + *P. philippii*; *P. guy* + *P. yaruqui*; and a clade including *P. longirostris* and *P. malaris*), disagreement is substantial in terms of how these clades are related to one another and to other *Phaethornis* species. Importantly, our data strongly contradict the monophyly of the remaining two subgenera (*Anisoterus* and *Phaethornis*) proposed by Hinkelmann and Schuchmann (1997). Although hermit relationships were generally strongly supported in our study (19 of 21 inferred nodes received posterior probabilities ≥ 0.98), our more limited sampling relative to that of Hinkelmann and Schuchmann (1997) leaves some *Phaethornis* relationships uncertain. Nevertheless, because our data strongly reject Hinkelmann and Schuchmann’s proposed subgeneric taxonomy, we recommend abandoning the *Phaethornis* subgenera.

Mangoes

We propose that the informal grouping “Mangoes” be applied to a monophyletic assemblage including, but probably not limited to, the following traditionally recognized genera: *Androdon*, *Anthracothorax*, *Chrysolampis*, *Colibri*, *Doryfera*, *Eulampis*, *Heliactin*, *Heliotheryx*, *Polytmus*, and *Schistes*. Previous studies and taxonomic convention suggest that *Augastes*, *Avocettula*, and perhaps *Loddigesia* (because it is thought to be closely related to *Heliactin* and *Heliotheryx*, see below) may also be part of this group, although these genera were not included in the McGuire et al. (2007) investigation.

Several of the included genera (*Androdon*, *Anthracothorax*, *Chrysolampis*, *Colibri*, *Doryfera*, and *Eulampis*) have been placed near the beginning of traditional linear

sequences (e.g., Peters 1945; Meyer de Schauensee 1966; Schuchmann 1999; Dickinson 2003), and our phylogenetic estimate should not be controversial with respect to these taxa. Furthermore, Bleiweiss et al. (1997) included four of these traditionally basally-placed genera, as well as a fifth genus (*Heliothryx*) traditionally grouped with Coquettes and Bees in linear sequences, but *Heliothryx* was shown to have an ancestral configuration of the tensor patagii brevis wing musculature (Type 2; Zusi and Bentz 1982). Our results are in complete agreement with Bleiweiss et al. (1997), both in terms of inclusion of these taxa within the Mangoes clade, and in the branching relationships inferred for these species, and should therefore not be particularly surprising.

Our results indicate that three additional genera (*Heliactin*, *Polytmus*, and *Schistes*) also belong to this assemblage, despite their placement far from the Mangoes in traditional linear sequences. *Polytmus* has been allied with Emeralds in linear sequences, but was shown by Zusi and Bentz (1982) to have the relatively ancestral Type 2 condition of the tensor patagii brevis wing muscle. *Heliactin* and *Schistes* have traditionally been placed amongst Coquettes and Bees and were not studied by Zusi and Bentz (1982), so we do not yet know the condition of their wing musculature. However, these taxa have been listed immediately adjacent to *Heliothryx* in linear sequences (e.g., Peters 1945; Meyer de Schauensee 1966; Schuchmann 1999; Dickinson 2003), so our finding that all three genera are part of the Mangoes assemblage should perhaps be less surprising in this context. Also, *Schistes* shares with *Colibri* a tail pattern that is unique in the Trochilidae (Remsen and McGuire, unpublished). *Heliactin* was previously found to be nested within Mangoes by Altshuler et al. (2004), and also shares an attenuated bill tip with *Heliothryx* and *Schistes*.

Our results disagree in a number of respects with relationships postulated by Schuchmann (1999). For example, Schuchmann suggested that *Androdon* and *Doryfera* would prove to be a monophyletic sister taxon of all other trochilines, a hypothesis consistent with most linear sequences for hummingbirds and with proposals for a third hummingbird subfamily, Doryferinae, to accommodate these two genera (Schuchmann 1995). Our results strongly reject this phylogenetic arrangement because *Androdon* and *Doryfera* are clearly nested within the monophyletic Mangoes assemblage and are each more closely related to other Mango genera than to one another. Schuchmann (1999) further proposed that all remaining trochilines could be divided into two clades, one to consist of *Campylopterus*, *Orthorhyncus*, *Abeillia*, *Klais*, *Stephanoxis*, *Topaza*, *Florisuga*, *Anthracothorax*, *Colibri*, *Eulampis*, *Avocettula*, and *Chrysolampis*. Our analyses indicate that this set of taxa is not monophyletic, and the various genera are

actually widely dispersed on the hummingbird phylogeny. For example, we found, as noted above, that *Topaza* and *Florisuga* together form a monophyletic unit that may be the sister clade of all other hummingbirds; *Campylopterus*, *Orthorhyncus*, *Abeillia*, *Klais*, and *Stephanoxis* are strongly placed within the Emeralds clade; and *Anthracothorax*, *Chrysolampis*, *Colibri*, and *Eulampis* (and presumably *Avocettula* as well) reside within the Mangoes clade.

Andean clade

Gerwin and Zink (1998) used the terms “Andean clade” and “High Andean clade” for hummingbirds corresponding to the Brilliants and Coquettes, respectively (this terminology was attributed to a personal communication from R. Zusi). Schuchmann (1999), on the other hand, considered the “Andean Clade” to include all Coquettes and Brilliants, as well as *Patagona gigas*. Because the implied contents of Gerwin and Zink’s (1998) “Andean” and “High Andean” clades are the same as for Brilliants and Coquettes, and because these two primarily Andean assemblages form a well-supported monophyletic unit, we follow Schuchmann (1999) in referring to Brilliants and Coquettes together as the “Andean Clade,” but note that the clade does not include *Patagona*. This phylogenetic hypothesis is at odds with the DNA-DNA hybridization study of Bleiweiss et al. (1997), which found that Brilliants are more closely related to Emeralds, Mountain Gems, and Bees than to Coquettes.

In terms of relationships within the Andean Clade, Schuchmann (1999) suggested that the clade consists of five subunits, for which he predicted the taxonomic content. Our results suggest that the five subunits are broadly paraphyletic, and in some cases include representatives from both the Coquettes and Brilliants.

Coquettes

We suggest that the informal taxonomic name “Coquettes” be applied to the following monophyletic assemblage of genera, all of which are part of the “Andean Clade”: *Adelomyia*, *Aglaiocercus*, *Chalcostigma*, *Discosura*, *Heliangelus*, *Lesbia*, *Lophornis*, *Metallura*, *Opisthoprora*, *Oreonympha*, *Oreotrochilus*, *Oxypogon*, *Phlogophilus*, *Ramphomicron*, and *Sephanoides*. Additional taxa likely to be nested within this group, but not included in the McGuire et al. (2007) study, are *Polyonymus*, *Sappho*, and *Taphrolesbia*, each of which is placed near coquette species in traditional linear sequences. This expanded use of the term “Coquettes” beyond *Lophornis*, *Discosura*, and *Popelairia* is a logical extension of the usage of Bleiweiss et al. (1997).

García-Moreno et al. (1999) provided a phylogenetic hypothesis for *Metallura* metaltail hummingbirds that

contradicted the conventional view that the genus can be divided into three natural groups, including the species *M. phoebe* and *M. tyrianthina*, and the *M. aeneocauda* species group or superspecies (comprised of all remaining *Metallura* species; Graves 1980; Heindl and Schuchmann 1998). More specifically, García-Moreno et al. (1999) found that *M. phoebe* was nested deeply within the *M. aeneocauda* ‘treeline superspecies.’ Despite inclusion of only four *Metallura* species in our study, our results contradict those of García-Moreno et al. (1999) in that we found strong support for a more traditional placement of *M. phoebe* as the sister of *M. tyrianthina* + our two included representatives of the *M. aeneocauda* superspecies (*M. aeneocauda* and *M. williami*). We note that the García-Moreno study was based on 855 bp of mitochondrial data (Cytb, ND2, and ND5), that our own mitochondrial data provided weakly supported contradictory relationships between *M. phoebe* and other *Metallura* species, and that our BFib data provided the primary support for *M. phoebe* as the sister taxon of *M. tyrianthina*, *M. aeneocauda*, and *M. williami*.

Although we sampled only two species of *Chalcostigma*, they did not form a monophyletic group, with *C. ruficeps* nested within a clade that also consists of the monotypic genera *Oreonympha* and *Oxypogon*. Based on plumage, Schuchmann and Heindl (1997) proposed that *Chalcostigma* consisted of two major groups, one of which included both species sampled by us. Therefore, we refrain from formal recommendations for changing classification without more thorough taxon sampling. Schuchmann and Heindl (1997) and Heindl and Schuchmann (1998) noted that similarities in plumage and morphology between *C. ruficeps* and the genus *Metallura* suggested that the two genera were sisters. This hypothesis is confirmed by our analysis.

Brilliant

We follow Bleiweiss et al. (1997) in applying the informal name “Brilliant” to the following monophyletic assemblage of genera, all of which also belong to the more inclusive “Andean Clade”: *Aglaeactis*, *Boissonneaua*, *Coeligena*, *Ensifera*, *Eriocnemis*, *Haplophaedia*, *Heliodoxa*, *Lafresnaya*, *Ocreatus*, *Pterophanes*, *Urochroa*, and *Urosticte*. *Clytolaema* is likely nested within this group because it is sometimes considered congeneric with *Heliodoxa* (e.g., Willis and Schuchmann 1993). Schuchmann (1985) proposed that *Chalcostigma* shared a common ancestor with *Aglaeactis* and *Pterophanes*, but our analysis shows that *Chalcostigma* is clearly in the Coquette group.

Whereas most nodes on the McGuire et al. (2007) tree received strong support (posterior probability values $\geq 95\%$), the genus *Heliodoxa* provides an interesting case because we did not generate strongly supported

resolution for this group. First, we did not find strong support for the monophyly of the genus relative to *Urochroa bougueri*, which might be nested within *Heliodoxa* (the posterior probability of *Heliodoxa* monophyly is only 0.91 with a 0.09 posterior probability that *Urochroa* is nested within *Heliodoxa*). Furthermore, only three of six interior nodes within *Heliodoxa* were significantly supported. Two of these three strongly supported nodes were congruent with both of the trees presented by Gerwin and Zink (1998), and the third (*H. xanthogenys* + *H. branickii*) is consistent with Gerwin and Zink’s (1998) UPGMA tree but not with their Distance-Wagner tree. Notably, our phylogenetic hypothesis is consistent with the Gerwin and Zink (1998) finding that *H. aurescens* (formerly in its own genus, *Polyplancta*) is indeed nested deeply within *Heliodoxa* (although the deeper nodes in the *Heliodoxa* tree have posterior probabilities < 0.95 , all of the trees in the posterior distribution nevertheless place *H. aurescens* within this *Heliodoxa* clade).

Based on display behavior and plumage, Schuchmann (1997) proposed that *Ocreatus* and *Urosticte* were sister genera, and that these two were the sister to *Eriocnemis* and *Haplophaedia*. Our data confirm the sister relationships of *Ocreatus* and *Urosticte*, and of *Eriocnemis* and *Haplophaedia*, but the two pairs are not closely related to one another other than being Brilliant.

Schuchmann et al. (2001) noted that vocal and plumage characters indicated that *Boissonneaua*, *Urosticte*, and *Aglaiocercus* might form a monophyletic group, but our data demonstrate that the former two taxa are Brilliant and the latter is a Coquette. However, *Boissonneaua* and *Urosticte* do form a monophyletic unit in our analysis if *Ocreatus* is included.

Mountain gems

We follow Bleiweiss et al. (1997) in applying the informal name “Mountain Gems” to the following monophyletic assemblage of genera: *Eugenes*, *Heliomaster*, *Lampornis*, and *Panterpe*. Although not included in the McGuire et al. (2007) study, *Hylonympha* and *Sternoclyta* were placed in the synonymy of *Eugenes* by Renner and Schuchmann (2004), suggesting inclusion within this clade. *Lamprolaima* might also be nested within this group based on size, plumage patterns, soft-part coloration, and position in linear sequences (Peters 1945).

The phylogenetic relationships of *Lampornis* were investigated by García-Moreno et al. (2006). In their study, they found *Lampornis* to be polyphyletic, with *L. hemileucurus* more closely related to *Panterpe insignis* (and perhaps other non-*Lampornis* species) than to the remainder of the otherwise monophyletic *Lampornis* assemblage. Although McGuire et al. (2007) included only three species

of *Lampornis*, our results were somewhat at odds with those of García-Moreno et al. (2006). For example, we found weak support for *Lampornis* monophyly (posterior probability of only 0.60), including *L. hemileucurus*. More importantly, we did obtain strong support (posterior probability = 1.0) for a monophyletic assemblage that consists of *Panterpe insignis*, *Heliomaster longirostris*, and *Eugenes fulgens*, which contradicts the finding of García-Moreno et al. (2006) that *Panterpe* and *H. hemileucurus* form a monophyletic unit to the exclusion of *H. longirostris* and *E. fulgens*. The disagreement between our trees presumably is tied to our inclusion of ND4 and BFib data, along with the AK1 and ND2 data analyzed by García-Moreno et al. (2006). Despite these minor differences in our trees, we emphasize that we agree with García-Moreno et al. (2006) that *Lampornis* monophyly is dubious and would benefit from further study.

Bees

We follow Bleiweiss et al. (1997) in applying the informal name “Bees” to the following monophyletic assemblage of genera: *Archilochus*, *Calliphlox*, *Calypte*, *Chaetocercus*, *Myrtis*, *Rhodopis*, *Selasphorus*, and *Stellula*. However, we note that *Stellula calliope* is clearly nested within *Selasphorus*, and we therefore recommend that *Stellula* be placed in the synonymy of *Selasphorus*, which has priority. Additional taxa likely to be nested within this monophyletic assemblage based on size, plumage patterns, soft-part coloration, and their positions within linear sequences include *Atthis*, *Calothorax*, *Doricha*, *Eulidia*, *Mellisuga*, *Microstilbon*, *Myrmia*, *Tilmatura*, and *Thaumastura*.

Emeralds

The large and taxonomically complex assemblage here referred to as “Emeralds” consists of at least the following genera: *Amazilia* [including Schuchmann’s (1999) *Agyrtia*, *Polyerata*, and *Saucerottia*], *Aphantochroa*, *Campylopterus*, *Chalybura*, *Chlorestes*, *Chlorostilbon*, *Chrysuronia*, *Damophila*, *Elvira*, *Eupherusa*, *Hylocharis*, *Klais*, *Lepidopyga*, *Microchera*, *Orthorhynchus*, *Taphrospilus*, and *Thalurania*. Size, plumage patterns, soft-part coloration, and positions within linear sequences (e.g., Peters 1945; Meyer de Schauensee 1966) suggest that the following additional genera may be nested within this group: *Abeillia*, *Cyanophaia*, *Cynanthus*, *Eupetomena*, *Goethalsia*, *Goldmania*, *Leucippus*, *Leucochloris*, *Phaeochroa*, *Stephanoxis*, and *Trochilus*.

Our phylogenetic results with respect to *Chlorostilbon melanorhynchus*, *Chlorostilbon mellisugus*, and *Chlorestes notata* are interesting if not yet conclusive. Each of our genetic markers provides strong support for the monophyly

of this small group of species, as suggested by linear sequences. However, our mtDNA and nuclear genetic data disagree with respect to the topological arrangement within this clade. The nuclear markers both support monophyly of *Chlorostilbon* with *Chlorestes notata* as its sister taxon. The mitochondrial data, on the other hand, strongly support a sister taxon relationship between *Chlorestes notata* and *Chlorostilbon mellisugus* to the exclusion of *Chlorostilbon melanorhynchus*. Combined data analyses strongly support the mitochondrial arrangement (*Chlorostilbon* paraphyly), but we believe it would be a mistake to accept this result uncritically. Indeed, the fact that two independent nuclear loci are consistent with the long-standing taxonomic arrangement (*Chlorostilbon* monophyly) suggests to us that the mtDNA data might be biased in some manner, perhaps reflecting introgressive hybridization or incomplete lineage sorting.

Schuchmann (1999) attempted to deconstruct the taxonomically complex genus *Amazilia*, which in recent classifications includes approximately 30–32 species (American Ornithologists’ Union 1998; Dickinson 2003; Remsen et al. 2007), into four less inclusive genera (*Agyrtia*, *Amazilia*, *Polyerata*, and *Saucerottia*). This attempt appears to have failed for two primary reasons. First, *Amazilia* (sensu stricto) appears not to be a monophyletic assemblage. McGuire et al. (2007) found that *Chrysuronia oenone*, *Damophila julie*, three species of *Hylocharis* (*H. cyanus*, *H. grayi*, and *H. sapphirina*), and *Lepidopyga caeruleocauda* are all nested within the subset of *Amazilia* included in their analysis. If these phylogenetic results were valid (see caveats below), then an attempt to partition *Amazilia* species into smaller genera without accounting for these extra-*Amazilia* taxa had little chance for success. Nevertheless, even if we were to ignore the relevant non-*Amazilia* genera, two of the four genera proposed by Schuchmann (1999) would appear not to be monophyletic (*Agyrtia* and *Polyerata*; see also Weller 2000). We do not propose an alternative taxonomy at this time for two reasons. First, *Amazilia* and related genera are notoriously difficult to identify (especially females) and it is possible that this could have impacted our phylogenetic study. However, we confirmed the identifications of voucher specimens or sequenced additional individuals for species with unexpected phylogenetic placements such as *C. oenone*, *D. julie*, *H. cyanus*, *H. grayi*, *H. sapphirina*, and *L. caeruleocauda*. Second, a cautious approach is necessary because hybridization is frequent among hummingbirds, even among genera, and mtDNA capture is a plausible explanation for radical conflict between gene trees and species trees; thus, more individuals and more nuclear genes should be sampled before the Emerald generic classification is revised. Third, we believe the scope of the “*Amazilia* problem” is even larger than shown here and that other genera are also likely nested within this clade. Because

at least one of the genera (*Hylocharis*) nested within *Amazilia* has nomenclatural priority, it is possible that *Amazilia* will eventually be synonymized with another genus. We believe it would be irresponsible to suggest a radical new taxonomy in which, for example, all currently recognized species of *Amazilia*, *Chrysuronia*, *Damophila*, and *Lepidopyga* are transferred to *Hylocharis*, only to revise it dramatically again in the near future when we confirm our preliminary finding (unpublished data) that *Trochilus* is also nested within *Amazilia* (which would require that all of these same species be transferred from *Hylocharis* to *Trochilus*). Ultimately, we believe that a convincing systematic treatment of this difficult group will require detailed morphological and genetic studies with dense intraspecific and interspecific sampling.

Species not accommodated within this taxonomic framework

We have only confirmed that one taxon, *Patagona gigas* (the giant hummingbird), cannot be accommodated within this informal taxonomic framework. In our analyses, this species was found to be the sister taxon of a large clade that consists of the Emeralds, Mountain Gems, and Bees with a modest posterior probability of 92.4%. Only two alternative placements for *P. gigas* received posterior probabilities greater than zero—these included 5.0% posterior probability for a sister taxon relationship with the Bees + Mountain Gems clade, and 2.6% posterior probability for a sister group relationship with Emeralds. Given that 97.4% of the posterior density supports *Patagona* as a relatively deeply divergent sister taxon of two or three of the major clades recognized here rather than as the sister taxon of a single major clade, we consider *Patagona gigas* worthy of separate consideration in the larger framework that we have developed for hummingbirds.

One additional species, *Anthocephala floriceps*, cannot be accommodated at this time within this framework because we did not have access to genetic samples and we simply have no data upon which to hypothesize its phylogenetic affinities. That said, we believe it unlikely that this species will prove to be a deeply divergent lineage residing outside of any of the principle clades of hummingbirds, as is the case for *Patagona gigas*.

A phylogenetic taxonomy for hummingbirds

We propose a phylogenetic taxonomy for hummingbirds to provide a formal framework for higher-level (super-generic) relationships. Phylogenetic taxonomies differ from traditional Linnaean taxonomies in a number of

respects. First, they are unranked, thereby explicitly rejecting the notion that named higher taxa are somehow equivalent to one another in an evolutionary sense. Second, they are defined on the basis of phylogenetic descent rather than on type specimens. Third, they are more flexible and stable in the sense that they are less likely to require replacement if new information suggests an alternative phylogenetic arrangement.

The taxonomy provided here does not directly address the taxonomic standing of individual species or the content of genera (although we provided a few such recommendations above in the discussion of the informal taxonomy). Our taxonomy deviates from traditional classifications of hummingbirds in a number of important ways. First, for the time being, we refrain from using the name Trochilinae because this traditionally recognized taxon appears to be polyphyletic. However, the name can be used in the future if Hermits are eventually found to be the sister taxon of all other hummingbirds. Second, each of the major clades of hummingbirds is assigned a formal name codifying the informal taxonomy proposed by Bleiweiss et al. (1997) and expanded upon by Altshuler et al. (2004) and herein. We appreciate that the ornithological community may prefer to view these taxa as having the rank of tribe within Linnaean classification, and, with one exception, we consequently applied clade names that are consistent in form with Linnaean tribe names. The exception is for the Hermits, which have traditionally been assigned to the subfamily Phaethornithinae. We see no reason to create a new name for this taxon and instead apply the current name (without changing its spelling) as a clade name consistent with the PhyloCode. Our application of a phylogenetic taxonomy presents a complication because naming conventions in the PhyloCode (2006) require that these names be based on the type species within the clade in question, and McGuire et al. (2007) did not include all of the appropriate type species in their phylogenetic study. Specifically, our phylogenetic study did not include *Lampornis amethystinus*, *Mellisuga minima*, or *Trochilus polytmus*, each of which will serve as the type species for a named major clade of hummingbirds in our proposed taxonomy. However, we have unpublished data (to appear in a subsequent publication) for *Lampornis amethystinus*, *Mellisuga minima*, and *Trochilus polytmus* that strongly place these species in the clades for which they will serve as the designated types.

The format of our taxonomy requires further explanation. First, we have defined each of the hummingbird crown-clades using branch-modified node-based names (see Wyss and Meng 1996). A branch-modified node-based name is defined as the most inclusive crown clade that contains some descendent species, but does not include species in alternative clades. Thus, these definitions are similar to those of stem-group names in that any newly

discovered species or perhaps previously unstudied species that is found to branch from the stem leading to a crown group effectively resets the position of the crown-group node. We have selected this approach for two reasons. First, we want this taxonomy to be able to accommodate newly discovered species that could represent sister taxa of major clades of hummingbirds without requiring the creation of new clade names or redefinition of clade names designated here. Second, we want the taxonomy to be flexible enough to accommodate future phylogenetic hypotheses that might (1) place previously unstudied taxa at the base of one or more of the major clades of hummingbirds, or (2) place one or more taxa that we now believe to be nested within a major clade at the base of that major clade without nullifying our proposed clade names. Branch-modified node-based names can satisfy this need, whereas conventional node-based names tend not to satisfy at least one of these criteria (see, for example, the clade name definitions of Joyce et al. 2004).

In the following sections, the abbreviation CCN refers to “Converted Clade Name” and NCN refers to “New Clade Name” (see PhyloCode 2006). “Converted Clade Names” are simply names that have already been applied to hummingbirds within the Linnaean framework that we redefine here under the guidelines of the PhyloCode, whereas “New Clade Names” are applied here for the first time under any context. The abbreviation “orig.” refers to the original taxonomic reference for the species in question.

Trochilidae Vigors, 1825 (CCN)

Pantrochilidae (NCN)

Definitions—“*Trochilidae*” refers to the crown clade arising from the most recent common ancestor of *Florisuga* (orig. *Trochilus*) *mellivora* (Linnaeus 1758), *Topaza* (orig. *Trochilus*) *pella* (Linnaeus 1758), *Phaethornis* (orig. *Trochilus*) *superciliosus* (Linnaeus 1766), *Polytmus* (orig. *Trochilus*) *guainumbi* (Pallas 1764), *Lesbia* (orig. *Ornismya*) *nuna* (Lesson 1833), *Coeligena* (orig. *Ornismya*) *coeligena* (Lesson 1833), *Patagona* (orig. *Trochilus*) *gigas* (Vieillot 1824), *Lampornis amethystinus* Swainson 1827, *Mellisuga* (orig. *Trochilus*) *minima* (Linnaeus 1758), and *Trochilus polytmus* Linnaeus 1758. This definition is intended to include all extant hummingbird species. “*Pantrochilidae*” refers to the panstem that includes crown *Trochilidae*, and is intended to provide a taxonomic framework for fossil taxa stemming from the branch leading to crown group hummingbirds, which appears to be the case for the fossil taxa *Argornis caucasicus*, *Eurotrochilus inexpectatus*, *Jungornis tessellatus*, and *Parargornis messelensis* (Mayr 2003a, b, 2004).

Florisugini (NCN)

Definitions—“*Florisugini*” is a branch-modified node-based name that refers to the most inclusive crown clade that contains *Florisuga* (orig. *Trochilus*) *mellivora* (Linnaeus 1758), but does not include *Phaethornis* (orig. *Trochilus*) *superciliosus* (Linnaeus 1766), *Polytmus* (orig. *Trochilus*) *guainumbi* (Pallas 1764), *Lesbia* (orig. *Ornismya*) *nuna* (Lesson 1833), *Coeligena* (orig. *Ornismya*) *coeligena* (Lesson 1833), *Patagona* (orig. *Trochilus*) *gigas* (Vieillot 1824), *Lampornis amethystinus* Swainson 1827, *Mellisuga* (orig. *Trochilus*) *minima* (Linnaeus 1758), and *Trochilus polytmus* Linnaeus 1758. Given the phylogenetic estimate presented here, this taxon includes *Topaza pella*, *T. pyra*, *Florisuga mellivora*, and *F. fusca*. This definition is intended to allow sufficient flexibility to accommodate newly discovered extant sister species to the clade that includes *Florisuga* and *Topaza*. “*Florisugini*” thus corresponds to the informal grouping “Topazes.”

Phaethornithinae Gould, 1861 (CCN)

Definitions—“*Phaethornithinae*” is a branch-modified node-based name that refers to the most inclusive crown clade that contains *Phaethornis* (orig. *Trochilus*) *superciliosus* (Linnaeus 1766), but does not include *Florisuga* (orig. *Trochilus*) *mellivora* (Linnaeus 1758), *Polytmus* (orig. *Trochilus*) *guainumbi* (Pallas 1764), *Lesbia* (orig. *Ornismya*) *nuna* (Lesson 1833), *Coeligena* (orig. *Ornismya*) *coeligena* (Lesson 1833), *Patagona* (orig. *Trochilus*) *gigas* (Vieillot 1824), *Lampornis amethystinus* Swainson 1827, *Mellisuga* (orig. *Trochilus*) *minima* (Linnaeus 1758), and *Trochilus polytmus* Linnaeus 1758. This definition is intended to include all extant hummingbirds currently recognized formally and informally as “Hermits,” including genera such as *Anopetia* and *Ramphodon* not included in the present study that could represent sister branches of the included hermit taxa.

Polytmini (NCN)

Definitions—“*Polytmini*” is a branch-modified node-based name that refers to the most inclusive crown clade that contains *Polytmus* (orig. *Trochilus*) *guainumbi* (Pallas 1764), but does not include *Florisuga* (orig. *Trochilus*) *mellivora* (Linnaeus 1758), *Phaethornis* (orig. *Trochilus*) *superciliosus* (Linnaeus 1766), *Lesbia* (orig. *Ornismya*) *nuna* (Lesson 1833), *Coeligena* (orig. *Ornismya*) *coeligena* (Lesson 1833), *Patagona* (orig. *Trochilus*) *gigas* (Vieillot 1824), *Lampornis amethystinus* Swainson 1827, *Mellisuga* (orig. *Trochilus*) *minima* (Linnaeus 1758), and *Trochilus polytmus* Linnaeus 1758. This definition corresponds to a clade that we have referred to informally as “Mangoes.”

The definition is intended to allow sufficient flexibility to accommodate more detailed phylogenetic findings, such as placement of taxa such as *Augastes* and *Avocettula* or yet to be discovered species on the branch leading to this clade.

Lesbiini (NCN)

Definitions—“*Lesbiini*” is a branch-modified node-based name that refers to the most inclusive crown clade that contains *Lesbia* (orig. *Ornismya*) *nuna* (Lesson 1833), but does not include *Florisuga* (orig. *Trochilus*) *mellivora* (Linnaeus 1758), *Phaethornis* (orig. *Trochilus*) *superciliosus* (Linnaeus 1766), *Polytmus* (orig. *Trochilus*) *guainumbi* (Pallas 1764), *Coeligena* (orig. *Ornismya*) *coeligena* (Lesson 1833), *Patagona* (orig. *Trochilus*) *gigas* (Vieillot 1824), *Lampornis amethystinus* Swainson 1827, *Mellisuga* (orig. *Trochilus*) *minima* (Linnaeus 1758), and *Trochilus polytmus* Linnaeus 1758. This definition corresponds to a clade that we have informally referred to as “Coquettes.” The definition is intended to allow sufficient flexibility to accommodate more detailed phylogenetic findings, such as placement of taxa such as *Polyonymus*, *Sappho*, *Taphrolesbia*, or yet to be discovered species on the branch leading to this crown clade.

Coeligenini (NCN)

Definitions—“*Coeligenini*” is a branch-modified node-based name that refers to the most inclusive crown clade that contains *Coeligena* (orig. *Ornismya*) *coeligena* (Lesson 1833), but does not include *Florisuga* (orig. *Trochilus*) *mellivora* (Linnaeus 1758), *Phaethornis* (orig. *Trochilus*) *superciliosus* (Linnaeus 1766), *Polytmus* (orig. *Trochilus*) *guainumbi* (Pallas 1764), *Lesbia* (orig. *Ornismya*) *nuna* (Lesson 1833), *Patagona* (orig. *Trochilus*) *gigas* (Vieillot 1824), *Lampornis amethystinus* Swainson 1827, *Mellisuga* (orig. *Trochilus*) *minima* (Linnaeus 1758), and *Trochilus polytmus* Linnaeus 1758. This definition corresponds to a clade that we have informally referred to as “Brilliant.” The definition is intended to allow sufficient flexibility to accommodate more detailed phylogenetic findings, including the possible placement of taxa such as *Clytolaema rubricauda*, *Loddigesia mirabilis* or yet to be discovered species on the branch leading to this crown clade.

Patagonini (NCN)

Definitions—“*Patagonini*” is a branch-modified node-based name that refers to the most inclusive crown clade that contains *Patagona* (orig. *Trochilus*) *gigas* (Vieillot 1824), but does not include *Florisuga* (orig. *Trochilus*) *mellivora* (Linnaeus 1758), *Phaethornis* (orig. *Trochilus*)

superciliosus (Linnaeus 1766), *Polytmus* (orig. *Trochilus*) *guainumbi* (Pallas 1764), *Lesbia* (orig. *Ornismya*) *nuna* (Lesson 1833), *Coeligena* (orig. *Ornismya*) *coeligena* (Lesson 1833), *Lampornis amethystinus* Swainson 1827, *Mellisuga* (orig. *Trochilus*) *minima* (Linnaeus 1758), and *Trochilus polytmus* Linnaeus 1758. This definition is intended to allow sufficient flexibility to accommodate more detailed phylogenetic findings, including the possible elevation of *Patagona gigas peruviana* to species status or placement of yet to be discovered species on the branch leading to this crown clade.

Lampornithini (NCN)

Definitions—“*Lampornithini*” is a branch-modified node-based name that refers to the most inclusive crown clade that contains *Lampornis amethystinus* Swainson 1827, but does not include *Florisuga* (orig. *Trochilus*) *mellivora* (Linnaeus 1758), *Phaethornis* (orig. *Trochilus*) *superciliosus* (Linnaeus 1766), *Polytmus* (orig. *Trochilus*) *guainumbi* (Pallas 1764), *Lesbia* (orig. *Ornismya*) *nuna* (Lesson 1833), *Coeligena* (orig. *Ornismya*) *coeligena* (Lesson 1833), *Patagona* (orig. *Trochilus*) *gigas* (Vieillot 1824), *Mellisuga* (orig. *Trochilus*) *minima* (Linnaeus 1758), and *Trochilus polytmus* Linnaeus 1758. This definition corresponds to a clade that we have informally referred to as “Mountain Gems.” The definition is intended to allow sufficient flexibility to accommodate more detailed phylogenetic discoveries, including the possible placement of taxa such as *Lamprolaima*, or yet to be discovered species on the branch leading to this crown clade.

Mellisugini (NCN)

Definitions—“*Mellisugini*” is a branch-modified node-based name that refers to the most inclusive crown clade that contains *Mellisuga* (orig. *Trochilus*) *minima* (Linnaeus 1758), but does not include *Florisuga* (orig. *Trochilus*) *mellivora* (Linnaeus 1758), *Phaethornis* (orig. *Trochilus*) *superciliosus* (Linnaeus 1766), *Polytmus* (orig. *Trochilus*) *guainumbi* (Pallas 1764), *Lesbia* (orig. *Ornismya*) *nuna* (Lesson 1833), *Coeligena* (orig. *Ornismya*) *coeligena* (Lesson 1833), *Patagona* (orig. *Trochilus*) *gigas* (Vieillot 1824), *Lampornis amethystinus* Swainson 1827, and *Trochilus polytmus* Linnaeus 1758. This definition corresponds to a clade that we have informally referred to as “Bees.” The definition is intended to allow sufficient flexibility to accommodate more detailed phylogenetic findings, including likely placement of taxa such as *Atthis*, *Calothorax*, *Doricha*, *Eulidia*, *Mellisuga*, *Microstilbon*, *Myrmia*, *Tilmatura*, *Thaumastura*, or yet to be discovered species on the branch leading to this crown clade.

Trochilini (NCN)

Definitions—“Trochilini” is a branch-modified node-based name that refers to the most inclusive crown clade that contains *Trochilus polytmus* Linnaeus, 1758, but does not include *Florisuga* (orig. *Trochilus*) *mellivora* (Linnaeus 1758), *Phaethornis* (orig. *Trochilus*) *superciliosus* (Linnaeus 1766), *Polytmus* (orig. *Trochilus*) *guainumbi* (Pallas 1764), *Lesbia* (orig. *Ornismya*) *nuna* (Lesson 1833), *Coeligena* (orig. *Ornismya*) *coeligena* (Lesson 1833), *Patagona* (orig. *Trochilus*) *gigas* (Vieillot 1824), *Lampornis amethystinus* Swainson 1827, and *Mellisuga* (orig. *Trochilus*) *minima* (Linnaeus 1758). This definition corresponds to taxa that we have informally referred to as “Emeralds.” The definition is intended to allow sufficient flexibility to accommodate more detailed phylogenetic discoveries, including the likely placement of taxa such as *Abeillia*, *Cyanophaia*, *Cynanthus*, *Eupetomena*, *Goethalsia*, *Goldmania*, *Hylonympha*, *Leucippus*, *Leucochloris*, *Phaeochroa*, *Stephanoxis*, *Sternoclyta*, *Trochilus*, or yet to be discovered species on the branch leading to this crown clade.

Zusammenfassung

Eine übergeordnete Taxonomie für Kolibris

Im Rahmen einer kürzlich publizierten phylogenetischen Schätzung für 151 Kolibris stellen wir eine erweiterte informelle Taxonomie bereit, sowie eine formale phylogenetische Taxonomie für Trochilidae, die den Regeln von PhyloCode folgt, jedoch mit der hierarchischen Nomenklatur des Linnéschen Systems in Einklang bleibt. Wir vergleichen die kürzlich publizierte phylogenetische Hypothese mit denen vorheriger übergeordneter und taxonomisch begrenzterer phylogenetischer Studien. Wir empfehlen die Anerkennung neun neuer Kladennamen unter dem PhyloCode, von denen im Linnéschen System acht mit Triben übereinstimmen und einer mit einer Subfamilie.

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