



Pseudasthenes, a new genus of ovenbird (Aves: Passeriformes: Furnariidae)

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Abstract

Phylogenetic analysis of the family Furnariidae (Aves: Passeriformes) indicates that the genus *Asthenes* is polyphyletic, consisting of two groups that are not sister taxa. *Pseudasthenes*, a new genus of ovenbird, is described for one of these groups. The four species included in the new genus, formerly placed in *Asthenes*, are *P. humicola*, *P. patagonica*, *P. steinbachi*, and *P. cactorum*.

Key words: *Asthenes*, *Oreophylax*, *Schizoeaca*, phylogeny, taxonomy

Asthenes Reichenbach 1853, a genus of the Neotropical avian family Furnariidae, currently contains 22 species of small ovenbirds restricted to Andean and southern South American temperate and subtropical regions, where they inhabit open areas dominated by rocks, shrubs and grasses (Remsen 2003). Members of the genus, commonly known as canasteros, are extremely diverse in behavior, ecology, and nest architecture, suggesting that *Asthenes* is not monophyletic (Pacheco *et al.* 1996; Zyskowski & Prum 1999; Remsen 2003; Vasconcelos *et al.* 2008).

A recently published phylogeny of the Furnariidae provided the first genetic evidence of lack of monophyly in *Asthenes* (Irestedt *et al.* 2006). This phylogeny included two species of *Asthenes*, one of which—*A. cactorum* Koepcke (Cactus Canastero)—was sister to *Pseudoseisura* Reichenbach, whereas the other—*A. urubambensis* (Chapman) (Line-fronted Canastero)—formed a clade with *Oreophylax* Hellmayr and *Schizoeaca* Cabanis. Gonzalez and Wink's (2008) phylogeny of the Synallaxinae included three species of *Asthenes*. They found that *A. cactorum* and *A. humicola* (Kittlitz) (Dusky-tailed Canastero) formed a clade that was sister to *Pseudoseisura*, whereas *A. urubambensis* formed a clade with *Schizoeaca* and *Oreophylax*. In a broader genus-level study of the infraorder Furnariides, Moyle *et al.* (2009) found *Asthenes* to be paraphyletic with respect to *Schizoeaca* in that *S. helleri* Chapman (Puna Thistletail) was nested within a group that contained *A. humilis* (Cabanis) (Streak-throated Canastero), *A. urubambensis*, and *A. baeri* (Berlepsch) (Short-billed Canastero). These findings suggested the need for a new phylogenetic classification for taxa currently included in *Asthenes* and related genera.

As part of a project to reconstruct the phylogenetic relationships of all species in the Furnariidae from DNA sequences, our extensive taxon-sampling allowed us to determine conclusively that the genus *Asthenes* consists of two groups that are not sister taxa. One group consists of four species of *Asthenes* (*A. cactorum*, *A. steinbachi* (Hartert) (Steinbach's Canastero), *A. patagonica* (d'Orbigny) (Patagonian Canastero), and *A. humicola*), whereas the second group consists of all remaining species of *Asthenes* as well as all species sampled from the genus *Schizoeaca* and *Oreophylax*. The type species of *Asthenes* (*A. sordida* (Lesson), currently considered a subspecies of *A. pyrrholeuca* (Vieillot) (Sharp-billed Canastero)) belongs to the large second group. Because no generic name is available for the clade consisting of *A. cactorum*, *A. steinbachi*, *A.*

patagonica, and *A. humicola* (Cory 1919; Cory & Hellmayr 1925; see classification below) here we describe a new genus for these four species:

***Pseudasthenes*, genus nov.**

Type species. *Synallaxis patagonica* d'Orbigny, 1839

Included species. *Asthenes patagonica* (d'Orbigny 1839), *Asthenes cactorum* Koepcke 1959, *Asthenes humicola* (Kittlitz 1830), *Asthenes steinbachi* (Hartert 1909).

Diagnosis. We were unable to identify a synapomorphic phenotypic character for the genus, but the four species share the following features: small furnariids (15–22 g), with predominantly gray and brown plumage and no streaks on dorsal parts; gular patch feathers black and white, or dull orange (*P. cactorum*) but never a combination of black and orange; tail slightly longer than wing (tail/wing ratio 1.1–1.3), graduated (rectrix 6/rectrix 1 ratio 0.55–0.70), and composed of 12 blunt rectrices with well-integrated barbs (except for the tip in some species). Phylogenetic diagnosis: the most inclusive crown clade that includes *Asthenes patagonica* and *A. humicola* but not *Pseudoseisura lophotes* or *Spartonoica maluroides* (d'Orbigny & Lafresnaye) (Bay-capped Wren-Spintail).

Etymology. The generic name, from the Greek *pseudo* (false) and *asthenes* (insignificant, strengthless), denotes the outward resemblance of species of this genus to species of *Asthenes* but highlights the fact that they are not closely related. The name is feminine in gender.

Genetic analyses. A preliminary genetic analysis of our data from all furnariid species found that *Pseudasthenes* was sister to a clade composed of *Pseudoseisura* and *Spartonoica*. This preliminary analysis also indicated that *Asthenes*, as currently recognized, is not monophyletic because *Schizoeaca* and *Oreophylax* are nested within it. To demonstrate that *Asthenes* is not monophyletic, and to propose a new hypothesis for phylogenetic relationships among *Asthenes*, *Schizoeaca*, and *Oreophylax*, we present an analysis of a subset of taxa from this larger study. This restricted analysis includes all species of *Asthenes* except *A. heterura* (Berlepsch) (Maquis Canastero) and *A. berlepschi* (Hellmayr) (Berlepsch's Canastero), all species of *Schizoeaca* except *S. coryi* (Berlepsch) (Ochre-browed Thistletail), and *Oreophylax moreirae* (Ribeiro) (Itatiaia Spintail). We also included in the analysis the furnariids *Furnarius rufus* (Gmelin) (Rufous Hornero), *Leptasthenura aegithaloides* (Kittlitz) (Plain-mantled Tit-Spintail), *Cranioleuca erythroptus* (Sclater) (Red-faced Spintail), *Thripophaga fusciceps* Sclater (Plain Softtail), *Phacellodomus rufifrons* (Wied-Neuwied) (Rufous-fronted Thornbird), *Spartonoica maluroides*, *Xenerpestes singularis* (Taczanowski & Berlepsch) (Equatorial Graytail), *Pseudoseisura lophotes*, *Philydor pyrrhodes* (Cabanis) (Cinnamon-rumped Foliage-gleaner), *Automolus infuscatus* (Sclater) (Olive-backed Foliage-gleaner), and *Xenops minutus* (Sparrman) (Plain Xenops) (Table 1). We used the dendrocolaptid species *Dendrocolaptes sanctithomae* (Lafresnaye) (Northern Barred Woodcreeper) to root the tree.

TABLE 1. Tissue samples used in the genetic analysis.

Taxon	Museum	Sample ID	Locality
<i>Furnarius rufus</i>	AMNH	DOT10431	ARGENTINA: prov. Neuquén; depto. Confluencia, Centenario.
<i>Leptasthenura aegithaloides</i>	AMNH	DOT10306	ARGENTINA: prov. Neuquén; depto. Anelo, Sierra Auca Mahuida.
<i>Schizoeaca perijana</i>	ICN	AMC879	COLOMBIA: depto. Cesar; Mun. Manaure, Sábana Rubia.
<i>S. fuliginosa fuliginosa</i>	LSUMNS	B30039	ECUADOR: prov. Carchi; 8 km W Tufino.
<i>S. fuliginosa plengei</i>	LSUMNS	B8233	PERU: depto. Pasco; Millpo, E Tambo de Vacas on Pozuzo-Chaglla trail.
<i>S. vilcabambae</i>	FMNH	390681	PERU: depto. Junin; Cordillera Vilcabamba, headwaters Rio Pomureni.
<i>S. griseomurina</i>	LSUMNS	B34804	PERU: depto. Cajamarca; Cordillera del Condor; Picorana.

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<i>S. palpebralis</i>	LSUMNS	B49625	PERU: depto. Junin; E Comas, ca. 45 km NE Huancayo.
<i>S. helleri</i>	AMNH	DOT2479	BOLIVIA: depto. La Paz; prov. Franz Tamayo, Tojoloque, near Queara.
<i>S. harterti</i>	LSUMNS	B1271	BOLIVIA: depto. La Paz; 1 km S Chuspipata.
<i>Oreophylax moreirae</i>	DZUFMG	2841	BRAZIL: Minas Gerais; município de Catas Altas, Serra do Caraça, Pico do Inficionado.
<i>Asthenes pyrrholeuca</i>	LSUMNS	B56783	ARGENTINA: prov. Chubut; 22 km N Pta. Mugryn on Provincial road 1 to Pto. Lobos.
<i>A. baeri</i>	AMNH	DOT12134	ARGENTINA: prov. Buenos Aires; depto. Partido Patagones, ca. 35 km E Carmen de Patagones, on Ruta National 3.
<i>A. humicola</i>	AMNH	DOT12194	CHILE: prov. Chacabuco; Colina, El Potezuelo.
<i>A. patagonica</i>	LSUMNS	B56798	ARGENTINA: prov. Chubut; 75 km W Puerto Madryn, Estancia Sierra Colorada on Provincial Route 8.
<i>A. pudibunda</i>	LSUMNS	B103915	PERU: depto. Ayacucho; km 48 on Nazca-Puquio Road.
<i>A. ottonis</i>	LSUMNS	B61395	PERU: depto. Cusco; 1 km E Huacarpay.
<i>A. modesta</i>	LSUMNS	B103883	PERU: depto. Tacna; Tacna-Ilave Road, 25 km NE Tarata.
<i>A. cactorum</i>	LSUMNS	B103812	PERU: depto. Ica; 24 km on Nazca-Purquio Road.
<i>A. humilis</i>	FMNH	391862	PERU: depto. Lima; Maticuna.
<i>A. dorbignyi</i>	LSUMNS	95386	BOLIVIA: depto. La Paz; Huajchilla, 18 rd km S Calacoto.
<i>A. steinbachi</i>	AMNH	DOT10390	ARGENTINA: depto. Anelo; Sierra Auca Mahuida.
<i>A. luizae</i>	UFMG	B3066	BRAZIL: Minas Gerais; município de Cardeal Mota, Serra do Cipó.
<i>A. wyatti</i>	LSUMNS	B103905	PERU: depto. Puno; km 44 Juliaca-Arequipa Road ca. 18 road km E Santa Hucia.
<i>A. sclateri</i>	AMNH	DOT12103	ARGENTINA: prov. Córdoba; depto. Punilla, Pampa de Achala, 8 km E El Condor on Provincial Route 20.
<i>A. anthoides</i>	LSUMNS	B56816	ARGENTINA: prov. Chubut; 16 km WNW Rio Pico, Estancia Tres Valles Provincial Route 19.
<i>A. hudsoni</i>	USNM	B06349	URUGUAY: depto. Soriano; ca 9 km N of Cardona, at Estancia Santa Emilia.
<i>A. urubambensis</i>	LSUMNS	B8311	PERU: depto. Pasco; Millpo, E Tambo de Vacas on Pozuzo-Chaglla trail.
<i>A. flammulata</i>	LSUMNS	B32093	PERU: depto. Cajamarca; Quebrada Lanchal 8 km ESE Sallique.
<i>A. virgata</i>	LSUMNS	B61350	PERU: depto. Junin; 2 km N Casapalca.
<i>A. maculicauda</i>	AMNH	DOT2484	BOLIVIA: depto. La Paz; prov. Franz Tamayo, Tojoloque, Near Queara.
<i>Cranioleuca erythroptis</i>	LSUMNS	B1364	PANAMA: prov. Darién; 9 km NW Cana on slopes Cerro Pirre.
<i>Thripophaga fusciceps</i>	LSUMNS	B7607	BOLIVIA: depto. Beni; Cercado, 6 km by rd. SE Trinidad.
<i>Phacellodomus rufifrons</i>	AMNH	DOT2305	BOLIVIA: depto. Santa Cruz; prov. Velasco; 300 m N of Rio Mercedes.
<i>Spartonoica maluroides</i>	AMNH	DOT12089	ARGENTINA: prov. Buenos Aires; Reserva Punta Rasa.
<i>Xenerpestes singularis</i>	LSUMNS	B6301	ECUADOR: prov. Pichincha; Yanacocha, N Slope of Cerro Pichincha.
<i>Pseudoseisura lophotes</i>	AMNH	DOT6112	BOLIVIA: depto. Santa Cruz; prov. Cordillera, Izozog, Comunidad Karapari, Estancia San Julian, 1000 m W of Parapet.
<i>Philydor pyrrhodes</i>	AMNH	DOT8864	VENEZUELA: Amazonas; Mrakapiwie.
<i>Automolus infuscatus</i>	LSUMNS	B4283	PERU: depto. Loreto; Lower Río Napo region, E bank Río Yanayacu, 90 km N Iquitos.
<i>Xenops minutus</i>	AMNH	DOT8845	VENEZUELA: Amazonas; Mrakapiwie.
<i>Dendrocolaptes sanctithomae</i>	AMNH	DOT3689	COSTA RICA: prov. Puntarenas; 0.8 km NW Cuatro Cruces on Route 1.

Tissue collections: AMNH—American Museum of Natural History, New York City, USA; DZUFMG—Coleção Ornitológica do Departamento de Zoologia da Universidade Federal de Minas Gerais, Belo Horizonte, MG, Brazil; FMNH—Field Museum of Natural History, Chicago, USA; ICN—Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Columbia; LSUMNS—Louisiana State University Museum of Natural Science, Baton Rouge, USA; UFMG—Laboratório de Biodiversidade e Evolução Molecular da Universidade Federal de Minas Gerais, Belo Horizonte, MG, Brazil; USNM—National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.

Using the Qiagen DNeasy kit, genomic DNA was extracted from 25 mg of pectoral muscle following the manufacturer's protocol. We amplified and sequenced three mitochondrial genes (ND3, CO2, and ND2), as well as the autosomal nuclear gene beta-fibrinogen intron 7 (Bf7), following methods described in Chesser *et al.* (2007). For at least one individual per genus, two additional nuclear protein-coding genes (RAG1 and RAG2) were sequenced. Most of the RAG sequences from were taken from Moyle *et al.* (2009); samples of *Xenerpestes singularis*, *Pseudoseisura lophotes*, and *Oreophylax moreirae* were amplified and sequenced for this study, according to methods described in Moyle *et al.* (2009). Following alignment and the exclusion of unique inserts from Bf7, the six-gene concatenated dataset included 6,972 base pairs.

In model-based phylogenetic inference, there is a trade-off between modeling the evolutionary process as closely as possible and the risk of over parameterization (Sullivan & Joyce 2005; McGuire *et al.* 2007). In preliminary analyses using the Akaike Information Criterion (Sullivan & Joyce 2005) we identified the General Time Reversible model of nucleotide substitution with gamma distributed rate variation across sites (GTR + Γ) and a fully partitioned dataset (a different model for each position of each coding gene [15] and the nuclear intron) as the best model and partitioning regime. We then performed a Bayesian analysis as implemented in MRBAYES 3.1 (Altekar *et al.* 2004; Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003) on CIPRES Portal v1.15 (Miller *et al.* 2009). The Bayesian posterior probability density was estimated by Metropolis-coupled Markov chain Monte Carlo in two independent runs. Each run consisted of four incrementally heated chains, continued for 25 million generations, and was sampled every 2500 generations. All chains reached stationarity, the independent runs converged (split frequencies < 0.01), and all parameters met benchmark ESS values (>200) as evaluated in Tracer v1.4.1 (Drummond & Rambaut 2007). After discarding the first 5 million generations as burn-in, we computed a majority-rule consensus tree. Following methods in Chesser *et al.* (2009), we also performed a Maximum Likelihood (ML) analysis. The best tree from this analysis was identical to the majority-rule consensus tree; therefore, we do not include the ML results here.

All individuals of *Pseudasthenes* formed a strongly supported clade (posterior probability = 1.0) sister to the *Pseudoseisura-Spartonoica* clade (Fig. 1). All other *Asthenes* species (hereafter *Asthenes sensu stricto*), together with *Oreophylax moreirae* and all sampled species of *Schizoeaca*, formed a monophyletic group. These results demonstrate that *Pseudasthenes* and *Asthenes sensu stricto* do not form a clade. Although several authors have suggested that *Asthenes* is not monophyletic (Pacheco *et al.* 1996; Zyskowski & Prum 1999; Remsen 2003; Vasconcelos *et al.* 2008), the pattern of relationships that we found had not been predicted.

Asthenes is usually subdivided into at least two informal subgroups based on differences in plumage pattern, habitat, and nest architecture: a group of plain-plumaged species that inhabit deserts and dry forests and make nests of sticks, and a group of streaked species that inhabit grassy areas and make nests of grasses (Pacheco *et al.* 1996; Collias 1997; Remsen 2003). We recovered a strongly supported clade that corresponds to the streaked group of canasteros. Members of this lineage include *A. humilis*, *A. wyatti* (Sclater & Salvin) (Streak-backed Canastero), *A. sclateri* (Cabanis) (Puno Canastero), *A. anthoides* (King) (Austral Canastero), *A. hudsoni* (Sclater) (Hudson's Canastero), *A. urubambensis*, *A. flammulata* (Jardine) (Many-striped Canastero), *A. virgata* (Sclater) (Junin Canastero), and *A. maculicauda* (Berlepsch) (Scribble-tailed Canastero). In addition, we found that *A. modesta* (Eyton) (Cordilleran Canastero), a plain-looking species that constructs stick nests, is part of this clade.

On the other hand, the plain-plumaged, stick-nesting canasteros, considered by many to be a natural group, consist of at least two major clades (in addition to *A. humicola*, discussed above). Four belong to the newly described genus *Pseudasthenes*. Two other species, *A. dorbignyi* (Reichenbach) (Rusty-vented Canastero) and *A. baeri*, form a clade sister to the remaining species of *Asthenes sensu stricto* (Fig. 1). There

is a resemblance in morphology and habits between these two *Asthenes* species and *Pseudasthenes*. Further, they show a pattern of geographic replacement similar to that found in a species complex or even a superspecies (Remsen 2003). After careful examination of specimens of these species, mostly study skins but also some skeletons, we were unable to find diagnostic characters that unequivocally separate *A. dorbignyi* and *A. baeri* from all species of *Pseudasthenes*, especially because of plumage similarities of the former with *P. cactorum* and *P. steinbachi*.

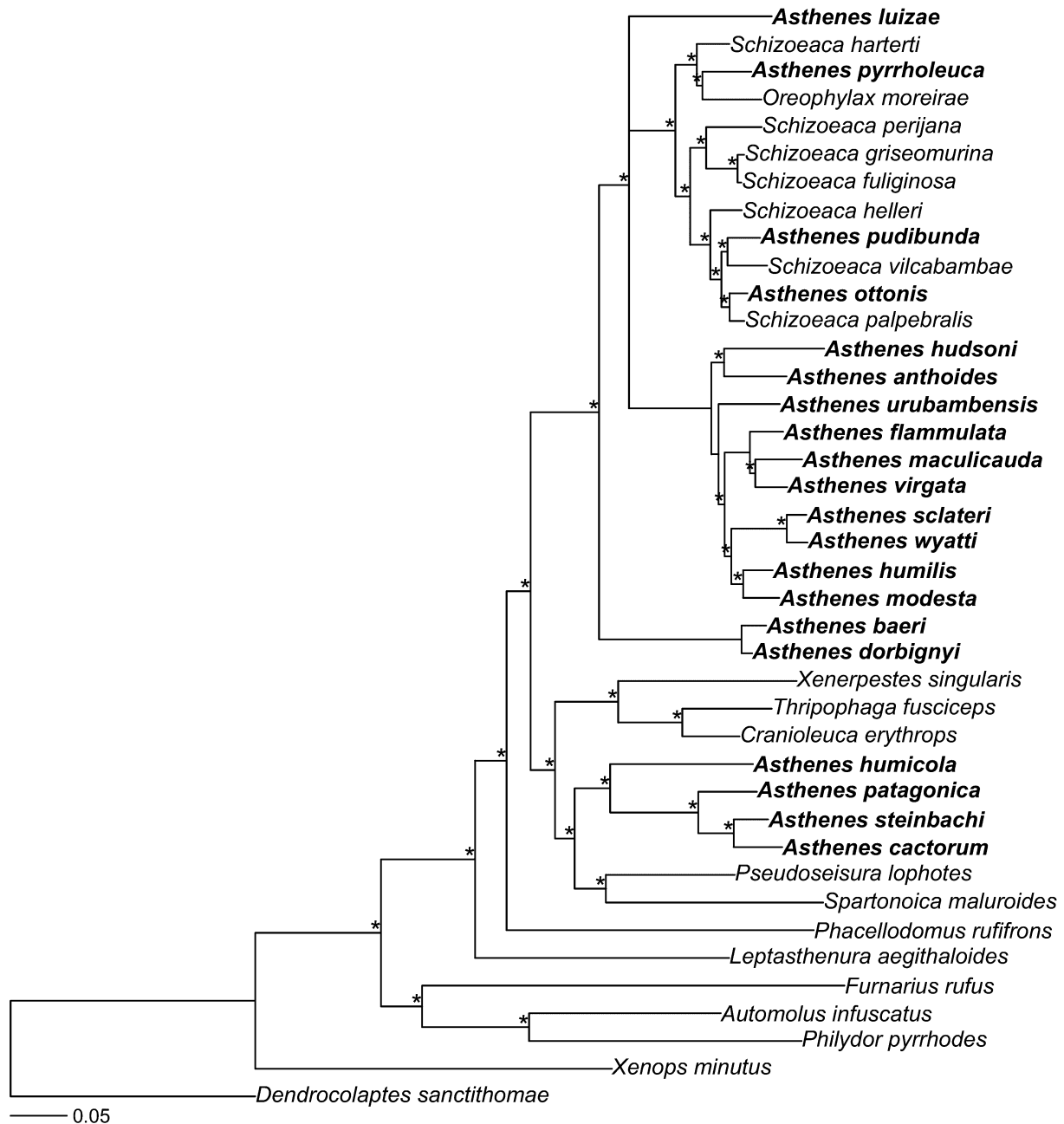


FIGURE 1. A simplified majority-rule Bayesian consensus tree of the Furnariidae (see text) that highlights the lack of a sister relationship between *Pseudasthenes* and *Asthenes* as well as the paraphyly of *Asthenes*, *Schizoeaca*, and *Oreophylax*. Asterisks represent nodes with a posterior probability of 1.0.

After transferring the corresponding species to *Pseudasthenes*, *Asthenes* remains paraphyletic because *Oreophylax moreirae* and all species of *Schizoeaca* are nested within it. We found a well-supported clade (posterior probability = 1.0) that includes all species of *Schizoeaca* and *Oreophylax* as well as three long-tailed species of *Asthenes*: *A. pudibunda* (Sclater) (Canyon Canastero), *A. ottonis* (Berlepsch) (Rusty-fronted

Canastero), and *A. pyrrholeuca*. The close relationship of the *Schizoeaca* thistletails and the monotypic genus *Oreophylax* is not surprising given their similarities in morphology, nesting behavior, habitat, and voice (Vaurie 1980; Remsen 2003; B. Whitney, pers. comm.), and a close relationship between *Asthenes* and *Schizoeaca* was previously suspected on the basis of similar throat patch configurations (Remsen 2003). However, the polyphyly of *Schizoeaca* with respect to the three long-tailed *Asthenes* listed above is surprising given the phenotypic distinctness of *Schizoeaca*, especially in tail morphology. Moreover, *Schizoeaca* species were considered homogeneous to the point of being treated as a single species in the past (Vaurie 1980).

The position of *A. luizae* Vielliard (Cipo Canastero) within *Asthenes sensu stricto* was unresolved; this species formed a trichotomy with the two main *Asthenes* clades. Pearman (1990) proposed, on the basis of voice and plumage, that its closest relative might be *A. dorbignyi* or *A. patagonica*. Vasconcelos *et al.* (2008), summarizing this and additional evidence, noted that all traits that it shared with other *Asthenes* were potentially plesiomorphic and concluded that its sister species could not be determined from the phenotypic data available. In fact, our data indicate this species is not closely related to any of the other *Asthenes*, including the species mentioned by Pearman (1990) and Vasconcelos *et al.* (2008), and forms a separate lineage within *Asthenes sensu stricto*.

The relationships of the three species not included in this study can be inferred tentatively from phenotypic characters. *Asthenes berlepschi* is almost certainly closely related to *A. dorbignyi* and may be a subspecies of *A. dorbignyi* (Cory & Hellmayr 1925; Bond & Meyer de Schauensee 1942; Fjeldså & Krabbe 1990). The second missing species, *A. heterura*, has been considered closely related to (Cory & Hellmayr 1925; Bond 1945), sister species to (Vaurie 1980), or conspecific with (Meyer de Schauensee 1966) *A. pudibunda*. Pearman (2001), however, noted that *A. heterura* is sufficiently similar to *A. pyrrholeuca* in plumage that they can easily be confused in the field and even in the hand. Because *A. pudibunda* and *A. pyrrholeuca* are not sister species the specific placement of *A. heterura* is better regarded as uncertain, although it probably belongs to the long-tailed *Asthenes/Schizoeaca/Oreophylax* clade. *Schizoeaca coryi* is similar to other *Schizoeaca* thistletails in plumage, tail structure, and habitat (Remsen 1981, 2003), and it presumably forms part of the same clade.

We recommend the following provisional classification of *Asthenes* and *Pseudasthenes*, based on our phylogeny and the rationale provided above for the missing species:

Genus *Asthenes* Reichenbach 1853

- Asthenes coryi* (Berlepsch)
- Asthenes perijana* (Phelps)
- Asthenes fuliginosa* (Lafresnaye)
- Asthenes griseomurina* (Sclater)
- Asthenes pudibunda* (Sclater)
- Asthenes heterura* (Berlepsch)
- Asthenes vilcabambae* (Vaurie)
- Asthenes palpebralis* (Cabanis), type of *Schizoeaca* Cabanis
- Asthenes ottonis* (Berlepsch) type of *Pseudosiptornis* Cory
- Asthenes helleri* (Chapman)
- Asthenes harterti* (Berlepsch)
- Asthenes moreirae* (Ribeiro), type of *Oreophylax* Hellmayr
- Asthenes pyrrholeuca* (Vieillot), type of *Asthenes*
- Asthenes modesta* (Eyton)
- Asthenes humilis* (Cabanis)
- Asthenes wyatti* (Sclater & Salvin)
- Asthenes sclateri* (Cabanis)
- Asthenes anthoides* (King), type of *Eusiptornoides* Cory

Asthenes hudsoni (Sclater)
Asthenes urubambensis (Chapman)
Asthenes flammulata (Jardine), type of *Siptornoides* Cory
Asthenes virgata (Sclater)
Asthenes maculicauda (Berlepsch)
Asthenes luizae Vielliard
Asthenes dorbignyi (Reichenbach)
Asthenes berlepschi (Hellmayr)
Asthenes baeri (Berlepsch)

Genus *Pseudasthenes* genus nov.

Pseudasthenes humicola (Kittlitz)
Pseudasthenes patagonica (d'Orbigny), type of *Pseudasthenes*
Pseudasthenes steinbachi (Hartert)
Pseudasthenes cactorum (Koepcke)

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