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# Phylogeny of Thripophagini ovenbirds (Aves: Synallaxinae: Furnariidae)

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In this study, we address the evolutionary relationships and discuss the biogeographical history of a complex and diverse group of ovenbirds, the Thripophagini. We reconstruct the phylogeny and estimate the time of divergence of this group, using sequences from two complete mitochondrial genes (cytochrome b and NADH subunit 2) from a total of 115 fresh tissue samples. The results provide a better understanding of the phylogenetic relationships of the taxa within this group, some of which require a thorough taxonomic revision. We discuss the biogeographical history of the group, and find parallels with other previously studied Andean birds which may indicate that tectonic and climatic events might, at least in part, be linked to its diversification through the uplift of the Andes, the creation of new montane habitats and barriers, the evolution of Amazonian drainages and landscapes, and the climatic oscillations of the Pleistocene.

ADDITIONAL KEYWORDS: Andean biogeography – Andean diversification – Andean uplift – ovenbirds – Thripophagini.

## INTRODUCTION

Moyle *et al.* (2009) introduced the name Furnariides to designate the infraorder of suboscine birds that was previously known as Furnariida (Irestedt *et al.*, 2002; Ericson *et al.*, 2003; Ericson & Johansson, 2003). This group includes ~651 species of Neotropical birds primarily distributed in South America throughout a broad range of habitats (Remsen *et al.*, 2018), and numerous studies have confirmed their monophyly (Irestedt *et al.*, 2001, 2002; Chesser, 2004; Hackett *et al.*, 2008; Claramunt, 2010). Within the infraorder, the Furnariidae – or ovenbirds – comprise almost 300 recognized species (Sibley & Ahlquist, 1990; Moyle *et al.*, 2009; Remsen *et al.*, 2018), and has been described as being one of the most diverse avian groups (Claramunt, 2010).

Within the Furnariidae, the Synallaxinae include two tribes, Thripophagini and Synallaxini (Moyle *et al.*, 2009). The tribe Thripophagini includes the genera *Acrobatornis*, *Metopothrix*, *Xenerpestes*, *Limnoctites*, *Cranioleuca*, *Siptornis*, *Thripophaga* and *Roraima* (Moyle *et al.*, 2009). Of these, *Siptornis* is distributed throughout the Andean highlands, whereas the species within *Thripophaga*, *Xenerpestes* and *Cranioleuca* are distributed both in the Andean highlands and in portions of the Neotropical lowlands (i.e. the Amazon Basin, the Atlantic Forest, the Pantepui, the Chocó, the Caatinga, the Pampas, and the Chaco); *Cranioleuca* is also found in the Central American highlands. Finally, the species of *Acrobatornis*, *Limnoctites*, *Roraima* and *Metopothrix* occur in isolated areas of the South American lowlands (Fig. 1). The tribe Thripophagini comprises a heterogeneous array of taxa, in terms of both morphology and ecology (Remsen, 2003; Claramunt, 2010). The diversity of nest morphology within the ovenbird family is so high that Irestedt *et al.* (2009) have suggested that it might be one of the factors that contributed to their high diversification rates, and

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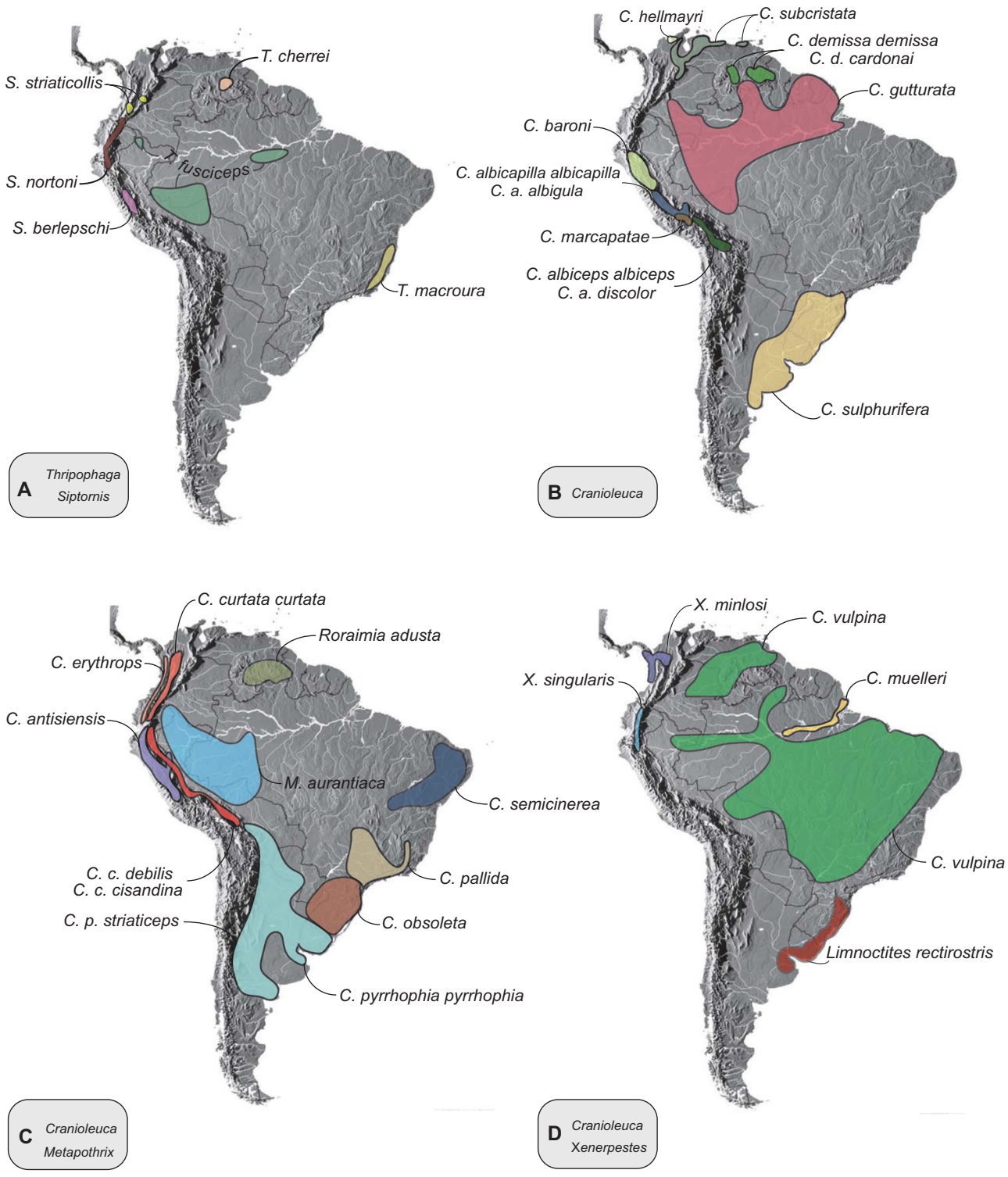


**Figure 1.** Distribution of the taxa within Thripophagini: A, *Siptornis* and *Thripophaga*; B, part of the genus *Cranioleuca* [*C. gutturata*, which needs to be renamed, as well as *Limnoctites sulphurifera* are included here (see text)]; C, part of the genus *Cranioleuca* and Metopothrix; D, part of *Cranioleuca* and Xenerpestes. Distributions were taken from del Hoyo *et al.* (2019).

they posit this feature might have allowed the group to colonize and diversify into new environments.

The high morphological diversity of this group has resulted in extensive taxonomic flux in the arrangement of its taxa, and there remain doubts regarding the taxonomic status of some taxa. Here, we follow the taxonomy in del Hoyo & Collar (2016). There is a need to clarify the boundaries of the genus *Thripophaga*, as Vaurie (1980) and Irestedt *et al.*, (2009) have suggested that it does not form a monophyletic group. Within *Cranioleuca*, *C. vulpecula* was considered to be a subspecies of *C. vulpina* (Cory & Hellmayr, 1925; Peters, 1951, Meyer De Schauensee, 1970; Ridgely & Tudor, 1994), although Zimmer (1997) considered that they were separate species based on morphological, vocal and ecological characters. Belton (1985) placed *C. obsoleta* as a subspecies of *C. pyrrhophia* based on 'intermediate specimens', although Claramunt (2002) argued that there was no strong support for interbreeding between these two species. On the other hand, *C. pyrrhophia* has three described subspecies: *C. p. pyrrhophia*, *C. p. striaticeps* and *C. p. rufipennis* (Cory & Hellmayr, 1925; Peters, 1951). Each of them is diagnosably distinct with regard to plumage, and they have disjunct distributions (Fig. 1C). Sibley & Ahlquist (1990) and Maijer & Fjeldsa (1997) proposed that *C. henricae*, *C. pyrrhophia* and *C. obsoleta* form a 'superspecies', a claim that was supported by the results of García-Moreno *et al.* (1999). According to S. Claramunt (pers. comm.) there is reason to believe that *C. henricae* might be a hybrid between *C. p. rufipennis* and *C. curtata debilis*, as *C. henricae* has some intermediate morphological features between these taxa. These two species are currently allopatric, with *C. p. rufipennis* found in the arid woodlands of La Paz and north-west Cochabamba, and *C. c. debilis* in the humid montane forests of Bolivia (the Yungas) south to Santa Cruz, but geographical overlap between these species may occur in as yet unsurveyed localities. *Cranioleuca demissa* has two described subspecies (Fig. 1B), *C. d. demissa* from the tepuis of the Duida subcentre of endemism (Cracraft, 1985), and *C. d. cardonai* (Phelps & Dickerman, 1980) from the tepuis of the Gran Sabana subcentre of endemism (Cracraft, 1985). *Cranioleuca erythrops* has three subspecies, *C. e. erythrops*, *C. e. rufigenis* and *C. e. griseigularis* (Cory & Hellmayr, 1925; Peters, 1951), all of which are diagnosably distinct based on plumage, and possess disjunct distributions. *Cranioleuca curtata cisandina*, *C. c. curtata* and *C. c. debilis* (Fig. 1C) are subspecies of *C. curtata* (Peters, 1951), although Cory & Hellmayr (1925) recognized *C. c. cisandina* as a separate species. *Cranioleuca antisiensis* is described as having two subspecies, *C. a. antisiensis* and *C. a. palamblae* (Cory & Hellmayr, 1925), each of them diagnosably distinct with regard to plumage, and with allopatric distributions (Fig. 1C). *Cranioleuca baroni* has three described subspecies, *C. b. baroni*, *C. b. capitalis* (Cory & Hellmayr, 1925; Peters, 1951) and *C. b. zaratensis*, which was described by Koepcke (1961a). Although each of these taxa is diagnosably distinct based on plumage, Fjeldsa & Krabbe (1990) proposed that *C. pyrrhophia* may form a superspecies with *C. antisiensis* and *C. baroni*, and that *C. curtata* should be treated as conspecific with *C. erythrops*. *Cranioleuca baroni* and *C. antisiensis* have been previously reported as being conspecific by Koepcke (1961b) and Fjeldsa & Krabbe (1990), but Cory & Hellmayr (1925) and Peters (1951) considered them as separate species. Although Remsen (2003: 187) noted that these two species had 'clearly distinct populations at the extreme of their ranges', *C. baroni* and *C. antisiensis* are allopatric, with *C. baroni* distributed in northern and central Peru in semi-arid woodlands, whereas *C. antisiensis* is found from southern Ecuador to northern Peru in montane or subandean humid forests, so this argument alone is no reason for considering them as conspecific.

Irestedt *et al.* (2009) suggested that the radiation of Synallaxinae ovenbirds took place during the last 15 Mya, a time frame that was later corroborated by Derryberry *et al.* (2011), when the uplift of the Andes, and later the glaciations of the Pleistocene, were reshaping the landscape in South America, including the river systems and precipitation patterns (Hooghiemstra *et al.*, 2000; Hoorn *et al.*, 2010). Numerous authors have suggested that these tectonic and climatic changes had a strong influence on the diversification of Andean groups (Bates & Zink, 1994; Bleiweiss, 1998; Pérez-Emán, 2005; Cadena *et al.*, 2007; Chaves *et al.*, 2007; Lutz *et al.*, 2013; Quintero *et al.*, 2013; Ceccarelli *et al.*, 2016). The tribe Thripophagini, due to its diversity and distribution, can be used to test the idea that certain events within Earth's history, such as the orogenesis of the Andes and the glacial–interglacial periods of the Pleistocene, played an important role in its biotic assemblage. Thus, in this study we reconstruct the phylogeny and estimate the time of divergence of the Thripophagini, using sequences from two mitochondrial genes, and use this phylogenetic hypothesis to infer some of the biogeographical history of the group.

## MATERIAL AND METHODS

### Habitat characterization and ancestral character-state reconstruction

To correlate current habitat distribution with the biogeographical history within Thripophagini, we characterized the ecological habitat in which each species breeds based on Fjeldsa & Krabbe (1990),

Remsen (2003) and Hooghiemstra *et al.* (2006). We divided forested vegetation into tropical lowland or wet forest (sea level to 1000–1200 m), subandean or lower montane forest (800–2300 m), Andean or upper montane forest (2300–3300 m) and *subpáramo* belt (3200–3600 m). Open vegetation in the Andes is dominated by the *páramo* (3500 to ~4200 m), above the tree line, containing bunch-forming grasses, with a diverse assemblage of herbaceous plants and small shrubs scattered among them (Neill, 1999), whereas open vegetation in the lowlands is divided into swamps, woodlands, Chaco and Pampas (Table 1). Each individual was classified into the following areas of endemism based on Cracraft (1985): Gran Sabana, Duida, northern Ecuador, southern Ecuador, northern Peru, central Peru, southern Peru, Austral Andes, Napo, Inambari, Para, Rondonia, Chaco, Caatinga, Patagonia, Pampean, eastern Panama, Coiba Island and Central American highlands (Table 1).

### Sampling, DNA extraction and amplification

Thorough sampling is essential for understanding the temporal and spatial patterns of diversification within any group. As many of the described species within the tribe Thripophagini have two or more recognized subspecies, we included as many of them as possible in order to test hypotheses of phylogenetic species limits with independent DNA data. For taxonomy, we consulted Peters (1951), Meyer De Schauensee (1970), Fjeldsa & Krabbe (1990), Ridgely & Tudor (1994), Remsen (2003) and Remsen et al. (2018). The species names in this paper follow del Hoyo & Collar (2016), and we adhere to the phylogenetic species concept coined by Cracraft (1997).

A total of 115 fresh tissue samples were included in the molecular analysis (Table 1), and sequences for some outgroups were obtained from GenBank (Table 1). Extractions were performed using the DNeasy kit (Qiagen), and the complete cytochrome b (*cyt b*) and NADH subunit (*ND2*) mitochondrial DNA (mtDNA) genes were amplified using general primers (Sorenson *et al.*, 1999). Amplifications were performed using GoTaq Polymerase (Promega). Amplification products were visualized by electrophoresis, and purified using Multiscreen PCR plates (Millipore). Purified PCR products were sequenced with the same primers used during amplifications, and run on a 3730 Automated DNA Sequencer (Perkin-Elmer, ABI) following standard protocols (Applied Biosystems, 2009).

### Phylogenetic analyses

Sequences were edited and examined for the presence of stop or nonsense codons using Sequencher 4.5 (GeneCodes Corporation). The incongruence length difference (ILD) test (Farris *et al.*, 1995) was performed in PAUP v.4.0b10 (Swofford, 2002) to assess the level of incongruence of phylogenetic signal between the two mitochondrial genes. Three independent analyses were performed. Maximum-parsimony (MP) was implemented in PAUP v.4.0b10 (Swofford, 2002), using PAUPRat (Nixon, 1999) with 10% of the characters perturbed, 200 iterations and ten independent parsimony replicates. Branch support was estimated through non-parametric bootstrapping (Felsenstein, 1985) in PAUP v.4.0b10 (Swofford, 2002), via a heuristic search, TBR branch swapping, and 1000 replicates with ten random stepwise addition sequence replicates. Maximum-likelihood (ML) was performed using GARLI (Zwickl, 2006), with GTR+G+I as the nucleotide substitution model, estimating base frequencies and the proportion of invariant sites. Two parallel analyses were run, which were automatically terminated when no significant improvements in topology were found after 2 million generations. Bayesian inference (BI) was implemented in MrBayes v.3.1.1 (Huelsenbeck & Ronquist, 2001) using a partitioned model approach to account for potential differences in evolutionary model parameters between the two genes. The best model for each gene partition was selected using MrModeltest 2.3 (Nylander, 2004). Two independent analyses were run using four simultaneous Markov chains for 10 million generations, with trees being sampled every 1000 generations, keeping 9000 trees from each analysis. The resulting 18 000 sampled trees were used to compute posterior probabilities for each node. During all searches, *Asthenes steinbachi*, *Asthenes pyrrholeuca*, *Schizoeaca helleri*, *Synallaxis ruficapilla*, *Synallaxis azarae* and *Hellmayrea gularis* were used as outgroups (Moyle *et al.*, 2009). All analyses were run on the CIPRES portal v.3.1 (Miller *et al.*, 2010).

### Divergence time estimates

Irestedt *et al.* (2009) calculated the divergence dates within the Furnariides, and according to their results, the ovenbird–woodcreeper radiation started to diverge at ~33 Mya, while the Synallaxines started to diverge at ~19 Mya. We used their results to estimate divergence times within the Thripophagini using BEAST (Drummond & Rambaut, 2007). To account for the uncertainty of using results from a previous analysis, which carry a level of uncertainty themselves, three independent analyses were run using priors based on the mean as well as the upper- and lower-bound confidence intervals reported by Irestedt *et al.* (2009), to provide a very conservative bracket for the estimated dates. Thus, the priors for the node between *Phacellodomus* and the remainder of the Synallaxines were set at 15, 17.45 and 22.5 Mya (node A, Table 2), those between *Hellmayrea gularis*

**Table 1.** List of taxa included in this study

| Voucher number | Species | Habitat | Area of endemism | Country | Locality |
|---|---|---|---|---|---|
| ANSP 19117 | *Xenerpestes singularis* | Lower montane/ subandean forest | Southern Ecuador | Ecuador | Zamora Chinchipé, Panguri; ~12 km NE San Francisco del Vergel |
| LSUMZ 6031 | *X. singularis* | Lower montane/ subandean forest | Southern Ecuador | Ecuador | Morona Santiago, W Slope Cordillera del Cutucú |
| LSUMZ 44674 | *X. singularis* | Lower montane/ subandean forest | Northern Peru | Peru | San Martín, ~24 km ENE Florida |
| LSUMZ 40432 | *Metopothrix aurantiacus* | Tropical lowland forest | Napo | Peru | Loreto, Amazonas, I Resaro, 78 km NE Iquitos, 80 m |
| LSUMZ 7367 | *M. aurantiacus* | Tropical lowland forest | Napo | Peru | Loreto, ~86 km SE Juanjui on E bank upper Rio Pauya |
| ANSP 19149 | *Siptornis nortoni* | Lower montane/ subandean forest | Southern Ecuador | Ecuador | Zamora Chinchipé, Panguri; ~12 km NE San Francisco del Vergel |
| LSUMZ 6202 | *S. striaticollis* | Lower montane/ subandean forest | Southern Ecuador | Ecuador | Morona Santiago, W Slope Cordillera del Cutucú, S trail from Logroño |
| ANSP 17662 | *Cranioleuca gutturata* | Tropical lowland forest | Napo | Ecuador | Morona Santiago |
| LSUMZ 1122 | *C. gutturata* | Tropical lowland forest | Inambari | Bolivia | La Paz, Rio Beni, ~20 km by river N Puerto Linares |
| LSUMZ 1150 | *C. gutturata* | Tropical lowland forest | Inambari | Bolivia | La Paz, Rio Beni, ~20 km by river N Puerto Linares |
| LSUMZ 42859 | *C. gutturata* | Tropical lowland forest | Napo | Peru | Loreto, ~54 km NNW mouth of Rio Morona, on east bank |
| LSUMZ 4819 | *C. gutturata* | Tropical lowland forest | Napo | Peru | Loreto, S Rio Amazonas, ~10 km SSW mouth Rio Napo on east bank |
| LSUMZ 2022 | *C. gutturata* | Tropical lowland forest | Napo | Peru | Pasco, km 41 on Villa Rica, Puerto Bermudez highway |
| AMNH 12009 | *Roraima adusta* | Montane forest | Gran Sabana | Venezuela | Bolivar |
| AMNH 11993 | *R. adusta* | Montane forest | Gran Sabana | Venezuela | Bolivar |
| AMNH 12044 | *R. adusta* | Montane forest | Gran Sabana | Venezuela | Bolivar |
| AMNH 9471 | *R. adusta* | Montane forest | Gran Sabana | Venezuela | Bolivar, Auyan Tepui |
| AMNH 12034 | *R. adusta* | Montane forest | Gran Sabana | Venezuela | Bolivar |
| AMNH 12040 | *R. adusta* | Montane forest | Gran Sabana | Venezuela | Bolivar |
| AMNH 9479 | *R. adusta* | Montane forest | Gran Sabana | Venezuela | Bolivar |

**Table 1.** *Continued*

| Voucher number | Species | Habitat | Area of endemism | Country | Locality |
|---|---|---|---|---|---|
| LSUMZ 52023 | *Limnoctites rectirostris* | Fresh water marshes | Pampas | Uruguay | Cerro Largo, Sierra de los Rios, Arroyo Sarandi, Paso Montaraz |
| LSUMZ 52022 | *L. rectirostris* | Fresh water marshes | Pampas | Uruguay | Rivera, Estancia Trinidad, COFUSA |
| LSUMZ 52021 | *L. rectirostris* | Fresh water marshes | Pampas | Uruguay | Rocha, Arroyo sauce del Peñon |
| NMNH B20846 | *L. sulphurifera* | Fresh water marshes | Pampas | Uruguay | Rocha |
| LSUMZ 7607 | *Thripophaga fusciceps* | Tropical lowland forest | Rondonia | Bolivia | Beni, Cercado 6 km by road SE Trinidad |
| ZMUC 129685 | *C. m. marcapatae* | Andean/upper montane forest | Southern Peru | Peru | Puno, 5 km from Soqapata, Carabaya |
| ZMUC 129687 | *C. m. marcapatae* | Andean/upper montane forest | Southern Peru | Peru | Puno, 5 km from Soqapata, Carabaya |
| FMNH 390678 | *C. m. weskei* | Andean/upper montane forest | Central Peru | Peru | Junin, Cordillera Vilcabamba, headwaters Rio Pomureni |
| LSUMZ 1231 | *C. a. albiceps* | Andean/upper montane forest | Southern Peru | Bolivia | La Paz, ~1 km S Chuspipata |
| ZMUC 127007 | *C. a. discolor* | Andean/upper montane forest | Southern Peru | Bolivia | Cochabamba, Pujyani, Cocapata 3860 m |
| ZMUC 129798 | *C. a. discolor* | Andean/upper montane forest | Southern Peru | Bolivia | Cochabamba, Sivingani, Ayopaya Range |
| ZMUC 126973 | *C. a. discolor* | Andean/upper montane forest | Southern Peru | Bolivia | Cochabamba, Coca-pata 4050 m |
| LSUMZ 25422 | *C. muelleri* | Tropical lowland forest | Inambari | Brazil | Amazonas, Rio Solimoes, Ilha Marchantaria, ~15 km S Manaus |
| LSUMZ 25423 | *C. muelleri* | Tropical lowland forest | Inambari | Brazil | Amazonas, Rio Solimoes, Ilha Marchantaria, ~15 km S Manaus |
| LSUMZ 25425 | *C. vulpina* | Tropical lowland forest | Inambari | Brazil | Amazonas, Rio Solimoes, Ilha Marchantaria, ~15 km S Manaus |
| LSUMZ 25426 | *C. vulpina* | Tropical lowland forest | Inambari | Brazil | Amazonas, Rio Solimoes, Ilha Marchantaria, ~15 km S Manaus |

**Table 1.** *Continued*

| Voucher number | Species | Habitat | Area of endemism | Country | Locality |
|---|---|---|---|---|---|
| LSUMZ 35506 | *C. vulpina* | Tropical lowland forest | Para | Brazil | Mato Grosso: Island do Ludovico on rio Teles Pires, 32 km NE |
| ANSP 19338 | *C. vulpecula* | Tropical lowland forest | Napo | Ecuador | Napo, Río Napo/Aguarico 150 m |
| ANSP 19346 | *C. vulpecula* | Tropical lowland forest | Napo | Ecuador | Napo, Río Napo/Aguarico 150 m |
| LSUMZ 25424 | *C. vulpecula* | Tropical lowland forest | Inambari | Brazil | Amazonas, Rio Solimoes, Ilha Marchantaria, ~15 km S Manaus |
| LSUMZ 3181 | *C. vulpecula* | Tropical lowland forest | Napo | Peru | Loreto, Isla Ronsoco, Rio Napo opposite Libertad, 80 km N Iquitos |
| LSUMZ 43020 | *C. vulpecula* | Tropical lowland forest | Napo | Peru | Loreto, River island in Rio Marañon at mouth of Rio Morona |
| ZMUC 125748 | *C. vulpecula* | Tropical lowland forest | Napo | Ecuador | Napo, Río Napo/Aguarico 150 m |
| LSUMZ 7372 | *C. vulpecula* | Tropical lowland forest | Napo | Peru | Loreto, Amazonas, I Pasto, 80 km NE Iquitos, 80 m |
| FMNH 399207 | *C. semicinerea* | Tropical forest/woodlands | Caatinga | Brazil | Pernambuco, Taquaritinga |
| NMNH B15858 | *C. d. cardonai* | Montane forest | Gran Sabana | Guyana | Mount Roraima |
| KU 4066 | *C. d. cardonai* | Montane forest | Gran Sabana | Guyana | N slope of Mount Roraima |
| LSUMZ 7418 | *C. d. demissa* | Montane forest | Duida | Venezuela | Amazonas, Cerro de la Neblina Camp VII, 1800 m |
| LSUMZ 7421 | *C. d. demissa* | Montane forest | Duida | Venezuela | Amazonas, Cerro de la Neblina Camp VII, 1800 m |
| LSUMZ 46740 | *C. dissita* | Tropical lowland forest | Coiba Island | Panama | Veraguas, Isla Coiba, Playa Hermosa, old airstrip |
| LSUMZ 46741 | *C. dissita* | Tropical lowland forest | Coiba Island | Panama | Veraguas, Isla Coiba, Playa Hermosa, old airstrip |
| ANSP 15773 | *C. e. erythrops* | Lower montane/ subandean forest | Northern Ecuador | Ecuador | Carchi |
| ANSP 18492 | *C. e. erythrops* | Lower montane/ subandean forest | Northern Ecuador | Ecuador | Manabi |
| ZMUC 136850 | *C. e. erythrops* | Lower montane/ subandean forest | Northern Ecuador | Ecuador | Pichincha, Tandayapa, 1600 m |

**Table 1.** *Continued*

| Voucher number | Species | Habitat | Area of endemism | Country | Locality |
|---|---|---|---|---|---|
| LSUMZ 26465 | *C. e. rufigenis* | Lower montane/ subandean forest | Central America | Panama | Chiriquí, Dist Gualaca, Cordillera Central |
| LSUMZ 28182 | *C. e. rufigenis* | Lower montane/ subandean forest | Central America | Panama | Chiriquí, Dist Gualaca, Cordillera Central |
| LSUMZ 16052 | *C. e. rufigenis* | Lower montane/ subandean forest | Central America | Costa Rica | Heredia, Fin~La Fortuna, 4 km SE Virgen del Socorro |
| LSUMZ 1364 | *C. e. griseigularis* | Lower montane/ subandean forest | Eastern Panama | Panama | Darién, ~9 km NW Cana, on slopes of Cerro Pirre |
| LSUMZ 2144 | *C. e. griseigularis* | Lower montane/ subandean forest | Eastern Panama | Panama | Darién, ~6 km NW Cana |
| ANSP 18961 | *C. a. antisiensis* | Lower montane/ subandean forest | Southern Ecuador | Ecuador | Loja |
| ANSP 16757 | *C. a. antisiensis* | Lower montane/ subandean forest | Southern Ecuador | Ecuador | Loja |
| LSUMZ 31683 | *C. a. palamblae* | Lower montane/ subandean forest | Northern Peru | Peru | Cajamarca, El Espino |
| LSUMZ 31684 | *C. a. palamblae* | Lower montane/ subandean forest | Northern Peru | Peru | Cajamarca, El Espino |
| LSUMZ 437 | *C. a. palamblae* | Lower montane/ subandean forest | Northern Peru | Peru | Piura, Cruz Blanca, 33rd km SW Huancabamba |
| ZMUC 126067 | *C. a. palamblae* | Lower montane/ subandean forest | Southern Ecuador | Ecuador | Azuay, St. Isabel to Girón, 1750 m |
| ANSP 20211 | *C. c. cisandina* | Lower montane/ subandean forest | Northern Ecuador | Ecuador | Sucumbios, Cascada de San Rafael |
| LSUMZ 6032 | *C. c. cisandina* | Lower montane/ subandean forest | Southern Ecuador | Ecuador | Morona Santiago, West slope of Cordillera del Cutucu |
| LSUMZ 8175 | *C. c. cisandina* | Lower montane/ subandean forest | Central Peru | Peru | Pasco, Cushi |
| LSUMZ 43852 | *C. c. cisandina* | Lower montane/ subandean forest | Northern Peru | Peru | San Martín, ~24 km ENE Florida |
| LSUMZ 43876 | *C. c. cisandina* | Lower montane/ subandean forest | Northern Peru | Peru | San Martín, ~24 km ENE Florida |
| ANSP 19793 | *C. c. cisandina* | Lower montane/ subandean forest | Southern Ecuador | Ecuador | Zamora Chinchipé, Cord. del Condor; above Chinapinza |

**Table 1.** *Continued*

| Voucher number | Species | Habitat | Area of endemism | Country | Locality |
|---|---|---|---|---|---|
| ZMUC 124821 | *C. b. baroni* | Andean/upper montane forest (dry) | Central Peru | Peru | Pasco, upper Huallaga, Pariamarca |
| ZMUC 139654 | *C. b. baroni* | Andean/upper montane forest (dry) | Central Peru | Peru | Ancash, Cordillera Blanca, Gague, Huaraz |
| ZMUC 124835 | *C. b. baroni* | Andean/upper montane forest (dry) | Central Peru | Peru | Ancash, Cordillera Blanca, Quebrada Pucavado |
| FMNH 391889 | *C. b. baroni* | Andean/upper montane forest (dry) | Central Peru | Peru | Ancash, Yungay Morococha |
| FMNH 391888 | *C. b. baroni* | Andean/upper montane forest (dry) | Central Peru | Peru | Ancash, Yungay Morococha |
| ZMUC 124837 | *C. b. baroni* | Andean/upper montane forest (dry) | Central Peru | Peru | Ancash, Cordillera Blanca, Rurichinchay |
| ZMUC 124836 | *C. b. baroni* | Andean/upper montane forest (dry) | Central Peru | Peru | Ancash, Cordillera Blanca, Quebrada Pucavado |
| FMNH 391884 | *C. a. (b.) zaratensis* | Andean/upper montane forest (dry) | Central Peru | Peru | Oyon, Lima |
| FMNH 391887 | *C. a. (b.) zaratensis* | Andean/upper montane forest (dry) | Central Peru | Peru | Oyon, Lima |
| FMNH 391891 | *C. b. zaratensis* | Andean/upper montane forest (dry) | Central Peru | Peru | Oyon, Lima |
| LSUMZ 3597 | *C. a. (b.) capitalis* | Andean/upper montane forest (dry) | Central Peru | Peru | Huanuco, Quebrada Huaunash, 4 km by road NW Nuevas Flores |
| LSUMZ 49622 | *C. a. albicapilla* | Andean/subparamo (dry) | Central Peru | Peru | Junin, Lampa, ~39 km ENE Huancayo |
| LSUMZ 49643 | *C. a. albicapilla* | Andean/subparamo (dry) | Central Peru | Peru | Junin, Lampa, ~39 km ENE Huancayo |
| ZMUC 129647 | *C. a. albigula* | Andean/subparamo (dry) | Southern Peru | Peru | Cusco, Quelcamachay, Santa Teresa, La Convención |
| FMNH 391882 | *C. a. albigula* | Andean/subparamo (dry) | Southern Peru | Peru | Urubamba, Cuzco, Peru |
| ZMUC 124797 | *C. a. albigula* | Andean/subparamo (dry) | Southern Peru | Peru | Apurimac, Abancay, 3200 m |
| ZMUC 124802 | *C. a. albigula* | Andean/subparamo (dry) | Southern Peru | Peru | Apurimac, 7 km S Cotaruse |
| ZMUC 124799 | *C. a. albigula* | Andean/subparamo (dry) | Southern Peru | Peru | Apurimac, Abancay, 3200 m |
| ZMUC 124810 | *C. a. albigula* | Andean/subparamo (dry) | Southern Peru | Peru | Cusco, Chainapuerto |
| ZMUC 125553 | *C. a. albigula* | Andean/subparamo (dry) | Southern Peru | Peru | Cusco, Calca, 4150 m |
| ZMUC 129669 | *C. a. albigula* | Andean/subparamo (dry) | Southern Peru | Peru | Cusco, Mantanay Urubamba |

**Table 1.** *Continued*

| Voucher number | Species | Habitat | Area of endemism | Country | Locality |
|---|---|---|---|---|---|
| LSUMZ 40864 | *C. a. albigula* | Andean/subparamo (dry) | Southern Peru | Peru | Cusco, Mantanay ~11 km NW Urubamba |
| ZMUC 124838 | *C. p. striaticeps* | Andean/upper montane forest (dry) | Austral Andean | Bolivia | Cochabamba, 10 km SW Aiquile |
| ZMUC 126243 | *C. p. striaticeps* | Andean/upper montane forest (dry) | Austral Andean | Bolivia | Chuquisaca, Palmarcito |
| LSUMZ 18683 | *C. p. striaticeps* | Andean/upper montane forest (dry) | Austral Andean | Bolivia | Santa Cruz, Cordillera, Estancia Pereforación, ~130 km E Charagua |
| LSUMZ 31658 | *C. p, striaticeps* | Andean/upper montane forest (dry) | Austral Andean | Bolivia | Santa Cruz, El Tambo, 14 km SE Comarapa |
| LSUMZ 6570 | *C. p. striaticeps* | Andean/upper montane forest (dry) | Austral Andean | Bolivia | Santa Cruz, 2.5 km N Tambo |
| ZMUC 126275 | *C. p. striaticeps* | Andean/upper montane forest (dry) | Austral Andean | Bolivia | Potosí, Parinolqui Pampa |
| ZMUC 126990 | *C. albicapila* (*striaticeps*) | Andean/upper montane forest (dry) | Austral Andean | Bolivia | Cochabamba, Cassay Vinto Coca-pata. 4050 m |
| NMNH B05938 | *C. p. pyrrhophia* | Semi-humid to arid Chaco | Chaco center | Argentina | Corrientes, Argentina |
| LSUMZ 25814 | *C. p. pyrrhophia* | Semi-humid to arid Chaco | Chaco center | Paraguay | Alto Paraguay, Madrejón |
| LSUMZ 51988 | *C. p. pyrrhophia* | Semi-humid to arid Chaco | Pampas | Uruguay | Cerro Largo, Rio Negro, Paso Mazangano |
| LSUMZ 52000 | *C. p. pyrrhophia* | Semi-humid to arid Chaco | Pampas | Uruguay | Colonia, Conchillas, Estancia el Topadro |
| LSUMZ 51990 | *C. p. pyrrhophia* | Semi-humid to arid Chaco | Pampas | Uruguay | Rio Negro, Isla de Lobos |
| LSUMZ 51992 | *C. p. pyrrhophia* | Semi-humid to arid Chaco | Pampas | Uruguay | Rivera, Rio Negro, Paso Mazangano |
| LSUMZ 51991 | *C. p. pyrrhophia* | Semi-humid to arid Chaco | Pampas | Uruguay | Alto Paraguay, Madrejón |
| LSUMZ 51995 | *C. p. pyrrhophia* | Semi-humid to arid Chaco | Pampas | Uruguay | Durazno, Estancia San José |
| LSUMZ 52005 | *C. p. pyrrhophia* | Semi-humid to arid Chaco | Pampas | Uruguay | Rio Negro, Isla de Lobos |
| ZMUC 125817 | *C. henricae* | Andean/upper montane forest (dry) | Southern Peru | Bolivia | La Paz, Inquisiví, 2350 m |
| ZMUC 128396 | *C. henricae* | Andean/upper montane forest (dry) | Southern Peru | Bolivia | La Paz/Cochabamba |

**Table 1.** *Continued*

| Voucher number | Species | Habitat | Area of endemism | Country | Locality |
|---|---|---|---|---|---|
| ZMUC 125818 | *C. henricae* | Andean/upper montane forest (dry) | Southern Peru | Bolivia | La Paz, Inquisiví, 2350 m |
| LSUMZ 22647 | *C. c. debilis* | Lower montane/ subandean forest | Southern Peru | Bolivia | La Paz, Prov. B. Saavedra, 83 km by road E Charzani, Cerro Asunta |
| LSUMZ 22894 | *C. c. debilis* | Lower montane/ subandean forest | Southern Peru | Bolivia | La Paz, La Paz, Prov. B. Saavedra, 83 km by road E Charzani |
| KU 3846 | *C. obsoleta* | Tropical woodlands | Chaco center | Paraguay | San Rafael National Park, Parabel |
| AMNH 10390 | *Asthenes steinbachi* | Lower montane/ subandean forest (dry) | Patagonia | Argentina | Neuquen |
| AMNH 10412 | *Asthenes pyrrholeuca* | Lower montane/ subandean forest (dry) | Patagonia | Argentina | Neuquen, Departamento Anelo |
| AMNH 2479 | *Schizoea~helleri* | *Paramo* and elfin forest | Rondonia | Bolivia | Franz Tamayo, Tojoloque, near Queara |
| AMNH 2448 | *Synallaxis ruficapilla* | Tropical lowland forest | Chaco center | Argentina | Misiones, San Ignacio |
| AMNH 2771 | *Synalaxis azarae* | Lower montane/ subandean forest | Austral Andean | Bolivia | Bautista Saavedra |
| AMNH 18799 | *Hellmayrea gullaris* | Andean/upper montane forest | Southern Ecuador | Ecuador | |
| | *Leptasthenura pileata* | | GenBank AY590045 | | |
| | *Phacellodomus rufifrons* | | GenBank GQ140100 | | |

Institutions: AMNH: American Museum of Natural History; KU: Natural History Museum & Biodiversity Research Center, The University of Kansas; LSUMNS: Museum of Natural Science, Louisiana State University; ANSP: Academy of Natural Sciences, Philadelphia; NMNH: National Museum of Natural History; FMNH: Field Museum of Natural History; ZMUC: University of Copenhagen Museum of Zoology.

**Table 2.** Dates of diversification (Mya) for the tribe Thripophagini and their confidence intervals estimated by BEAST; nodes correspond to those of Figure 3

| Node | Lower bound* | Mean† | 95% CI‡ | Upper bound§ |
|---|---|---|---|---|
| Node A | 15 | 17.45 | | 22.5 |
| Node B | 13.7 | 16.38 | | 21.5 |
| Node C | 13.4 | 15.63 | | 20.3 |
| 1 | 11.8 | 13.3 | 11.4–15.1 | 17.5 |
| 2 | 9.3 | 11.2 | 9.3–13.1 | 14.7 |
| 3 | 7.4 | 8.9 | 6.7–11.4 | 11.8 |
| 4 | 7.0 | 8.4 | 6.7–10.1 | 11.0 |
| 5 | 4.8 | 5.8 | 4.5–7 | 7.6 |
| 6 | 4.5 | 5.4 | 4.3–6.6 | 7.1 |
| 7 | 2.3 | 2.7 | 1.8–3.7 | 3.6 |
| 8 | 4.3 | 5.1 | 4.1–6.3 | 6.7 |
| 9 | 3.6 | 4.4 | 3.4–5.3 | 5.7 |
| 10 | 1.2 | 1.5 | 0.8–2.1 | 1.9 |
| 11 | 2.8 | 3.4 | 2.7–4.2 | 4.4 |
| 12 | 2.3 | 2.8 | 1.9–3.7 | 3.7 |
| 13 | 1.8 | 2.2 | 1.4–3 | 2.9 |
| 14 | 2.3 | 2.8 | 2.2–3.5 | 3.7 |
| 15 | 1.7 | 2.1 | 1.5–2.7 | 2.7 |
| 16 | 0.3 | 0.4 | 0.2–0.7 | 0.5 |
| 17 | 0.9 | 1.1 | 0.7–1.6 | 1.5 |
| 18 | 0.2 | 0.3 | 0.07–0.5 | 0.3 |
| 19 | 1.7 | 2.2 | 1.6–2.7 | 2.8 |
| 20 | 1.5 | 1.9 | 1.3–2.4 | 2.4 |
| 21 | 0.6 | 0.7 | 0.3–1.1 | 1 |
| 22 | 1.6 | 2 | 1.5–2.5 | 0.9 |
| 23 | 1.4 | 1.8 | 1.3–2.3 | 2.3 |
| 24 | 0.9 | 1.1 | 0.6–1.6 | 1.4 |
| 25 | 0.6 | 0.7 | 0.4–1 | 0.9 |

*Mean divergence dates obtained using the lower-bound confidence interval reported by Irestedt *et al.* (2009) as a prior.
†Mean divergence dates obtained using the mean reported by Irestedt *et al.* (2009) as a prior.
‡95% confidence interval for the divergence dates using the reported mean as a prior.
§Mean divergence dates obtained using the upper bound confidence interval reported by Irestedt *et al.* (2009) as a prior.

and the rest of the clade were 13.7, 16.38 and 21.5 Mya (node B, Table 2), and those for the node that splits *Asthenes* + *Schizoeaca* from the rest of the group were 13.4, 15.63 and 20.3 Mya (node C, Table 2). In all cases a normal distribution prior with a standard deviation of 1.0 Myr was used on the ages of the calibrated nodes, which allows for a bidirectional distribution of the uncertainty during the estimation (Ho & Phillips, 2009). For this analysis, a reduced matrix of both *ND2* and *cyt b* genes was used, containing only one or two individuals per basal taxonomic unit, plus *Leptasthenura* as the outgroup (Moyle *et al.*, 2009). The model parameters for BEAST were computed using BEAUti, with the following settings: GTR + invariant sites as the nucleotide substitution model, a relaxed, uncorrelated lognormal clock model, and a Yule process as the tree prior. A chain length of 10 million was used, and after a burn-in of 1000 the resulting trees were summarized via TreeAnnotator v.1.5.1, using the maximum clade credibility option as target tree type, and mean heights for node heights, whereas the consensus was visualized and edited using FigTree v.1.31 (Rambaut, 2009).

## RESULTS

### Phylogenetic analyses

The sequences from both *cyt b* (1092 bp) and *ND2* (1041 bp) genes (available in GenBank) were aligned manually in Sequencher 4.5 (GeneCodes Corporation) and checked for the presence of stop codons (there were none). The results of the ILD test rejected incongruence between the genes ($P > 0.05$). The ten

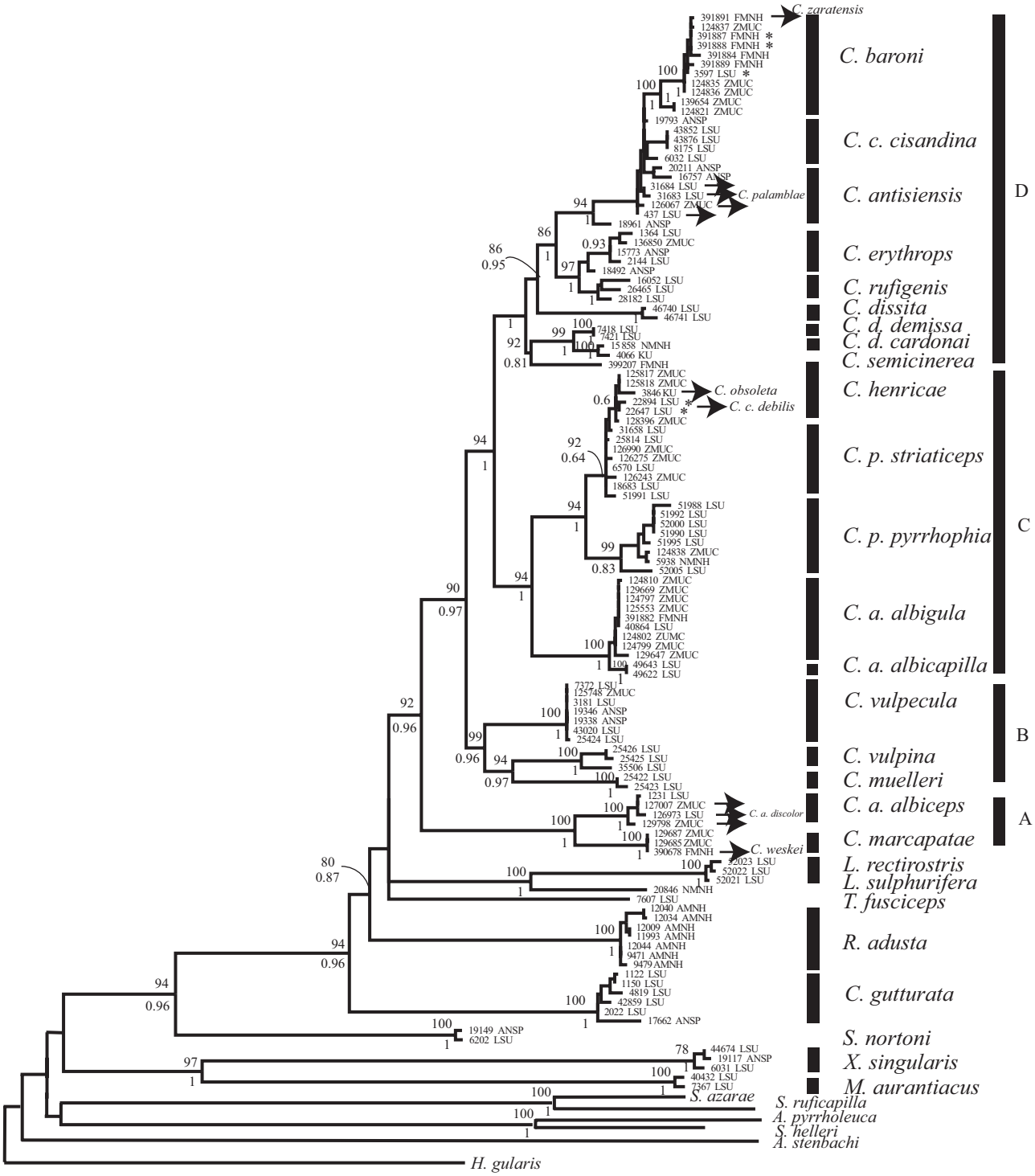


**Figure 2.** Maximum-likelihood phylogram of the tribe Thripophagini. Bootstrap support values are depicted above branches, while posterior probabilities are given below. Voucher numbers correspond to those in Table 1. Individuals of *C. c. debilis* nested within *C. henricae* are marked with an asterisk, as well as those of *C. antisiensis* nested within *C. baroni* (see text and Table 1).

replicates of the MP searches yielded between 165 and 184 MP trees of 1791 steps each, and the majority consensus of them (not shown). For the BI analysis, the GTR+I+G model of substitution was selected for *cyt b*, while the HKY+I+G model was selected for *ND2* through MrModeltest v.2.3 using the Akaike's information criterion (AIC). The arithmetic mean of the Bayes factor for the two simultaneous BI analyses was lnL −11 898.28. The ML analysis had a final score of lnL = −11 769.9675, and Figure 2 presents the ML phylogram with bootstrap support values as well as posterior probabilities from the BI analysis.

Topologies from the three analyses largely agree, although in the ML analysis *Thripophaga* was sister to the clade of *Cranioleuca* + *Limnoctites*, in the BI analysis *Limnoctites* was sister to the clade of *Cranioleuca* + *Thripophaga*, and in the MP analysis the clade of *Limnoctites* + *Thripophaga* was sister to *Cranioleuca*. Also, the placement of *C. obsoleta* differs among the three analyses: in the ML analysis it was nested within *C. henricae*, whereas in the MP and BI analyses it was not, and was sister to the clade of *C. p. pyrrophia* + *C. p. striaticeps*. Nevertheless, both in the case of the relationships among *Cranioleuca*, *Limnoctites* and *Thripophaga*, and in the placement of *C. obsoleta*, the conflicting nodes had low support in all three analyses.

Within the Thripophagini, *Xenerpestes* and the monotypic genus *Metopothrix* form a well-supported clade (Fig. 2). This clade is sister to the rest of the tribe, in which *Siptornis* is sister to a well-supported clade containing the polyphyletic *Cranioleuca*, as well as *Roraima*, *Limnoctites* and *Thripophaga* (Fig. 2). Within this clade, the taxon currently classified as *Cranioleuca gutturata* does not belong to the genus *Cranioleuca*, and thus a new genus will be erected to reflect its different taxonomic position (Fig. 2; taxonomic work in progress). This species is sister to the rest of the clade. *Roraima*, in turn, is sister to the clade that contains *Limnoctites*, *Thripophaga* and *Cranioleuca* (Fig. 2). As previously mentioned, there is no agreement across analyses with respect to the relationships among these three genera. The branch length of the node leading to this clade is very short, suggesting that the split among the three might have happened almost simultaneously. Within *Limnoctites*, *L. rectirostris* is sister to *Cranioleuca sulphuriphera* (*Limnoctites sulphiriphera*), and the latter should therefore be considered as part of *Limnoctites* instead of *Cranioleuca*.

Excluding *C. gutturata* and *L. sulphuriphera*, which are not closely related to the other species within *Cranioleuca* (Fig. 2), the remainder of the species in this genus form a well-supported monophyletic group. *Cranioleuca* can be partitioned into four clades, A–D (Fig. 2). Clade A contains *C. marcapatae marcapatae*, *C. m. weskei*, *C. albiceps discolor* and *C. a. albiceps*. The two subspecies within *C. albiceps* (*C. a. abiceps* and *C. a. discolor*) were not recovered as different clades in the molecular phylogeny. The same was true for those within *C. marcapatae*: *C. m. marcapatae* and *C. m. weskei* (Remsen, 1984), which were recovered in the same clade (Fig. 2).

Clade B is unique in that it is the only one containing species found solely in Amazonia (Fig. 1D). The results from our molecular phylogeny suggest that *C. vulpecula* and *C. vulpina* are indeed different taxa, and show that they are not each other's sister species, as *C. vulpina* is sister to *C. muelleri*, and together they are sister to *C. vulpecula* (Fig. 2).

Clade C contains *Cranioleuca albicapilla albicapilla*, *C. albicapilla albigula*, *C. pyrrhophia*, *C. striaticeps*, *C. henricae* and *C. obsoleta*. Within it *C. a. albicapilla* and *C. a. albigula* are sister groups in the molecular phylogeny (Fig. 2). Clade C is sister to the one formed by the *pyrrhophia* species-group, which contains *C. pyrrhophia pyrrhophia*, *C. p. striaticeps*, *C. p. rufipennis*, *C. henricae* and *C. obsoleta*. In our analyses, the position of *C. obsoleta* varied, and was not supported in any of them. Thus, there is a need to include more samples of *C. obsoleta*, as having only one individual is probably the cause of this lack of resolution. Moreover, we found that *C. p. pyrrhophia* and *C. p. striaticeps* belong to separate clades (Fig. 2), although there is one individual of *C. p. striaticeps* nested within *C. pyrrhophia*. Moreover, within *C. p. striaticeps*, we found one bird labelled as *C. a. albicapilla* (ZMUC 126990) that, because of its distribution (Cochabamba; Table 1), is probably a mislabelled individual belonging to *C. p. striaticeps*, as *C. a. albicapilla* does not reach Bolivia (Fig. 1B; Remsen, 2003). *Cranioleuca p. striaticeps* and *C. henricae* are paraphyletic on the gene tree (Fig. 2), and within *C. henricae*, we found two individuals of *C. curtata debilis* (LSUMNS 22647, LSUMNS 22894). *Cranioleuca henricae* is diagnosably distinct in plumage from *C. curtata debilis*, *C. p. rufipennis* and *C. p. striaticeps*. *Cranioleuca p. rufipennis* was not sampled in the molecular phylogeny.

Clade D contains *Cranioleuca semicinerea*, *C. demissa*, *C. d. cardonai*, *C. dissita*, *C. erythrops*, *C. rufigenis*, *C. griseigularis*, *C. antisiensis*, *C. palamblae*, *C. curtata*, *C. curtata debilis*, *C. cisandina*, *C. b. baroni*, *C. b. capitalis* and *C. b. zaratensis*. The two subspecies within *C. demissa*, *C. d. demissa*, and *C. d. cardonai*, are sister groups in the molecular phylogeny, and together they are sister to *C. semicinerea* (Fig. 2). This clade is sister to another that contains *C. dissita*, from Coiba Island (Fig. 1D), which in turn is sister to the remainder of the group. *Cranioleuca dissita* was traditionally recognized as a subspecies of *C. vulpina* (Wetmore, 1957), but the results of this study show that it belongs a different clade, not related to the former

(Fig. 2). The remainder of the group is divided into two clades. The first contains *C. erythrops* and *C. erythrops rufigenis*, and the other *C. antisiensis*, *C. cisandina* and *C. baroni* (Fig. 2). *Cranioleuca e. griseigularis* was not recovered as a separate species in the molecular phylogeny, as the two individuals included were nested within *C. erythrops.* The two described subspecies of *C. antisiensis*, *C. antisiensis antisiensis* and *C. a. palamblae*, are nested in the same clade. The same is true for the three subspecies described for *C. baroni*, i.e. *C. baroni baroni*, *C. b. capitalis* and *C. b. zaratensis*, which, although diagnosably distinct based on plumage, were not recovered as different clades in the molecular phylogeny (Fig. 2). We also found that *C. baroni*, *C. antisiensis* and *C. cisandina* are recovered as part of the same clade, while *C. pyrrhophia* is part of a different group (clade C). Although *C. baroni*, *C. antisiensis* and *C. cisandina* are paraphyletic with regard to mtDNA with respect to each other, each is diagnosably distinct in plumage. The results of the molecular phylogeny (Fig. 2) show that some individuals identified as *C. antisiensis* were nested within *C. baroni* (FMNH 391887, FMNH 391884, LSUMNS 3597). However, the distributions of these specimens in central Peru (Table 1) suggest that these might be individuals from *C. b. capitalis* (LSUMNS 3597) and *C. b. zaratensis* (FMNH 391887, FMNH 391884), as *C. antisiensis* (Fig. 1c) only reaches northern Peru (Remsen, 2003).

### Divergence among major clades

As uncertainty in calibrations can greatly affect estimates of rate variation and their interpretation (Ho & Phillips, 2009; Smith, 2009; Smedmark*et al.*, 2010), probabilistic calibration priors were used, which are more appropriate in dealing with uncertainty than point calibrations (Drummond *et al.*, 2006). Moreover, a normally distributed prior was used on the ages of calibrated nodes, as it allows for a conservative bidirectional distribution of the uncertainty during the estimation (Ho & Phillips, 2009).

The mean values reported in Table 2 are derived from calibrating nodes A, B and C (Fig. 3) using the values reported by Irestedt *et al.* (2009), including their 95% confidence intervals (CI), whereas the ranges correspond to the upper- and lower-bound confidence intervals reported by Irestedt *et al.* (2009). The means obtained by using the upper- and lower-bound confidence intervals should not be interpreted as confidence intervals themselves, but rather as extremely conservative estimates.

The results from the means obtained in the analyses using the upper- and lower-bound confidence intervals reported by Irestedt *et al.* (2009) as priors are highly congruent with the results from the 95% CIs for the reported mean (Table 2). This congruence suggests that the conservative estimation of the divergence dates is similar to the confidence intervals recovered when using the mean. Throughout the biogeographical discussion only the mean dates are used, as they represent the set of trees with the highest posterior density (Drummond & Rambaut, 2007), and as such the date with the highest posterior credibility. According to the results, the tribe Thripophagini diverged from the Synallaxini around 13.3 Mya (95% CI 11.4–15.1 Mya; node 1, Fig. 3). The clade of *Metopothrix* and *Xenerpestes* diverged ~11.2 Mya (95% CI 9.3–13.1 Mya; node 2, Fig. 3), whereas the split between *Siptornis striaticollis nortoni* and the rest of the Thripophagini took place around 8.4 Mya (95% CI 6.7–11.4 Mya; node 4, Fig. 3), and the split leading to *C. gutturata* and the rest of the clade took place around 5.8 Mya (95% CI 4.5–7 Mya; node 5, Fig. 3). *Roraima* split from the rest of the tribe ~5.6 Mya (95% CI 4.3–6.6 Mya; node 6, Fig. 3), while the next split gave origin to the *Limnoctites* + *Thripophaga* + *Cranioleuca* clade, around 5.1 Mya (95% CI 4.1–5.3 Mya; node 8, Fig. 3). Within *Cranioleuca* the split between clade A and the rest of the genus occurred at 4.4 Mya (95% CI 3.4–5.3 Mya; node 9, Fig. 3), clade B split from clades C + D around 3.4 Mya (95% CI 2.7–4.2 Mya; node 11, Fig. 3), and clades C and D split around 2.8 Mya (95% CI 2.2–3.5 Mya; node 14, Fig. 3).

## DISCUSSION

### Spatial and temporal patterns of diversification

The split between the tribes Synallaxini and Thripophagini took place at a time when the eastern Cordillera of the Central Andes was at about 30% of its current elevation (Gregory-Wodzicki, 2000), whereas the northern Andes had only attained half of their present elevation by the middle to late Miocene (Graham, 2009). Thus, it may be inferred that the common ancestor of Thripophagini was distributed in the lowlands or low montane forests. Divergence between *Xenerpestes* and *Metopothrix*, the sister group to other thripophagines, took place ~8.9 Mya. *Metopothrix* is distributed in the lowlands of the Napo area of endemism, whereas *X. singularis* is distributed along the eastern slope of the Andes of Ecuador and northern Peru, in the humid montane forest. The split between these two allopatric species coincides with active uplift of the northern Andes (Hoorn *et al.*, 1995; Hooghiemstra *et al.*, 2006; Graham, 2009), so their divergence might be related to this event. This uplift created new environments while at the same time creating ecological barriers altitudinally between newly isolated species. It is important to mention that

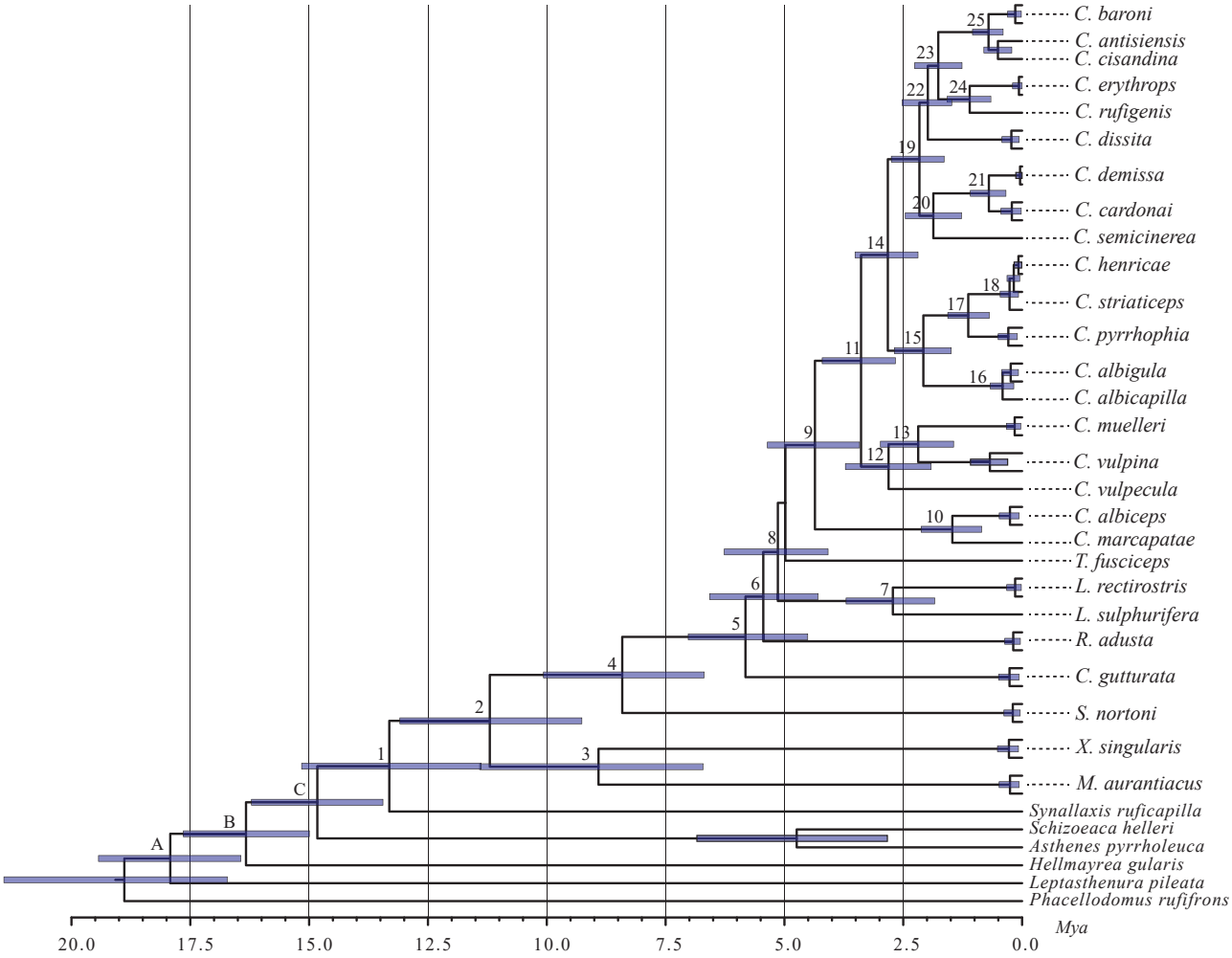


**Figure 3.** Estimated dates of divergence for species in the tribe Thripophagini, calculated by BEAST. Numbers above nodes correspond to those in Table 2. Purple horizontal bars depict confidence intervals.

although *Xenerpestes* has three recognized species, only one, *X. singularis*, was included in this analysis, so further studies are needed within this clade. The next clade to split was that of *Siptornis straticollis nortoni*, which is distributed along the east slope of the Andes of northern Peru. This split took place ~8.4 Mya. Given its timing, it is possible that the origin of this deep lineage is also related to Andean uplift, so further studies are needed within this clade.

*Roraima adusta* is distributed in the Pantepui region. Reconstruction of the ancestral character-state for the node leading to *R. adusta* is equivocal. *Cranioleuca gutturata* is the sister group to the remainder of the thripophagines, including *R. adusta*, and is distributed in the tropical forest, *varzea* and *tierra firme* of the Amazon basin. *Roraima adusta* diverged around 5.4 Mya. Although some authors have suggested that the tepuis were recently colonized from the northern Andes (Chapman, 1931; Mayr & Phelps, 1967; Cook, 1974; Haffer, 1974), probably as a result of the climatic oscillations of the Pleistocene (Chapman, 1931; Cook, 1974; Haffer, 1974), others suggest that some species found in this region might have descended from taxa that at some point were more widespread across northern South America (Braun *et al.*, 2005; Brumfield & Edwards, 2007; Mauck & Burns, 2009). In the case of *R. adusta*, its ancestor was probably distributed in the surrounding lowlands of the Pantepui. However, the process by which its ancestor was isolated from the lowlands to the Pantepui is not clear.

The split leading to the clade *Limnoctites* + *Thripophaga* + *Cranioleuca* took place ~5.1 Mya. Again, the reconstruction of the ancestral state of this node was equivocal. Moreover, because the phylogenetic relationships among these three genera are not resolved, it is not possible to make further

biogeographical inferences of the events that gave rise to this group.

Within *Cranioleuca*, the split between clade A and the rest of the genus occurred at ~4.4 Mya. *Cranioleuca a. albiceps* and *C. m. marcapatae* are distributed in the upper montane or Andean forest of Peru and Bolivia, respectively. However, the reconstruction of the ancestral character state leading to this clade is equivocal. Because the closest genera to *Cranioleuca* – *Thripophaga* and *Limnoctites* – are distributed in the lowlands, it can be inferred that the ancestor of *Cranioleuca* was also distributed in the lowlands. If this is so, a vicariance event due to uplift of the Andes could be the cause of this split, as the eastern Bolivian cordillera gained almost half of its current height in the last 6–10 Myr (Graham, 2009), and if the ancestor of *Cranioleuca* was distributed along the slopes of the Andes at lower altitudes, it could have been uplifted along with the Andes. *Cranioleuca a. albiceps* split from *C. m. marcapatae* between 1.2 and 1.9 Mya, with a mean of 1.5 Mya. These two species are separated by the Apurimac River Valley, and their divergence is more or less contemporary with that of the hummingbirds *Schistes chapmani* and *S. geoffroyi* (~2.5 Mya; Quintero & Perktas, 2017), and the parrots *Hapalopsittaca melanotis melanotis* and *H. m. peruviana* (~1 Mya; Quintero *et al.*, 2013), which have the same distribution and are divided by this same biogeographical barrier. The divergence of these three pairs of disjunct species at about the same time supports the hypothesis that vicariance of all three pairs may be associated with the formation of this valley, as redundant patterns are more likely to be caused by the same process than to independent processes such as dispersal in each of the three lineages.

Clade B is the only one within *Cranioleuca* that is composed entirely of Amazonian species. *Cranioleuca muelleri* inhabits *varzea* forests, *C. vulpina* is found in *varzea* forests, riverine forests and flooded savannah woodlands (Zimmer, 1997), and *C. vulpecula* is found in successional forests in islands of the Amazon river and its 'white-water tributaries' (Zimmer, 1997). This clade was isolated in Amazonia between 2.3 and 3.7 Mya, with a mean of around 2.8 Mya. Campbell *et al.* (2006) and Ribas *et al.*, (2012) have suggested that this coincides with the establishment of the Amazon drainage.

Clades C and D split ~2.8 Mya. As described by Vaurie (1980) and Garcia-Moreno *et al.* (1999), clade C includes southern species distributed in woodlands and dry forests, which construct nests supported from the bottom, whereas clade D contains northern species that are mainly distributed in the humid submontane forests (the exception being *C. baroni*, which is found in drier zones and higher habitats) and which construct pendant nests (Vaurie, 1980; Garcia-Moreno et al., 1999). It is not clear what event or events isolated these two clades, and further analyses are needed.

Within clade C, the divergence between *C. p. pyrrhophia*, *C. p. striaticeps*, *C. henricae* and *C. obsoleta* of the Austral Andes and the Pampas, and that between *C. albicapilla* and *C. a. albigula* from central and southern Peru, were initiated around 1.7 and 2.7 Mya, with a mean at ~2.1 Mya. As in the case of *C. m. marcapate*/*C. a. albiceps*, the Andean species of the two subclades within clade C are divided by the Apurimac river valley, and their divergence is contemporary with that of the other pairs of species that share this distribution, such as the parrots *H. m. melanotis* and *H. m. peruviana* (Quintero et al., 2013), and the hummingbirds *Schistes chapmani* and *S. geoffroyi* (Quintero & Perktas, 2017). Thus, the split between *C. a. albicapilla* + *C. a. albigula* and the clade including *C. p. pyrrhophia*, *C. p. striaticeps*, *C. henricae* and *C. obsoleta* serves as further evidence that the formation of biogeographical barriers, in this case the Apurimac river valley, is a major contributor to the isolation and diversification of these clades. The clade of *C. p. pyrrhophia*, *C. p. striaticeps*, *C. henricae* and *C. obsoleta* diverged around 1.1 Mya. *Cranioleuca p. striaticeps* is allopatric to *C. p. pyrrhophia*, with *C. p. striaticeps* found in the dry woodlands of the Bolivian Andes, and *C. pyrrhophia* distributed in the dry areas of the Chaco and the Pampas. Diversification of these latter two taxa may have been related to the shift of the montane vegetation during the glacial periods of the Pleistocene, when the upper montane forest descended to altitudes that correspond to the current montane and tropical lowland forest (Hooghiemstra et al., 2000). As dry vegetation is present within the distributions of both species, the descent of vegetation zones during glaciations may have created a dry corridor that allowed the common ancestor of this species to reach lower altitudes. During the interglacial this connection might have been lost, isolating *C. p. striaticeps* from *C. p. pyrrophia*. No biogeographical inferences regarding *C. henricae* and *C. obsoleta* can be drawn at this time, until their taxonomic status has been resolved. However, given that *C. henricae* is paraphyletic for mtDNA with respect to *C. p. striaticeps*, and the individuals of *C. c. debilis* are nested within *C. henricae*, this lends support to the idea that *C. henricae* could in fact be a hybrid. There is a need to conduct a detailed morphological and phylogeographical analysis of *C. henricae* to clarify its relationships.

Within group D, the clade containing *C. demissa cardonai*, *C. d. demissa* and *C. semicinerea* diverged from the remainder of the clade between 1.7 and 2.8 Mya, with a mean of 2.2 Mya. The split between *C. semicinerea* of the dry Caatinga forest in eastern Brazil and *C. d. cardonai* and *C. d. demissa* of the humid montane forests of the

Pantepui took place around 1.9 Mya. The divergence between these two clades may be related to vicariance due to the dry glacial intervals during the Pleistocene, which further isolated dry areas such as the Caatinga from the surrounding humid areas such as those of the Pantepui (Hooghiemstra et al., 2000). Once in the Pantepui, the ancestor of *C. d. cardonai* + *C. d. demissa* may have reached the montane forests of the tepuis during the cycles of vertical shifting of the montane forest belts of the glacial/interglacial periods (Rull, 2005). Further biogeographical studies are needed to understand the split between *C. d. cardonai* of the Gran Sabana, and *C. d. demissa* of the Duida. *Cranioleuca dissita* split from the rest of the clade ~0.7 Mya. *Cranioleuca dissita* is distributed on Isla Coiba, in the Veragua Archipelago of Panama. Coiba is part of a system of volcanic oceanic islands uplifted at the end of the Tertiary (Castroviejo & Ibáñez, 2001). It is not clear what event may have caused the split of this taxon, and reconstruction of the ancestral character state is equivocal for this node. However, it is possible that a dispersal event may have been responsible. Finally, the next split divided the remainder of clade D into two groups: *C. e. erythrops* (western Ecuador) + *C. e. rufigenis* (Central America) from *C. b. baroni*, *C. c. cisandina* and *C. a. antisiensis* from the Andes. This split took place ~1.8 Mya. At present it is not possible to reconstruct the events that may have been responsible for the split of these two clades, as the rest of the species from the northern Andes are missing from the analysis. *Cranioleuca e. erythrops* from western Ecuador, and *C. rufigenis* from west Panama and Costa Rica diverged from each other ~1.1 Mya, after the Isthmus of Panama was already in place (Coates *et al.*, 1992). The clade that contains *C. c. cisandina*, *C. a. antisiensis* and *C. b. baroni* diverged ~0.7 Mya, so each of the species within it is very recent (Fig. 3). *Cranioleuca c. cisandina*, *C. a. antisiensis* and *C. b. baroni* have allopatric distributions, with *C. c. cisandina* and *C. a. antisiensis* distributed in humid montane forests at lower altitudes than *C. b. baroni*, which in turn is found in dry upper montane or Andean forests. The reconstruction of the ancestral distributions suggests that the ancestor of this clade was distributed in southern Peru. The difference in habitat between the humid montane *C. c. cisandina*, *C. a. antisiensis* and the upper montane, drier *C. b. baroni* may be an indication that the split between these taxa may have been related to vegetation changes during the climatic oscillations of the Pleistocene (Hooghiemstra *et al.*, 2000).

## CONCLUSIONS

The broad sampling and the use of basal taxonomic units in this study allowed us to better understand the diversity and evolutionary relationships of this group of birds, as well as an indication of its complex biogeographical history. Our phylogenetic findings again highlight the importance of framing any evolutionary study within a phylogenetic context. Further phylogeographical studies are needed to establish the species limits within the complex formed by *C. a. antisiensis*, *C. b. baroni* and *C. c. cisandina*, as well as to clarify the species status of *C. henricae*. Further work will also clarify the status of several subspecies that we recovered as genetically distinct. It is important to take into account the limitations of the present analysis given the exclusive use of mitochondrial genes. Further studies should include more thorough sampling for this diverse and complex group, and include nuclear genes.

Our results indicate that the diversification of this group seems to have been influenced, at least in part, by the uplift of the Andes, the creation of new montane habitats and barriers, the evolution of Amazonian drainages and landscapes, and the climatic oscillations of the Pleistocene.

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