

Short communication

A new genus for the Andean Green Pihás (Cotingidae)

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The diverse Neotropical suboscine passerines account for more than a tenth of all avian species. Most radiations within this group have received little systematic scrutiny since the historically standard classifications of Hellmayr (Cory & Hellmayr 1924, 1925, 1927, Hellmayr 1929). Recent advances in phylogenetic analysis and molecular systematics have produced exciting new opportunities for understanding higher-level phylogenetic relationships, species limits and evolutionary history of the Neotropical suboscine clade.

To maintain congruence between avian classification and developments in phylogenetic research, it is important to revise avian taxonomy to reflect new, well supported systematic findings. Often a traditional classification can be made phylogenetically meaningful with a minimum of changes: e.g. synonymizing a monotypic genus that renders another genus paraphyletic or ahistorical. Some results, however, require that new names be created to classify previously unrecognized clades accurately.

The cotingas (Cotingidae) are a diverse Neotropical family. Although the limits of the family have been in dispute for years, they are currently recognized to include the traditional genera of Snow (1979), the plantcutters (*Phytotoma*) (Lanyon & Lanyon 1988, Prum *et al.* 2000), Sharpbill (*Oxyruncus*) (Sibley *et al.* 1985, Sibley & Ahlquist 1990, Prum *et al.* 2000), the tityras (*Tityra*) (Prum 1990, Prum *et al.* 2000) and the *Schiffornis* group of Prum and Lanyon (Prum & Lanyon 1989, Prum *et al.* 2000) *Schiffornis*, *Laniocera*, *Laniisoma*, *Pachyramphus*, *Xenopsaris* and *Iodopleura*.

Snow (1982: 111) was first to suggest that the Andean green pihás – *subalaris* and *cryptolophus* – may be distantly related to the rest of the piha species within the traditional genus *Lipaugus* – *vociferans*, *unirufus*, *fuscocinereus*, *lanioides*, and *streptophorus*. Subsequently, in a test of the monophyly of the cotingas, Prum (1990) documented that *Lipaugus* species were morphologically quite divergent. The hindlimb arteries of *Lipaugus vociferans* revealed the derived heteromerous condition, typical

of most cotingas and manakins, in which the main arterial supply to the hindlimb is via the femoral artery (*A. femoralis*). In contrast, the main hindlimb arteries of both species of Andean green pihás, *Lipaugus subalaris* and *L. cryptolophus*, were ischiadic (*A. ischiadica*), an apparent reversal within cotingas to the primitive state found in most birds that also occurs in the cotinga genera *Rupicola*, *Phoenicircus*, *Carpornis*, *Pipreola*, *Ampelioides* and *Oxyruncus* (Prum 1990). Subsequent research on cotinga syringeal morphology (Prum unpubl. data) has revealed additional phylogenetically informative morphological differences between the Andean green pihás and the other members of *Lipaugus*. Most recently, a phylogenetic analysis of DNA sequences from a mitochondrial protein coding gene, cytochrome *b* (Prum *et al.* 2000), further supports the conclusion that the genus *Lipaugus* as traditionally constituted (Hellmayr 1929, Snow 1979) is polyphyletic.

In Prum (1990), I suggested that the species *subalaris* and *cryptolophus* be removed from *Lipaugus* Boie 1828, but I placed them erroneously in the genus *Lathria* Swainson 1837, which had been applied to these piha species in some previous classifications (e.g. Sclater 1888). Subsequently, D. F. Stotz (*in litt.*) brought to my attention that the type *Lathria* Swainson 1837 is *Muscicapa plumbea* Lichtenstein = *Muscicapa vociferans* Wied which is also the type species of the genus *Lipaugus*. Stotz correctly observed that the genus *Lathria* is thus not available for *subalaris* and *cryptolophus* if the type of *Lathria* remains in *Lipaugus*. He further opined that another junior synonym of *Lipaugus*, *Turdampelis* Lesson 1844, was unavailable for a genus including *subalaris* and *cryptolophus* alone, because the type of *Turdampelis* is *Turdampelis lanioides* Lesson, which I suggest should be included within *Lipaugus*. Thus, no genus name is available to include the newly recognized clade of *cryptolophus* and *subalaris*, and there are no strong data to support their placement in any other available cotingid genus. Herein, I propose a new genus name to include the species of this distinct clade of Andean green pihás:

Snowornis gen. nov.

Type species. *Lipaugus subalaris* Sclater. 1861. *Proceedings of the Zoological Society of London*, p. 210. Ecuador, Rio Napo.

Diagnosis. The genus is diagnosed by a combination of traits: (1) the insertion of the M. tracheolateralis on the lateral syringeal membranes between the A1 and B1 syringeal supporting elements, (2) the absence of intrinsic syringeal musculature, (3) mainly ischiadic hindlimb arterial supply, (4) largely olive-green plumage, with yellow eye ring, and yellow underwing coverts, and (5) partially concealed black crown patch in male or both sexes.

Etymology. The genus *Snowornis* is named in honour of Dr David W. Snow for his many contributions to our understanding of the ecology, behaviour, and systematics

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of the cotingas and manakins, and for his original insights into the role of frugivory in the evolution of polygyny and lek behaviour.

DISCUSSION

The diagnosis of the new genus *Snowornis* includes the species *S. subalaris* and *S. cryptolophus*, and excludes all other cotinga species. The recognition of *Snowornis* is justified by data from arterial and syringeal morphology, plumage, and mitochondrial DNA sequences that all support the monophyly of *Snowornis* and its distinctness from *Lipaugus*.

The members of *Snowornis* are easily diagnosed by the presence of largely olive-green plumage, yellow eye ring, yellow underwing coverts and a partially concealed black crown (Snow 1982). This black crown is found in both sexes of adult *cryptolophus*, but only in male *subalaris*. None of these plumage features occur in *Lipaugus*. The crown patch is clearly derived within cotingas and constitutes a distinct synapomorphy of the new genus. *Snowornis subalaris* can be further distinguished by its grey tail, undertail coverts and belly, whereas *S. cryptolophus* is characterized by entirely green tail and underparts.

Since Prum (1990), I have made additional observations of the hindlimb arterial supply in *Lipaugus*. In addition to *L. vociferans*, the derived femoral artery condition is also present in *unirufus*, *fuscocinereus* and *streptophorus*. (As yet, no spirit specimens are available for *L. lanioides* or *Chirocylla uropygialis*, Wood *et al.* 1982.) So, the derived femoral artery is uniformly present in all available members of *Lipaugus* and absent in *Snowornis*. The absence of the femoral state in *Snowornis* is a derived loss that is probably synapomorphy of *Snowornis* or a synapomorphy shared by *Snowornis* (Prum *et al.* 2000).

Recent syringeal observations document that *Lipaugus vociferans*, *L. unirufus*, *L. fuscocinereus*, and *L. streptophorus* all have a pair of intrinsic syringeal muscles that originate on the ventral surface of the syringeal element A4 and insert on the A1/B1 lateral membranes (Prum pers. obs.). These intrinsic muscles are derived within cotingas and a synapomorphy of *Lipaugus*. The loud and highly modulated vocalizations of *L. vociferans* (the Screaming Piha), *L. unirufus*, *L. fuscocinereus* and possibly *L. streptophorus* (Ridgely & Tudor 1994) imply that these intrinsic muscles function directly in vocal modulations. Similar vocalizations with rapid, intense volume modulations are known from *L. lanioides* and *Chirocylla uropygialis* (Ridgely & Tudor 1994), for which no syringeal specimens are available. Based on their vocal behaviour, however, it appears likely that *L. lanioides* and *C. uropygialis* also have these derived intrinsic muscles and are members of the monophyletic *Lipaugus* clade. In contrast, the syringes of *Snowornis subalaris* and *S. cryptolophus* lack intrinsic syringeal muscles, which is the general plesiomorphic condition for cotingas. The syringes of *S. subalaris* and *S. cryptolophus* are also quite distinct in

numerous other features from those of the members of *Lipaugus* (Prum pers. obs.). Both species of *Snowornis* are much less vocal than *Lipaugus* species. The vocalization of *S. subalaris* has been described as a 'clear and ringing two-noted whistle: churrrrrrr-ee!' (Ridgely & Tudor 1994). The vocalizations of *S. cryptolophus* are unknown.

A recent phylogenetic analysis of sequences from the mitochondrial protein coding gene cytochrome *b* supported a single phylogeny for 32 species representing 26 genera of cotingas (Fig. 1) (Prum *et al.* 2000). The phylogeny includes four main clades of cotingas which may be recognized as subfamilies: Tityrinae, Phytotominae, Rupicolinae and Cotinginae. The analysis included four species of pihas representing both genera: *S. subalaris*, *S. cryptolophus*, *L. unirufus* and *L. fuscocinereus* (Fig. 1). Among the 32 cotinga species analysed, the percentage sequence divergence over the 375 base pairs from the 3' end of the mitochondrial cytochrome *b* gene analysed var-

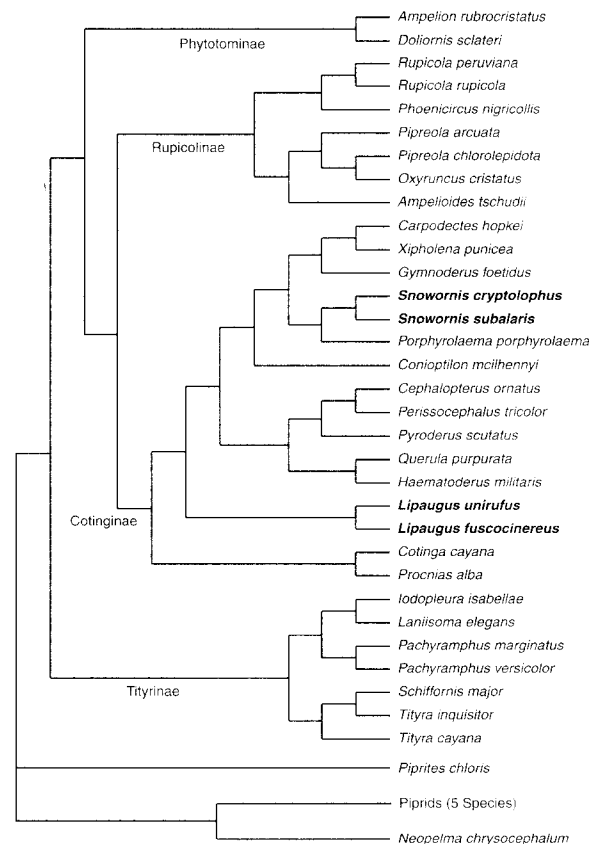


Figure 1. Single most parsimonious phylogenetic hypothesis for 32 cotinga species based on 375 base-pair sequences from the 3' end of the mitochondrial protein coding gene cytochrome *b* (Prum *et al.* 2000). This molecular phylogenetic hypothesis supports the monophyly of *Snowornis*, the monophyly of *Lipaugus* excluding *S. subalaris* and *S. cryptolophus*, and a distant phylogenetic relationship between *Snowornis* and *Lipaugus* within the subfamily Cotinginae. Species of *Snowornis* and *Lipaugus* are shown in boldface.

ied from 4.3% (*Cephalopterus ornatus* vs. *Perissocephalus tricolor*) to 25.7% (*Carpodectes hopkei* vs. *Laniisoma elegans*). Percentage observed sequence divergence between *S. subalaris* and *S. cryptolophus* was 10.8% and between *L. unirufus* and *L. fuscocinereus* was 12.8%. In contrast, the average percentage sequence divergence between the species of *Lipaugus* and *Snowornis* was 20.2% (19.0–21.2%). Furthermore, the most parsimonious phylogenetic hypothesis for these data identified both *Lipaugus* and *Snowornis* as exclusive monophyletic groups, and both of these clades were more closely related to other lineages within the subfamily Cotinginae (Fig. 1). Many of the specific branches within the Cotinginae in this hypothesis of phylogeny are not strongly supported (Prum *et al.* 2000). For example, there is little support for a sister group relationship between *Snowornis* and *Porphyrolaema*. However, the molecular data do not support any close relationship between *Snowornis* and *Lipaugus*.

In summary, derived features of the syrinx and molecular sequences support the monophyly of *Lipaugus* excluding *subalaris* and *cryptolophus*. As suggested by Remsen *et al.* (1982), *Chirocylla uropygialis* is distinguished only by its autapomorphous wing feather specializations, and should be placed within *Lipaugus*. *Lathria*, *Turdampelis*, and *Chirocylla* are all junior synonyms of *Lipaugus*. Derived plumage traits and molecular sequences support the monophyly of *Snowornis*, including only *subalaris* and *cryptolophus*. Additional variation in hindlimb arteries and molecular sequences further supports the conclusion that these two lineages of pihas are not closely related within the Cotinginae. Although the current hypotheses for the relationships among *Lipaugus*, *Snowornis*, and other cotinga genera are by no means final, data from different sources corroborate that the two genera of pihas are not closely related.

Snowornis subalaris and *S. cryptolophus* remain poorly known in nature (Snow 1982, Ridgely & Tudor 1994). The few reported observations indicate that these species are generally quiet denizens of humid upper tropical and humid lower montane forests of the Andes where they feed on both insects and fruit. *S. subalaris* apparently produces a clear two-note whistled call (Snow 1982, Ridgely & Tudor 1994), but there are no indications of lek behaviour in either species, as in many *Lipaugus* (Snow 1982, Ridgely & Tudor 1994). However, *Snowornis* belongs in Cotinginae which includes many other polygynous species. Further research on the natural history and phylogenetic relationship of the Andean green pihas will further elucidate the patterns of morphological, behavioural and ecological evolution within the cotingas. Lastly, continuing to refer to *S. subalaris* and *S. cryptolophus* as pihas would merely perpetuate the misimpression that these species are closely related to *Lipaugus*. Therefore, I recommend that *S. subalaris* and *S. cryptolophus* be referred to in English as the Grey-tailed Cotinga and the Olivaceous Cotinga respectively.

This paper is dedicated to Dr David W. Snow for his inspirational work on the display behaviour, breeding systems and evolution of manakins and cotingas. Douglas F. Stotz kindly pointed out the taxonomic error in my earlier paper (Prum 1990). Critical molecular and morphological specimens for this work were provided by the Academy of Natural Sciences of Philadelphia, American Museum of Natural History, British Museum (Natural History), Field Museum of Natural History, Louisiana State University Museum of Natural Science, and US National Museum of Natural History. The manuscript has been improved by comments from K. Bostwick, S. Hilty, A.T. Peterson, M. Robbins, K. Zyskowski, and two anonymous reviewers. This research was supported by a grant from the National Science Foundation (DEB-9318273).

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