Taxonomy, vocalisations, syringeal morphology and natural history of *Automolus roraimae* (Furnariidae)

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The White-throated Foliage-gleaner *Automolus roraimae* has been a subject of taxonomic and nomenclatural debate almost since its description in 1884. Described as *Philydor albigularis* by Salvin & Godman (1884) from Mt. Roraima, Guyana, it was transferred to *Automolus* by Sclater (1890). Hellmayr (1917) proposed that the name *Philydor albigularis* was a homonym of *Philydor albogularis* Spix (*Av. Bras*. 1, 1824: 74), and was therefore unavailable. Because both *Philydor albigularis* Salvin & Godman, 1884, and *Philydor albogularis* Spix, 1824, had been subsequently transferred to *Automolus*, Hellmayr determined that the name *Automolus albigularis* was also a homonym of *Automolus albogularis* (now *A. leucophthalmus*), and was equally unavailable. Hellmayr (1917: 199) proposed a new name, *Automolus roraimae*, and designated the type as being from the Venezuelan side of Mt. Roraima. Some subsequent authors (e.g. Peters 1951, Vaurie 1980) interpreted nomenclatural rules differently, and retained the name of *A. albigularis*, whereas others (e.g. Meyer de Schauensee 1970) followed Hellmayr (1917) in using *A. roraimae*. E. Eisenmann (p. 342 *in* Vaurie 1980), invoking Arts. 57 and 59(a) of the *International code of zoological nomenclature*, determined that the names *albigularis* and *albogularis* represent homonymous variable spellings, and are therefore primary homonyms under the Code. This solidified Hellmayr's (1917) interpretation, and subsequent authors (e.g. Ridgely & Tudor 1994, Hilty 2003, Remsen 2003) have adhered to the name *Automolus roraimae*.

However, confusion surrounding *Automolus roraimae* did not end with the resolution of its name. Wetmore & Phelps (1956) described *Philydor hylobius* (Neblina Foliage-gleaner) from two specimens (one tail-less adult and one juvenile) collected on Cerro de la Neblina in southernmost Venezuela. Mayr (1971) followed Wetmore & Phelps in recognising *P. hylobius*, and noted its similarity and probable relationship to the Black-capped Foliage-gleaner *P. atricapillus* of the Atlantic Forest of south-east Brazil. Vaurie (1980: 277) went further, stating that '*hylobius* needs more study, but seems to represent only an isolated population of *Philydor atricapillus*.' Dickerman *et al*. (1986) subsequently demonstrated that the two specimens of '*Philydor hylobius*' were, in fact, an erythristic adult and a juvenile of *Automolus roraimae*, differing from typical adults primarily in the ochraceous-tawny (rather than creamy white) supercilium and throat. The juvenile differed further in the presence of dusky scalloped fringes to the ventral feathers. Thus, *Philydor hylobius* Wetmore & Phelps, 1956, is a junior synonym of *Automolus roraimae* Hellmayr (Dickerman *et al*. 1986).

Throughout the period of nomenclatural confusion surrounding *Automolus roraimae* there has been ongoing speculation as to whether the species belongs in *Automolus*. Ridgely & Tudor (1994) suggested that it is better placed in *Philydor*, where it was described. Kratter & Parker (1997) seemed to suggest a closer relationship of *A. roraimae* to the genus *Syndactyla*, and Hilty (2003: 495) noted that whereas the species is 'almost certainly not an *Automolus*' its plumage characters are suggestive of *Philydor*, and its vocalisations of *Syndactyla* and *Anabazenops*. Remsen (2003) in the most comprehensive and recent treatment of the Furnariidae, reiterated all of these possibilities, but retained *roraimae* in *Automolus* pending further analysis.

During field work in the Sierra de Lema, Bolívar, Venezuela (KJZ) and Mt. Roraima, Guyana (MBR), we observed and tape-recorded multiple White-throated Foliage-gleaners. Our observations and recordings caused us to independently conclude that, based on vocal and ecological characters, it should be transferred from *Automolus* to *Syndactyla*. Generic transfers within the so-called 'foliage-gleaner clade' (subfamily Philydorinae) have been commonplace (Remsen 2003), particularly in recent years, as taxonomists have had access to a suite of vocal, ecological and molecular data unavailable to earlier workers (Parker *et al*. 1995, Kratter & Parker 1997, Robbins & Zimmer 2005). In an earlier paper (Robbins & Zimmer 2005), we presented evidence that the Planalto Foliage-gleaner (previously *Philydor dimidiatum*) should be transferred to *Syndactyla*. Here, we present vocal, syringeal, behavioural and ecological data that lead us to believe that *Automolus roraimae* is more closely related to species currently included in *Syndactyla* than to species currently in *Automolus* or *Philydor*.

Methods

We assume that vocalisations of foliage-gleaners, like those of other suboscines, are mostly or entirely inherited (Kroodsma 1984, 1989, Kroodsma & Konishi 1991), and consequently provide potentially informative characters for systematic study (Parker *et al*. 1995, Kratter & Parker 1997, Zimmer 1997, 2002, Remsen 2003). To analyse vocalisations, we assembled tape-recordings of all but one (*Philydor novaesi*) of the currently recognised species of *Automolus*, *Syndactyla*, *Philydor*, *Anabazenops* and *Simoxenops*. Our inventory provided sufficient material for most species in these groups, but we supplemented it with material from other recordists, and, in three instances, with material from commercially available compilations of bird recordings (see below). Sample sizes (=number of individuals) for each species are as follows: *Automolus roraimae* (9); *A. infuscatus* (79); *A. paraensis* (39); *A. leucophthalmus* (102); *A. ochrolaemus* (73); *A. rubiginosus* (8); *A. melanopezus* (7); *A. rufipileatus* (39); *Philydor rufum* (21); *P. lichtensteini* (35); *P. pyrrhodes* (6); *P. erythropterum* (15); *P. erythrocercum* (23); *P. atricapillus* (20); *P. ruficaudatum* (7); *Syndactyla subalaris* (22); *S. rufosuperciliata* (40); *S. guttulata* (1); *S. ruficollis* (8); *S. dimidiata* (15); *Simoxenops ucayalae* (14); *Anabazenops dorsalis* (28); and *Anabazenops fuscus* (38). We made auditory comparisons of all recordings, and visual comparisons of spectrograms of each species. Vocalisations selected for illustration here were deemed representative based on auditory comparison of the entire inventory, and on visual comparison of spectrograms of a smaller sample. Data accompanying recordings reproduced as spectrograms are provided in the figure legends. Locations and recordists for all recordings examined are given in Appendix 1.

Our study was conducted in conjunction with investigations into the taxonomic relationships of *Syndactyla dimidiata* (Robbins & Zimmer 2005), *Automolus infuscatus* (Zimmer 2002) and *A. leucophthalmus* (Zimmer 2008). In those papers, we presented spectrograms of *Syndactyla ucayalae*, six species of *Philydor* (*lichtensteini*, *atricapillus*, *erythropterum*, *erythrocercum*, *pyrrhodes* and *rufum*), and four species of *Automolus* (*infuscatus*, *paraensis*, *leucophthalmus* and *rufipileatus*). Additionally, Kratter & Parker (1997) published spectrograms of *Anabazenops fuscus* and *A. dorsalis*. Rather than duplicate previous work, we refer readers to those publications to view spectrograms of the vocal characters described verbally below. These spectrograms are cross-referenced in the Results section.

To facilitate interpreting our vocal data the following commercial sound compilations should be consulted: *Syndactyla rufosuperciliata* (Schulenberg 2000b); *S. subalaris* (Moore *et al*. 1999, Schulenberg 2000b); *S. guttulata* (Boesman 1999); *S. ruficollis* (Coopmans *et al*. 2004); *Simoxenops striatus* (Schulenberg 2000a); *S. ucayalae* (Schulenberg *et al*. 2000, Marantz &

Zimmer 2006); *Philydor rufum* (Moore *et al*. 1999, Lysinger *et al*. 2005); *P. fuscipenne* (Jahn *et al*. 2002); *P. erythrocercum* (Moore 1996, Schulenberg 2000a, Schulenberg *et al*. 2000, Lysinger *et al*. 2005, Marantz & Zimmer 2006); *P. pyrrhodes* (Moore 1996, Schulenberg *et al*. 2000, Marantz & Zimmer 2006); *P. erythropterum* (Moore 1996, 1997, Schulenberg *et al*. 2000, Marantz & Zimmer 2006); *P. ruficaudatum* (Schulenberg *et al*. 2000, Lysinger *et al*. 2005, Marantz & Zimmer 2006); *Anabazenops dorsalis* (Schulenberg *et al*. 2000, Lysinger *et al*. 2005, Marantz & Zimmer 2006); *Automolus ochrolaemus* (Schulenberg *et al*. 2000, Jahn *et al*. 2002, Marantz & Zimmer 2006); *A. infuscatus* (Schulenberg *et al*. 2000); *A. paraensis* (Marantz & Zimmer 2006); *A. rufipileatus* (Schulenberg *et al*. 2000, Marantz & Zimmer 2006); *A. rubiginosus* (Schulenberg *et al*. 2000, Jahn *et al*. 2002, Lysinger *et al*. 2005); and *A. melanopezus* (Schulenberg *et al*. 2000). Note that recordings from these sources are not included in our inventory, although the recordings of *Simoxenops striatus* (T. A. Parker recording from Bolivia; Schulenberg 2000) and *Philydor fuscipenne* (M. Lysinger recordings; Jahn *et al*. 2002) were consulted.

For comparison, vocalisations were categorised as loudsongs or calls. Loudsongs were consistently patterned multi-note vocalisations (Isler *et al*. 1997) given seemingly in the context of territorial advertisement. Vocalisations characterised as calls usually were structurally simple (typically involving well-spaced repetition of identical notes or pairs of notes), and most often were given in the context of contact notes between mates, as aggression calls during territorial conflicts with conspecifics, or in response to playback. Exceptions are noted in the results below. Our tape-recordings were made with Sony TCM-5000 and Sony TC-D5 Pro II recorders and Sennheiser ME-80, MKH-70 and ME-67 shotgun microphones. Spectrogram illustrations were made by P. R. Isler on a Macintosh G4 computer using Canary version 1.2.1 (Bioacoustics Research Program, Cornell Lab. of Ornithology, Ithaca, NY) and Canvas graphics software (version 5.0.3, Deneba Software, Miami, FL).

Syringes were cleared and double-stained following protocol in Cannell (1988), which distinguished cartilaginous (blue) and ossified (red) tissues. Several syringeal characters were analysed, including tracheal rings named as A and B elements, *Processi vocales* shape, *Membranae tracheales* characteristics, the *sternotrachealis*, *tracheolateralis* and *vocalis* muscles, and the presence or absence of some syringeal structures such as the 'drum' (a cylinder composed of two or more complete, fused A-elements). Nomenclature follows Ames (1971). Both before and after clearing and staining, syringes were placed in a small dissecting dish for examination under binocular magnification of 20–60×. CK examined syringeal characters of taxa listed in Appendix 2.

To assess plumage characters, we examined representative study skins of *Automolus roraimae*, and all currently recognised species in *Automolus, Philydor* (except *P. novaesi*), *Syndactyla* and *Anabazenops* (see Acknowledgments for institutions).

Behavioural and habitat data are from field work conducted by KJZ (Sierra de Lema, Bolívar, Venezuela) in 1987, 1991, 1992 and 2004, and by MBR (Guyana: north slope of Mt. Roraima, 05º06′N, 60º44′W) in 2001. All measurements used in behavioural data (distances, heights, etc.) are estimates.

Results

Vocalisations.—The loudsong of *A. roraimae* (Figs. 1a–c) is a slow, harsh rattle that peaks in amplitude mid-song and accelerates at the end. It typically comprises a stuttering prelude or preamble of higher frequency but lower amplitude notes with a distinctly nasal quality, that accelerates into a higher amplitude series of frequency-modulated, fairly evenly paced,

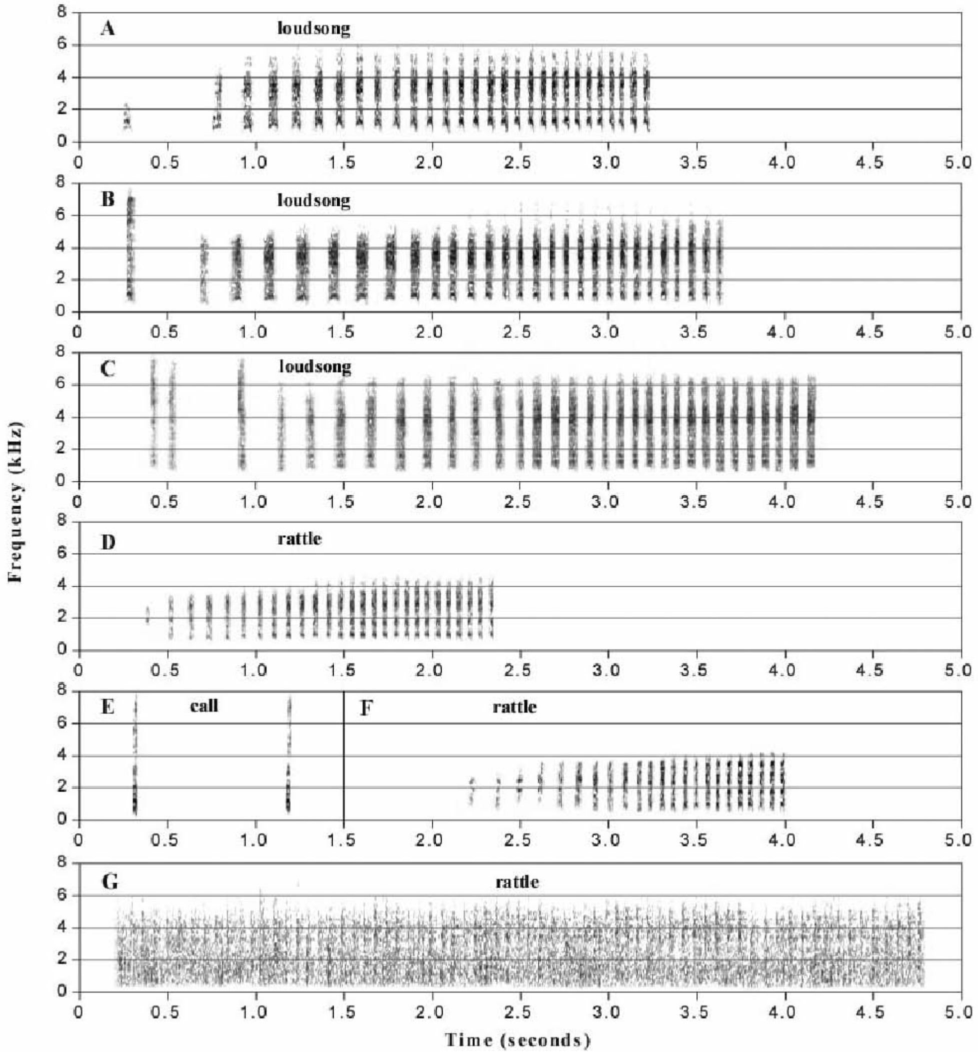


Figure 1. Vocalisations of *Automolus roraimae*. (a) loudsong, Mt. Roraima, Guyana (M. B. Robbins). (b) loudsong, Sierra de Lema, Bolívar, Venezuela (K. J. Zimmer). (c) loudsong, Sierra de Lema, Bolívar, Venezuela (K. J. Zimmer). (d) rattle, Sierra de Lema, Bolívar, Venezuela (K. J. Zimmer). (e) calls, Mt. Roraima, Guyana (M. B. Robbins). (f) rattle, Sierra de Lema, Bolívar, Venezuela (K. J. Zimmer). (g) long rattle, Sierra de Lema, Bolívar, Venezuela (K. J. Zimmer).

and strident, scratchy notes that may rise and fall somewhat in frequency (4–6 kHz) before accelerating to an abrupt conclusion. The harsh, distinctly scratchy quality of the notes is denoted in the spectrograms (Figs. 1a–c) by their relatively broad width. *Roraimae* loudsong was translated accurately by Hilty (2003: 494) as '*tzik . . . chek . . . tzik. .jjza-jjza-jjza-jza ja'ja'-ja'ja'ja*, the *jjza* series very harsh'. Loudsongs showed substantial variation, both within and among individuals. Songs varied greatly in overall length (2.0–5.0 seconds), and particularly in the presence or absence of a preamble, its length, and the extent to which it stuttered (vs. being evenly paced). These differences appeared to be exacerbated by playback and, depending on the degree of agitation, the differences within a single individual's songs could be marked. Some of the observed variation may be the result of sexual differences.

Apart from loudsongs, two other types of vocalisations were recorded from *roraimae*. One is a single-noted or doubled *TCHACK* or *ZHICK* (6–8 kHz) with a harsh yet nasal quality (Fig. 1e). These calls are given as contact notes between pair members that are separated while foraging. They are also given as aggression calls in response to playback. Individuals of a presumed pair gave single-note calls that differed qualitatively, with the calls of one bird sounding harsher, whereas the other sounded more nasal. The other vocalisation type is a harsh-sounding rattle, generally evenly paced but rising and falling slightly in frequency (*c*.4–6 kHz), and varying greatly in length (1–7 seconds) (Figs. 1d, 1f, 1g). As noted with loudsongs, variation in the rattle call length appears to be as great within individuals as between individuals, and is particularly susceptible to the influence of playback. Rattle calls are often given immediately before or after loudsongs, but are also given as antagonistic calls in response to playback. Birds responding to playback consistently give longer rattles.

Our song analyses included all five currently recognised species of *Syndactyla* (*subalaris*, *ruficollis*, *rufosuperciliata*, *guttulata* and *dimidiata*). Loudsongs of these species (Figs. 2a, 2c, 2e, 2g, 2h; *guttulata* not shown) are remarkably similar in pattern and quality, and consist of a series of nasal or scratchy, chattering notes (1.5–8.5 seconds in duration, delivered at *c*.5–8 kHz) that usually accelerate markedly toward the end and often terminate abruptly. The terminal, more closely spaced notes are usually less nasal or scratchy in quality compared to the introductory and middle song notes, as evidenced by note-width differences. As in *roraimae*, songs of the four *Syndactyla* (only one song of *guttulata* was available, so it was excluded from this part of the analysis) vary greatly in length, and somewhat in frequency shifts and pace changes (acceleration or deceleration within the song), both within and among individuals. These parameters are influenced by playback and the bird's state of agitation. Calls of all five *Syndactyla* species (Figs. 2b, 2d, 2f, 2i) are also remarkably uniform between species, consisting of a harsh, nasal *TCHEK*, *TCHECH* or *TCHAK* (6–8 kHz), and a harsh, generally evenly paced rattle of varying length, delivered at *c*.4–6 kHz (Fig. 2j; *guttulata* is not shown).

Loudsongs of *Simoxenops ucayalae* resemble those of *A. roraimae* and the five *Syndactyla* in being a long series of closely spaced, harsh notes with a distinctly nasal quality (Robbins & Zimmer 2005; Figs. 2g–h). They are lower in frequency (*c*.3–4 kHz) than the loudsongs of *Syndactyla*, but vary similarly in overall song-length (*c*.3–5 seconds), frequency shifts, and pace changes (acceleration and deceleration) between songs from the same individual. As in *roraimae* and the *Syndactyla* species, this variation is influenced by playback and by the degree of agitation of the responding bird. In contrast to the five *Syndactyla*, the loudsongs of *Simoxenops ucayalae* typically accelerate more markedly over the first part of the song and slow toward the end, but still end abruptly. In this respect, they are most similar to loudsongs of *Syndactyla dimidiata*, which often begin with a preamble of closely spaced notes that then slow to the main series of more widely spaced nasal notes. Loudsongs of *S. ucayalae* are also similar to those of *Syndactyla dimidiata* in often beginning with a stuttering start of lower frequency and lower amplitude notes. Our inventory contains only a single recording of *Simoxenops striatus*, precluding generalisations about its vocalisations; however, loudsongs of the single *striatus* example are similar to those of *ucayalae* in pattern and quality. The call of *S. ucayalae* is a harsh, nasal *TCHAK* (Robbins & Zimmer 2005; Fig. 2i), similar to that of *roraimae* and the five *Syndactyla* species surveyed.

In contrast to *Syndactyla* and *Simoxenops*, the seven species of *Automolus* show little internal cohesion in vocal characters, which may indicate that the latter genus is not monophyletic. The loudsongs of *A. infuscatus* and *A. rufipileatus* are slightly descending rattles similar to one another in pace, pitch and note shape, but which differ in length and pattern. The rattle of each species comprises an evenly paced series of rapid similar notes delivered

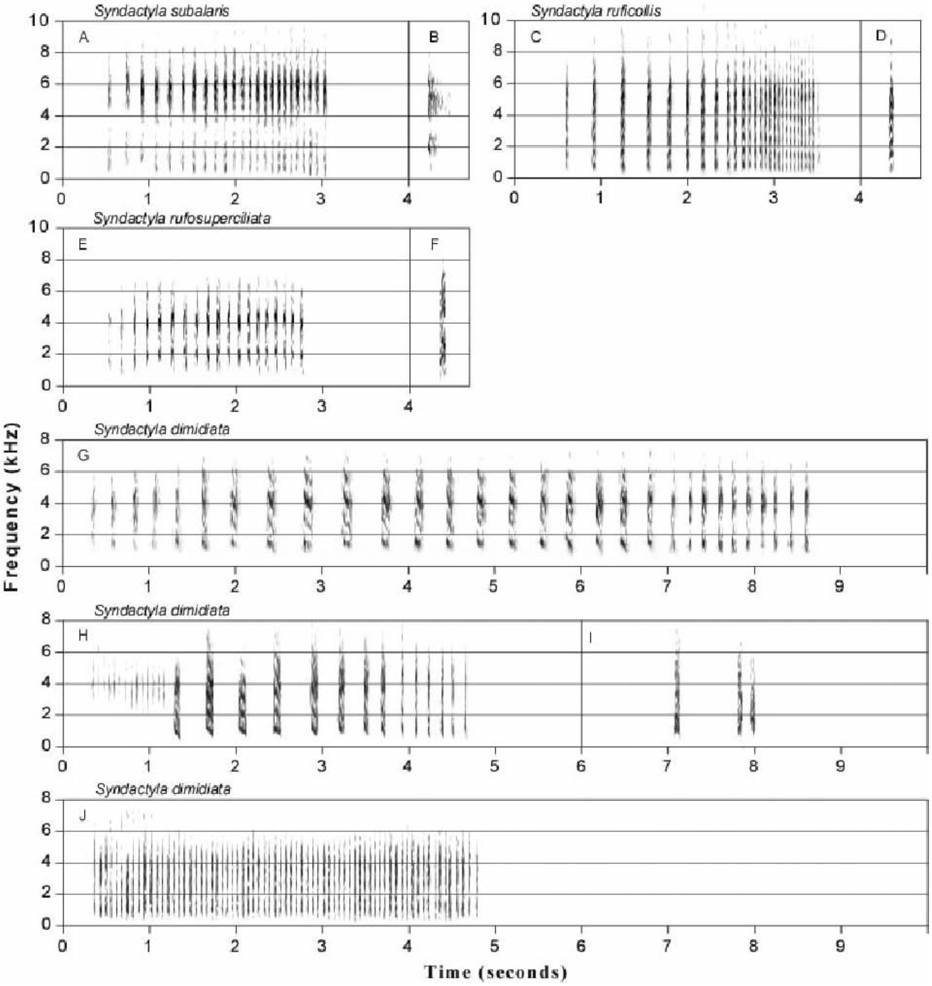


Figure 2. Vocalisations of various species of *Syndactyla* foliage-gleaners. (a) *Syndactyla subularis*: natural song, Monteverde Cloud Forest Reserve, Costa Rica (March 1994). (b) *Syndactyla subularis*: single-note call, Cerro de la Muerte, Costa Rica (March 1997). (c) *Syndactyla ruficollis*: natural song, Abra Porculla, dpto. Piura, Peru (24 January 2001). (d) *Syndactyla ruficollis*: single-note call, Abra Porculla, dpto. Piura, Peru (24 January 2001). (e) *Syndactyla rufosuperciliata*: natural song, Serra do Caraça, Minas Gerais, Brazil (6 September 2001). (f) *Syndactyla rufosuperciliata*: single-note call, Itatiaia National Park, Rio de Janeiro, Brazil (21 October 1998). (g) *Syndactyla dimidiata*: responsorial song of male–female duet, Brasília National Park, Distrito Federal, Brazil (20 August 2002). (h) *Syndactyla dimidiata*: initiating song of male–female duet, Brasília National Park, Distrito Federal, Brazil (20 August 2002). (i) *Syndactyla dimidiata*: call notes, Brasília National Park, Distrito Federal, Brazil (20 August 2002). (j) *Syndactyla dimidiata*: rattle call in response to playback, Patos de Minas, Minas Gerais, Brazil (27 December 1996; A. Whittaker). All recordings by K. J. Zimmer unless otherwise noted. All spectrograms by P. R. Isler.

at a rate too fast for the human ear to clearly distinguish individual notes (Zimmer 2002; Figs. 4, 7). The loudsong of *A. paraensis* is a loud series of 2–17 well-spaced, frequency-modulated notes, each of which has a particularly harsh, grating quality (Zimmer 2002; Fig. 3). The number of notes and the length of songs frequently vary within a song bout from the same individual. Categorisation of *A. ochrolaemus* songs is difficult as a result of the high degree of geographic vocal variation within the complex, the nature of which is the subject of ongoing investigation. However, loudsongs of the four recognised South American subspecies of *ochrolaemus* (*pallidigularis*, *ochrolaemus*, *turdinus* and *auricularis*) are similar to one another in consisting of a descending series of 4–8 countable, nasal notes (but lacking frequency modulation, and thus, any scratchy or harsh quality), often with a low-amplitude, terminal rattle. The loudsongs of *A. rubiginosus* also vary geographically, but all can be categorised as consisting of slowly delivered, two-syllabled or diphthongal nasal notes resembling vocalisations of some *Synallaxis* spinetails (pers. obs.) and totally unlike the loudsongs of any other *Automolus*. The loudsong of *A. melanopezus* is also divergent, consisting of 2–3 well-differentiated, introductory *WHIP* notes, followed by a rapid, uncountable burst of closely spaced notes. The loudsong of *A. leucophthalmus* consists of a barely countable series of 2–12 closely spaced doublets, the individual notes of which are clear in tone and lack frequency modulation (Zimmer 2008; Figs. 3–4). The subspecies *A. leucophthalmus lammi* differs from others in the complex in that the loudsong consists of a countable series of closely spaced, frequency-modulated notes or doublets, each of which has a particularly harsh, grating quality, similar to that of the song notes of *A. paraensis* (Zimmer 2008; Fig. 2). As in *A. paraensis*, all subspecies of *A. leucophthalmus* vary the number of notes and length of songs within an individual song bout.

As is the case with loudsongs, calls of the seven species of *Automolus* differ noticeably from those of *A. roraimae*, *Syndactyla* and *Simoxenops*, and vary markedly within the genus. The most common call of *A. paraensis* is a loud, single-noted *quip* or *queep* with a distinctly liquid quality (Zimmer 2002; Figs. 3e–g). A less frequently given long call is a series of 4–10 *quip* notes that accelerate after the initial note and then slow toward the end (Zimmer 2002; Fig. 3h). The most commonly heard call from *A. infuscatus* is a two-noted *chik-uh* or *chik-it*, in which the first note is higher pitched than the second (Zimmer 2002; Figs. 5a–b, g–h). A sharp, squeaky, single-noted *chik* is also given (Zimmer 2002; Figs. 5c, d, i). All taxa in the *A. leucophthalmus* complex give single-note *kwek* and double-noted *kwek-kwaah* calls (Zimmer 2008; Figs. 2i–j, 3g–i, 4d–e) that are similarly liquid in quality, and possibly homologous to the calls of *A. paraensis* and *A. infuscatus*. *A. leucophthalmus* also has a long call of 8–20, liquid *weck* notes, with or without a differentiated preamble, which varies both geographically and individually (Zimmer 2008; Figs. 2g–h, 3e–f). Calls of *A. ochrolaemus* are difficult to characterise due to geographic variation between subspecies, but most taxa give a harsh, somewhat buzzy single-noted *djurr*, *jraah* or some permutation thereof, which is completely different in quality from the calls of *paraensis*, *infuscatus* and *leucophthalmus*. The typical call of *A. rufipileatus* is a guttural, single-noted *jowp*, closer to the calls of the *A. ochrolaemus* complex, but still quite different. Our relatively small inventories of *A. melanopezus* and *A. rubiginosus* contain only loudsongs, precluding any generalisations concerning their respective calls.

The eight species of *Philydor* surveyed can be divided into three vocal groups based on differences in loudsongs. The first group includes Ochre-breasted Foliage-gleaner *P. lichtensteini* and the various subspecies comprising the Rufous-rumped Foliage-gleaner *P. erythrocercum*. Loudsongs of these species (Robbins & Zimmer 2005; Figs. 3a, 3d) consist of a countable series of distinctly spaced, sharp or squeaky notes. The second group includes Black-capped Foliage-gleaner *P. atricapillus*, Chestnut-winged Foliage-gleaner *P. erythropterus* and Cinnamon-rumped Foliage-gleaner *P. pyrrhodes*. Loudsongs in this group (Robbins & Zimmer 2005; Figs. 3b–c, 3e) consist of a long series of uncountable, closely spaced notes that form a trill. In general, these songs show relatively slight changes in frequency from start to finish, although the song of *P. pyrrhodes* is distinguished by a distinct change in amplitude beginning with the middle third of the song (Robbins & Zimmer 2005; Fig. 3e). The third group includes Buff-fronted Foliage-gleaner *P. rufum*, Rufous-tailed Foliage-gleaner *P. ruficaudatum*, and Slaty-winged Foliage-gleaner *P. fuscipenne*. Loudsongs of these species (Robbins & Zimmer; Fig. 3f) are somewhat intermediate (relative to those of the other two groups) with respect to the number of notes and the spacing. They could be characterised as rattles that change in pace and/or frequency (sometimes several times) over the course of the song, and that have a more 'staccato' or 'ratchet' quality. None of the eight species considered here has a loudsong whose notes could be characterised as imparting (either individually, or in entirety) a 'nasal' or 'scratchy' quality. In marked contrast to *A. roraimae*, the various *Syndactyla* species and *Simoxenops ucayalae*, none of the eight species of *Philydor* showed any tendency for marked intra-population variation in song characters, either within or among individuals. Also in contrast to *A. roraimae*, *Syndactyla* spp., and *Simoxenops ucayalae*, the *Philydor* species did not conspicuously alter the length or patterns of their loudsongs in response to playback. However, in response to playback, *P. pyrrhodes* does regularly give a long, low-amplitude rattle call that is similar to the loudsong but without shifts in amplitude, pace, or frequency (KJZ unpubl.).

Calls of the eight *Philydor* species (excluding *novaesi*) show no unifying threads, and vary considerably between species. Calls from our inventory are as follows: (a) *erythrocercum*—an explosive, somewhat squeaky *SQUEET!* or an ascending, loud *WHEEEK!*; (b) *ruficaudatum*—a thin, brittle rattle *tsissiitt* with the quality of a waxwing (*Bombycilla*); (c) *fuscipenne*—a thin, sharp *cheet* or *steet*, and a short, stacatto *chidideet*; (d) *rufum*—a hard *JIK!*; (e) *atricapillus*—a squealing, loud *SKEW* or *SPREE*, and a loud series of 3–4 ascending whistled *TWEEEET* notes; (f) *lichtensteini*—a thin, abbreviated fast rattle *skit't't'r'r'r'tt*; (g) *erythropterum*—a shrill *KREEEAH* or *KREEER*; (h) *pyrrhodes*—a hard *chidit* or *chikit*, and, in response to playback, a prolonged, low-amplitude rattle (sometimes lasting up to 30 seconds).

Vocalisations of the two *Anabazenops* (Kratter & Parker 1997; Fig. 3) are similar in many respects and, although exhibiting some similarities in pattern, are very different in tonal quality, note shape, pace and frequency from those of *A. roraimae* or *Syndactyla*. The loudsong of *Anabazenops dorsalis* is a series of 5–25 widely spaced clucking notes that start quickly before slowing to an even pace, and which have an overall flat pattern of peak frequency (*c*.1.5–2.5 kHz), but which peak in amplitude mid-song (*kek-kek-kek CLOCK CLOCK CLOCK CLOCK CLOCK CLOCK*). As in *roraimae*, all *Syndactyla* species and *Simoxenops*, *Anabazenops dorsalis* loudsongs are variable within and among individuals, in both the number of notes and in the presence or absence and length of any stuttering preamble. This variation seems, in part, a function of agitation level. Foliage-gleaners in agonistic encounters or ones responding to playback generally give longer songs, and are more likely to include a lower amplitude, chattering preamble to the song. The most commonly heard call of *A. dorsalis* is a single-note *jek*, which is a somewhat harsher version of the introductory notes of the loudsong. Less frequently heard is a long, harsh chatter or rattle of variable length (up to 84 seconds) that resembles a lower amplitude version of the rattle call of a Ringed Kingfisher *Megaceryle torquata*. This call is most frequently given in agonistic encounters with conspecifics or following playback. A shortened and more stuttering version of this call is often given as the chattering prelude to the loudsong. The loudsong of *Anabazenops fuscus* is a similar but somewhat faster paced series of 4–30+ countable, evenly paced *jeck* notes (*c*.2.0–3.0 kHz), which may or may not be preceded by a lower amplitude, chattering preamble. The chatter call of *A. fuscus* can vary in length, but never reaches the extremes of >60 seconds of *A. dorsalis*. As in *A. dorsalis*, there is much inter- and intra-individual variation in the songs of *A. fuscus*, primarily pertaining to the length of the song and the presence or absence of the chattering preamble. Other calls of *A. fuscus* include a harsh, single-note *jeck*, similar to the individual notes of the song, and an arresting series of 2–7, loud, squealing notes. Mated pairs of both *Anabazenops* commonly engage in antiphonal duets, which are variable in nature. These often involve one member of the pair giving a typical loudsong, while the other gives a sustained chatter or rattle call.

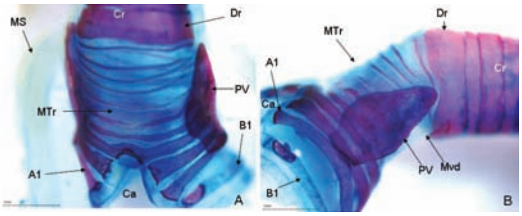
Syringeal morphology.—The *A. roraimae* syrinx is a typical tracheophone syrinx, with B and the first two A elements divided. Two narrow flat bars (*Processi vocales*) are fused posteriorly by elastic connective tissue to the lateral surfaces of the A-1 and A-2 elements (Figs. 3a–b). In lateral view this structure is broader caudally, thinner cranially, but 'rounded' in shape (Fig. 3b). The *Membranae tracheales* begin at the A-3 element, which is complete. This membrane has 6–7 crossbars that are A elements, none of which is exceptionally thin (within the *Membranae* each element is about one-fifth the width of the unmodified A-element). This structure is limited caudally by A-3, and the cranial limit is A-10 or A-11, so it consists of 7–8 small membranes. All elements within the limits of the *Membranae tracheales* cross it dorsally and ventrally (Fig. 3a). At the end of the *Membranae tracheales* there is a cylinder composed of two complete, partially fused A-elements forming a drum ('Dr' in Fig. 3).

The extrinsic muscle *M. tracheolateralis* inserts immediately cranial to the drum, whereas *M. sternotrachealis* inserts directly on the cranial end of the *Processus vocalis*. The intrinsic muscle pair *M. vocalis dorsalis* originates on the lateral and dorsolateral cranial edge of the drum, and the *M. vocalis ventralis* muscle pair originates on the lateral and ventrilateral surfaces of the same elements. These muscles insert on the dorsal or ventral caudal portion of the *Processus vocalis,* respectively (see characters 19 and 20, Appendix 3, for more details).

In lateral views of other *Automolus* syringes analysed, the caudal portion of the *Processus vocalis* is much wider than the cranial extreme, which is in all cases more acute than in *A. roraimae* (Fig. 4a, c, e, g, i and k; character 12, Appendix 3, especially so in some cases, like *A. infuscatus*, Fig. 4a). In *Automolus* species, when syringes are viewed ventrally (Fig. 4b, d, f, h, j and 1), the crossbars are thinner, being almost absent in *A. rubiginosus* (Fig. 4h, character 9, Appendix 3). The drums are thicker, with more elements that are more strongly fused (characters 15–14, Appendix 3, respectively). Although Raposo *et al*. (2006) found that the extent of element fusion within Dendrocolaptinae syringes is intraspecifically variable, we found no variation among three *roraimae* syringes examined.

The *Philydor* syringes (Fig. 5a–j) also have a *Processus vocalis* with an acute cranial extreme, except in *P. lichtensteini*. On the other hand, *P. pyrrhodes*, *P. erythrocercum* and *P. lichtensteini* have a pair of 'horns' on the ventral side of this structure (character 11, Appendix 3). This is particularly interesting because 'horns' in the *Processi vocales* were only known on both the ventral and dorsal sides of *Geositta* and dendrocolaptid species; indeed, this character was considered a Dendrocolaptinae synapomorph. The significance of this finding is the subject of an ongoing investigation by CK. The drum is strong and completely fused in *P. atricapillus*, *P. erythrocercum* and *P. pyrrhodes,* but there is no drum in *P. rufum* and *P. lichtensteini* (see character 14, Appendix 3). Although the number and extent of element fusion that comprise the drum may vary intraspecifically, it nonetheless is possible to identify the same extent of drum strength among individuals of the same species. The crossbars in the *Membranae tracheales* are very thin, especially in *P. rufum*.

Of *Syndactyla* syringes analysed, *dimidiata* (Figs. 5k–1, 6c–d), *subalaris* (Fig. 6g–h) and *rufosuperciliata* (Fig. 6a–b) had characteristics very similar to those of *A. roraimae*, with the *Processus vocalis* lacking an acute cranial extreme, having a 'rounded' shape in lateral view, and a drum with only two fused or semi-fused elements (=no well-developed drum) and *Membranae tracheales* with well-developed (not extremely thin) crossbars. Except for the lateral view of *Processus vocalis* of *A. leucophthalmus* (Fig. 4i), which is similar to that of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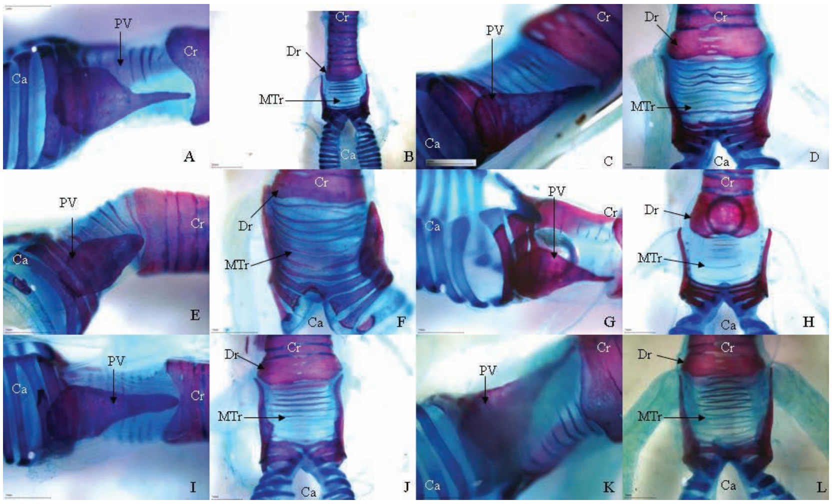
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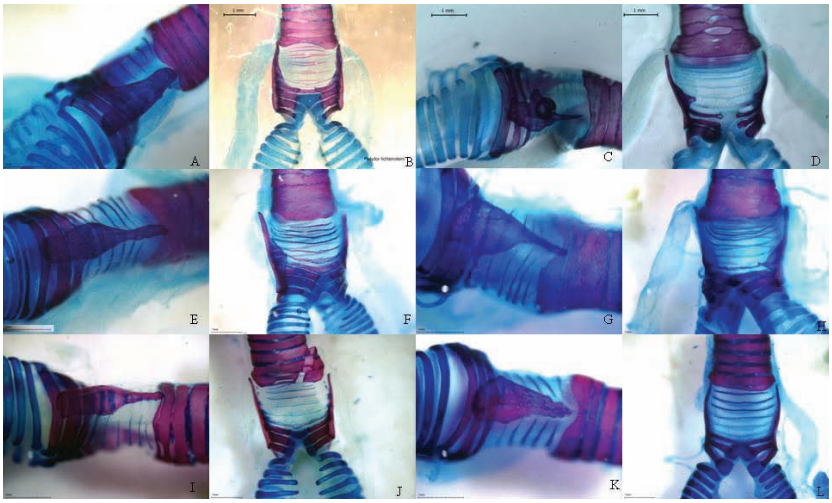
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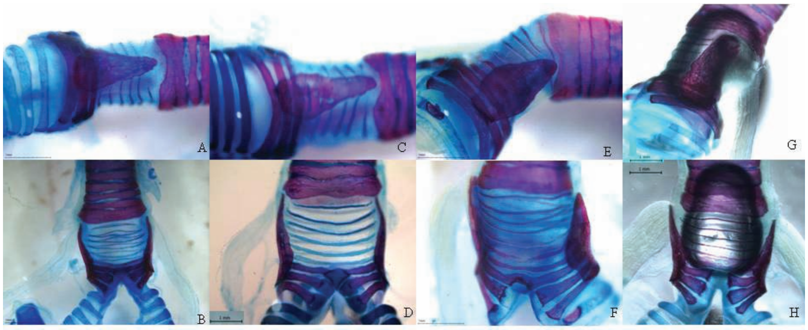
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6

Syndactyla dimidiata (Fig. 5k), these characteristics are not found in other *Automolus* and *Philydor* examined.

Characteristics of syringeal extrinsic and intrinsic muscles (*M. tracheolateralis*, *M. sternotrachealis*, and *M. vocalis ventralis* and *dorsalis*), were the same in *A. roraimae* and all other species analysed (see characters 17, 18, 21 and 22, Appendix 3), except for the caudal insertion of the intrinsic muscles (characters 19 and 20, Appendix 3).

Behaviour.—In the Sierra de Lema (Bolívar, Venezuela) and on the north slope of Mt. Roraima, Guyana, individuals or presumed pairs of *A. roraimae* occupied stunted, melastome-dominated, mossy forest, where they were most frequently seen at the edge of disturbed areas in a large matrix of pristine forest. Individuals were encountered more often than pairs, members of which foraged mostly in fairly close association with their presumed mates, maintaining contact through regular vocalisations. At Sierra de Lema, *roraimae* regularly associated with mixed-species flocks of other insectivores, but was nearly as often found away from such flocks. In contrast, during late March–early April 2001 on Mt. Roraima, birds were breeding and were not associated with mixed-species flocks. Specimen data from two females indicate that they had just laid eggs on 29 March and 5 April (KUMNH 93464–5). When associated with mixed-species flocks, individual foliage-gleaners exhibited a particular tendency to stay close to pairs of Streak-backed Antshrikes *Thamnophilus insignis*, following closely behind the antshrikes whenever they moved any significant distance. *A. roraimae* foraged *c*.0.5–9.0 m above ground, but primarily at 1–6 m, and often so low to the ground that their movements were obscured by dense vegetation. Progression was through a rapid series of short hops, or 'hitching', from side to side, in which the orientation of the body was changed relative to the position of the substrate, from one hop to the next. Much foraging was vertically directed along the main trunks of small trees and slender saplings, but individuals also moved in a lateral path along more open limbs and through vine tangles. Foliage-gleaners frequently wrapped their tails around slender trunks or branches as a sort of brace, particularly when moving vertically. Foraging birds regularly flicked both wings simultaneously, a movement that was usually accompanied by a simultaneous shallow vertical flick of the tail. Arthropod prey was mostly perch-gleaned from branch or vine surfaces by reaching, followed by a quick stab of

Captions to plates on opposite page:

Figure 3. Alizarine Red and Alcian Blue cleared and stained *Automolus roraimae* syrinx. (a) ventral view. (b) lateral view. References: A1: ring A1, B1: ring B1, Ca: Caudal part of the syrinx, Cr: Cranial part of the syrinx, Dr: Drum, MS: *Sternotrachealis* muscle, MTr: *Membrana trachealis*, Mvd: *Vocalis dorsalis* muscle, PV: *Processus vocalis*.

Figure 4. Alizarine Red and Alcian Blue cleared and stained syrinx of (a) *Automolus infuscatus* lateral view. (b) *A. infuscatus* ventral view. (c) *Automolus ochrolaemus* lateral view. (d) *A. ochrolaemus* ventral view. (e) *Automolus roraimae* lateral view. (f) *A. roraimae* ventral view. (g) *Automolus rubiginosus* lateral view. (h) *A. rubiginosus* ventral view. (i) *Automolus leucophthalmus* lateral view. (j) *A. leucophthalmus* ventral view. (k) *Automolus rufipileatus* lateral view. (1) *A. rufipileatus* ventral view. References: Ca: Caudal part of the syrinx, Cr: Cranial part of the syrinx, PV: *Processus vocalis*, MTr: *Membranae tracheales*, Dr: Drum.

Figure 5. Alizarine Red and Alcian Blue cleared and stained syrinx of (a) *Philydor lichtensteini* lateral view. (b) *P. lichtensteini* ventral view. (c) *Philydor erythrocercum* lateral view. (d) *P. erythrocercum* ventral view. (e) *Philydor atricapillus* lateral view. (f) *P. atricapillus* ventral view. (g) *Philydor pyrrhodes* lateral view. (h) *P. pyrrhodes* ventral view. (i) *Philydor rufum* lateral view. (j) *P. rufum* ventral view. (k) *Syndactyla dimidiata* lateral view. (1) *S. dimidiata* dorsal view.

Figure 6. Alizarine Red and Alcian Blue cleared and stained syrinx of (a) *Syndactyla rufosuperciliata* lateral view. (b) *S. rufosuperciliata* ventral view. (c) *Syndactyla dimidiata* lateral view. (d) *S. dimidiata* ventral view. (e) *Automolus roraimae* lateral view. (f) *A. roraimae* ventral view. (g) *Syndactyla subalaris* lateral view. (h) *S. subalaris* ventral view.

the bill. Acrobatic manoeuvres, such as hanging, were regularly employed, and on several occasions birds used their bill to hammer at nodes of branches, stems or dead leaves, frequently probing into moss on trunks or arboreal leaf litter suspended in vines. KJZ videotaped one individual that clung to a hanging dead branch while hammering and probing in the fractured end with its bill, much in the manner of a *Xenops*. Singing birds assumed a fairly upright (*c*.60–70º) position, usually on a more open branch. The tail was vibrated to the rhythm of the song, and the throat feathers were distinctly ruffled.

Discussion

The generic relationships of the many foliage-gleaners comprising the Philydorinae have long been disputed. Vaurie (1980) employed an expanded concept of the genus *Philydor* that included, among many others, the currently recognised genera *Syndactyla* and *Simoxenops*. Although Vaurie's views failed to gain wide acceptance, the generic placement of some foliage-gleaners has shifted among *Automolus*, *Philydor* and *Syndactyla*, suggesting that the plumage characters currently used to separate these genera are not well defined. The taxon *Syndactyla mirandae* was described from Goiás, Brazil, and for a time was treated as a subspecies of Buff-browed Foliage-gleaner *S. rufosuperciliata*, before it was determined to be synonym of *P. dimidiatum* (Remsen 2003). *P. dimidiatum*, in turn, was subsequently transferred to *Syndactyla* (Robbins & Zimmer 2005) as was Rufous-necked Foliage-gleaner *Automolus ruficollis* (Parker *et al*. 1985, Ridgely & Tudor 1994).

The presence or absence of streaking on either the upper- or underparts has traditionally been treated as a major plumage distinction within the Philydorinae (e.g. Vaurie 1980). Within the currently recognised *Syndactyla*, the trans-Andean *ruficollis* and *dimidiata* of south-central Brazil and east-central Paraguay are most divergent from the others in being largely unstreaked (Robbins & Zimmer 2005). The emphasis in earlier classifications on the presence or absence of streaking accounts for the placement of *ruficollis* and *dimidiata* in *Automolus* and *Philydor,* respectively. With the recent generic transfer of these species, *Syndactyla*, as currently constituted, now comprises a gradient of species, from heavily streaked on both dorsal and ventral surfaces (*subalaris*, *guttulata*), to heavily streaked only on the ventral surface (*rufosuperciliata*), to strongly flammulated ventrally (*ruficollis*), to only vaguely flammulated below (*dimidiata*). In an earlier paper (Robbins & Zimmer 2005), we recommended that the genus *Simoxenops* be subsumed into *Syndactyla*, and pointed out that the inclusion of (then) *Philydor dimidiatum* in *Syndactyla* bridged the perceived plumage morphological gap between *Syndactyla* and *Simoxenops*.

The ongoing debate as to whether *A. roraimae* belongs in *Automolus* or *Philydor* has been similarly based almost entirely on the perceived importance of plumage characters. Historically, there has been little or no discussion of the possibility that *roraimae* is a *Syndactyla*, primarily because *roraimae* is unstreaked, and prior to 1985, all species included in *Syndactyla* were boldly streaked. In addition to lacking streaking, *roraimae* has a striking white or cream-coloured throat that contrasts strongly with the darker underparts, and a bold white supercilium that contrasts strongly with the dark ear-coverts. In these characters, and in its overall plumage pattern, *roraimae* bears a striking resemblance to *Anabazenops dorsalis*, a species previously placed in *Automolus* based on plumage similarities to *Automolus infuscatus*, but since transferred to *Anabazenops* largely on the basis of vocal and ecological characters (Kratter & Parker 1997). Vaurie (1980: 293) used the shared characters of uniformly coloured upperparts (excluding the tail and rump), pale whitish throat and absence of streaking to suggest a possible close relationship between *A. infuscatus*, *A. leucophthalmus* and *Anabazenops dorsalis*, inexplicably excluding *A. roraimae* (which shares all of the same characters) from the discussion. In his key to *Automolus*, Vaurie (1980: 298) further noted that *A. albigularis* (=*roraimae*) and *dorsalis* also share a distinctly well-defined whitish supercilium and postocular streak.

Despite the striking similarity in plumage pattern of *roraimae* to these other species, it is increasingly apparent that such plumage similarities do not reflect phylogenetic relationships. Dusky-cheeked Foliage-gleaner *Anabazenops dorsalis* has been shown to belong in *Anabazenops* despite its plumage similarities to *Automolus infuscatus*, and all plumage characters used by Vaurie (1980) to unite those species can also be found in *Philydor erythrocercum*. Indeed, until recently (Dickerman *et al*. 1986) the emphasis on plumage characters in elucidating relationships among the foliage-gleaners had resulted in the classification of the juvenile of *roraimae* as a distinct species in a separate genus from the adult! The use of alternative plumage characters could lead to a completely different interpretation of generic relationships. The *roraimae* juvenile plumage differs from that of adults in having the supercilium and the underparts tinged rich ochraceous-buff, and in having dusky fringes to many of the breast feathers (Dickerman *et al*. 1986, Hilty 2003, Remsen 2003), a juvenile vs. adult plumage distinction which parallels that found in *Syndactyla subalaris* (Vaurie 1980, Remsen 2003), but which is without parallel in any species of *Automolus* (Kratter & Parker 1997, Remsen 2003). Unlike *roraimae*, none of the nine currently recognised species of *Philydor* has a well-defined white throat that contrasts strongly with much darker underparts, nor does any species of *Philydor* or *Automolus* possess a bold white supercilium and postocular streak. Conversely, two species of *Syndactyla*, *subalaris* and *guttulata*, are similar to *roraimae* in having a distinct pale supercilium and dark underparts that contrast strongly with a well-delineated pale (whitish or pale buff) throat, the principal difference being that those species are also boldly streaked above and below. In having a distinctly white throat and supercilium, *roraimae* most closely approaches *Anabazenops* (*dorsalis* and *fuscus*), but neither of these has sharply delineated, contrasting dark underparts, and *fuscus* has a bold, white hindcollar.

Other morphological characters are more suggestive of a close relationship between *A. roraimae* and *Syndactyla*. Like all *Syndactyla*, and both species of *Simoxenops*, *A. roraimae* has an upturned mandible, or 'ascending gonys' (Vaurie 1980, Remsen 2003), although the angle is not nearly as pronounced as in *Simoxenops*. Kratter & Parker (1997) presented morphometric data for 18 species of foliage-gleaners, including *roraimae,* three other species currently included in *Automolus* (*infuscatus*, *melanopezus* and *ochrolaemus*), and *Syndactyla rufosuperciliata*. In bill-length, bill-width, bill-depth and wing-chord, *roraimae* was distinctly smaller than the other three species of *Automolus*, but nearly identical to *S. rufosuperciliata*.

Additionally, syringeal morphology, which has been considered an important higher taxonomic character in suboscines, including Furnariidae (Müller 1878, Ames 1971, Remsen 2003) supports a relationship between *roraimae* and *Syndactyla*, whilst showing *roraimae* to be distinct from both *Automolus* and *Philydor* in *Processus vocalis* shape in lateral view, drum strength, and width of elements crossing the *Membranae tracheales.*

Excluding *A. roraimae*, *Automolus* and *Philydor* species examined had syringes in which the *Processi vocales* had an acute proximal extreme (except *A. leucophthalmus*) and a stronger drum consisting of more fused elements, as well as a *Membrana trachealis* in which the crossbars were extremely narrow or nearly lacking. In each of these characters, syringes of both *roraimae* and *S. dimidiata* more resembled those of the *Syndactyla* species examined (Fig. 6), thereby adding support for the inclusion of these two species within *Syndactyla*. Unfortunately, *Simoxenops* syringeal material was not available.

Because of the inherited nature of vocalisations within the suboscines (Lanyon 1978, Kroodsma 1984, Kroodsma 1989), vocalisations are often a strong indication of relationships within this group. Within the Furnariidae, vocalisations in concert with morphological and behavioral aspects have been used to elucidate relationships at the species and generic levels (Parker *et al*. 1985, Whitney & Pacheco 1994, Kratter & Parker 1997, Zimmer 1997, Remsen 2003, Robbins & Zimmer 2005). Indeed, Vaurie's (1971, 1980) systematic revisions of this family, which did not include vocal information, but were based primarily on plumage and external structural characters, led to conclusions that have not been generally accepted by the ornithological community (Fitzpatrick 1982, Sibley & Monroe 1990, Ridgely & Tudor 1994, Remsen 2003).

Vocal characters may provide the strongest argument for the relatedness of *roraimae* to *Syndactyla*. Loudsongs of the five *Syndactyla* species represented in our inventory were remarkably uniform in pattern and note quality. Calls of these species were also strikingly similar to one another. Indeed, vocalisations of all five are so similar that they are easily confused by the uninitiated listener. All are united by the harsh, nasal quality of their notes in both loudsongs and in calls, the accelerating pattern of the loudsong, the often stuttering start to the loudsong, and the variation in loudsong length, changes of pace, and frequency shifts displayed by individuals, particularly in response to playback.

The vocalisations of *A. roraimae* are strikingly similar to those of *Syndactyla*, and are not similar to those of any of the other recognised species of *Automolus, Philydor* or *Anabazenops*, none of which shares the distinctive nasal, scratchy quality that immediately distinguishes *roraimae*, *Syndactyla* and *Simoxenops*. Vocal similarities between *Simoxenops* and *Syndactyla* were first noted by Parker (1982), and have been amplified by subsequent authors (Parker & Bates 1992, Ridgely & Tudor 1994, Remsen 2003, Robbins & Zimmer 2005).

Willard *et al*. (1991) described the foraging behaviour of *roraimae* as primarily by 'probing in medium to large arboreal bromeliads', Kratter & Parker (1997) reported searches of clasping sheaths around bamboo nodes, and Hilty (2003) noted it probing in dead palm fronds. Behaviourally, *roraimae* is also a closer fit with *Syndactyla* in gleaning primarily from branch or vine surfaces, employing hammering or chiseling motions of the bill, in hitching up vertical trunks, and in often foraging apart from mixed-species flocks. The hammering or chiseling of substrates has been noted for *S. guttulata* (Hilty 2003), *S. rufosuperciliata* (Remsen 2003), *S. dimidiata* (Robbins & Zimmer 2005) and *S. ruficollis* (pers. obs.), and is a primary search manoeuvre of both *Simoxenops* (Parker 1982, Parker & Bates 1992, Zimmer *et al*. 1997, Remsen 2003). Conversely, this behaviour is rare or absent among species of *Automolus* and *Philydor*, most of which are dead-leaf specialists (Remsen 2003). One study, conducted in south-east Peru, showed that 88–100% of all search manoeuvres by each of four species of *Automolus* (*infuscatus*, *ochrolaemus*, *melanopezus* and *rufipileatus*) were directed to dead leaves. Less rigorously quantified observations of the foraging behaviour of *A. paraensis* and *A. leucophthalmus* from Brazil (Zimmer 2002, 2008) suggested that those two species directed more than 75% of their search manoeuvres to dead leaves as well. Although *roraimae* frequently inspects arboreal leaf-litter, such manoeuvres do not, in our experience, constitute an obvious majority of all foraging manoeuvres, nor is any such specialisation indicated in the scant literature (Willard *et al*. 1991, Hilty 2003, Remsen 2003). B. M. Whitney is cited (Kratter & Parker 1997) as having described the foraging behaviour of *roraimae* as being similar to that of *Syndactyla*, but without further elaboration. Although all *Syndactyla* species regularly associate with mixed-species flocks, they are less habitual in their attendance than are the species of *Philydor*, most of which are inveterate members of such flocks, and rarely encountered away from them (pers. obs.; Remsen 2003). Unlike the two species of *Anabazenops* (Kratter & Parker 1997), *roraimae* does not show any strong specialisation on bamboo.

In vocal characters, syringeal morphology, morphometrics and foraging behaviour, *roraimae* is much more like currently recognised species of *Syndactyla* than currently recognised species of *Automolus* or *Philydor*. It is somewhat divergent from *Syndactyla* with respect to its adult plumage pattern (although more similar in its juvenile plumage), which more closely resembles some *Automolus* and *Anabazenops*. Based on all other characters, these plumage similarities appear convergent and not reflective of relationship.

Taxonomic recommendation

We recommend that '*Automolus*' *roraimae* be placed in the genus *Syndactyla*; the name would thus become *Syndactyla roraimae* (Hellmayr). Because the adult plumage pattern of *roraimae* is unique among *Syndactyla*, whereas the vocalisations of all species in the genus are similar, it is difficult to identify its sister. Accordingly, we suggest that in a linear sequence, *roraimae* be placed at the beginning of the *Syndactyla*, reflecting its plumage uniqueness. At the same time, we acknowledge that a molecular-based analysis is required to recover phylogenetic relationships within the genus.

Hellmayr (1925) coined the English name of White-throated Automolus for *A. roraimae* and White-throated Foliage-gleaner has been used by most subsequent authors (e.g., Meyer de Schauensee 1970, Ridgely & Tudor 1994, Remsen 2003). Although not inaccurate, the modifier 'White-throated' could just as readily describe *A. leucophthalmus*, *A. infuscatus*, *A. paraensis* and *A. ochrolaemus pallidigularis*, as well as *Anabazenops fuscus* and *A. dorsalis*. Hilty (2003) used the English name of Tepui Foliage-gleaner for *A. roraimae.* Given that *roraimae* is a restricted-range species endemic to the Tepui Endemic Bird Area (Stattersfield *et al.* 1998, Remsen 2003), and that within this region it is found only in montane evergreen forest, primarily on the slopes and tops of tepuis, the name Tepui Foliage-gleaner is not only appropriate but is also more informative. We therefore recommend adopting the English name of Tepui Foliage-gleaner for *Syndactyla roraimae*.

Acknowledgements

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APPENDIX 1

Recording locations and recordists. Numbers following each name represent the number of individual birds recorded by the recordist at each site.

Automolus roraimae.—GUYANA: Mt. Roraima (M. B. Robbins, 4; MLNS 130494–7). VENEZUELA: Sierra de Lema, Bolívar (S. L. Hilty, 1; K. J. Zimmer, 4).

Automolus ochrolaemus.—BRAZIL: Alta Floresta region, Mato Grosso (K. J. Zimmer, 6); Borba region, Amazonas (K. J. Zimmer, 4); Lábrea region, Amazonas (K. J. Zimmer, 1); Manaus region, Amazonas (K. J. Zimmer, 2); Maués, Amazonas (K. J. Zimmer, 1); Rio Roosevelt, Amazonas (K. J. Zimmer, 1). COSTA RICA: Arenal (K. J. Zimmer, 2); Braulio Carrillo National Park (K. J. Zimmer, 9); Las Cruces OTS Station (K. J. Zimmer, 13); La Selva OTS Station (K. J. Zimmer, 1); Río Sierpe (K. J. Zimmer, 2). ECUADOR: Tiputini Biodiversity Center, Napo (K. J. Zimmer, 3). PANAMA: Nusagandi (K. J. Zimmer, 7). PERU: Hacienda Amazonia, dpto. Madre de Dios (K. J. Zimmer, 2); Manu Wildlife Center, dpto. Madre de Dios (K. J. Zimmer, 4); Tambopata Research Center, dpto. Madre de Dios (K. J. Zimmer, 2). VENEZUELA: Alechiven Camp, Amazonas (K. J. Zimmer, 4); Escalera Road, Bolívar (K. J. Zimmer, 4); Hato Las Nieves, Bolívar (K. J. Zimmer, 2); Junglaven Camp, Amazonas (K. J. Zimmer, 3).

Automolus infuscatus.—BOLIVIA: Suarez, Pando (T. A. Parker, 1). BRAZIL: Lábrea region, Amazonas (K. J. Zimmer, 1); left bank of rio Negro, north of Manaus, Amazonas (M. Cohn-Haft, 1; A. Whittaker, 1); Palmari Lodge, rio Javari, Amazonas (K. J. Zimmer, 5); Porongaba, Acre (A. Whittaker, 2); São Gabriel da Cachoeira, Amazonas (K. J. Zimmer, 3); Serra do Navio, Amapá (K. J. Zimmer, 1). ECUADOR: La Selva Lodge, Napo (R. A. Behrstock, 2; G. H. Rosenberg, 1); Santiago, Morona-Santiago (M. B. Robbins, 3; MLNS 49248, 49284, 77244); Tiputini Biodiversity Center, Napo (K. J. Zimmer, 15). GUYANA: Iwokrama Reserve (R. S. Ridgely, 1; M. B. Robbins, 1; MLNS 125886); Waruma River (M. B. Robbins, 3; MLNS 85740, 85755, 85760); Baramita (M. B. Robbins, 1; MLNS 125887). PERU: south bank of río Napo, 80 km north of Iquitos, dpto. Loreto (T. A. Parker, 2; G. H. Rosenberg, 1); Quebrada Sucusari, dpto. Loreto (T. A. Parker, 6); Yanamono, dpto. Loreto (G. H. Rosenberg, 2); Cocha Cashu, Manu National Park, dpto. Madre de Dios (T. A. Parker, 1); Tambopata Reserve, dpto. Madre de Dios (M. L Isler, 1; L. Kibler, 3; M. Palmer, 2; T. A. Parker, 16; G. H. Rosenberg, 1; A. van den Berg, 4; K. J. Zimmer, 1)

Automolus paraensis.—BRAZIL: Alta Floresta region, Mato Grosso (K. J. Zimmer, 20); Borba region, Amazonas (K. J. Zimmer, 2); Caxiuanã Forest Reserve, Pará (K. J. Zimmer, 11); Rio Roosevelt, Amazonas (K. J. Zimmer, 1); Serra dos Carajás, Pará (K. J. Zimmer, 5).

Automolus leucophthalmus.—BRAZIL: Augusto Ruschi Reserve, Espírito Santo (K. J. Zimmer, 4); Boa Nova, Bahia (A. Whittaker, 1); Caetés, Espírito Santo (K. J. Zimmer, 2); Crasto Reserve, Sergipe (K. J. Zimmer, 9); Fazenda Palmeiras, Bahia (K. J. Zimmer, 12); Iguaçu National Park, Paraná (K. J. Zimmer, 33); Itabeguara, Alagaos (K. J. Zimmer, 1); Linhares CVRD Reserve, Espírito Santo (K. J. Zimmer, 3); Murici Reserve, Alagaos (K. J. Zimmer, 5; C. A. Marantz, 3); Porto Seguro, Bahia (K. J. Zimmer, 2); Santa Teresa, Espírito Santo (K. J. Zimmer, 4); Serra do Caraça Natural Reserve, Minas Gerais (K. J. Zimmer, 2); Sooretama Biological Reserve, Espírito Santo (K. J. Zimmer, 1); Ubatuba, São Paulo (K. J. Zimmer, 17); Una Ecological Park, Bahia (K. J. Zimmer, 2); Volta Velha Reserve, Santa Catarina (K. J. Zimmer, 2)

Automolus melanopezus.—ECUADOR: Tiputini Biodiversity Center, Napo (K. J. Zimmer, 3). PERU: Tambopata Research Center, dpto. Madre de Dios (K. J. Zimmer, 4).

Automolus rubiginosus.—COSTA RICA: Las Cruces OTS Station (K. J. Zimmer, 4). ECUADOR: Tinalandia, Pichincha (K. J. Zimmer, 1); Tiputini Biodiversity Center, Napo (K. J. Zimmer, 2). VENEZUELA: Santa Elena, Bolívar (K. J. Zimmer, 1).

Automolus rufipileatus.—BRAZIL: Alta Floresta region, Mato Grosso (K. J. Zimmer, 19); Boa Vista, Roraima (K. J. Zimmer, 1); Fazenda Rancho Grande, Rondônia (K. J. Zimmer, 1); Rio Roosevelt, Amazonas (K. J. Zimmer, 1); São Gabriel da Cachoeira, Amazonas (K. J. Zimmer, 1); Serra dos Carajás, Pará (K. J. Zimmer, 6). PERU: Hacienda Amazonia, dpto. Cusco (K. J. Zimmer, 1); Manu Wildlife Center, dpto. Madre de Dios (K. J. Zimmer, 5); Tambopata Research Center, dpto. Madre de Dios (K. J. Zimmer, 3). VENEZUELA: Rio Caura, Bolívar (K. J. Zimmer, 1).

Philydor ruficaudatum.—BRAZIL: Serra dos Carajás, Pará (K. J. Zimmer, 5); Alta Floresta, Mato Grosso (K. J. Zimmer, 2).

Philydor erythrocercum.—BRAZIL: Caxiuanã Forest Reserve, Pará (K. J. Zimmer, 3); Fazenda Rancho Grande, Rondônia (K. J. Zimmer, 1); Alta Floresta region, Mato Grosso (K. J. Zimmer, 5); Lábrea region, Amazonas (K. J. Zimmer, 2); Maués, Amazonas (K. J. Zimmer, 1); Rio Mapiá, Borba region, Amazonas (K. J. Zimmer, 1); Rio Roosevelt, Amazonas (K. J. Zimmer, 5); Serra dos Carajás, Pará (K. J. Zimmer, 3); Tupana Lodge, Amazonas (K. J. Zimmer, 1). ECUADOR: Tiputini Biodiversity Station, Napo (K. J. Zimmer, 1).

Philydor erythropterum.—BRAZIL: Alta Floresta, Mato Grosso (K. J. Zimmer, 1); Fazenda Rancho Grande, Rondônia (K. J. Zimmer, 4); Lábrea region, Amazonas (K. J. Zimmer, 1); Rio Roosevelt, Amazonas (K. J. Zimmer, 2); Tupana Lodge, Amazonas (K. J. Zimmer, 1). ECUADOR: Tiputini Biodiversity Station, Napo (K. J. Zimmer, 4). PERU: Manu Wildlife Center, dpto. Madre de Dios (K. J. Zimmer, 2).

Philydor lichtensteini.—BRAZIL: Iguaçu National Park, Paraná (K. J. Zimmer, 25); Volta Velha Reserve, Santa Catarina (K. J. Zimmer, 3). PARAGUAY: dptos. Caazapá and Concepción (M. B. Robbins, 7; MLNS 120472–7).

Philydor atricapillus.—BRAZIL: Augusto Ruschi Reserve, Espírito Santo (K. J. Zimmer, 1); Fazenda Palmeiras, Bahia (K. J. Zimmer, 1); Garuva, Paraná (K. J. Zimmer, 1); Iguaçu National Park, Paraná (K. J. Zimmer, 6); Perequê, Rio de Janeiro (K. J. Zimmer, 1); Ubatuba region, São Paulo (K. J. Zimmer, 5); Una Ecological Park, Bahia (K. J. Zimmer, 1); Volta Velha Reserve, Santa Catarina (K. J. Zimmer, 3). PARAGUAY: dpto. Caazapá (M. B. Robbins; MLNS 120471).

Philydor rufum.—BRAZIL: Itatiaia National Park, Rio de Janeiro (K. J. Zimmer, 14); Augusto Ruschi Reserve, Espírito Santo (K. J. Zimmer, 1), Caetés, Espírito Santo (K. J. Zimmer, 3). PERU: Manu Wildlife Center, dpto. Madre de Dios (K. J. Zimmer, 1); Tambopata Research Center, dpto. Madre de Dios (K. J. Zimmer, 1). VENEZUELA: Henri Pittier National Park (K. J. Zimmer, 1)

Philydor pyrrhodes.—BRAZIL: Alta Floresta region, Mato Grosso (K. J. Zimmer, 1). GUYANA: Acari Mts., Rupununi, Barima River (M. B. Robbins, 3; MLNS 120478–80). PERU: Tambopata Research Center, dpto. Madre de Dios (K. J. Zimmer, 1). VENEZUELA: Yapacana National Park, Amazonas (K. J. Zimmer, 1).

Anabazenops dorsalis.—BRAZIL: Alta Floresta region, Mato Grosso (K. J. Zimmer, 20). PERU: Manu Wildlife Center, dpto. Madre de Dios (K. J. Zimmer, 2); Tambopata Research Center, dpto. Madre de Dios (K. J. Zimmer, 6).

Anabazenops fuscus.—BRAZIL: Boa Nova, Bahia (K. J. Zimmer, 1); Itatiaia National Park, Rio de Janeiro (K. J. Zimmer, 32); Santa Teresa region, Espírito Santo (K. J. Zimmer, 5).

Syndactyla subalaris.—COSTA RICA: Cerro de la Muerte (K. J. Zimmer, 1); Monteverde Cloud Forest Reserve (K. J. Zimmer, 12); Tapanti Faunal Reserve (K. J. Zimmer, 1). ECUADOR: Morona-Santiago (M. B. Robbins, 2; MLNS 41285 and 41287). PANAMA: Chiriquí (M. B. Robbins, 2; MLNS 120481–2; K. J. Zimmer, 2). PERU: Abra Patricia, dpto. San Martín (K. J. Zimmer, 2).

Syndactyla rufosuperciliata.—BRAZIL: Itatiaia National Park, Rio de Janeiro (K. J. Zimmer, 17); Espírito Santo (K. J. Zimmer, 2); São Francisco de Paula region, Rio Grande do Sul (K. J. Zimmer, 13); Serra do Caraça, Minas Gerais (K. J. Zimmer, 4); Serra da Graciosa, Paraná (K. J. Zimmer, 1). PARAGUAY: dpto. Caazapá (M. B. Robbins, MLNS 120483). PERU: Cosñipata Road, dpto. Cusco (K. J. Zimmer, 2).

Syndactyla guttulata.—VENEZUELA: Palmichal, Carabobo (P. Boesman, 1).

Syndactyla ruficollis.—ECUADOR: Loja (M. B. Robbins MLNS 57080). PERU: Abra Porculla, dpto. Piura (K. J. Zimmer, 6); Tumbes Reserved Zone, dpto. Tumbes (K. J. Zimmer, 1).

Syndactyla dimidiata.—BRAZIL: Brasília National Park, Distritio Federal (K. J. Zimmer, 5); Emas National Park, Goiás (K. J. Zimmer, 4); Patos de Minas, Minas Gerais (A. Whittaker, 1); Retiro das Pedras, Distrito Federal (K. J. Zimmer, 3). PARAGUAY: San Luis National Park (M. B. Robbins, 2; MLNS 120469–70).

Syndactyla (=*Simoxenops*) *ucayalae*.—BRAZIL: Alta Floresta region, Mato Grosso (K. J. Zimmer, 8); Serra dos Carajás, Pará (K. J. Zimmer, 4). PERU: Tambopata Research Center, dpto. Madre de Dios (K. J. Zimmer, 2).

APPENDIX 2

Syringes examined with country, sex, and institution catalogue numbers.

Anabacerthia variegaticeps.—PANAMA: male (KUNHM 86939)

Automolus roraimae.—GUYANA: females (KUNHM 93465; KUNHM 93464; NMNH 626785)

Automolus ochrolaemus.—GUYANA: male (KUNHM 92922)

Automolus infuscatus.—GUYANA: male (KUNHM 92921)

Automolus leucophthalmus.—PARAGUAY: male (KUNHM 88042)

Automolus rufipileatus.—GUYANA: male (KUNHM 89746)

Automolus rubiginosus.—ECUADOR: unsexed (KUNHM 65571); GUYANA: male (NMNH 621751)

Berlepschia rikeri.—GUYANA: male (NMNH 621990)

Hyloctistes subulatus.—PERU: male (KUNHM 87368)

Philydor erythrocercum.—GUYANA: males (KUNHM 89748–49)

Philydor lichtensteini.—PARAGUAY: male (KUNHM 88359)

Philydor atricapillus.—PARAGUAY: male (KUNHM 88043)

Philydor rufum.—PARAGUAY: male (KUNHM 87925)

Philydor pyrrhodes.—GUYANA: male (KUNHM 94833)

Syndactyla subalaris.—PANAMA: male (KUNHM 86937).

Syndactyla rufosuperciliata.—PARAGUAY: male (KUNHM 87921).

Syndactyla dimidiata.—PARAGUAY: female (KUNHM 88363); male (KUNHM 92935).

Thripadectes rufobrunneus.—PANAMA: male (KUNHM 86942)

APPENDIX 3

Syringeal characters from *Automolus*, *Philydor*, *Syndactyla* and related group species.

	1–5	6–10	11–15	16–20	21–22
Anabacerthia variegaticeps	10100	12011	1210?	?1120	00
Automolus roraimae	00111	1[12]201	03111	11111	00
Automolus ochrolaemus	00110	13202	01124	01120	01
Automolus infuscatus	00110	12113	01123	11121	01
Automolus leucophthalmus	00111	13114	02124	11121	00
Automolus rufipileatus	00120	13112	11123	01111	00
Automolus rubiginosus	00110	1002[01]	011[12][12]	11100	00
Berlepschia rikeri	20001	10211	02114	01133	00
Hyloctistes subulatus	00110	13114	01124	11120	00
Philydor erythrocercum	00101	12013	11122	01121	00
Philydor lichtensteini	00110	11211	22110	11110	01
Philydor atricapillus	00110	?2203	00023	11120	00
Philydor rufum	00110	11011	00010	01121	00
Philydor pyrrhodes	01121	11211	21122	11110	00
Syndactyla subalaris	00110	11200	13121	11121	00
Syndactyla rufosuperciliata	00111	11211	03120	11110	00
Syndactyla dimidiata	00111	11[02]11	0311[01]	11100	00
Thripadectes rufobrunneus	00111	03013	01123	01122	00

Description of syringeal characters

A and B elements: 1—Bronchial bifurcation beginning at element: (0) A-2, (1) A-3; 2—The composition of the elements is both osseous and cartilaginous from the element: (0) A-3, (1) A-2; 3—Ventral widening of the element A-3: (0) absent, (1) present; 4—Elements A-2 and A-3: (0) not fused, (1) dorsally fused, (2) dorsally and ventrally fused.

Membranae tracheales: 5—Caudal extreme of the ventral *Membrana trachealis* at element: (0) A-4, (1) A-3; 6—Caudal extreme of the dorsal *Membrana trachealis* at element: (0) A-2, (1) A-3; 7—Cranial extreme of the ventral *Membrana trachealis* at element: (0) A-9, (1) A-10, (2) A-11, (3) A-12; 8—*Membrana trachealis* elements are: (0) cartilaginous, (1) both, cartilaginous and ossified, (2) ossified; 9—*Membrana trachealis*: (0) with narrow elements, (1) with very narrow elements, (2) almost without elements.

Processi vocales: 10—Number of elements at the extension of *Processi vocales*: (0) 9, (1) 10, (2) 11, (3) 12, (4) 13; 11—Horns in *Processi vocales*: (0) absent, (1) present ventrally, short, (2) present ventrally, long; 12—*Processi vocales*: (0) narrow caudal extreme with narrowed cranial extreme, (1) broad caudal extreme with narrow cranial extreme, (2) broad cranial extreme and broader caudal extreme, (3) rounded; 13—Outline in lateral view of *Processus vocalis*: (0) it narrows abruptly, (1) it narrows smoothly.

Drum: 14—Drum A elements: (0) not fused (=no drum), (1) partially fused, (2) totally fused; 15—Drum cranial limit at element: (0) A11, (1) A12, (2) A13, (3) A14, (4) A15; 16—Elements which comprise the drum are: (0) more narrow dorsally and ventrally, (1) with uniform width.

Muscles—Intrinsic muscles: 17—Intrinsic muscles: (0) absent, (1) present; 18—Cranial insertion of *M. vocalis ventralis* and *dorsalis*: (0) anterior to the drum, (1) in the drum; 19—Insertion of ventral intrinsic muscles at element: (0) A-3, (1) A-4, (2) A-5, (3) A-6; 20—Insertion of dorsal intrinsic muscles at element: (0) A-3, (1) A-4, (2) A-5, (3) A-6. *Extrinsic muscles*: 21—*M. sternotrachealis* cranial insertion: (0) at the cranial extreme of *Processi vocales*, (1) at the cranial extreme of *Processi vocales* and the A elements cranial to *Membranae tracheales*; 22—*M. tracheolateralis* caudal insertion: (0) cranial to the drum or the element immediately cranial to *Membranae tracheales*, (1) in the drum or the element immediately cranial to *Membranae tracheales*.