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PHYLOGENY AND CLASSIFICATION OF *AUTOMOLUS* FOLIAGE-GLEANERS AND ALLIES (FURNARIIDAE)

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Abstract. We investigate phylogenetic relationships among the foliage-gleaners of the genera *Automolus*, *Hyloctistes*, *Hylocryptus*, and *Clibanornis* (Furnariidae) by means of DNA sequences of mitochondrial and nuclear genes. The genus *Automolus* is not monophyletic because *A. rubiginosus* and *A. rufipectus* are more closely related to *Hylocryptus* and *Clibanornis* and because *Hyloctistes* is nested within the main *Automolus* clade. *Hylocryptus erythrocephalus* and *H. rectirostris* are not sister species; the former is part of the *A. rubiginosus* complex, whereas the latter is sister to *Clibanornis dendrocolaptoides*. Two species, *A. infuscatus* and *A. rubiginosus*, are not monophyletic, indicating the need for further taxonomic revision. On the basis of our phylogenetic analyses and of quantitative assessments of phenotypic variation, we propose a new classification for *Automolus* and allies, including the description of a new subgenus.

Key words: *classification,* Cryptomolus, *foliage-gleaners, neotropical birds, Philydorini, phylogeny.*

Filogenia y Clasificación de *Automolus* y Géneros Relacionados (Aves: Furnariidae)

Resumen. Investigamos las relaciones filogenéticas de los géneros *Automolus*, *Hyloctistes*, *Hylocryptus* y *Clibanornis* (Furnariidae) mediante secuencias de ADN de genes mitocondriales y nucleares. El género *Automolus* no es monofilético porque *A. rubiginosus* y *A. rufipectus* están más relacionados con *Hylocryptus* y *Clibanornis* y porque *Hyloctistes* está incluido dentro del clado principal de *Automolus*. *Hylocryptus erythrocephalus* y *H. rectirostris* no son especies hermanas; la primera es parte del complejo de *A. rubiginosus* mientras que la segunda es hermana de *Clibanornis dendrocolaptoides*. Dos especies, *A. infuscatus* y *A. rubiginosus*, no son monofiléticas, lo que sugiere la necesidad de una revisión de los límites de las especies en el grupo. A la luz de estos resultados, complementados con un análisis de heterogeneidad morfométrica, proponemos una nueva clasificación para *Automolus* y géneros relacionados, incluyendo la descripción de un subgénero nuevo.

INTRODUCTION

The genus *Automolus* is composed of medium-sized foliage-gleaners (Furnariidae: Philydorini) inhabiting tropical and subtropical humid forests in Central and South America. Because of their lack of distinguishing morphological characteristics, in the past, assessments of affinities and taxonomic limits in *Automolus* have been speculative (e.g., Vaurie 1980). However, a combination of relatively large size, plain plumage, straight bill, and slightly elongated crown feathers sets most species of *Automolus* apart from most other foliage-gleaners (Cory and Hellmayr 1925, Parker 1979, Vaurie 1980, Ridgely and Tudor 1994). All *Automolus* species inhabit the forest undergrowth, where they glean invertebrates from the vegetation, in particular from dead leaves, debris, and, to a lesser degree, epiphytes (Remsen and Parker 1984, Rosenberg 1997, Remsen 2003). Also, like most other foliage-gleaners, *Automolus* species nest in burrows dug in earthen banks (Vaurie 1980, Zyskowski and Prum 1999, Remsen 2003).

Recently acquired field data on habitat, behavior, and vocalizations have provided additional evidence for relationships among the foliage-gleaners (Kratter and Parker 1997, Robbins and Zimmer 2005, Zimmer et al. 2008). Three species formerly placed in *Automolus* have been transferred to other genera on the basis of vocalizations, nest placement, habitat, feeding behavior, and morphology (Remsen et al. 2012). Ridgely and Tudor (1994) transferred *Automolus*

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ruficollis to *Syndactyla* on the basis of vocal, behavioral, and plumage similarities (Parker et al. 1985). *Automolus dorsalis* nests in a hollow bamboo stem instead of underground (Kratter 1994) and shares with *Anabazenops fuscus* characteristics related to specialization on bamboo (microhabitat, feeding behavior, morphology), vocalizations, and plumage, strongly suggesting a close relationship that led Kratter and Parker (1997) to transfer *dorsalis* to *Anabazenops*. Finally, on the basis of vocal, syringeal, morphometric, and behavioral similarities, Zimmer et al. (2008) transferred *Automolus roraimae* to *Syndactyla*. With these changes, *Automolus* has become phenotypically more cohesive.

A comprehensive molecular phylogenetic analysis of the Furnariidae supported all these recent changes but also revealed new relationships that render the currently defined *Automolus* nonmonophyletic (Derryberry et al. 2011). *Automolus rubiginosus* is more closely related to the genera *Hylocryptus* and *Clibanornis* than it is to other *Automolus*, and *Hyloctistes subulatus* is embedded within *Automolus* (Derryberry et al. 2011). Plumage and vocal similarities between *A. rubiginosus* and *Hylocryptus* had been noted previously (Chapman 1919, Vaurie 1971, Paynter 1972). Recently, Krabbe (2008) found that vocalizations of *A. rubiginosus rufipectus*, endemic to the Santa Marta Mountains of northern Colombia, were different from those of other members of the *A. rubiginosus* complex and remarkably similar to those of *H. erythrocephalus*. He suggested that *rufipectus* deserves species status, a proposal now accepted by the South American Classification Committee of the American Ornithologists' Union (Remsen et al. 2012), and that it may be related to *Hylocryptus*. In addition to this, the remarkable phenotypic variation and wide geographic distribution of *A. rubiginosus* warrant an evaluation of its monophyly in the context of a broad phylogenetic analysis of the foliage-gleaners. Previously, the relationships of *A. rubiginosus*, *A. rufipectus*, and *H. erythrocephalus* could not be resolved with certainty, but Derryberry et al. (2011) found that that the genus *Hylocryptus* is not monophyletic because *H. rectirostris* is sister to *Clibanornis dendrocolaptoides*. Here we analyze phylogenetic relationships of members of *Automolus*, *Hyloctistes*, *Hylocryptus*, and *Clibanornis* in more detail with an expanded dataset including multiple samples per species. With the results of the phylogenetic analyses, we analyze patterns of morphometric variation and propose a new generic classification considering morphological heterogeneity under alternative classification schemes.

METHODS

PHYLOGENETIC ANALYSIS

We analyzed samples of all currently recognized species of *Automolus*, *Thripadectes*, *Hyloctistes*, *Clibanornis*, and *Hylocryptus*, including all major geographic groups in the *A. ochrolaemus, A. infuscatus*, and *A. rubiginosus* species complexes (Appendix; available at http://dx.doi.org/10.1525/cond.2013.110198). We also included samples of two other genera of the Philydorini (*Philydor* and *Ancistrops*) and *Synallaxis*, *Furnarius*, and *Xenops* as outgroups (Appendix). For all specimens, we amplified and sequenced the mitochondrial genes NADH dehydrogenase subunit 3 (ND3) and cytochrome oxidase subunit II (COII) and intron 7 of the nuclear gene β-fibrinogen (BF7). We also sequenced the gene NADH dehydrogenase subunit 2 (ND2) from at least one specimen per species. We included protein-coding sequences of nuclear RAG genes 1 and 2 for the major lineages (Appendix). Details of PCR primers and laboratory methods followed Derryberry et al. (2011). Protein-coding sequences were aligned by eye and BF7 intron sequences were aligned with MUSCLE 3.8 (Edgar 2004).

We coded single-nucleotide heterozygotes with IUPAC ambiguity symbols and used numerical algorithms (Dmitriev and Rakitov 2008) to reconstruct allele sequences of heterozygotes for insertions or deletions. First, ambiguous bases were called with the Heterozygote plugin in Geneious Pro 5.4.2 (Drummond et al. 2011) for both the forward and reverse chromatograms. Then, we reconstructed allelic sequences with Indelligent version 1.2 (http://ctap.inhs.uiuc.edu/dmitriev/indel.asp). We checked the accuracy of allelic reconstructions by comparing results for the forward and reverse readings. Finally, using both forward and reverse readings, we assembled the long and short alleles separately. New sequences were deposited in Genbank (accession numbers KC835403–KC835521)

We ran maximum-parsimony analysis in PAUP* (Swofford 2003). Heuristic searches consisted of 100 runs of stepwise random taxon additions followed by tree-bisection–reconnection branch-swapping rearrangements with a maximum of 1000 optimal trees kept in each replicate. We assessed clade support by nonparametric bootstrapping with 1000 replicates and the same heuristic-search parameters, except that only 10 rounds of random additions were used.

Maximum-likelihood inference was implemented in RAxML version 7.0.4 (Stamatakis et al. 2008) on the Cipres Portal version 2.2 (Miller et al. 2010) by means of the general time-reversible model of nucleotide substitution with rate heterogeneity among sites modeled by a gamma distribution (GTR + Γ). We ran separate analyses for mitochondrial and nuclear sequences as well as a concatenated analysis. We evaluated various partitioning schemes and used Akaike's information criterion (second-order estimator AIC_c) to choose the optimal partitioning strategy (Sullivan and Joyce 2005, McGuire et al. 2007). The three linkage groups (mtDNA, BF7, RAG genes) were always treated separately. Coding regions were further partitioned by gene, by codon position, and by both gene and codon position. Partition by both gene and codon position was optimal (lowest AIC_c) for the concatenated dataset and the mtDNA dataset, whereas partition by codon position only was optimal for the RAG dataset when analyzed separately. Clade support was assessed with the fast bootstrap algorithm implemented in RAxML (Stamatakis et al. 2008).

We generated trees for each linkage group and evaluated whether the three groups were congruent before performing a

concatenated analysis. We evaluated congruence across linkage groups (mtDNA, RAG genes, BF7) in a reduced dataset, including only species for which sequences of all genes were available (the taxon sampling corresponding to the RAG sequences), and evaluated sequence data for each linkage group on the maximum-likelihood trees of the other two linkage groups. We assessed the significance of log-likelihood differences between trees by the Shimodaira and Hasegawa (1999) test (SH) in RAxML (*–fh* option). We used a stringent significance level (0.01) to correct for multiple comparisons (a total of six tests). Using the same test, we also evaluated the monophyly of particular groups by comparing the optimal (unconstrained) maximum-likelihood tree with one in which the monophyly of a group was constrained (under the constraint *–g* option in RAxML).

MORPHOMETRICS

We measured eight external features on 168 study skins representing all 45 species of foliage-gleaners in the Philydorini. We measured at least three males per species except for *Automolus rufipectus*, of which only one specimen was available. We measured bill length from the anterior border of the nostril to the tip of the bill and bill width at the level of the anterior border of the nostrils. Two wing measurements were taken from the carpal joint without flattening the natural curvature of the closed wing: length to the tip of the longest primary and length to the tip of the first secondary. Two tail-length variables were measured from the base of the central rectrices, to the tip of the central rectrix and to the tip of the outer rectrix. Tarsus length and hallux length with claw were measured according to Baldwin et al. (1931). S. C. made all measurements with a Mitutoyo Digimatic Point Caliper (resolution 0.01 mm) with an output interface.

Morphometric variables were log transformed, allowing measurements differing in the same proportion to be analyzed on an arithmetic scale (Gingerich 2000). We conducted a principal component analysis on the log-transformed variables to visualize the distribution of clades in the morphospace and to assess the degree of overlap and similarity of particular clades.

We estimated the morphometric heterogeneity of all nonmonotypic genera in the Philydorini to guide decisions of taxon ranking (Claramunt et al. 2010). The approach consists of calculating multivariate variances as a measure of heterogeneity for taxa in different classification schemes. A classification scheme resulting in more homogeneous taxa will be preferred over one resulting in more heterogeneous taxa. We used the total variance as a multivariate descriptor of variation (Van Valen 1974) together with a variance-partitioning technique to estimate the separate contribution of size and shape to the total variation (Darroch and Mosimann 1985). The "log-size" of each specimen is calculated as the average of the eight log-transformed variables. A vector of shape ("log-shape") for each specimen is obtained by subtracting the "log-size" from each variable. Variances are then calculated for different clades from the original logged data (overall variance) and the log-shape data (shape variance). The total variance is the sum of all variances of individual traits (Van Valen 1974). Finally, the difference between the total overall variance and the total shape variance is the contribution of size to the total variation (Darroch and Mosimann 1985). We calculated approximate standard errors for estimates of variances by using a jackknifing method in which we repeated the estimation procedure while excluding one specimen at a time; we then calculated the standard deviation of the estimate by the standard formula (Van Valen 2005).

Using the methods described above, we estimated size and shape variances for various clades in the Philydorini. In particular, we compared monophyletic, nonmonotypic genera of foliage-gleaners with alternative ranking schemes for some genera in the *Automolus* group. In addition to the genera in the *Automolus* group, we estimated the heterogeneity of a monophyletic *Anabacerthia* (including *A. ruficaudata* and *A. lichtensteini*, formerly in *Philydor*), *Anabazenops*, a monophyletic *Philydor* (including only *P. pyrrhodes*, *P. atricapillus*, and *P. novaesi*), and *Syndactyla* (including *Simoxenops*) (see Derryberry et al. 2010 and Remsen et al. 2012 for details).

CLASSIFICATION

We propose a classification of *Automolus* and allies following phylogenetic principles (Cracraft 1974) and the Linnaean system of nomenclature (International Commission on Zoological Nomenclature 1999). Even under these principles there is room for multiple classification schemes regarding names, ranking, and the order of taxa in the linear sequence. We adopted the following ancillary criteria for assigning names to clades: (1) minimize changes that alter the content of traditional named taxa; (2) to avoid potential instability, name only strongly supported clades; and (3) avoid creation of heterogeneous groups, as determined by the heterogeneity analysis explained above. We used "phyletic sequencing" as a way of ordering taxa and encoding phylogenetic information without the need for naming all clades in a tree (Nelson 1972, Cracraft 1974). In this method, the named taxon listed first is sister to the taxa listed below it, e.g., the relationship [A, (B, C)] can be represented in the sequence as either "A, B, C" or "A, C, B" with no need for the clade (B, C) to be named. In the case of unnamed clades, we generated the linear sequence by "ladderizing" the species tree, i.e., clades with fewer species are listed first; e.g., if C has fewer species than B, then "A, C, B" is preferred. After these sequencing rules are applied, only sister species remain in an arbitrary order. Sister species were ordered according to geography, e.g., if B is distributed between A and C, then "A, B, C" is preferred. When geographic patterns are not clear, we placed the species distributed to the south or to the east last (Peters 1951).

RESULTS

PHYLOGENY

Across all three linkage groups (mtDNA, BF7, and RAG), phylogenetic trees were largely congruent for well-supported relationships (bootstrap values >85%). The resolution of the BF7 tree, however, was poor, and only some terminal relationships were well supported. Moreover, the BF7 tree showed one specimen of *Hyloctistes subulatus* as sister to *Philydor pyrrhodes* (100% bootstrap), whereas it grouped with the other two *H. subulatus* in the mtDNA tree. In addition, a specimen of *A. rubiginosus* from Mexico (MZFC 11202) was heterozygous, and the two alleles, phased with the Indelligent algorithm, were not recovered as sister in the BF7 tree. Although the fit of BF7 sequences was not significantly worse on the mtDNA and RAG trees (results of SH tests not significant), the BF7 tree was a significantly worse fit to both the mtDNA and RAG sequences (likelihood ratio 76.9 and 32.8, respectively; $P < 0.01$ in both SH tests). For comparison, the mtDNA and RAG datasets were not significantly incongruent (likelihood ratios 29.5 and 5.7, results of both SH tests not significant). These results suggest that the phylogenetic signal in BF7 sequences is weaker than, and incongruent with, that of the other two linkage groups, and that the incongruence cannot be explained solely by the stochasticity of the substitution process in DNA sequences. Other processes such as incomplete lineage sorting or gene paralogy may be also involved. For these reasons, we performed a concatenated analysis using only mtDNA and RAG sequences. The following results are based on the concatenated analysis.

The genus *Automolus*, as currently recognized, is not monophyletic (Fig. 1). The *A. rubiginosus* complex is most closely related to *Clibanornis* and *Hylocryptus*, whereas the other *Automolus* species are sister to *Thripadectes*. These basal relationships are well supported independently by the mtDNA and RAG datasets when analyzed separately (bootstrap values >90 %). Even after the *A. rubiginosus* complex is excluded from *Automolus* (hereafter *Automolus* sensu stricto), the genus is not monophyletic because *Hyloctistes* is embedded within it (Fig. 1). A tree in which *Hyloctistes* is outside *Automolus* sensu stricto is significantly less likely than the unconstrained tree (likelihood ratio = 77, SH test $P < 0.01$).

Automolus sensu stricto is composed of two strongly supported subclades (Fig. 1). One subclade contains *A. rufipileatus* and *A. melanopezus*, the other *Hyloctistes*, *A. ochrolaemus*, and the *A. infuscatus* complex (including *A. leucophthalmus*, *A. lammi*, and *A. paraensis*, Fig. 1). The monophyly of *Automolus* sensu stricto is only weakly supported; it is well supported by RAG sequences (97% bootstrap) but not by mtDNA sequences, which show *A. rufipileatus* and *A. melanopezus* sister to *Thripadectes* (albeit with low bootstrap support). However, the SH test indicates that the RAG and mtDNA topologies do not differ significantly (likelihood ratio 5.7, SH test not significant). Basal relationships within the *Hyloctistes*/*A. ochrolaemus*/*A. infuscatus* clade are not well resolved. A tree in which *Hyloctistes* is sister to an *A. ochrolaemus*/*A. infuscatus* clade is not significantly worse than the ML tree (likelihood ratio = 2.7, SH test $P > 0.05$).

The two species of *Hylocryptus* are not sister taxa; instead, *H. rectirostris* is sister to *Clibanornis dendrocolaptoides*, whereas *H. erythrocephalus* is embedded within the *A. rubiginosus* complex. Enforcing the monophyly of *Hylocryptus* resulted in a significantly less likely tree (likelihood ratio = 209, SH test $P < 0.01$). Finally, *A. rufipectus* is also nested within *A. rubiginosus,* making the latter species paraphyletic. A tree in which both *H. erythrocephalus* and *A. rufipectus* were excluded from the *A. rubiginosus* complex was a poorer fit to the sequence data (likelihood ratio = 64, SH $0.05 > P > 0.01$), as were trees in which only *H. erythrocephalus* (likelihood ratio = 70, SH $0.05 > P > 0.01$) or only *A. rufipectus* (likelihood ratio = 28, SH $0.05 > P > 0.01$) was excluded from *A. rubiginosus*.

Another species not recovered as monophyletic was *Automolus infuscatus*, because *A. i. badius* from northern Amazonia was outside the *infuscatus*/*leucopthalmus* clade (Fig. 1). Mitochondrial sequences suggest *A. i. badius* is closer to *Hyloctistes*, but without strong support (Fig. 1).

MORPHOMETRICS

The three major clades identified in the molecular analysis (*Automolus* sensu stricto, *Thripadectes*, and the *Clibanornis*/*Hylocryptus* clade) occupy different parts of the morphospace defined by the eight measurements (Fig. 2), albeit with some overlap. Principal component 1 (PC1) had negative loadings for all variables, with higher loadings for tail and foot variables (Fig. 2). Principal component 2 (PC2) had positive loadings for wing and tail variables and negative loadings for bill length and foot variables (Fig. 2). Species of *Automolus* sensu stricto (squares in Fig. 2) tend to have shorter bills and smaller feet. Species of *Thripadectes* are characterized by medium to large overall size (low PC1) and long wings and tails (high PC2). Species in the *Clibanornis*/*Hylocryptus* clade (triangles in Fig. 2) occupy a wide range of sizes (PC1), but are characterized by mostly negative values of PC2, indicating relatively longer bills and large feet.

To restore the monophyly of *Automolus* one could include in it all species of *Automolus*, *Hyloctistes*, *Thripadectes*, *Hylocryptus*, and *Clibanornis* (hereafter *Automolus* sensu lato). However, the morphological analysis suggests that such a genus would be unusually heterogeneous in shape (Fig. 3). Some genera of the Philydorini, such as *Syndactyla*, are heterogeneous in size, and others, such as *Clibanornis*, are heterogeneous in shape, but only *Automolus* sensu lato would be heterogeneous in both size and shape. Splitting *Automolus* sensu lato into three (*Automolus* sensu stricto, *Thripadectes*, and *Clibanornis*) or four genera (as before but *Hylocryptus* separated from *Clibanornis*)

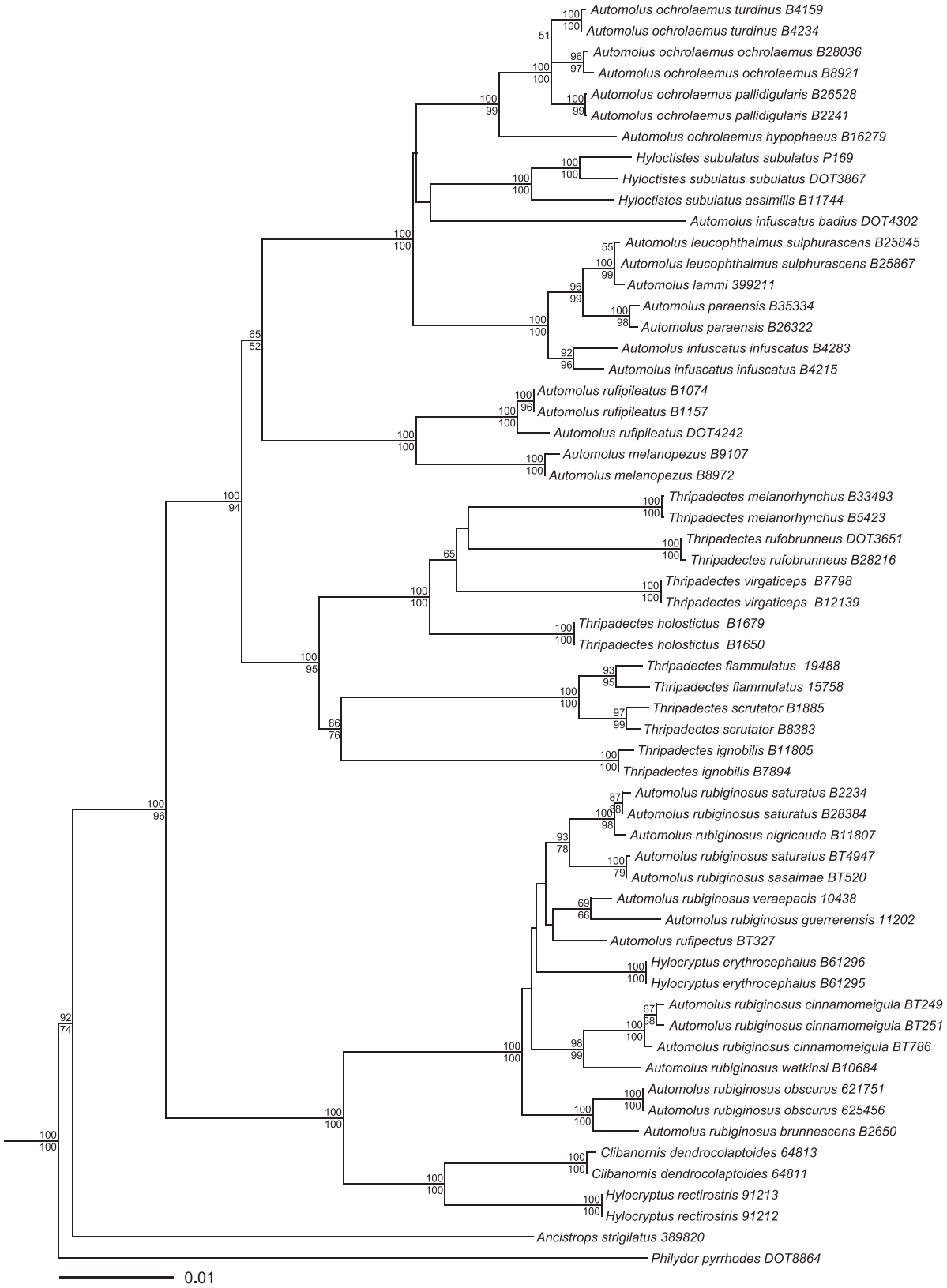

FIGURE 1. Maximum-likelihood tree of concatenated mitochondrial and RAG sequences for *Automolus* foliage-gleaners and allies (Furnariidae). Bootstrap values are indicated above (maximum-likelihood analysis) and below (maximum-parsimony analysis) branches.

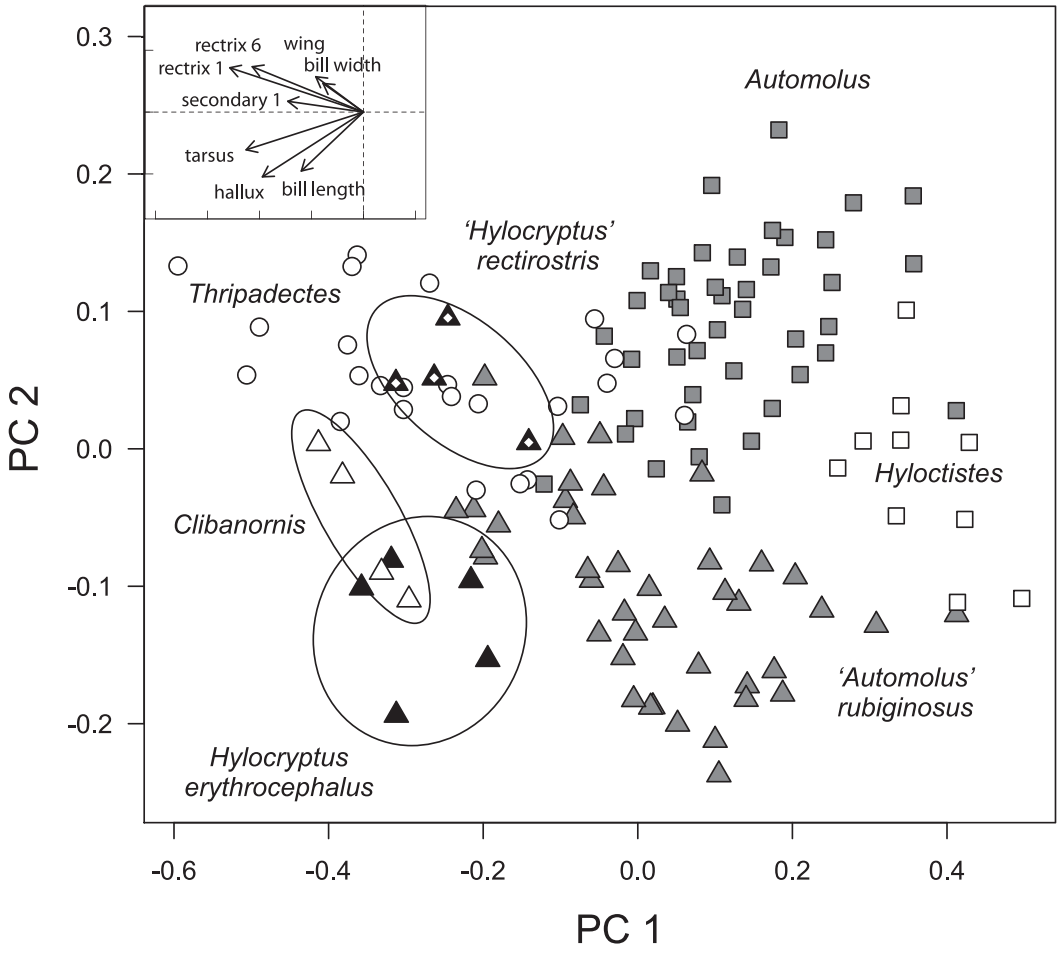

FIGURE 2. Principal component analysis of eight variables from the external anatomy of *Automolus* and allies. Major clades are indicated by squares (*Automolus*/*Hyloctistes*), circles (*Thripadectes*), and triangles (*Clibanornis*/*Hylocryptus*/*A. rubiginosus* complex). PC 1 and PC 2 explained 66% and 13% of the variance, respectively. The inset shows character loadings.

would result in taxa with levels of heterogeneity comparable to those of other genera in the Philydorini, such as *Anabazenops*, *Philydor*, *Syndactyla*, and *Anabacerthia*. *Clibanornis* sensu lato, including *C. dendrocolaptoides*, *Hylocryptus*, and the *Automolus rubiginosus* complex, is more heterogeneous in shape than other genera, but splitting it into two genera, *Clibanornis* (for *C. dendrocolaptoides* and *Hylocryptus rectirostris*) and *Hylocryptus* (for *Hylocryptus erythrocephalus* and the *A. rubiginosus* complex), results in relatively homogeneous genera. In both cases, however, standard errors around variance estimates indicate that levels of heterogeneity of the resultant clades overlap widely with those of other genera in the Philydorini.

DISCUSSION

We found that *Automolus*, as currently defined, is not monophyletic. Members of the *A. rubiginosus* complex, including *A. rufipectus,* are more closely related to *Clibanornis* and *Hylocryptus* than to other species of *Automolus*. Even if one were to redefine *Automolus* by excluding the *rubiginosus* complex, the genus would still not be monophyletic because of the position of *Hyloctistes*. Before Ridgway (1909) described the genus *Hyloctistes*, *H. subulatus* was generally included in *Automolus*. Ridgway (1909) believed that *Hyloctistes* was closer to *Philydor*, presumably because of its foot morphology (Ridgway 1911). A much longer bill distinguished *Hyloctistes* from *Philydor*, whereas the degree of syndactyly distinguished it from *Automolus* (Ridgway 1909). The new genus *Hyloctistes* was adopted in most classifications. In our examination of specimens, however, we could not identify any consistent difference in degree of syndactyly between *Hyloctistes* and *Automolus*. Furthermore, aside from the dark and striped plumage, some subspecies of *H. subulatus*, such as the short-billed *H. s. assimilis*, are morphologically similar to some *Automolus* species, and some overlap in morphology is evident in the morphometric space (Fig. 2). In habitat and behavior, *Hyloctistes* is similar to other *Automolus* species but with a tendency, at least in some subspecies, to forage higher

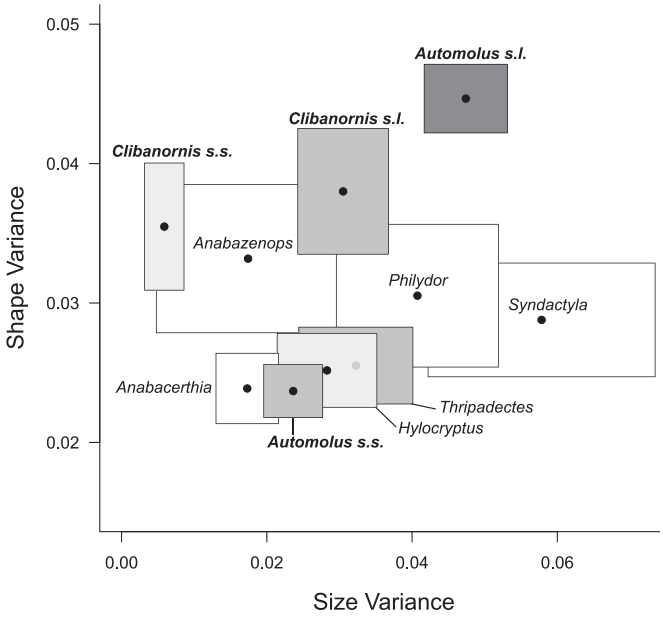

FIGURE 3. Morphometric-heterogeneity analysis based on eight variables from the external anatomy of five traditional polytypic genera and four alternatives for delimitation of genera in the *Automolus*/*Clibanornis* group according to the results of the phylogenetic analysis. Variance was partitioned into a size and a shape component by Darroch and Mosimann's (1985) method. *Automolus* sensu lato (s. l.) includes *Hyloctistes*, *Thripadectes*, *Hylocryptus*, and *Clibanornis*. *Automolus* sensu stricto (s. s.) includes *Hyloctistes* but not *Thripadectes* nor the *A. rubiginosus*/*Clibanornis* clade. *Clibanornis* sensu stricto includes *C. dendrocolaptoides* and *H. rectirostris*. *Clibanornis* sensu lato also includes *Hylocryptus* and the *A. rubiginosus* complex. *Hylocryptus* includes *H. erythrocephalus* and the *A. rubiginosus* complex. Boxes represent one standard deviation below and above the point estimate.

above the ground and in more varied substrates such as vines, palm fronds, and major branches near main trunks (Remsen 2003). Also, like other *Automolus* species, *Hyloctistes subulatus* nests in burrows dug in earthen banks (Remsen 2003) and uses rachises of compound leaves as its primary nest material (Zyskowski and Prum 1999).

Clibanornis, *Hylocryptus*, and the *A. rubiginosus* complex form a strongly supported clade. Although affinities between *Hylocryptus* and the *A. rubiginosus* complex have been hypothesized on the basis of similarities in morphology (Chapman 1919) and nest architecture (Zyskowski and Prum 1999), phylogenetic relationships were not well represented in previous taxonomies. Chapman (1919) described *Hylocryptus* for *H. erythrocephalus* primarily because of the morphology of its bill, which distinguished the new bird from other members of the *A. rubiginosus* complex. Much later, Zimmer (1936) transferred *Automolus rectirostris* to *Hylocryptus* on the basis of alleged similarities in bill shape and plumage. Since then, most authors accepted a close affinity between *erythrocephalus* and *rectirostris*, even suggesting that they be considered conspecific (Vaurie 1971, Paynter 1972). Our analysis demonstrates that these taxa are not sister to each other: *erythrocephalus* is part of the *rubiginosus* complex, whereas *rectirostris* is sister to *Clibanornis dendrocolaptoides* (Fig. 1, see also Derryberry et al. 2011). We also found that these two species are not particularly similar morphologically, other than being larger than most other foliage-gleaners (Fig. 2).

The affinities of *Clibanornis dendrocolaptoides* were completely uncertain before genetic data became available. Sclater and Salvin (1873) described *Clibanornis* in the subfamily Furnariinae as being similar to *Furnarius*. Cory and Hellmayr (1925) listed it between *Coryphistera* and *Cinclodes*, in the same subfamily, without providing any rationale. Vaurie (1971, 1980) merged *Clibanornis* into *Phacellodomus*, in the subfamily Synallaxinae, on the basis of alleged behavioral and morphological similarities. Analysis of DNA sequences, however, demonstrated that none of these hypotheses was correct: *C. dendrocolaptoides* belongs in the Philydorini (Irestedt et al. 2009). Our analyses further revealed that *C. dendrocolaptoides* is sister to *H. rectirostris* (Fig. 1, see also Derryberry et al. 2011).

Our results provide insights on relationships and species limits among members of the *A. rubiginosus* complex. We found that *H. erythrocephalus* and *A. rufipectus* are not only part of the *A. rubiginosus* complex but are actually nested within *A. rubiginosus*. Merging *H. erythrocephalus* and *A. rufipectus* into a highly polytypic *A. rubiginosus* seems unjustified because plumage, morphometric, and vocal characteristics suggest that more than one species is involved (Chapman 1917, Cory and Hellmayr 1925, Vaurie 1980, Remsen 2003, Krabbe 2008). Several forms now considered subspecies of *A. rubiginosus* were described as species, and some of them were maintained as such even after the use of subspecies in ornithology became widespread (Chapman 1917, Cory and Hellmayr 1925). Evidence for conspecificity of these forms is lacking, and Peters (1951) merged them into a single species without analyses of geographic variation, reproductive compatibility, or phylogenetic affinities. As in many other avian groups, especially in the neotropics, a degree of overall morphological similarity was used uncritically to rank former species as subspecies under the paradigm of using polytypic species to indicate relatedness and simplify taxonomy. Revisions of species limits are revealing that many good species have been lumped erroneously (e.g., in the Furnariidae, Zimmer 2002, 2008, Simon et al. 2008, Areta and Pearman 2009, d'Horta et al. 2013).

Our preliminary examination of plumage variation suggests that *A. rubiginosus* is composed of five phenotypically coherent groups largely congruent with clades recovered in the phylogenetic analysis. The Central American subspecies *rubiginosus*, *guerrerensis*, *veraepacis*, and *fumosus*, although not homogeneous, form a coherent morphological group, and

our two samples from Mexico, representing *guerrerensis* and *veraepacis*, formed a clade in both the mtDNA and BF7 trees. Although genetic samples of *fumosus* (the isolated taxon from Costa Rica and Panama) were not available, this form is very similar in plumage to *veraepacis*, part of the nominate group. South American subspecies occurring west of the Andes (*nigricauda*, *saturatus*, and *sasaimae*) are darker than any others of *A. rubiginosus* and together were treated as a separate species by Chapman (1917) and Cory and Hellmayr (1925). These three subspecies form a clade in both mtDNA and BF7 trees. Within this clade, *nigricauda* and *saturatus* are the darkest and have a blackish tail; *saturatus* is darker on average, but many individuals cannot be distinguished from *nigricauda* on this basis; *sasaimae* is similar but has a brown tail. Lack of monophyly in mitochondrial DNA of *saturatus* in relation to the other two subspecies (Fig. 1) may result from incomplete lineage sorting or gene flow. In any case, this suggests that the three subspecies are better considered a single lineage. The lighter coloration of *sasaimae* may be related to its inhabiting a dryer area and so represent local adaptation in a few plumage loci rather than a species-level divergence. East of the Andes, there are three distinctive morphological groups: (1) *A. r. cinnamomeigula* from the foothills of the Eastern Andes above the Llanos of Colombia is distinctively rufous overall; (2) *A. watkinsi* from the foothills of central and southern Peru has little rufous overall, distinctive dark scaling on the throat, and a rufous nape; and (3) birds from the foothills of northern Amazonia are mostly brownish but with a conspicuous cinnamon-rufous throat. This third group includes *obscurus* and *venezuelanus* from the Guiana Shield as well as *caquetae* from southern Colombia and *brunnescens* from eastern Ecuador and northeastern Peru. A close relationship between the birds of western and northeastern Amazonia has not been hypothesized before despite their striking similarity. We could not find diagnostic differences between these four taxa (contra Meyer de Schauensee 1947). In agreement with this, our results supported a close relationship between our samples from northeastern Peru and from Guyana (Fig. 1). Detailed analysis of character variation and relationships using larger samples will be necessary to test the validity of this preliminary assessment and to determine species limits in the *A. rubiginosus* complex.

Our analysis also clarified relationships among members of the *A. infuscatus* complex. Using a combination of plumage, morphometric, and vocal data, Zimmer (2002, 2008) revised species limits in this group. He separated *A. paraensis* from *A. infuscatus* (Zimmer 2002) and *A. lammi* from *A. leucophthalmus* (Zimmer 2008) primarily on the basis of marked differences in songs and calls. He also noted that the vocalizations of *A. paraensis* were most similar to those of *A. lammi*. Our results (Fig. 1) support the separation of *A. paraensis* from *A. infuscatus* because the former is more closely related to the Atlantic Forest species *A. lammi* and *A. leucophthalmus* than it is to *A. infuscatus*. The *A. paraensis*/*lammi*/*leucophthalmus* clade is well supported by the phylogenetic analysis of sequence data (100% bootstrap, Fig. 1) and by a synapomorphic 5-bp deletion in the BF7 intron. On the other hand, we did not find *A. paraensis* and *A. lammi* to be sister taxa as suggested by vocal similarities (Zimmer 2002). Finally, we found that subspecies *A. i. badius* from northern Amazonia is not closely related to nominate *A. infuscatus* and may lie outside the *A. infuscatus* complex. Because we could not resolve its exact position in the tree with any confidence, the possibility that *A. i. badius* is sister to the *A. infuscatus* complex cannot be ruled out. In that case, the *A. infuscatus* clade including *A. i. badius* may be considered a superspecies (Zimmer 2002, Remsen 2003) or even a single polytypic species. However, evidence suggests that multiple species are involved (Zimmer 2002, 2008). Although the vocal and morphological differences between *A. i. badius* and *A. i. infuscatus* are subtle, they are diagnostic. *A. i. badius* can be distinguished from *A. i. infuscatus* by the rusty instead of olive-brown crown and by a loudsong with significantly fewer notes (<25 notes, Zimmer 2002). In addition, *A. i. infuscatus* lacks a characteristic shared by *A. infuscatus*, *A. lammi*, and *A. leucophthalmus*: the posterior malar feathers of those three species are whitish like the throat, resulting in a sharp contrast between the malar and auricular regions; in *A. i. badius*, the posterior malar feathers form a gradient between the dark auriculars and the whitish throat (S. C., pers. obs.). DNA sequences of the other two subspecies of *A. infuscatus* were not available for analysis, but the characters mentioned above indicate that *A. i. cervicalis* from the eastern Guiana Shield is allied to *A. i. badius*, whereas *A. i. purusianus*, from the Amazon–Madeira interfluvium, is allied to *A. i. infuscatus* (see also Zimmer 2002). Therefore, *A. infuscatus* may consist of two species: (1) *A. infuscatus* (including *purusianus*) from western Amazonia and (2) *A. cervicalis* (including *badius*), restricted largely to the Guiana Shield. A denser sampling of all forms is required to confirm this hypothesis.

The improved understanding of the affinities of *Hylocryptus* and *Clibanornis* provided by our study calls for a revision of previous ideas about the process of diversification in this group. Paynter (1972), assuming a close affinity between *H. erythrocephalus* and *H. rectirostris*, advanced a biogeographic hypothesis to explain the widely separated distributions of this pair of species, suggesting that their ancestor was distributed across the Amazon basin during a glacial period when the region was covered by dry or seasonally dry forests; subsequently, the expansion of humid forest separated the two species (Paynter 1972). Therefore, Paynter's hypothesis implies the ancestral *Hylocryptus* was extirpated from the Amazon basin by climate change. In contrast, the relationships revealed by our phylogeny suggest a different scenario. First, because the clade including the two traditionally defined species of *Hylocryptus* is composed not only of seasonal-forest

species but also of humid-forest species, the range of possibilities for the habitat of the ancestor is wider. Second, because sister lineages tend to be geographic neighbors (e.g., *H. rectirostris* and *C. dendrocolaptoides*), one need not invoke extinction of populations to account for disjunct distributions. Finally, phenotypes seem to have changed rapidly and sometimes convergently. Our results suggest that plumage color is associated with habitat. Lineages that occupy seasonally dry forests, like *H. erythrocephalus* and *H. rectirostris*, have paler plumage than lineages that occupy humid forests, like most other members of the *A. rubiginosus* complex. The darkest forms are found in the most humid regions, as exemplified by *A. r. nigricauda* and *A. r. saturatus*, which inhabit the extremely humid Chocó. Therefore, color variation in this group is consistent with Gloger's rule (Zink and Remsen 1986), a phenomenon also documented for other furnariids (Claramunt 2002, Remsen 2003, Areta and Pearman 2009). Convergence in coloration and size may thus have resulted in superficial morphological similarities between *H. erythrocephalus* and *H. rectirostris* that misled previous subjective assessments of relationships.

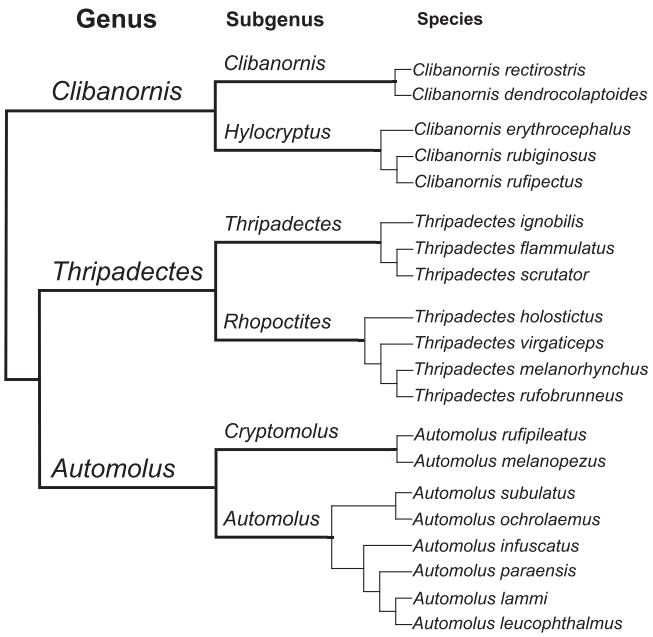

FIGURE 4. Phylogenetic tree with new classification of *Automolus* and allies.

CLASSIFICATION OF *AUTOMOLUS* AND ALLIES

Considering our estimate of phylogenetic relationships and the criteria explained in the methods, we propose a new classification for *Automolus* and allies. We based our classification and applied phyletic sequencing on a reduced tree comprising species-level taxa only (Fig. 4). Further research on species limits may result in changes in the linear sequence of species within subgenera, but we expect that our supraspecific classification will remain stable. Results of the analysis of morphometric heterogeneity argue against expansion of *Automolus,* which would result in an unusually heterogeneous genus (Fig. 3). We preferred to (1) rank the genera at a lower level, resulting in relatively homogeneous clades (Fig. 3) occupying different portions of the morphospace (Fig. 2), (2) preserve the genus *Thripadectes*, and (3) minimize changes in the content of the traditional genus *Automolus*. The heterogeneity analysis was ambiguous with respect to the use of *Hylocryptus*, which could be merged into an expanded *Clibanornis*. Maintaining these two genera would obscure the fact that they form a strongly supported monophyletic group, unless a nontraditional rank such as a supergenus is used. We preferred the use of *Clibanornis* sensu lato and recognize subclades as subgenera.

Our proposed classification fits well with major ecological divisions among these foliage-gleaners. The genus *Automolus* comprises species that inhabit lowland tropical humid forests and are primarily arboreal dead-leaf specialists (Remsen and Parker 1984, Rosenberg 1997, Remsen 2003). The genus *Thripadectes* comprises species that are also primarily arboreal but inhabit montane forests, including cloud forests (Remsen 2003). The genus *Clibanornis* comprises species that inhabit both humid and seasonal forests in montane areas or foothills and tend to forage in leaf litter (Remsen 2003, Krabbe 2008, Bodrati and Cockle 2006).

We describe a new subgenus for *Automolus rufipileatus* and *A. melanopezus*. They form a strongly supported clade that could not be represented in the classification by phyletic sequencing alone. In addition to the shared morphological characteristics mentioned in the diagnosis, both *A. rufipileatus* and *A. melanopezus* seem to be associated with stands of woody canes such as *Guadua* and *Gynerium* (Ridgely and Tudor 1994, Kratter 1997, Remsen 2003). The position of *Hyloctistes subulatus* is not strongly supported; it clustered with *Automolus infuscatus badius* in our analyses but appeared as sister to the *A. infuscatus*/*ochrolaemus* clade in Derryberry et al. (2011). If the latter placement is corroborated with more evidence, then *Hyloctistes* can be resurrected as a subgenus within *Automolus*. We opted for listing *subulatus* first, within the subgenus, but its final position may change with further data and how species limits are resolved in the *A. infuscatus* complex. Species flagged with an asterisk in the following classification are not monophyletic and require revision.

Genus *Clibanornis* Sclater and Salvin, 1873. Type: *Anabates dendrocolaptoides* Pelzeln, 1859

Subgenus *Clibanornis* Sclater and Salvin, 1873

Clibanornis rectirostris (Wied, 1831)

Clibanornis dendrocolaptoides (Pelzeln, 1859)

Subgenus *Hylocryptus* Chapman, 1919. Type: *Hylocryptus erythrocephalus* Chapman, 1919

Clibanornis erythrocephalus (Chapman, 1919)
Clibanornis rubiginosus (Sclater, 1856a)*
Clibanornis rufipectus (Bangs, 1898)

Genus *Thripadectes* Sclater, 1862. Type: *Anabates flammulatus* Eyton, 1849

Subgenus *Thripadectes* Sclater, 1862

Thripadectes ignobilis (Sclater and Salvin, 1879)
Thripadectes flammulatus (Eyton, 1849)
Thripadectes scrutator Taczanowski, 1874

Subgenus *Rhopoctites* Ridgway, 1909. Type: *Philydor rufobrunneus* Lawrence, 1867

Thripadectes holostictus (Sclater and Salvin, 1875)
Thripadectes virgaticeps Lawrence, 1874
Thripadectes melanorhynchus (Tschudi, 1844)
Thripadectes rufobrunneus Lawrence, 1867

Genus *Automolus* Reichenbach, 1853. Type: *Anabates leucophthalmus* Wied, 1821. Synonyms: *Ipoborus* Cabanis and Heine, 1859 (type: *A. leucophthalmus* Wied, 1821), *Automoliana* Strand, 1928 (type: *A. leucophthalmus* Wied, 1821), *Hyloctistes* Ridgway, 1909 (type: *Philydor virgatus* Lawrence, 1867).

Subgenus *Cryptomolus*, subgenus novum. Type: *Anabates rufipileatus* Pelzeln, 1859

Diagnosis: Similar to other species of *Automolus* (sensu stricto) but iris orange to red instead of whitish, yellow, or dark brown (Remsen 2003) and auricular and throat feathers uniformly colored, with no light stripes or dark borders forming flammulated patterns.

Etymology: a combination of "*cryptos*" (Greek for hidden or concealed) and "*molus*" the ending of the generic name *Automolus*, treated as a masculine noun in the nominative singular.

Automolus rufipileatus (Pelzeln, 1859)
Automolus melanopezus (Sclater, 1858)

Subgenus *Automolus* Reichenbach, 1853

Automolus subulatus (Spix, 1824)
Automolus ochrolaemus (Tschudi, 1844)
Automolus infuscatus (Sclater, 1856b)*
Automolus paraensis Hartert, 1902
Automolus lammi Zimmer, 1947
Automolus leucophthalmus (Wied, 1821)

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