Avian Diversification in the Andes: Understanding Endemism Patterns and Historical Biogeography

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ABSTRACT

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The Andes, along with the Amazon and Atlantic forests, harbor the richest avifauna in the world with roughly one third of all the world's species of birds. Many biogeographical studies have sought to explain the origin and diversification of Andean taxa. However, because of the Andes' extensive latitudinal span and complexity, there is no one single cause of origin or of diversification that can explain the diversity found in them.

Along the Andes, multiple biogeographic patterns of disjunction between highland and lowland sister-groups have been linked to Andean uplift. For example, Ribas *et al.* (2007) provided evidence that the spatio-temporal diversification in the monophyletic parrot genus *Pionus* is causally linked to Andean tectonic and palaeoclimate change through vicariance. Thus, if the Andes uplift is responsible for some of the patterns of montane-lowland disjunctions, it may be one of the mechanisms underlying the taxonomic assembly of the Andean montane avifauna.

In this dissertation I explored whether the origin and diversification of three groups of Andean birds—the exclusively Andean parrot genera *Hapalopsittaca*, the subclade of mangoes containing *Doryfera*, *Schistes*, and *Colibri*, and the ovenbirds of the tribe Thripophagini—can be linked to Earth history.

The results show that the origin of these Andean taxa can be explained through vicariance from their lowland sister-groups, mediated by the uplift of the Andes. Thus, this thesis proposes that geological events are directly responsible for originating diversity throughout montane environments. Once in the Andes, the diversification of these montane taxa can be explained by events such as the tectonic evolution of the Andes—which created canyons and valleys that may have caused the vicariance of continuous populations—as well as by the climatic oscillation of the Pleistocene, which caused altitudinal shifts, expansion, and contraction of the montane vegetation belts during the climatic oscillations of the Pleistocene.

In summary a significant part of the temporal patterns of origins and diversification of the three groups of birds included in this study can be linked to Earth history, both in terms of the tectonic history of the Andes and of the climatic events of the Pleistocene.

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CHAPTER 1

The Origin and Diversification of Andean Taxa: a Review

INTRODUCTION

The Andes, along with the Amazon and Atlantic forests, harbor the richest avifauna in the world (Stotz *et al.*, 1996; Nores, 2000; Rahbek & Graves, 2001) with roughly one third of all the world's species of birds. Although numerous studies have dealt with this diversity, there are many unanswered questions regarding the systematics, origins, and diversification of Andean taxa. Moreover, many studies addressing these topics were undertaken before the time of modern phylogenetic methods, were based on a biological species concept paradigm, or lacked a time-estimation component (e.g., Chapman, 1917, 1926; Vuilleumier, 1969; Vuilleumier & Simberloff, 1980; Remsen Jr, 1984; Fjeldså, 1985; Graves, 1985; Garcia-Moreno *et al.*, 1998; Poulsen & Krabbe, 1998; Chesser, 2000; Fjeldså & Rahbek, 2006; Mihoc *et al.*, 2006). As the literature grows, so do different views and opposing empirical examples on the origin and diversification of Andean taxa. Because of the Andes' extensive latitudinal span and complexity, it is likely that there is no one single pattern to explain the origin or single cause of diversification. Here I present some of the most relevant ideas that have been proposed to explain the origin and diversification of Andean groups.

ORIGINS OF ANDEAN TAXA

In his monograph of the birds of Colombia, Chapman (1917) proposed three sources for populations that colonized the high Andean habitats: the Guianan highlands, the Central American highlands, and the temperate lowlands of southern South America. Later in his monograph on the birds of Ecuador (1926), he suggested that the majority of birds found in the *páramo* and *puna* zone of the Andes were derived by primary differentiation of populations from the adjacent Amazonian lowlands, whereas other montane species must have come from contiguous regions. Although there are studies that present examples of Andean taxa whose sister group is distributed in one of more of these putative areas [e.g.: tropical lowlands for *Heliodoxa* hummingbirds (Gerwin & Zink, 1989), *Leptopogon* flycatchers (Bates & Zink, 1992), and *Pionus* parrots (Ribas *et al.*, 2007); Central America for the rodent genus *Akodon* (Patton & Smith, 1992) and *Buarremon* brush-finches (Cadena *et al.*, 2007); southern-temperate South America for the high Andean coot species (Fjeldså, 1985); southeastern coasts of South America for some *Thamnophilus* species (Brumfield & Edwards, 2007); North America for the legume genus *Lupinus* (Hughes & Eastwood, 2006)], the exact mechanism of their origin in montane environments is still highly debated.

Can Earth history explain the origin of Andean taxa?

Throughout this dissertation, the term Earth history refers both to tectonic processes and the climatic oscillations of the Pleistocene. Multiple biogeographic patterns of disjunction between highland and lowland sister-groups have been linked to Andean uplift. For example, Garcia-Moreno *et al.* (1999) found that the lower-elevation *Metallura tyrianthina* of the eastern slope of the Andes is the sister-group of a clade of higher-elevation *Metallura* hummingbirds and suggested that the diversification of this group may have been induced by Andean uplift. Later, Ribas *et al.* (2007) provided evidence that the spatio-temporal diversification in the monophyletic parrot genus *Pionus* is causally linked to Andean tectonic and palaeoclimate change through vicariance. These authors postulated three independent instances of highland-lowland diversification in *Pionus*. Likewise, Almeida *et al.* (2007) proposed a highland-lowland split in the rodent genus *Calomys* caused by uplift of the Andes.

If the Andes uplift is responsible for some of the patterns of montane-lowland disjunctions, it may be one of the mechanisms underlying the taxonomic assembly of the Andean montane avifauna (Ribas *et al.*, 2007). If some of the allopatric patterns found between the montane regions of the Andes and the adjacent lowlands have been a consequence of the uplift of this mountain chain, we would find that those montane and lowland groups form sister groups, with the lowland taxa being basal, and that the time of divergence between them coincide with the timing of the uplift of the Andes (Bates & Zink, 1994; Garcia-Moreno *et al.*, 1999: Almeida *et al.*, 2007; Ribas *et al.*, 2007). Furthermore, as the uplift would have created patterns of montane/lowland disjunction in several groups roughly at the same time, we would find a temporal congruence in the origin of many different montane groups from lowland ancestors. If, on the other hand, lowland-montane taxa pairs do not form sister groups, or if they do, but the timing of their divergence is not congruent with that of the uplift of the Andes, then alternative hypotheses would have to be invoked for the origin of Andean taxa.

There are many instances in which highland-lowland disjunctions have been overlooked (e.g. Dingle *et al.*, 2006; Brumfield & Edwards, 2007), mainly because many biogeographical studies include only highland or lowland groups in their analysis, do not frame questions in a phylogenetic context, do not take into account temporal patterns of diversification, or assume *a priori* that ecological factors alone are responsible for structuring altitudinal distributions. If we are to understand the relevance of these patterns for the origin of montane taxa, future biogeographic studies will need to include relevant highland and lowland groups, frame biogeographical questions in a phylogenetic context, and take into account temporal patterns of diversification.

In those cases in which the origin of Andean taxa cannot be explained by vicariance events between montane and lowland taxa due to the uplift of the Andes, the alternatives would be either vicariance or dispersal events from southern temperate regions (Fjeldså, 1985), from northern montane regions (Perez-Eman, 2005; Miller *et al.*, 2007; Weir *et al.*, 2008; Bonaccorso, 2009), or from the southeastern coast of South America (Brumfield & Edwards, 2007). In either case, the phylogenetic pattern would show a sister group relationship between taxa of the putative area and the Andes, and the basal clade would be distributed outside the Andes. If vicariance was responsible for the origin of these groups, then the timing of their split would be spatio-temporally congruent with Earth history events, and several groups would have been originated by the same event at the same time. Finally, long distance dispersal events from any of the aforementioned areas would have the same phylogenetic pattern than those that originated via vicariance, but there would not be temporal congruence between them and any given Earth history event.

SPECIATION OF ANDEAN GROUPS

Explanations for Andean diversification have focused on Earth history via the tectonic evolution of the Andes (Chapman, 1926; Cracraft, 1985; Garcia-Moreno *et al.*, 1998; Garcia-Moreno *et al.*, 2001; Perez-Eman, 2005; Fjeldså & Rahbek, 2006; Cadena *et al.*, 2007; Chaves *et al.*, 2007; Sedano & Burns, 2009), vegetation shifts during the Pleistocene (Van Der Hammen & González, 1963; Van Der Hammen *et al.*, 1973; Hooghiemstra, 1984; Van Der Hammen & Cleef, 1986; Van Der Hammen, 1989; Hooghiemstra & Van Der Hammen, 2004; Hooghiemstra *et al.*, 2006), ecological interactions such as competition and predation (Terborgh, 1971; Terborgh & Weske, 1975; Remsen & Graves, 1995b, a; Navas, 2003; Buckley & Roughgarden, 2005; Brumfield & Edwards, 2007), parapatric speciation along elevational gradients (Endler, 1977; Hall, 2005), and rapid radiation as a response to newly created habitats (Vuilleumier, 1970; von Hagen & Kadereit, 2001; Kadereit & von Hagen, 2003; Bell & Donoghue, 2005; Hughes & Eastwood, 2006).

Earth history as an explanation of the speciation within Andean groups

The influence of tectonics and climatic oscillations has been recognized as an important factor in the diversification of species in different biogeographic zones (Kohn & Fremd, 2008; Koscinski *et al.*, 2008; Antonelli *et al.*, 2009; Cossios *et al.*, 2009; Finarelli & Badgley, 2010; Hoorn et al, 2010). In the Andes, tectonic evolution created deep valleys that may have caused the vicariance of ancestral populations into new species, while the uplift of the different cordilleras may have isolated ancestral contiguous populations, causing them to diversify. Moreover, the climatic oscillations of the Pleistocene caused cyclic vertical shifts of the vegetation belts, while at the same time caused the expansion of some of these belts during glacial periods, allowing for dispersion and increased gene flow, which was interrupted during the interglacials, in which widespread populations were broken and isolated, sometimes causing their diversification. In order to link these Earth history events with the diversification of Andean groups, it is important to frame biogeographic questions in a phylogenetic frame, and to obtain a temporal estimate of their diversification.

Parapatric speciation along elevational gradients

Although Endler proposed that selection across vertical slopes might explain parapatric distributions (1977, 1982), few studies have tested this model in a phylogenetic framework. Those pairs of species that are assumed to be parapatric must be each other's sister species, but the lack of phylogenetic studies of groups with this kind of distribution preclude to test this hypothesis. Patton & Smith (1992) examined a series of paired highland-lowland species replacements of Andean *Akodon* mice. They found that populations from the same elevation across adjacent valleys were more closely related to each other than to populations that were vertically distributed within drainages. In this manner they were able to reject parapatric speciation as the mechanism underlying the divergence of highland and lowland populations in this group of rodents. Other studies have also falsified the hypothesis of parapatric speciation, such as those by Arctander & Fjeldså (1994) for *Scytalopus* in the Ecuadorian Andes, Hillis (1985) for the Andean Lizard *Pholidobolus*, and Dingle *et al.* (2006) for *Henicorhina* wrens. The only instance in which vertical montane speciation has been found is that of *Ithomiola* butterflies (Hall, 2005). This genus is distributed in lowland and montane regions throughout the

Neotropics. Hall (2005) found that basal species appear to be allopatrically distributed whereas most derived ones are elevationally parapatric. According to Hall (2005), the more derived the species, the higher elevational bands they occupy, with a sister species-pair occupying the highest elevational bands.

Although there may be other instances in which parapatric speciation is responsible of the diversification and current patterns of distribution of Andean taxa, it is clear that these questions have to be addressed in a phylogenetic framework in order to accept or falsify empirical observations.

Can competition explain diversification in the Andes?

Some studies have proposed competition as an alternative to parapatric speciation to explain elevational replacements, as in the case of the birds of the Cordillera Vilcabamba, Peru (Terborgh, 1971; Terborgh & Weske, 1975), the Andean lizard *Pholidobolus* (Hillis, 1985), the brush-finches of the genera *Atlapetes* (Remsen & Graves, 1995a) and *Buarremon* (Remsen & Graves, 1995b), and perhaps in some species of the genus *Thamnophilus* (Brumfield & Edwards, 2007). However, just as with many other instances of diversification, there are few studies that corroborate these hypotheses within a phylogenetic framework or with the requisite ecological studies on the ground.

Competition as a factor in speciation can be tested in cases in which pairs of species have restricted, complementary distributions where they coexist and broader elevational ranges where only one of them is present, as in the case of the brush-finches of the genus

Buarremon (Remsen & Graves, 1995b; Cadena, 2007). In Peru, Ecuador, and most of Colombia, where both taxa coexist, *B. brunneinucha* occupies the lower part of the gradient whereas *B. torquatus* is found at higher elevations. Furthermore, in some regions of northern South America and Central America the pattern is reversed, and in other areas, mid-montane populations of *B. brunneinucha* are found between high- and low-elevation populations of *B. torquatus*. Cadena (2007) tested whether competition could explain the distribution patterns of these two species through phylogenetic and population genetics analyses, and his results firmly reject potential roles for interspecific competition in the elevational zonation for *Buarremon*. Rather, he suggests that *B. brunneinucha* may have colonized the range of *B. torquatus* recently, so even if competition has played a role in these recent distributions, it cannot explain the distributional patterns throughout the whole range of these two species (Cadena, 2007). The results of this study add to others (Sorenson *et al.*, 2003; Flanagan *et al.*, 2004; De Chaine & Martin, 2006) that have found that ecological interactions have played only a small part in the evolutionary history of taxa, and thus are not sufficient to explain diversification.

Is there a south to north diversification pattern within Andean taxa?

Some authors have found south-to-north diversification patterns within Andean taxa, with more basal taxa distributed in the southern regions of the Andes, whereas more derived ones are found in the northern ranges. These patterns are proposed to be linked to the south-to-north uplift of the mountain range (Doan, 2003; Picard *et al.*, 2008). Doan (2003) tested this hypothesis using the monophyletic Andean lizard genus *Proctoporus*. Her results found that the southernmost species were the most basal, which is consistent with the south-to-north diversification pattern prediction. However, those species distributed in the northern Andes did not match this prediction. The Venezuelan and Trinidadian species did appear to be highly derived, but the Ecuadorian and Colombian species did not form a particular pattern in relation to them. This lack of pattern within Ecuador and Colombia suggests that a more dynamic model is needed to explain these distributions, and possibly Pleistocene climatic cycles may have been significant in their assemblage. Thus, the south-to-north diversification pattern hypothesis does appear to have predictive power with regard to large-scale distribution patterns in this group (Doan, 2003). Soejima *et al.* (2008) found a similar diversification pattern in the genus *Paranepheliinae* (Liabeae, Asteraceae). These authors found that the ancestor of *Paranepheliinae* may have originated in the southern Andes, whereas the progressive uplift of the range and subsequent climatic oscillations of the Pleistocene may have led to the expansion of their distribution toward the north, where it stopped at the Huancabamba Depression.

Phylogenetic signatures in the speciation of Andean taxa

Different modes of speciation throughout the Andes would be reflected by different phylogenetic patterns. As already mentioned, in case parapatric speciation is taking place, species that replace each other altitudinally would have to be sister taxa, with the most basal taxa distributed in the lower elevations, whereas the most derived one would be occupying the highest one (Hall, 2005). Events such as competition or range expansion may or may not take place between sister groups, but because these ecological events are expected to be very recent in the history of taxa (Cadena, 2007), they may not necessarily leave phylogenetic signatures.

If, on the other hand, diversification is caused by Earth history, then the resultant phylogenetic and biogeographic patterns would have to be spatially and temporally linked to it. Among Earth history explanations, diversification due to the tectonic evolution of the Andes—through the formation of canyons or valleys that intersected the cordilleras—or by vegetation shifting during the climatic events of the Pleistocene, would have caused the contemporaneous formation of multiple independent lineages, via fragmentation of ancestral taxa distributed in a previously continuous area (Perez-Eman, 2005; Cadena *et al.*, 2007; Miller *et al.*, 2007). However, if diversification of the Andes proceeded through expansion followed by long-distance dispersal, the phylogenetic patterns of different groups would not be congruent with each other, and would consist of clades of isolated groups with no particular structure among them (Miller *et al.*, 2007). In the case of south-to-north diversification patterns as the result of the south-to-north uplift of the Andean chain, the most basal taxa of the group presenting this pattern would have to be distributed in the southern Andes, with the most derived ones distributed in the northernmost ranges (Doan, 2003; Picard *et al.*, 2008; Soejima *et al.*, 2008). However, even when a south-to-north diversification may be the result of this temporal pattern of tectonic progression, some of these phylogenetic and biogeographic patterns may be obscured by more recent and complex events as mentioned by Doan (2003).

EXPLORING THE ORIGIN AND DIVERSIFICATION OF THREE GROUPS OF ANDEAN BIRDS

In this dissertation, I explore whether the origin and diversification the exclusively Andean parrot genera *Hapalopsittaca*, the subclade of mangoes *Doryfera*, *Schistes*, and *Colibri* (Mcguire *et al.*, 2009), and the ovenbirds of the tribe the Thripophagini (Moyle *et al.*, 2009)—can be linked to Earth history. Specifically, I will test the hypothesis of whether some of the allopatric patterns found between the montane regions of the Andes and the adjacent lowlands have been a consequence of the uplift of this mountain chain, and if the tectonic history of the Andes, as well as the climatic changes of the Pleistocene can explain the diversification of these groups.

AN EARTH HISTORY BACKGROUND TO UNDERSTANDING AVIAN DIVERSIFICATION IN THE ANDES

Geological and geographic setting of the northern and central Andes

The Andean range can be divided into three domains. The northern Andes, north of 2° S, correspond to part of Ecuador, Colombia, and Venezuela (Fig 1). The central Andes range from 2° to 33° 30' S, and can be divided into northern central Andes (2°S - 15°S), *Altiplano* subdomain (15° S - 24° S), *Puna* subdomain (24° S to 28° S), and southern flat slab subdomain (28° S - 33° 30' S). The northern central Andes correspond to the Andes of southern Ecuador and northern Peru, while the *Altiplano*-Puna subdomain corresponds to the Andes of central Peru, Bolivia, and northern Argentina (Fig. 1). Finally, the southern flat slab subdomain and the southern Andes (below 33° 30' S) are characteristic of the remainder of Argentina and Chile (Jordan *et al.*, 1983; Gregory-Wodzicki, 2000).

The northern Andes

The northern Andes comprise the Santa Marta Massif, the Venezuelan or Meridan Andes, and three main Andean ranges in Colombia—the Cordilleras Occidental, Central and Oriental (Fig. 1). These three cordilleras are known collectively as the Colombian Andes (Gregory-Wodzicki, 2000). The Sierra Nevada de Santa Marta reaches a maximum height of 5,700 m. This massif is the northernmost mountain considered to be part of the Andes (Fig. 1) and has never been connected to the rest of the Andean ranges, as it is isolated by wide alluvial plains (Simpson, 1975, Fjeldså & Krabbe, 1990). Santa Marta is bounded on the north by the Caribbean Sea and the plains of the lower Guajira Peninsula, on the west by the Magdalena River valley, and on the southeast by the valleys of the Rios Cesar and Ranchería (Tschanz *et al.*, 1974). Within the Colombian Andes, the Cordillera Occidental is the lowest with elevations averaging about 2000 m and with no snowcaps (Fjeldså & Krabbe, 1990). This cordillera is separated from the Cordillera Central by the Cauca Valley (Fig. 1). The Cordillera Central has elevations averaging 3000-3500 m, with high peaks (*nevados*), mainly in the Caldas-Quindío region (Fjeldså & Krabbe, 1990). The Magdalena Valley (Fig. 1) divides this cordillera from the Cordillera Oriental. The latter is a wide range with peaks averaging 2500-3500m, and a few higher massifs, such as the Sierra Nevada del Cocuy, which reaches 5493 m (Fjeldså & Krabbe, 1990). At 10°N, the Cordillera Oriental bifurcates to the northwest into the Santander massif and the Sierra de Perijá (Hoorn *et al.*, 1995), and to the northeast into the Mérida Andes (Fig. 1). Although a geographical continuation of the Colombian Andes, the Mérida Andes are of a different geological origin (Audemard & Audemard, 2002). The Santander massif and the Mérida Andes are separated by the Táchira saddle depression (Fig. 1; Hoorn *et al.*, 1995), a 40 km gap with a dry subtropical climate (Fjeldså & Krabbe, 1990).

The central Andes

The Andes of Ecuador are the narrowest part of the entire Andean range. They are subdivided into two main ridges known as the Cordillera Occidental and Cordillera Oriental, and a third ridge to the northeast, the Napo uplift, which reaches its maximum height in Colombia (Coltorti, 2000). The two main cordilleras are connected by transverse ridges (nudos) that create several interandine valleys known as the Central Valley system (Fjeldså & Krabbe, 1990). In northern Peru the Cordillera Oriental divides the catchments of the Huallaga River to the east and the Marañón River to the west, forming a major gap in the highlands known as the North Peru Low (Fig. 1; Bush *et al.*, 2005). In central Peru, the highlands are intersected from the east by several deep valleys, whereas in the south, from Cusco to Central Bolivia, the Eastern Cordillera (Cordillera Real) forms a continuous chain interrupted by two canyons in La Paz, Bolivia that have a significant altitudinal gradient towards the lowlands known as the *Yungas* (Fjeldså & Krabbe, 1990). In the north of Bolivia, the Cordilleras Oriental and Occidental, both with elevations exceeding 6000 m, drain the *Altiplano* plateau (~3800 m). The Cordillera Occidental is formed by a chain of volcanoes, whereas the Cordillera Oriental and the Altiplano basin are the result of folding and faulting (Garzione *et al.*, 2008). The inner drainage area of the *Altiplano* used to be covered by the Ballivian lake, that is now fragmented into Lake Titicaca to the north—which drains into Lake Popo—and Lakes

Uyuni and Coipasa to the south (Fjeldså & Krabbe, 1990). To the west of the Cordillera Occidental lies the Cordillera de la Costa, with elevations of 1000–1500 m, whereas to the east of the Cordillera Oriental lies the Subandean zone, with elevations at 400–1000 m, and the Chaco Basin (Jordan & Alonso, 1987; Allmendinger *et al.*, 1997). The Cordillera Oriental ends in the Tunari range in Cochabamba, Bolivia (Fjeldså & Krabbe, 1990).

Geological origins and uplift of the Andes

Origin and uplift of the northern Andes

The Cordillera Occidental is of volcanic origin, and was accreted to the Coast of South America in the Late Cretaceous (Winsemann, 1994), whereas parts of it were uplifted during the Miocene (Hooghiemstra *et al.*, 2006). On the other hand, the Cordilleras Central and Oriental are not of volcanic origin (Gregory-Wodzicki, 2000). The Cordillera Central rose between Late Oligocene and Middle Miocene (Hooghiemstra *et al.*, 2006, Graham 2009). However, the highest uplift rates for all three Cordilleras took place during the Plio-Pleistocene (Van Der Hammen, 1961; Harrington, 1962; Van Houten & Travis, 1968; Van Der Hammen *et al.*, 1973; Fabre, 1983; Kroonenberg *et al.*, 1990; Hoorn *et al.*, 1995; Gregory-Wodzicki, 2000; Hooghiemstra *et al.*, 2006; Graham 2009). The main range of the Cordillera Oriental is the best studied of the three, due to the availability of paleobotanical data from sediments at *ca*. 2550 m elevation in the surroundings of the high plain of Bogotá (Hooghiemstra *et al.*, 2006). The evidence from these sediments and that from geological data suggest that from the Middle Miocene through Early Pliocene the elevations were no more than 40% of their modern values, and increased significantly between 2 and 5 Mya at rates of 0.5–3 mm/yr, reaching modern elevations by around 2.7 Mya (Gregory-Wodzicki, 2000; Graham 2009; Hoorn *et al.*, 2010). To the north or the Cordillera Oriental, the Santander Massif began its uplift between 16 and 12 Mya (Kroonenberg *et al*., 1990), whereas the Mérida Andes were uplifted between 12 and 8 Mya (Albert *et al.*, 2006; Hoorn *et al*., 2010), and gained the final 1200-1500 m in the last 3-5 Mya, with an average uplift rate of 2-5 mm/yr (Audemard & Audemard, 2002).

Origin of the central Andes

The uplift of the central Andes began in the Cenozoic as a consequence of the subduction of the Nazca Plate, as it slowed its motion from *ca*. 15 to 5 cm/yr, as a result, perhaps of the collision of India with Asia (Lamb, 2004). The decrease in the subduction rate caused a decrease in the amount of sediments into the subduction zone, which in turn resulted in the build up of friction that ultimately initiated the uplift of the central Andes *ca*. 40 Mya (Lamb & Davis, 2003). The subduction of the Nazca Plate in the Peru-Chile trench before the Pliocene was quick and steep, giving rise to volcanic activity, whereas from the Pliocene onwards was slow and shallow with less volcanic activity (Graham, 2009). However, subduction only accounts for one fifth of the height of the Andes. The majority of the current height of the central Andes is the result of compression of the continent between the movements away from the Mid-Atlantic Ridge at the east, and resistance towards the subduction of the Nazca Plate at the west (Graham, 2009), along with a further reduction in the amount of sediments that flowed into the subduction zone as a result of the creation of the rain shadow to the west of the Andes *ca*. 15 Mya (Lamb &

Davis, 2003; Strecker *et al.*, 2009). Finally, thinning of the underlying lithosphere of the central Andes is another factor that generated surface uplift, by causing heating, weakening, and folding of the crust to high elevations (Garzione *et al.*, 2008; Graham, 2009).

Paleolevations of the central Andes have been reconstructed through many different methods. Through the study of an assemblage of a 6-7 Mya palynoflora recovered from the 3600-m high Pislepampa locality at the northeast of Cochabamba, Graham *et al.* (2001) suggested that from one-third to one-half of the uplift of the Cordillera Oriental has occurred since the deposition of this flora when it was part of the lower border of the cloud forest, with paleoelevations between 1200 and 1400 m (Graham *et al.*, 2001). Moreover, using the morphology of well preserved paleosurfaces that define Late Miocene paleodrainage systems, Barke & Lamb (2006) suggested that the best estimate of uplift for the Cordillera Oriental in the Bolivian Andes over the last 12–9 Mya has been 1705±695 m, whereas other studies (Gregory-Wodzicki *et al.*, 1998; Gregory-Wodzicki, 2000; Montgomery *et al.*, 2001; Ghosh *et al.*, 2006; Rowley & Garzione, 2007) suggest an uplift from 2000 to 4000 m after 10 Mya. Moreover, through the study of the Late Miocene upper Jakokkota flora from west-central Bolivia, Gregory-Wodzick (2002) estimated that at this time, the paleoelevation of the *Altiplano* was 1160 ± 600 m, so approximately two thirds of its modern elevation was obtained since the early Late Miocene, whereas through the studies of oxygen and clumped isotope data (Garzione *et al.*, 2006; Ghosh *et al.*, 2006) estimated that the Altiplano reached its current height *ca.* 6

Mya. Dates for the uplift of the Ecuadorian mountain chain show that its current height was attained between 5.5 Mya and 3.3 (Coltorti, 2000; Spikings & Crowhurst, 2004).

Vegetation of the northern Andes

The following description is for the vegetation distributed in the Cordillera Oriental of Colombia (Hooghiemstra *et al.*, 2006; Weng *et al.*, 2007), but can be extended to the whole of the northern Andes. The tropical lowland forest belt extends from sea level to 1000, (average annual temperatures: 22 °C to 13°C). Above the lowland forest zone, the subandean or lower montane forest belt extends from 1000 to 2300 m (average annual temperatures: 23°C to 19°C), followed by the Andean forest or upper montane forest that extends from 2300–2500 to 3200 m (average annual temperatures: 16°C to 9°C). Immediately above the upper forest line is the *subpáramo* belt, which extends from 3200 m to 3500 m (average annual temperatures: 9°C to 6°C), and is a transition zone from forest to open areas (Weng *et al.*, 2007). The *páramo* or *grasspáramo* belt extends from *ca*. 3500 m to *ca*. 4200 m (average annual temperatures: 6°C to 3°C), while the *superpáramo* belt can be found from *ca*. 4200 m up to snowline at *ca*. 4800 m (average annual temperatures: 3°C to 0°C). In the *superpáramo*, the vegetation is minimum and found only in patches due to daily ground frosts that cause unstable soil (Van't Veer & Hooghiemstra, 2000; Hooghiemstra *et al.*, 2006).

Development of the northern Andes' montane forests during the Neogene: Uplift of the Andes

The Andean uplift played a major role in the development and distribution of the present-day northern Andean flora in creating new habitats and serving as a route for temperate taxa to migrate into these newly formed environments (Hooghiemstra *et al.*, 2006). Thus, the present-day composition of the flora of the Colombian montane forest and *páramo* is the result of these two phenomena (Hooghiemstra *et al.*, 2006). Macro (fossil leaves, fruits, seeds) and microfossils (fossil pollen and spores) from the Late Miocene to Late Pleistocene contained in sediments in the basin and surrounding areas of Bogotá (at *ca.* 2550 m: Salto de Tequenedama I/II, Late Miocene; Río Frío, Early Pliocene; Subachoque- 39 and Facatativá-13, Middle Pliocene; Guasca, Late Pliocene) give a "snapshot" of the long-term paleoecological development of the northern Andes (Hooghiemstra *et al.*, 2000; Hooghiemstra *et al.*, 2006) and are the base of the knowledge of the development of the montane forests in the northern Andes. According to this data, during the Late Miocene this area of the Cordillera Oriental of Colombia was a lowland riverine environment (*ca.* 700 m elevation) dominated by tropical lowland taxa, similar to those found in the modern *várzea* forest of the Amazon basin (Hooghiemstra *et al.*, 2006). By Late Miocene to Early Pliocene, the floral composition changed from tropical lowland to subandean forest, as denoted by the change in proportions of lowland *vs* Laurasian families (75% to *ca*. 60% *vs* 10% to *ca*. 23%, respectively) suggesting an elevation of *ca*. 1000 m for the Cordillera Oriental. During the Middle Pliocene, the floral composition indicates that the area had reached an elevation of *ca*. 2000 m (Hooghiemstra *et al.*, 2006), whereas during the Late Pliocene it had reached elevations close to *ca*. 2600 m.

Development of the northern Andes' montane forest during the Quaternary: The climatic oscillations

During the climatic oscillations of the Quaternary, the vegetation of the Andes experimented a number of cyclic elevational shifts as a result of the changes in temperature between glacial-interglacial cycles (Van Der Hammen & González, 1963; Van Der Hammen *et al.*, 1973; Van Geel & Van Der Hammen, 1973; Hooghiemstra, 1984; Van Der Hammen, 1989; Hooghiemstra *et al.*, 1993; Hooghiemstra & Ran, 1994; Hooghiemstra & Cleef, 1995; Hooghiemstra & Van Der Hammen, 1998; Hooghiemstra *et al.*, 2000; Hooghiemstra *et al.*, 2006; Weng *et al.*, 2007), as well as to changes in precipitation and dropping levels in the concentration of atmospheric CO_2 (Boom *et al.*, 2001; Boom *et al.*, 2002).

The basin of Bogotá is presently situated in the Andean forest zone (upper montane forest belt), and is the floor of an old drained lake. This basin formed *ca*. 6 Mya as the Cordillera Oriental was going through a major uplift, and reached its present height (2550 m) between 4 and 3 Mya (Graham, 2009). The sedimentary basins of Bogotá contain uninterrupted sequences of lacustrine sediments that vary in age from the last two glacial cycles of the Fuquene basin (Van Geel & Van Der Hammen, 1973), to the complete sequence of Quaternary Ice Ages of the Bogotá basin through the 357 m deep core Funza-I (Hooghiemstra, 1984) and the 586 m deep core Funza-II (Hooghiemstra & Ran, 1994; Hooghiemstra & Cleef, 1995). The Funza pollen records show that the upper forest line of the northern Andes shifted during the Quaternary from *ca*. 2000 m during extreme glacial conditions, to *ca*. 3400-3700 m during peak interglacial conditions (Hooghiemstra *et al.*, 2000; Weng *et al.*, 2007), meaning that this basin was covered by *grasspáramo* during the glacial cycles, and by Andean forests during the interglacials (Weng *et al.*, 2007). Thus, these pollen records are representative of the history for the northernmost Andes of Colombia and Venezuela during the climatic cycles of the Plio-Pleistocene (Hooghiemstra *et al.*, 2000; Weng *et al.*, 2007).

According to the Funza pollen records, around 2.2-1.4 Mya cold climate became persistent, and the upper forest line reached 1900 m (Hooghiemstra *et al.*, 2000). Between 1.4 and 1.0 Mya cold climatic conditions (8°-12°C at 2500 m) were still common, and the upper limit of the lower montane or subandean forest reached higher elevations. At around 1.0 Mya *Alnus* reached the northern Andes (Hooghiemstra *et al.*, 2000). *Alnus* is a characteristic genus of the northern hemisphere, and its arrival to the high plains of Bogotá constitutes an indication that warm climate conditions had become persistent again (Bush, 2005), which caused that the upper limit of the lower montane forest belt reached its modern elevation of 2300 m (Hooghiemstra *et al.*, 2000). At *ca.* 600 kyr, *Quercus* reached the northern Andes (Bush, 2005), marking the beginning of a new type of montane forest beginning at *ca.* 130 kyr (Marchant *et al.*, 2002). During the Last Glacial Maximum (~20–18 kyr) *páramo* belt moved to lower elevations, becoming widespread in contrast to the small isolated islands it formed during interglacials (Simpson, 1975; Hooghiemstra *et al.*, 2000; Hooghiemstra *et al.*, 2006). Thus, glacial periods offered good opportunities for gene flow because *páramo* formed large continuous areas. Because the oscillations of the *páramo* were repeated many times during the Quaternary, they might have stimulated significant speciation and may explain why the currently restricted *páramo* biome has a high level of endemism (Hooghiemstra & Van Der Hammen, 2004; Hooghiemstra *et al.*, 2006).

Vegetation of the central Andes

Lower montane rain forest occurs on the eastern Andean slope of the central Andes between 700 and 2500 m, but it has the same characteristics of the cloud forests, namely constant high humidity, fog, mist, and abundant epiphytes on tree branches and trunks (Neill, 1999). This vegetation belt is replaced by the upper montane rain forest from 2500 m to *ca.* 3400–3600 m. The upper limits of the upper montane forest is known as elfin forest or *ceja andina*, characterized by lower tree canopies and twisted trees (Neill, 1999). *Grasspáramos* or *páramos* occur from about 3400 to over 4000 m, and are dominated by bunch forming grasses, with a diverse assemblage of herbaceous plants and small shrubs scattered among them (Neill, 1999). In very wet areas of the Cordillera Oriental of Ecuador, dwarf bamboo is found instead of bunchgrass *páramos*. On the slopes of northern and central Ecuador, from 4000–4500 m, shrub and cushion *páramos* are found above *grasspáramos*, with a non-continuous vegetation cover. Desert *páramo* vegetation is found at the highest elevations on the slopes of the highest volcanoes, near the lower limit of glaciers, with very sparse plant cover (Neill, 1999). The highlands of Peru and Bolivia are covered by a low steppic and alpine vegetation of plants, although is possible to find small local evergreen woodlands or bushlands as high as 5000 m (Fjeldså, 1992).

Climatic oscillations of the Quaternary in the central Andes

Paleoecological data from the high Andes of Peru and Ecuador are scarce, despite glacial geological evidence for periods of extensive glacier activity during the Late Pleistocene (Hansen & Rodbell, 1995). Palynological studies from the central Peruvian Andes suggest that major vegetation fluctuations were associated with the glacial-interglacial transition from the Late Pleistocene to the Holocene. A pollen and sediment record of a core from Laguna Baja in the eastern cordillera of northern Peru, at 3575 m, suggests several episodes of major vegetational and climatic change over the past 13,000 yr. According to it, the warm and moist environment appears to have been responsible for the development of an open mixed montane forest about 12,000 yr in northern Peru. Between *ca* 11,600 and 10,000 yr *páramo* was expanded at the expense of the mixed montane forest, suggesting a cooler and/or more arid interval. However, at about 10,000 yr ago, temperature and precipitation increased, which resulted in the replacement of *páramo* vegetation with wet montane forest. Humid conditions prevailed until the Middle Holocene, when increased aridity forced the wet montane forest downwards (Hansen & Rodbell, 1995). In Central Peru, the pollen records from Lake Pacucha, which lies at 3095 m, offer the only complete vegetation record of the cloud forest from the LGM to the present (Valencia *et al.*, 2010). During the LGM the vegetation belt at that zone shifted *ca*. 1300 m downslope, as suggested by the presence of open puna vegetation at Pacucha. Deglaciation began at around 16 cal. kyr, and as the forest began to shift up the vegetation changed to tree-line forest mixed with shrubs and ultimately to Andean forest. During the mid-Holocene, a dry event turned Lake Pacucha into a shallow, mostly saline pool. However, the vegetation surrounding this lake was not affected by these periods of drought, as evidenced by the pollen records. By 6-5.5 cal. kyr, the pollen sequence marks the most rapid vegetation change, that is explained by Human occupation, and that caused a decrease in tree species, and an increase in weeds an fires (Valencia *et al.*, 2010).

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Figure Legends

Figure 1. Map of South America showing the northern and central Andes, along with the main different ridges and geological gaps mentioned in the text. The northern Andes are depicted in orange, while the central Andes are depicted in green.

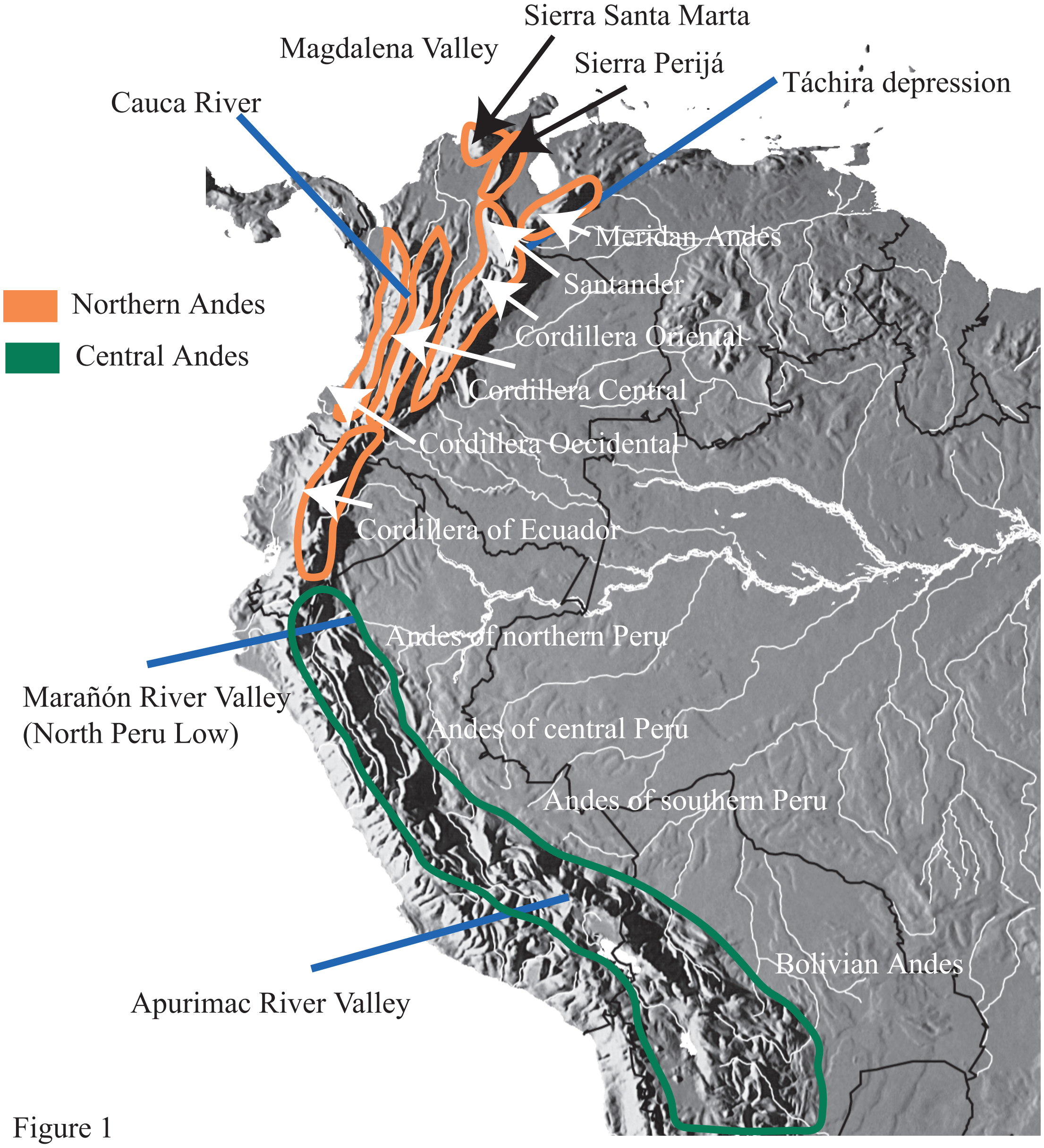
Sierra Santa Marta
Magdalena Valley
Sierra Perijá
Táchira depression
Cauca River
Meridan Andes
Santander
🟧 Northern Andes
🟩 Central Andes
Cordillera Oriental
Cordillera Central
Cordillera Occidental
Cordillera of Ecuador
Andes of northern Peru
Marañón River Valley
(North Peru Low)
Andes of central Peru
Andes of southern Peru
Bolivian Andes
Apurimac River Valley

Figure 1

CHAPTER 2

The Andean *Hapalopsittaca* Parrots (Psittacidae, Aves): Another Example of Montane-Tropical Lowland Vicariance

INTRODUCTION

Many studies have sought to understand the origin and diversification of the montane biota of the Andes. The most common hypotheses for the origin of this biota are long distance dispersal from lowland relatives, dispersion upslope followed by allopatry, and colonization from Central America. These ideas have been frequently combined to propose explanations that can account for the complexity found throughout the range. In his monograph of the birds of Colombia, for example, Chapman (1917) suggested that as the Andes increased in elevation, new habitats became available for colonization by latitudinal range expansion from areas with similar climates, such as the montane regions of Central America, as well as by altitudinal expansion caused by competition in the lowlands, which forced species to higher altitudes. Hooghiemstra *et al.* (2006) proposed that Andean uplift played a part in the development and distribution of the current Andean flora with many Neotropical lowland taxa colonizing montane habitats by adapting to new climatic conditions. Other authors proposed that montane groups arose by long-distance dispersal from lowland counterparts, including Van Der Hammen & Cleef (1986) for plants, as well as Gerwin & Zink (1989), Bleiweiss (1998), and Mcguire *et al.* (2007) for birds. Furthermore, Hooghiemstra postulated that the emerging Andes acted as a bridge that allowed temperate taxa to migrate from more temperate latitudes into the new montane habitats. In fact, the montane areas of Central America have frequently been identified as the source of Andean temperate colonizers, for example in birds (Hackett, 1995; Perez-Eman, 2005; Cadena *et al.*, 2007; Miller *et al.*, 2007; Da Costa & Klicka, 2008), rodents (*Akodon* mice; Patton & Smith, 1992), and plants (Malpighiaceae, Fabaceae, and Annonaceae; Antonelli *et al.*, 2009).

Although many authors have proposed that the uplift of the Andes, and the climatic changes of the Plio-Pleistocene have had a strong influence in the diversification of Andean biota (Bates & Zink, 1994; Bleiweiss, 1998; Cadena, 2007; Chaves *et al.*, 2007; Koscinski *et al.*, 2008; Cossios *et al.*, 2009), only a few (Bates & Zink, 1994; Bleiweiss, 1998) have linked the uplift with the origin of montane clades. In contrast, a biogeographic analysis of the parrot genus *Pionus* provided evidence that the origin of high montane Andean groups can be directly linked to Andean tectonic uplift and subsequent climatic oscillations (Ribas *et al.*, 2007).

This paper describes another phylogenetic and biogeographic pattern connecting high montane biotas to the lowlands, as exemplified by the exclusively montane parrot genus *Hapalopsittaca* and its sister genus *Pyrilia* [*Pyrilia* = *Gypopsitta* (Banks *et al.*, 2008), in Ribas *et al.,* 2005], which is exclusively distributed in the adjacent lowland forests of South and Central America, both east and west of the Andes (Ribas *et al.*, 2005). Furthermore, the monophyly of *Hapalopsittaca* is assessed, as Ribas *et al.* (2005) included only *H. pyrrhops* in their analysis, and reconstruct its spatial and temporal history. Finally, I will propose that although there might be multiple explanations for the origin of high Andean taxa, many biogeographical studies have missed important patterns by not sampling relevant highland and lowland taxa and not framing those studies in a temporal context, and by assuming *a priori* that ecological factors and/or long-distance dispersal are primarily responsible for processes of taxonomic assembly.

The study group

The genus *Hapalopsittaca* (Ridgway, 1912) is currently considered to comprise four species and seven subspecies. However, the taxonomic status of the species has changed several times. *H. m. peruviana* was described as a subspecies of *H. melanotis*, whereas the "amazonina" or "rusty-faced" group (Graves & Uribe Restrepo,1989) included two subspecies, *H. a. amazonina* and *H. a. theresae*, until Graves & Uribe Restrepo (1989) described a new subspecies, *H. a. velezi* from the Cordillera Central of Colombia, from three individuals that had been incorrectly identified as *H. fuertesi*. *H. pyrrhops* and *H. fuertesi* were originally described as distinct species, but Peters (1937) suggested treating them as conspecific with *H. amazonina*, a taxonomy that was later adopted by Meyer de Schauensee (1966). Graves & Uribe Restrepo (1989) were not able to find a sister-group relationship between *H. fuertesi* and *H. pyrrhops*, but grouped them along with the three subspecies of "amazonina," *H. a. amazonina*, *H. a. theresae*, and *H. a. velezi*, in the "*H. amazonina* superspecies."

All *Hapalopsittaca* have restricted distributions in the *páramos* and temperate humid montane forests, known colectively as "ceja de selva" (Fjeldså & Krabbe, 1990). *Páramos* occur in isolated patches that are isolated from other vegetation belts altitudinally (Fjeldså & Krabbe, 1990; Fjeldså, 1992), and in the humid tropical Andes, their vegetation is dominated by patches of mosses, lichens, bunchgrass, bamboo, sedges, ferns, tree ferns, bushes, and *Puya* bromeliads (Fjeldså & Krabbe, 1990). *H. melanotis* (Fig. 1) is the southernmost species, found in western Bolivia, in La Paz and Cochabamba, and has also the lowest altitudinal distribution of the genus at 1740-2500 m (Fjeldså & Krabbe, 1990). *H. peruviana* (Fig. 1) is found in central and southern Peru, from Huánuco and eastern Pasco, south to Cusco, in altitudes ranging from 2800–3450 m (Fjeldså & Krabbe, 1990). *H. pyrrhops* (Fig. 1) is distributed in Cajamarca, northern Peru, north to southern Ecuador at 2500-3500 m (Fjeldså & Krabbe, 1990). *H. velezi* (Fig. 1) is found on the northwestern flank of Nevado del Ruíz, on the Cordillera Central of Colombia*,* between 2250 and 2650 m, being replaced altitudinally by *H. fuertesi* (Fig. 1), which has been found at 2600-3800 m south of Caldas, east of Risaralda, northeast of Quindío and west of Tolima (Proaves, 2009). *H. amazonina* is distributed between 2200-3000 m, in the west slopes of the Cordillera Oriental, north to Santander, and Páramo de Tama, in northwestern Venezuela (Fjeldså & Krabbe, 1990). Finally, *H. theresae* (Fig. 1) is distributed between 2500-3000 m in Mérida and Táchira (Fjeldså & Krabbe, 1990). Little is known about of biology of the genus, but they have evolved to live at elevations and appear to have restricted latitudinal movements (Proaves, 2009).

Of the four recognized species of *Hapalopsittaca*, the IUCN Red List catalogues *H. melanotis* (comprising *H. melanotis* and *H. peruviana*) as of least concern, *H. pyrrhops*, and *H. amazonina* (comprising *H. theresae, H. amazonina and H. velezi*) as decreasing, and *H. fuertesi* as critically endangered (IUCN, 2010). Although recent records for *H. fuertesi* suggest that the population of this species has recently increased to *ca*. 160 individuals thanks to ongoing conservation efforts, this species is still considered critically endangered due to the clearing of habitat in its already-restricted range (IUCN, 2010). In the case of *H. theresae, H. amazonina,* and *H. velezi*, the historical ranges in the Cordilleras Central and Oriental of Colombia and Venezuela are largely deforested, and though it seems that Colombian populations (*H. amazonina* and *H. velezi*) are not declining, Venezuelan ones (*H. theresae*) are (IUCN, 2010). The same is true for the suitable habitat of *H. pyrrhops*, which is mostly fragmented and declining (IUCN, 2010). Finally, although not quantified, the population trend for *H. melanotis* (*H. melanotis* and *H. peruviana*) seems to be stable (IUCN, 2010). Because of their restricted habitats and low population numbers, acquiring genetic material of all the species in this genus is difficult, and tissue samples are scarce. Thus, this study relied heavily on toe pad samples from different collections to reconstruct their phylogenetic history. However, even these are not abundant, which prevented extensive sampling.

MATERIALS AND METHODS

Taxonomic units

Specimens housed in the American Museum of Natural History (AMNH) ornithology collection, as well as relevant literature (Graves & Uribe Restrepo, 1989; Fjeldså & Krabbe, 1990; Collar, 1997; Forshaw, 2006), were examined to determine basal, diagnosably distinct taxonomic units (or phylogenetic species; Cracraft 1997) within *Hapalopsittaca.* Specimens examined included individuals of all four traditionally recognized species and six of the seven subspecies: *H. amazonina* (five specimens), *H. velezi* (one specimen), *H. theresae* (six specimens), *H. fuertesi* (five specimens), *H.*

pyrrhops (one specimen), and *H. melanotis* (two specimens). No individuals of *H. peruviana* were available.

Molecular sampling

Mitochondrial sequences were obtained from 17 individuals representing all seven basal taxa within *Hapalopsittaca*. Tissue was available for one individual of *H. melanotis* (LSUMZ 107592) and two individuals of *H. pyrrhops* (ANSP 18917, 19184), whereas sequences for one individual of *H. pyrrhops* were taken from a previous study (Ribas *et al.*, 2005). Thus, the remainder sequences were obtained from toe pads. At least two individuals from each basal taxon, from different localities whenever possible, were included (Table 1). To test the monophyly of the genus, and to evaluate its phylogenetic position within Neotropical parrots, and specifically within the "amazons and allies" clade of Tavares *et al.* (2006), sequences from the related genera *Pionus, Pionopsitta, Pyrilia, Amazona, Alipiopsitta, Graydidascalus, Triclaria,* and *Brotogeris* were included. During all searches *Brotogeris* was used as outgroup. All sequences other than those of *Hapalopsittaca* were obtained from GenBank (Table 1).

DNA extraction, amplification, and sequencing

DNA extractions from both skin and tissue samples were performed with the DNeasy kit (Qiagen, Valencia CA, USA), adding DTT to the incubation buffer, and incubating overnight in the case of skins. The complete cytochrome *b* (cyt *b*) and the subunit 2 of the NADH (ND2) were amplified for all samples, using specifically designed primers for amplifying fragments of 200 - 350 bp, with 30 - 50 bp of overlapping between adjacent fragments (Table 2).

All amplifications were performed with GoTaq Hot Start Polymerase (Promega). Depending on the primers, annealing temperatures ranged from 50 to 55 degrees, and negative controls were included for all amplifications to rule out contamination. Amplification products were visualized by electrophoresis, and purified using Multiscreen PCR Plates (Millipore). The purified PCR products were sequenced with the same primers used for the amplifications on a 3730 Automated DNA Sequencer (Perkin-Elmer, ABI) following the standard protocol.

Phylogenetic analyses

Sequences were edited and corrected using Sequencher 4.5 (Gene Codes Corporation) and the incongruence length difference (ILD) test (Farris *et al.*, 1995) was performed in order to assess incongruence of phylogenetic signal between the two mitochondrial genes. Maximum parsimony (MP) and maximum likelihood (ML) searches were performed in PAUP v 4.0b10 (Swofford, 2002) for the combined set, while a Bayesian inference analysis (BI) was performed using MrBayes v 3.1.1 (Huelsenbeck & Ronquist, 2001). For the MP analysis heuristic tree searches, tree bisection reconnection (TBR), branch swapping, and 10000 random addition sequence replications were used. All characters were equally weighted and all substitutions were included. Support was assessed using non-parametric bootstrapping (Felsenstein, 1985) with 1000 replications. For the ML analysis, the best-fit model of nucleotide substitution was selected through

JModeltest 0.1.1 (Posada, 2008), using the Akaike Information Criterion (AIC). The ML analysis was performed via an heuristic tree search, TBR branch swapping, and 10 random addition replicates, and support was assessed by non-parametric bootstrapping (Felsenstein, 1985) with 100 replications and five random addition replicates. A partitioned model approach was used for the Bayesian analysis in order to account for potential differences in evolutionary model parameters between the two genes, and the best model for each data set was selected using MrModelTest 2.2 (Nylander, 2004), through the AIC criterion. Four simultaneous Markov chains for 10,000,000 generations were used, with trees being sampled every 1000 generations for a total of 10,000 trees, with 9,000 kept in each analysis. Three independent analyses were performed for the combined data set, and the 27,000 sampled trees obtained were used to compute the posterior probabilities of each node.

Estimation of divergence dates

Dates for the internal nodes of the phylogeny were calculated using BEAST v 1.5.2 (Drummond & Rambaut, 2007), which uses MCMC to infer time-measured phylogenies, weighting each tree proportionally to its posterior probability. For this analysis a reduced matrix was used, which contained a single individual per species of *Hapalopsittaca* and *Pionus*, three species of *Pyrilia*, and one each of *Alipiopsitta, Amazona, Graydidascalus,* and *Triclaria* (the latter genus was used as the outgroup). The model parameters for BEAST were selected using BEAUti, using the following settings: GTR + invariant sites as the substitution model, substitution rates estimation, a relaxed clock model to account for lineage-specific rate heterogeneity, and a Yule process as the tree prior. The priors for calibrating the nodes for the divergence dating analysis were obtained from a previous study that included nuclear gene-based (RAG-1 and RAG-2) calibrations of parrot diversification (Ribas *et al.*, 2007). In order to explore the uncertainty related to using calibrations from a previous study, three independent analyses were run using different sets of priors to calibrate the two basal nodes: the mean and the upper and lower-bound confidence intervals as reported by Ribas *et al.* (2007). Thus, the node separating (*Hapalopsittaca, Pyrilia*) from all other parrots (node A, Fig. 3) was fixed at 8.9, 16.9, and 34.5 Mya BP for RAG-2, and 10, 17.7, and 27.6 Mya BP for RAG-1, whereas the split between *Pionus* and *Graydidascalus brachyurus* (node B, Fig. 3) was fixed at 3.9, 9.2, and 18.5 Mya BP for RAG-2, and 5.2, 10.7, and 18.6 Mya BP for RAG-1. 95% confidence intervals were only estimated for the reported mean. During all analyses, a normal distribution was used, in which uncertainty is distributed in a bidirectional manner (Ho & Phillips, 2009), with a 1.0 My standard deviation for all the priors. The analysis ran for 10 M generations, and the results were analyzed via Tracer v1.41 (Rambaut & Drummond, 2007), summarized via TreeAnnotator v1.5.1 using the maximum clade credibility option as target tree type, and mean heights for node heights, while the summary tree was visualized and edited using FigTree v 1.3.1 (Rambaut, 2009).

RESULTS

Recognition of basal taxonomic units

Our analysis distinguishes seven diagnosably distinct taxa based on morphology (Appendix 1). Thus the four currently recognized biological species do not adequately represent the taxonomic diversity within the genus. The biospecies *Hapalopsittaca melanotis* has two different diagnosable taxa, H. *melanotis* and *H. peruviana,* whereas the biospecies *H. amazonina* is comprised of three diagnosably distinct forms: *H. amazonina, H. theresae*, and *H. velezi*. Only two forms, *H. pyrrhops* and *H. fuertesi,* are accurately represented by the current species classification as diagnosable units. All of these basal taxonomic units have disjunct distributions (Fig. 1) in areas that correspond to well-known areas of endemism (Cracraft, 1985; Fjeldså, 1992; Table 1).

Phylogenetic analyses

Sequences for the complete cyt *b* and ND2 genes were obtained for all individuals included in the study. Sequences were aligned manually, translated to confirm the correct reading-frame and checked for the presence of stop codons. The results of the ILD test rejected incongruence between the two genes ($p > 0.05$). The TrN+I+G model of substitution was selected for the analysis of the combined data set (ML), whereas for the BI analysis, GTR + I was selected for ND2, and HKY+I for cyt *b*.

The MP analysis of the combined set resulted in nine most parsimonious trees (2445 steps), the strict consensus of which (Fig. 2) agrees with the ML solution (Fig. 3) as well as the BI analyses in showing that *Hapalopsittaca* forms a well-supported monophyletic group and confirms that it is sister to *Pyrilia*, as found by Ribas *et al.* (2005). Thus, *Hapalopsittaca* is nested within Tavares *et al.*'s (2006) “amazons and allies” clade, which also includes the genera *Amazona*, *Alipiopsitta*, *Pionus*, *Graydidascalus*, *Pionopsitta, Triclaria*, *Myiopsitta*, and *Brotogeris*.

Once the monophyly of *Hapalopsittaca* and its sister-group relationship to *Pyrilia* were established, another analysis was undertaken that included only species of *Hapalopsittaca* and *P. pyrilia* as an outgroup. Results from the MP and ML analyses identify two highly supported clades within *Hapalopsittaca*, one central and one northern Andean. The central Andean clade includes *H. melanotis* from Bolivia and *H. peruviana* from southern and central Peru (Figure 4), whereas the remaining species form the northern clade. Within the northern clade, the MP tree shows that *H. fuertesi* from the Cordillera Central of Colombia is sister to *H. pyrrhops* of northern Peru and Ecuador (Fig. 4a). However, this result was not found by either the ML or the BI analyses, as in both cases, *H. pyrrhops* was sister to the clade of *H. amazonina, H. velezi and H. theresae,* and this whole clade was then sister to *H. fuertesi* (Fig. 4b). The relationships among *H. amazonina, H. theresae,* and *H. velezi* also varied between the analyses. In the MP analysis, *H. velezi* from the Cordillera Central of Colombia is sister to a paraphyletic assembly of *H. amazonina* from the Cordillera Oriental of Colombia and *H. theresae* from the Meridan Andes of Venezuela (Fig. 4a), whereas in the ML analysis the three species are paraphyletic for mtDNA (Fig. 4b), and in the BI *H. amazonina* is paraphyletic to *H. velezi*, and together they are sister to *H. theresae*. In all cases, the support for the relationships among these three taxa is low, so for now, it is not possible to establish with any confidence how they are related to each other. However, it is clear that each of them constitutes a basal taxonomic unit, as they have fixed morphological traits, and occupy disjunct distributions in recognized areas of endemism.

Estimation of divergence dates

As in any divergence dating analysis, uncertainty in calibrations can greatly affect estimates of rate variation and their interpretation (Ho & Phillips, 2009; Smith, 2009; Smedmark et al., 2010). Thus, in order to address this uncertainty, probabilistic calibration priors were used, which are more appropriate in dealing with uncertainty than point calibrations (Drummond et al., 2006). Moreover, as calibration priors were taken from the results of a previous study (Ribas et al., 2007), a normally distributed (symmetric) prior on the ages of calibrated nodes was used as it allows for a conservative bidirectional distribution of the uncertainty during the estimation (Ho & Phillips, 2009).

The mean values reported in table 3 are derived from the calibration of nodes A and B of Figure 5 for RAG-2 and RAG-1, and the range of values reported in table 3 include the upper- and lower-bound means for those genes using the mean and the upper and lower-bound confidence intervals as reported by Ribas et al. (2007). These upper- and lower-bound means should not be interpreted as confidence intervals, but rather as very conservative estimates of age-uncertainty (the 95% confidence intervals calculated directly in the analyses are shown on Table 3). Based on the BEAST analysis, the split between *Pyrilia* and *Hapalopsittaca* is estimated to have taken place between 12.1 (10-14.1 Mya BP 95% CI; RAG-2) and 12.9 (10.9-15 Mya BP 95% CI; RAG-1) Mya BP, whereas within *Hapalopsittaca*, the split between the northern and central Andean clades took place between 8.6 (6.6-10.5 Mya BP 95% CI; RAG-2) and 9.2 (7.2-11.1 Mya BP 95% CI; RAG-1) Mya BP. Within the central Andean clade, the split between H. *melanotis* and *H. peruviana* took place around 0.9 Mya BP (0.5-1.4 Mya BP 95% CI), whereas the basal split within the northern Andean clade occurred between 3.1 (2.2-4.1 Mya BP 95% CI; RAG-2) and 3.4 (2.4-4.4 Mya BP 95% CI; RAG-1) Mya BP, and that leading to *H. amazonina, H. theresae,* and *H. velezi* took place *ca* 0.4 (0.2-0.6 Mya BP 95% CI) Mya BP.

DISCUSSION

Phylogenetic analyses and recognition of basal taxonomic units

The results of this analysis indicate that all seven taxa within *Hapalopsittaca* are diagnosably distinct for plumage (Appendix 1), and the results of the phylogenetic analysis found support for *H. melanotis*, *H. peruviana*, *H. fuertesi, H. pyrrhops*, *H.velezi,* and *H. amazonina* as being distinct taxa in agreement with plumage diagnosis. Furthermore, most species of *Hapalopsittaca* have their ranges divided by arid river valleys that have been recognized as barriers to dispersal (Vuilleumier, 1969; Cracraft, 1985; Weir, 2009): *H. melanotis* and *H. peruviana* are divided by the Apurimac River Valley, *H. velezi* and *H. amazonina* by the Magdalena Valley, and *H. amazonina* and *H. theresae* by the Táchira depression, formed by the Torbes and Quinimari Rivers (Figure 1). All the above evidence constitute evidence that each of these basal taxonomic units qualifies as separate phylogenetic species. This has a significant implication for understanding their evolutionary history and biogeographic patterns. For example, *H. fuertesi* and *H. velezi* are the only two species of the genus that replace each other altitudinally in the Cordillera Central of Colombia, with *H. velezi* distributed from 2250-2650 m, whereas *H. fuertesi* is found between 2900 and 3350 m (Graves & Uribe Restrepo, 1989; Proaves, 2009). As these two species are not sister-taxa (Figs. 3 and 4), this observation constitutes another example (Hillis, 1985; Patton & Smith, 1992; Arctander & Fjeldså, 1994; Dingle *et al.*, 2006) contradicting the hypothesis of parapatric speciation (Terborgh, 1971; Endler, 1982), and highlighting the importance of using basal taxonomic units to understand evolutionary processes.

The paraphyly of *H. theresae* with respect to *H. amazonina* (Fig. 4a) in the MP tree, and to both *H. amazonina* and *H. velezi* in the ML phylogram (Fig. 4b), contrasts with the plumage diagnosis (Appendix 1) and disjunct distributions of each of these species. Although the phylogenetic pattern (Fig. 4) can be interpreted as a gene tree for these three species due to its recent divergence, it is also possible that the periods of *páramo* expansion during the glaciations of the Pleistocene (Van Der Hammen & González, 1963; Hooghiemstra, 1984; Hooghiemstra & Cleef, 1995; Hooghiemstra & Van Der Hammen, 2004; Hooghiemstra *et al.*, 2006; Mommersteeg, 1998) that ended after the Last Glacial Maximum, some 18,000 years ago (Hooghiemstra *et al.*, 2000) may have allowed some interchange between these three, currently disjunct species.

The biogeographic origin of *Hapalopsittaca*

Hapalopsittaca is the only genus within the "amazons and allies" clade that is exclusively distributed along the Andes. The sister clade to *Hapalopsittaca* + *Pyrilia* contains *Triclaria, Pionopsitta, Amazona, Alipiospsitta and Graydidascalus* (Tavares *et al.*, 2006), which are predominately lowland genera, as well as *Pionus* with lowland and highland species (Ribas *et al.*, 2007). This leads to the inference that the ancestral character-state of the branch leading to *Pyrilia* +*Hapalopsittaca* was lowland (Fig. 3). Since the montane *Hapalopsittaca* is allopatric relative to the lowland *Pyrilia*, the time of this split (~12.1 -12.9 Mya BP; Fig. 5, node 1) supports the hypothesis of vicariance by uplift of the Andes as a cause for this highland/lowland disjunction (see Almeida *et al.*, 2007; Ribas *et al.*, 2007). By *ca.* 14 Mya BP the Eastern Cordillera of Bolivia was at about 30% of its modern elevation (Gregory-Wodzicki, 2000) and reached its current altitude of *ca.* 4000 m in the last 6-10 Mya BP (Gregory-Wodzicki *et al.*, 1998; Gregory-Wodzicki, 2000; Graham *et al.*, 2001; Graham, 2009). The Cordillera Oriental of Colombia had not reached more than 40% of its current altitude by 5 Mya BP (Gregory-Wodzicky, 2000). Thus, the ancestor of *Hapalopsittaca* was likely distributed along the eastern slope of the Andean cordillera at a time when its height was similar to that at which the extant species of *Pyrilia* are found, and then was uplifted to higher altitudes. Given current data, however, it is not possible to know where in the Andes this initial split took place.

Within *Hapalopsittaca*, the split between central and northern Andean clades took place around ~8.6 to 9.2 Mya BP (Fig. 5, node 2). These two clades are separated by the Marañón River Valley, an important barrier for the distribution of birds (Vuilleumier, 1969; Cracraft, 1985). Picard *et al.*, (2008) suggested that the Andes of Central Peru were uplifted above 2000-2500 m by the late Miocene (Picard *et al.*, 2008), and there is evidence that major canyon incision in the Cordillera Blanca took place between 8 and 5 Mya BP (Montario *et al.*, 2005). These data suggest that the uplift of the Central Cordillera of Peru may have cause the ancestral populations of *Hapalopsittaca* to vicariate, and that the arid Marañón Valley might have acted as a barrier between these two newly vicariated clades.

The diversification within the north Andean clade (Fig. 5, node 3) took place around 3.1-3.4 Mya BP, when the Ecuadorian cordillera (Coltorti, 2000) and the Cordillera Oriental of Colombia (Graham, 2009) were experiencing their final uplift. These events could have isolated the ancestors of H. *amazonina, H. theresea*, and *H. velezi* in the Cordillera Oriental, from those of *H. pyrrhops* and *H. fuertesi* from northern Ecuador and the Central Cordillera of Colombia.

Speciation within both the northern and central clades of *Hapalopsittaca* took place in the last 1.7 Mya BP (Fig. 5, nodes 4, 5, and 6). Since no major orogenic events were taking place at that time, as the Cordillera Oriental and the Venezuelan Andes had attained their modern altitude, it is most likely that the cyclic climatic changes of the Pleistocene were the causal mechanism of their speciation. During this time, montane vegetation belts repeatedly shifted vertically during glacial and interglacial periods, and as a consequence, *páramo* vegetation changed from being isolated areas at the top of the upper forest line during the interglacials to becoming more widely distributed downslope during the glacial periods (Van Der Hammen & González, 1963; Hooghiemstra, 1984; Hooghiemstra & Cleef, 1995; Hooghiemstra & Van Der Hammen, 2004; Hooghiemstra *et al.*, 2006; Mommersteeg, 1998). The first record of *páramo* vegetation becoming widespread in the Cordillera Oriental of Colombia dates from ~2.7-2.2 Mya BP when there was a significant decrease of temperature at a global scale (Hooghiemstra *et al.*, 2000). From 2.2-1.0 Mya BP, the upper forest line reached 1900 m, and the *páramo* formed continuous areas that might have allowed the ancestral populations of this northernmost clade of *Hapalopsittaca* in the Cordillera Oriental to expand to the Central Cordillera of Colombia and to the Venezuelan Andes. However, around 350 Kya BP (Hooghiemstra *et al.*, 2000), warm climatic conditions again fragmented the *páramo* into small islands (Simpson, 1975; Hooghiemstra & Van Der Hammen, 2004). This could have caused the ancestral population to vicariate into the three current species—*H. amazonina*, *H. velezi*, and *H. theresea*—found today, as the diversification of this clade occurred around this time (Fig. 5, node 5). Thus, there is a spatio-temporal link between Andean glacial and interglacial periods, specifically the history of expansion and isolation of the *páramo* and divergence within the northernmost species of *Hapalopsittaca.* This account is most likely the same for the rest of the species of the genus, but in other regions, the vegetation record for the last 3.5 Mya has not been documented in detail as in the Cordillera Oriental.

Comparison of diversification patterns between Hapalopsittaca and Pionus

Because both *Pionus* and *Hapalopsittaca* belong to the "amazon and allies" clade (Tavares *et al.*, 2006), and both constitute examples of highland/lowland diversification patterns in the Andes, it is interesting to explore the coincidences and differences in temporal diversification patterns within these two groups.

In *Hapalopsittaca*, the transition between lowland and highland occurred between nodes 1 and 2 (Fig. 5), that is, between *ca.* 12 and 9 Mya BP. As the uplift of the Andes was gradual, this means that the ancestors of *Hapalopsittaca* might have been distributed along the eastern Andean slopes when the vegetation at the highest elevation corresponded to cloud forest (Graham, 2009), and then uplifted along with the mountain and its vegetation to higher altitudes, until eventually reaching the heights at which they are found today. On the other hand, Ribas et al. (2007) suggested that the three montane clades within *Pionus* were independently vicariated from their lowland ancestors much later in time than *Hapalopsittaca*, as the first lowland/highland vicariance event for *Pionus* (Fig 5, node 19) occurred at ~3.6–3.9 Mya BP. In both *Hapalopsittaca* and *Pionus*, the initial vicariance from lowland to highland can be linked to the uplift of the Andes in that in both clades their sister groups are distributed in the lowlands with no intervening species in mid-montane habitats, and the time of the split between lowland and highland taxa coincides with ongoing uplift. Furthermore, as all montane species within *Pionus* and *Hapalopsittaca* originated during the Pleistocene (Fig. 5, column D), their speciation can be associated with the climatic cycles of the Pleistocene, which repeatedly vertically shifted the vegetation belts, and caused the expansion and contraction of the *páramos*, causing a passive displacement and vicariance of the flora and fauna. Thus, the diversification history of these two montane groups suggests that the diversification and current ranges of many other highland taxa with lowland relatives might also be linked to the geological history of mountain chains.

CONCLUSIONS

As I have presented, the origin of *Hapalopsittca*, as well as that of other montane taxa, can be strongly associated with Earth history. Thus, it may be possible that the taxonomic assembly of mountain ranges can be, at least in part, explained by historical factors rather than by ecological ones and/or long-distance dispersal. In order to test this idea further, it is important to undertake more biogeographic studies in the Andes, as well as in other mountain ranges, which are framed in a phylogenetic context, use relevant highland and lowland taxa, include divergence time estimates, and use phylogenetic species rather than biospecies as units of study.

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FIGURE LEGENDS

Figure 1. Distribution of the species within *Hapalopsittaca*. Mayor biogeographical barriers relevant for the group are shown.

Figure 2. Maximum Parsimony tree for the combined set of cyt *b* and ND2 genes, including representatives from the “amazons and allies” clade (Tavares *et al*., 2006). Bootstrap support is indicated above the branches.

Figure 3. Maximum Likelihood phylogram for the combined set of cyt *b* and ND2 genes, including representatives from the “amazons and allies” clade (Tavares *et al*., 2006). Lowland taxa are presented in green, while montane taxa are in orange. Bootstrap support is indicated above the branches, while posterior probabilities are indicated below.

Figure 4. a) Maximum Parsimony tree for the genus *Hapalopsittaca*. Bootstrap support values for the MP analysis is shown on the left hand-side above branches. b) ML cladogram obtained using the (TrN+I+G) model of evolution, as calculated via JModeltest 0.1.1 (Posada, 2008), using the AIC information criterion. Bootstrap support is shown above branches, and Bayesian posterior probabilities below. Posterior probabilities were obtained from the 50% consensus from the remaining 90% sampled trees obtained after burn-in during two independent runs of a four simultaneous Markov chains for 10M generation analysis in MrBayes, using the (GTR + I) model of evolution

for ND2, and the (HKY+I) for cytb, which were calculated using MrModeltest 2.2 (Nylander, 2004).

Figure 5. Chronogram obtained in BEAST for a reduced matrix containing all species within *Hapalopsittaca* and *Pionus*, plus related species. Lowland taxa are presented in green, while montane ones are in orange. Purple horizontal lines represent CI, while vertical lines A-D correspond to relevant geological events. Numbers on branches correspond to nodes on table 3.

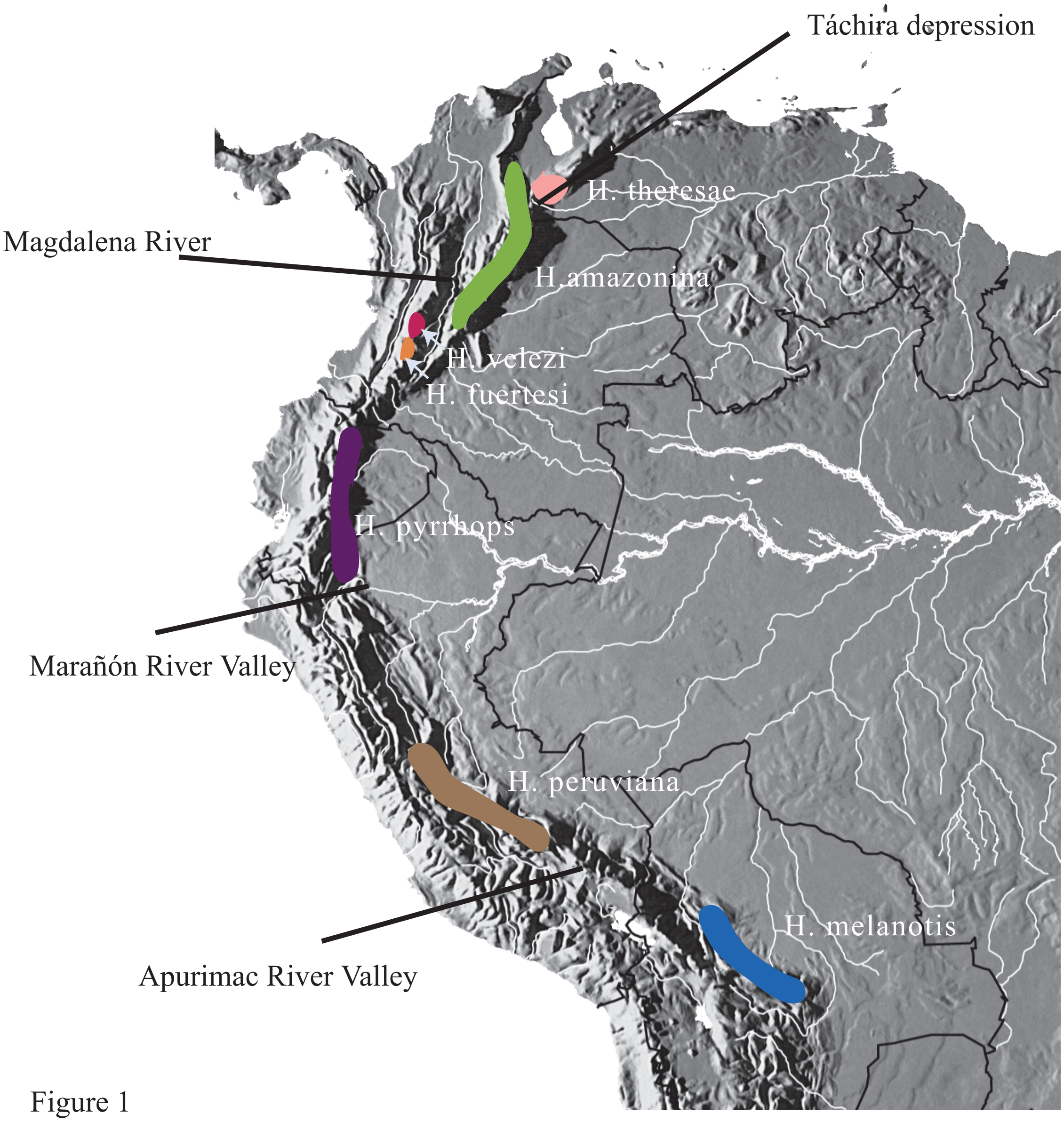

Táchira depression
H. theresae
Magdalena River
H.amazonina
H. velezi
H. fuertesi
H. pyrrhops
Marañón River Valley
H. peruviana
H. melanotis
Apurimac River Valley

Figure 1

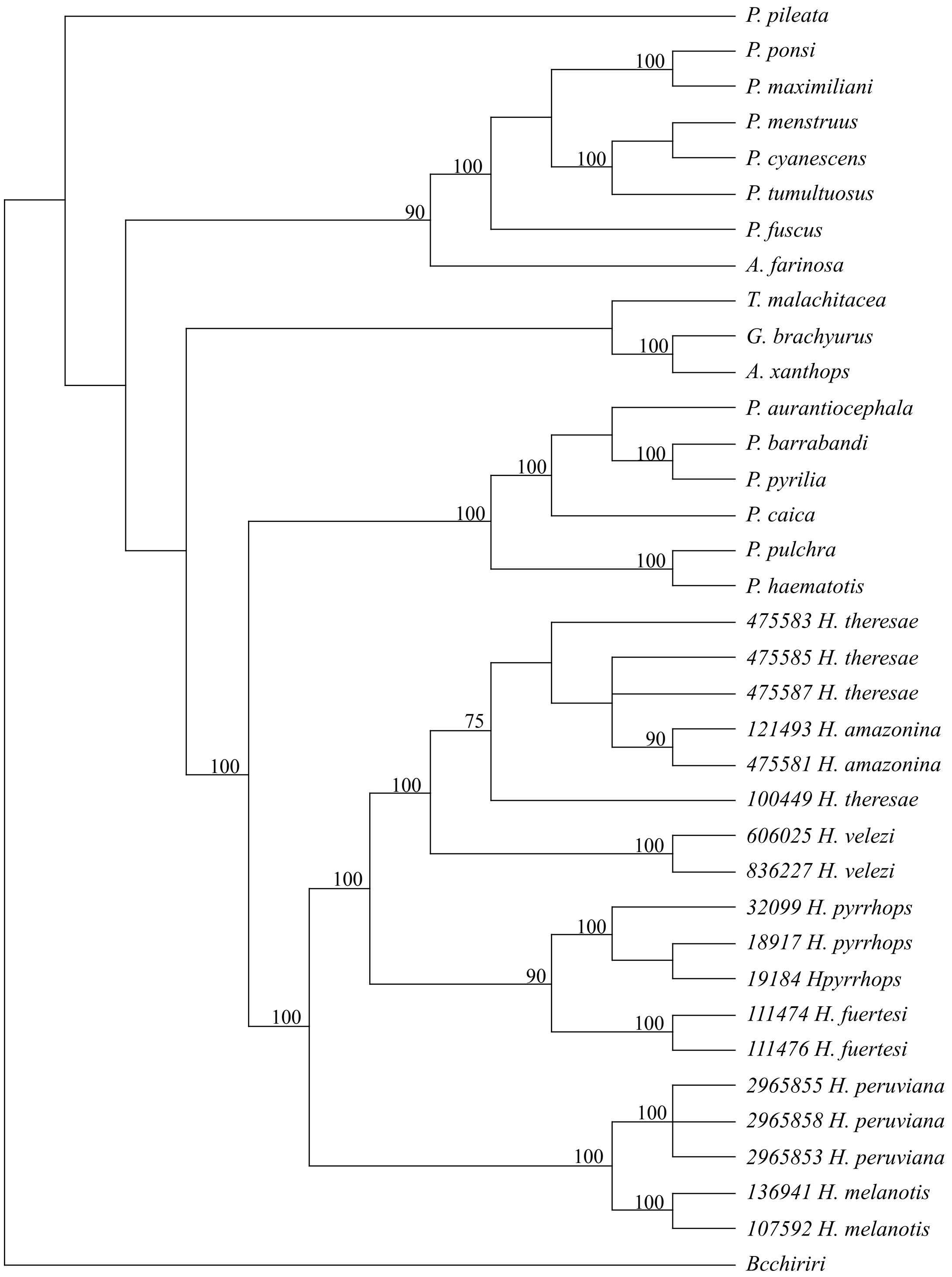

P. pileata
P. ponsi
P. maximiliani
P. menstruus
P. cyanescens
P. tumultuosus
P. fuscus
A. farinosa
T. malachitacea
G. brachyurus
A. xanthops
P. aurantiocephala
P. barrabandi
P. pyrilia
P. caica
P. pulchra
P. haematotis
475583 H. theresae
475585 H. theresae
475587 H. theresae
121493 H. amazonina
475581 H. amazonina
100449 H. theresae
606025 H. velezi
836227 H. velezi
32099 H. pyrrhops
18917 H. pyrrhops
19184 Hpyrrhops
111474 H. fuertesi
111476 H. fuertesi
2965855 H. peruviana
2965858 H. peruviana
2965853 H. peruviana
136941 H. melanotis
107592 H. melanotis
Bcchiriri
100
100
100
90
100
100
100
100
100
75
90
100
100
100
100
90
100
100
100
100
100

Figure 2

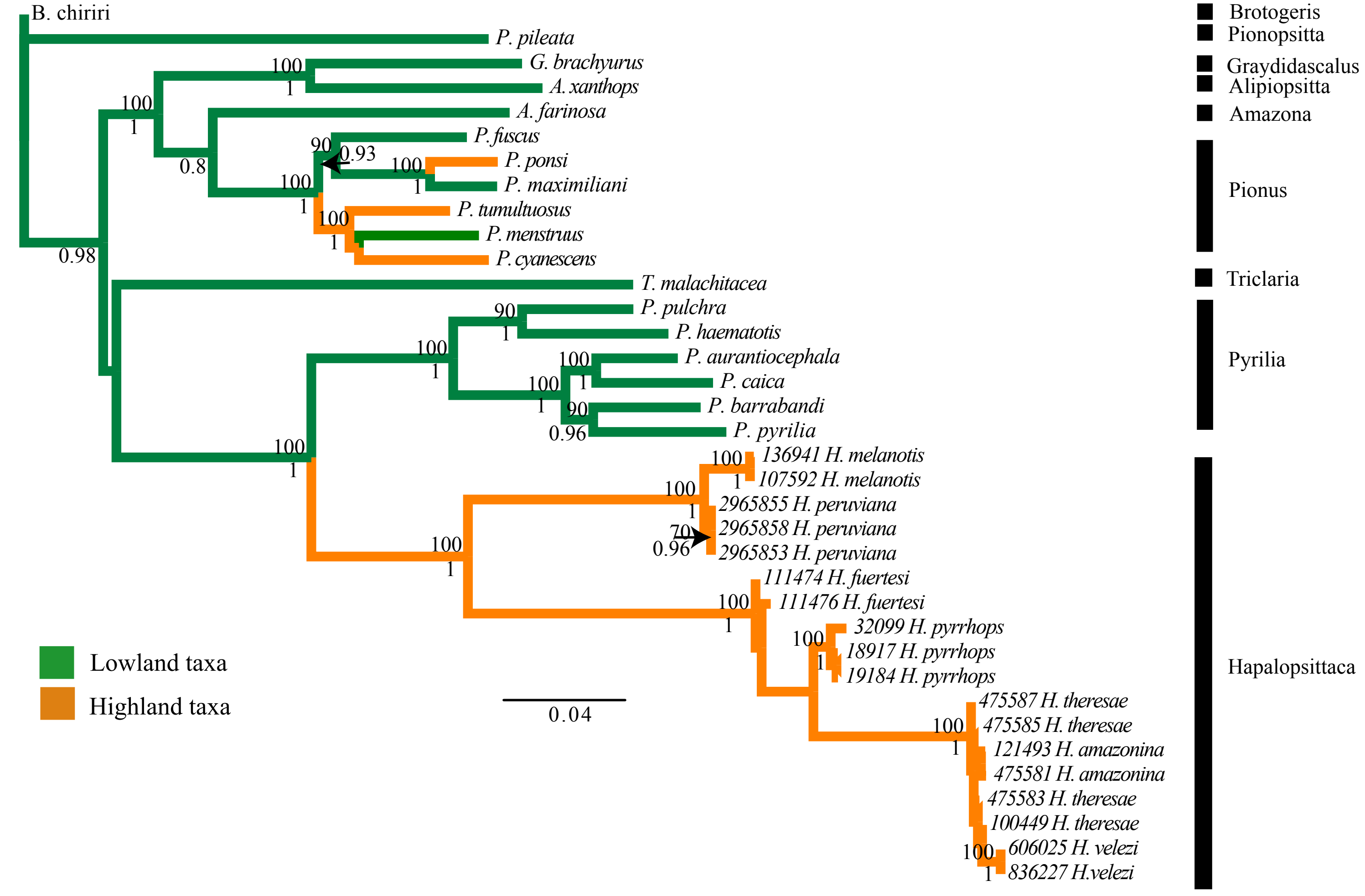
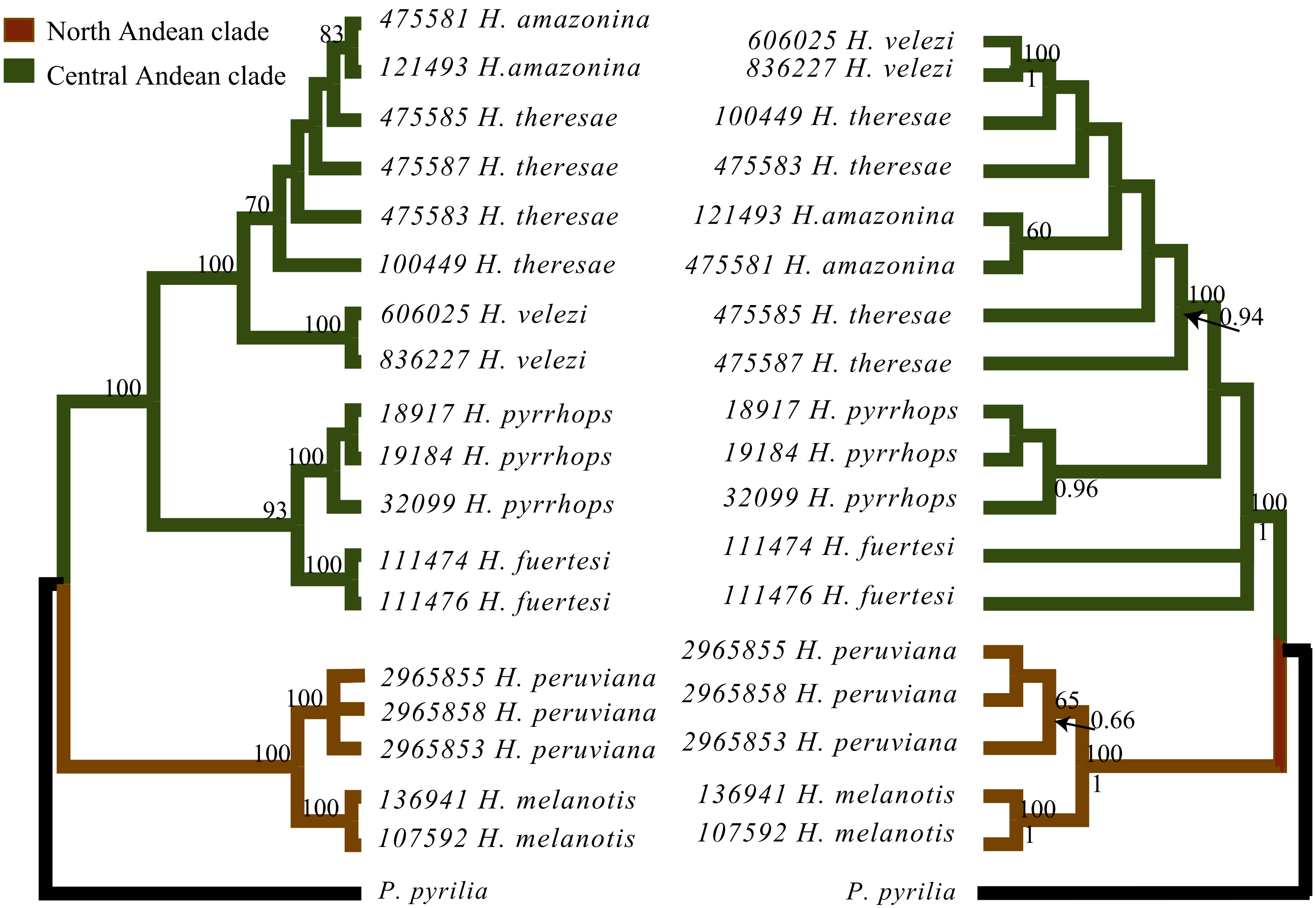

B. chiriri
P. pileata
100
G. brachyurus
1
A. xanthops
100
1
A. farinosa
0.8
90
0.93
P. fuscus
100
P. ponsi
100
1
P. maximiliani
1
P. tumultuosus
100
1
P. menstruus
P. cyanescens
0.98
T. malachitacea
90
P. pulchra
1
P. haematotis
100
1
100
P. aurantiocephala
100
1
1
P. caica
90
P. barrabandi
0.96
P. pyrilia
100
1
100
136941 H. melanotis
1
107592 H. melanotis
100
1
2965855 H. peruviana
70
2965858 H. peruviana
0.96
2965853 H. peruviana
100
1
111474 H. fuertesi
100
111476 H. fuertesi
1
32099 H. pyrrhops
100
18917 H. pyrrhops
1
19184 H. pyrrhops
475587 H. theresae
100
475585 H. theresae
1
121493 H. amazonina
475581 H. amazonina
475583 H. theresae
100449 H. theresae
100
606025 H. velezi
1
836227 H.velezi
Brotogeris
Pionopsitta
Graydidascalus
Alipiopsitta
Amazona
Pionus
Triclaria
Pyrilia
Hapalopsittaca
Lowland taxa
Highland taxa
0.04

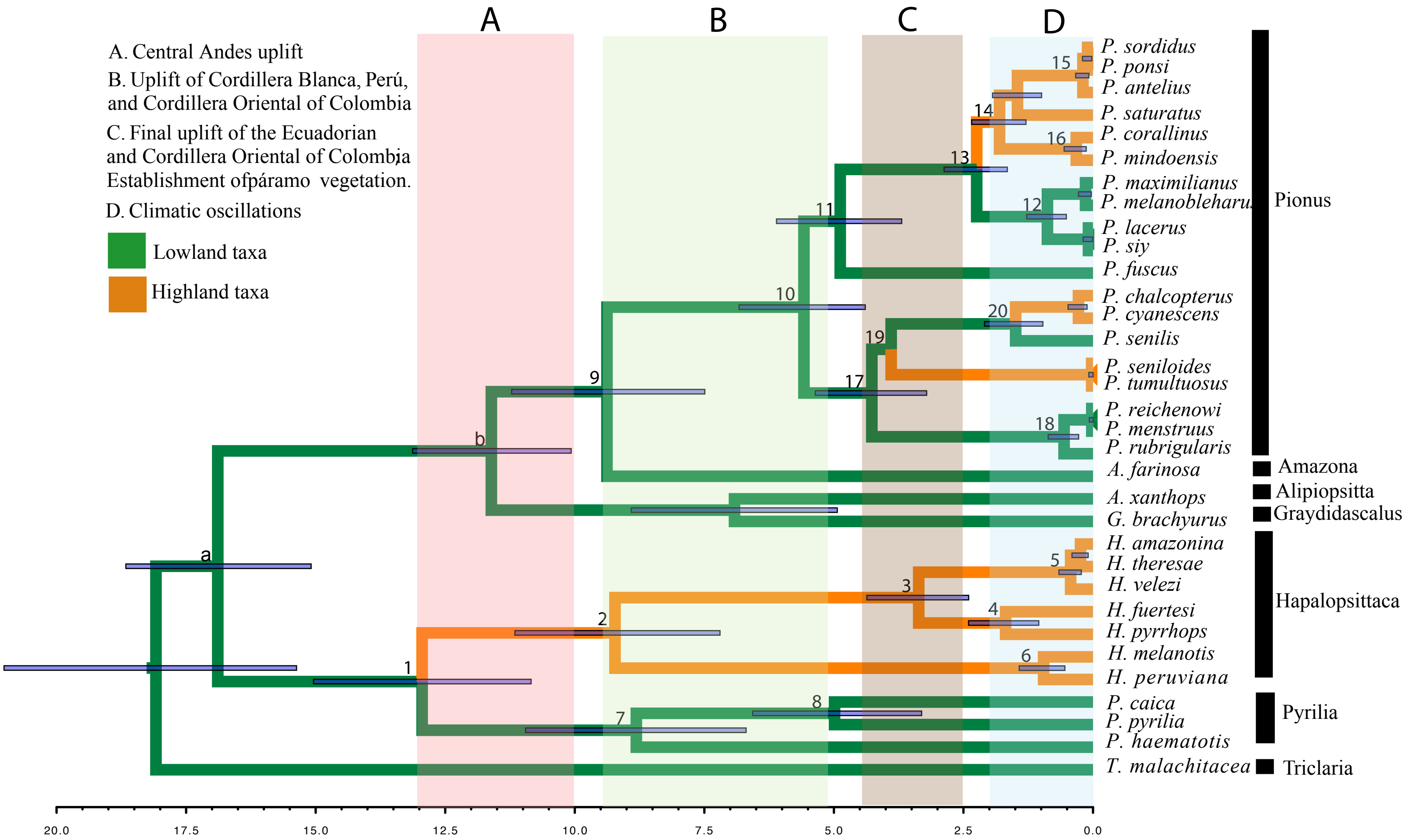
Figure 3



a) Maximum Parsimony

b) Maximum Likelihood

Figure 4


A
B
C
D
A. Central Andes uplift
B. Uplift of Cordillera Blanca, Perú, and Cordillera Oriental of Colombia
C. Final uplift of the Ecuadorian and Cordillera Oriental of Colombia, Establishment ofpáramo vegetation.
D. Climatic oscillations
🟩 Lowland taxa
🟧 Highland taxa
P. sordidus
P. ponsi
P. antelius
P. saturatus
P. corallinus
P. mindoensis
P. maximilianus
P. melanobleharus
P. lacerus
P. siy
P. fuscus
P. chalcopterus
P. cyanescens
P. senilis
P. seniloides
P. tumultuosus
P. reichenowi
P. menstruus
P. rubrigularis
A. farinosa
A. xanthops
G. brachyurus
H. amazonina
H. theresae
H. velezi
H. fuertesi
H. pyrrhops
H. melanotis
H. peruviana
P. caica
P. pyrilia
P. haematotis
T. malachitacea
Pionus
Amazona
Alipiopsitta
Graydidascalus
Hapalopsittaca
Pyrilia
Triclaria
a
b
1
2
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15
16
17
18
19
20
20.0
17.5
15.0
12.5
10.0
7.5
5.0
2.5
0.0

Figure 5

Table 1. Taxa of *Hapalopsittaca* for which ND2 and cyt *b* sequences were obtained, including voucher numbers, collection locality, and area of endemism in which each taxon is distributed.

Species	Voucher No	Locality	Area of Endemism
Hapalopsittaca pyrrhops	ANSP 18917	Loja, Ecuador	Southern Ecuador
Hapalopsittaca pyrrhops	ANSP 19184	Loja, Ecuador	Southern Ecuador
Hapalopsittaca pyrrhops	AY669487/AY669443	Cajamarca, Peru	Northern Peru
Hapalopsittaca fuertesi	AMNH 111474	Cauca, la Guneta, Colombia	Cordillera Central
Hapalopsittaca fuertesi	AMNH 111476	Cauca, Sta Isabel, Colombia	Cordillera Central
Hapalopsittaca theresae	AMNH 475585	El Escorial, Mérida, Venezuela	Merida Andes
Hapalopsittaca theresae	AMNH 475583	La Culata, Mérida, Venezuela	Merida Andes
Hapalopsittaca theresae	AMNH 475587	El Valle, Mérida Venezuela	Merida Andes
Hapalopsittaca theresae	AMNH 100449	El Escorial, Mérida Venezuela	Merida Andes
Hapalopsittaca amazonina	AMNH 475581	Bogotá, Colombia	Cordillera Oriental
Hapalopsittaca amazonina	AMNH 121493	El Roble, Fusagasugá, Colombia	Cordillera Oriental
Hapalopsittaca velezi	NMNH 606025	Caldas, Manizales, Colombia	Cordillera Central
Hapalopsittaca velezi	NMNH 606025	Caldas, Manizales, Colombia	Cordillera Central
Hapalopsittaca melanotis	AMNH 136941	Bolivia	Southern Peru
Hapalopsittaca melanotis	LSU 107592	La Paz, Bolivia	Southern Peru
Hapalopsittaca peruviana	FMNH 2965853	Huailaspampa, Huanaco, Peru	Central Peru
Hapalopsittaca peruviana	FMNH 2965855	Huailaspampa, Huanaco, Peru	Central Peru
Hapalopsittaca peruviana	FMNH 2965858	Huailaspampa, Huanaco, Peru	Central Peru

ANSP: Academy of Natural Sciences of Philadelphia; AMNH: American Museum of Natural History; NMNH: National Museum of Natural: History; LSU: Louisiana State University Museum of Natural Science; FMNH: Field Museum of Natural History.

Table 2. Primers used during amplification and sequencing.

Cytochrome *b*	
L1NPcytb	TTCGCACTATCYAYCYTAATTGC
R1Pcytb	CTCCTGTGTTTCAGGTTTCTTTG
L2Pcytb	ATGGGGCCTCATTCTTCTTT
R2Pcytb	TGAATGGGAGGAGGAAGTGT
L3Pcytb	AAACCTATTCTCCGCCATCC
R3Pcytb	GGTGAAGTTTTCGGGGTCTC
L4Pcytb	CTGCTGGGGCTTACAATCAT
R4 cytb	GTTCACAAGAC AATGTT
ND2	
L1PND2	GTTCAACCCCTTCCCTCACT
R1PNd2	AGTGAGGGATGACCCTTGAA
L2PNd2	CAGCATGTGTTCTGCTAACCA
R2PNd2	GGTGTTGGTTGTGTTCATGG
L3PNd2	TAACCTCCTCCRTYTTCCTCA
R3PNd2	TCTTGYTYRATGAGYTCYTGT
L4PNd2	TCCCCCACTAACAGGCTTCT
R4 ND2	GAAGGCCTTTGGTTTGTGTTATCCTAAG

Table 3. Estimates of divergence time (Myr BP) obtained by BEAST for RAG-2 and RAG-1. Nodes A and B are fixed, whereas nodes1 to 20 correspond to those of Fig. 5.

RAG-2					RAG-1				
Node	Lower bound[1]	Mean[2]	95% CI[3]	Upper-bound[4]	Node	Lower bound[1]	Mean[2]	95% CI[3]	Upper-bound[4]
A	8.9	16.9	-	34.5	A	10.0	17.7	-	27.6
B	3.9	9.2	-	18.5	B	5.2	10.7	-	18.6
1	5.7	12.1	10-14.1	25.1	1	6.8	12.9	10.9-15	25.6
2	4.1	8.6	6.6-10.5	17.6	2	4.9	9.2	7.2-11.1	18.0
3	1.5	3.1	2.2-4.1	6.5	3	1.8	3.4	2.4-4.4	7.1
4	0.7	1.6	0.9-2.2	3.3	4	0.9	1.7	1-2.4	3.8
5	0.2	0.4	0.2-0.6	0.8	5	0.2	0.4	0.2-0.6	1.0
6	0.4	0.9	0.5-1.3	1.8	6	0.5	0.9	0.5-1.4	2.1
7	3.9	8.2	6.2-10.4	17.0	7	4.7	8.8	6.7-10.9	17.3
8	2.2	4.6	2.9-6.2	9.5	8	2.6	5.0	3.3-6.6	9.8
9	2.5	5.2	4-6.4	10.4	9	3.0	5.6	4.4-1.7	10.7
10	2.2	4.5	3.4-5.7	8.9	10	2.6	4.9	3.7-6.1	9.1
11	1.0	2.1	1.5-2.7	4.3	11	1.2	2.2	1.7-2.9	4.5
12	0.4	0.8	0.5-1.2	1.7	12	0.5	0.9	0.5-1.3	2.0
13	0.8	1.7	1.2-2.2	3.4	13	1.0	1.8	1.3-2.3	4.0
14	0.6	1.3	0.9-1.8	2.8	14	0.8	1.4	1-1.9	3.1
15	0.09	0.2	0.07-0.3	0.4	15	0.1	0.2	0.08-0.3	0.5
16	0.1	0.3	0.1-0.5	0.6	16	0.2	0.3	0.1-0.5	0.8
17	1.9	4.0	2.3-5	8.0	17	2.3	4.3	3.2-5.3	8.4
18	0.2	0.5	0.2-0.8	1.0	18	0.3	0.5	0.3-0.9	1.3
19	1.8	3.6	-	7.3	19	2.1	3.9	-	7.5
20	0.7	1.4	0.9-2	2.8	20	0.8	1.5	1-2.1	2.9

1 Mean divergence dates obtained using the lower-bound CI reported by Ribas et al., 2007 as a prior

2 Mean divergence dates obtained using the mean reported by Ribas et al., 2007 as a prior

3 95% CI for the divergence dates using the reported mean as a prior

4 Mean divergence dates obtained using the upper-bound CI rerported by Ribas et al., 2007 as a prior

Supplementary 1

Description and distribution of each species of *Hapalopsittaca*

Hapalopsittaca pyrrhops (Salvin, 1876)

Diagnosis Forehead, lores, forecheeks and chin dark red; crown green tinged blue; hindcheeks and ear-coverts green, shaft-streaked greenish yellow; tail dark blue, green at base.

Altitudinal Range 2500-3500

Distribution From Cajamarca, northern Peru, north to southern Ecuador.

Hapalopsittaca fuertesi (Chapman, 1912)

Diagnosis Very narrow dull red frontal band; face and ear coverts yellow; crown blue; belly with a red patch; bend of wing to lesser wing-coverts, carpal edge, and lesser underwing coverts crimson; tail red with violet blue tip.

Altitudinal Range 2900-3350

Distribution. Cordillera Central of Colombia, Below Nevado de Santa Isabel, and a possible sighting near Ibague, Tolima.

Hapalopsittaca amazonina (Des Murs, 1845)

Diagnosis Forehead orange red, with red forecrown; lores pale yellow, extending below eye; chin and forecheeks dull orange-red; throat and breast olive; bend of wing to lesser wing coverts red; blue shoulder and secondaries; tail red tipped violet blue.

Altitudinal Range 2200-3000 m

Distribution Slopes of Cordillera Oriental in Colombia

Hapalopsittaca theresae (Hellmayr, 1915)

Diagnosis Similar to *H. amazonina*, but with forehead, chin, and forecheeks dark orange red; ear coverts dark olive; throat and upper breast olive brown.

Altitudinal Range 2500-3000 m

Distribution Extreme western Venezuela, from northern Táchira north to central Trujillo.

Hapalopsittaca velezi Graves & Restrepo, 1989

Diagnosis Forehead and cheecks dark orange brown; olivaceous crown; olivaceous yellow nape and hindneck; bend of wing, shoulder, lesser underwing coverts, and anterior median wing coverts bright red; alula and primary coverts dark blue.

Altitudinal Range 2250-2650 m

Distribution Above Manizales on the northwestern flank of Nevado del Ruíz, Central Cordillera of Colombia

Hapalopsittaca melanotis (Lafresnaye, 1847)

Diagnosis Green upperparts, yellowish underparts; lores and frontal band blue; crown blue gray; blue collar; ear-coverts black; upper wing coverts and outermost secondaries black; primaries mostly blue; tail tipped blue; narrow bare skin ring around eye.

Altitudinal Range 1740-2500 m

Distribution Isolated in central western Bolivia, in La Paz and Cochabamba.

Hapalopsittaca peruviana (Carriker, 1932)

Diagnosis Similar to *H. melanotis*; lores dark brown; ear-coverts brownish; reduced blue collar to narrow band across throat.

Altitudinal Range 2800–3450 m

Distribution Eastern slope of the Andes in central and southern Peru, from Huánuco and eastern Pasco south to Cusco.

CHAPTER 3

Phylogeny and Biogeography of a Subclade of Mangoes (Aves, Trochilidae)

INTRODUCTION

With more than 300 recognized species in more than 100 genera, hummingbirds are one of the most specious families of birds, and the second largest in the New World (Schuchmann, 1999; Dickinson, 2003). Although hummingbirds have been used as model systems in many different fields, many aspects of their evolutionary history and biogeography remain unknown. McGuire *et al.* (2007) conducted a molecular phylogenetic study that included individuals from each of the higher-level hummingbird groups and used the resulting phylogeny to explore several biogeographic questions, including the role played by mountains in the diversification of this group. Their results imply that hummingbirds diversified in the South American lowlands, in agreement with the findings of Bleiweiss (1998). Furthermore, they suggest that the diversification of this group has been complex, involving several vicariance and dispersal events, as with the exception of topazes and mountain gems, every major clade of hummingbird has species distributed in the Andes, a fact, that according to them, would require at least ten invasions and five dispersal events into and out of this mountain chain (McGuire *et al.*, 2007).

The subclade of mangoes comprising the genera *Doryfera, Schistes,* and *Colibri* (McGuire *et al.*, 2007; McGuire *et al.*, 2009) is distributed in the Andes, the Pantepui, the lowlands and highlands of Central and Mesoamerica, the southern Brazilian uplands, and the lowlands of South America, including the Chocó, the Amazon Basin, the Chaco, the

Cerrado, and the southeastern Brazilian coast (Fig. 1). As the reconstruction of the ancestral state for the common ancestor of the three most basal clades of hummingbirds (topazes, hermits, and mangoes) has a high (0.999) likelihood support of having been distributed in the lowlands (McGuire *et al.*, 2007), I take up the question of what events might account for the diversification of this subclade of mangoes into the Andes, and then a potential dispersal episode from the Andes to the lowlands. The possibility of the latter event is relevant to explore because, as Fjeldså (1995), and (Fjeldså & Rahbek, 2006) postulated, the Andes have played a significant role in the diversity of the lowlands and have functioned as the source of many bird species. There is indeed evidence of taxa that originated in the Andes and later diversified in the lowlands (Garcia-Moreno *et al.*, 1999; Burns & Naoki, 2004; Chesser, 2004; Haag *et al.*, 2007; Torres-Carvajal, 2007).

There have been many explanations of the origin and diversification of Andean taxa. The most prominent ones invoke long distance dispersal (Van Der Hammen & Cleef, 1986; Gerwin & Zink, 1989; Bleiweiss, 1998; McGuire *et al.*, 2007), ecological factors (Terborgh, 1971), or include a combination of the two (Chapman, 1917, 1926; Chaves *et al.*, 2007). As an alternative, the idea that Earth history can be directly linked to the origin and diversification of Andean taxa has been explored in many recent studies (Hughes & Eastwood, 2006; Almeida *et al.*, 2007; Ribas *et al.*, 2007; Picard *et al.*, 2008; this thesis). In this study, I reconstructed the phylogeny of the subclade of mangos that includes *Doryfera*, *Schistes,* and *Colibri*, and obtained an estimate of their age in order to investigate the linkage between their evolutionary history and the geological history of the areas in which they are distributed. The uplift of the Andes proceeded at different rates from south to north and from east to west (Gregory-Wodzicki, 2000), affecting taxa differently depending on the time and place of their initial diversification. Moreover, the climatic oscillations of the Pleistocene led to cyclic vertical shifts of the Andean vegetation belts between glacial and interglacial periods (Van Der Hammen & González, 1963; Van Der Hammen *et al.*, 1973; Hooghiemstra, 1984; Van Der Hammen & Cleef, 1986; Van Der Hammen, 1989; Hooghiemstra & Ran, 1994; Hooghiemstra & Cleef, 1995; Hooghiemstra *et al.*, 2000; Hooghiemstra & Van Der Hammen, 2004; Hooghiemstra *et al.*, 2006). These vegetation shifts may have allowed a passive interchange between montane and subandean forest taxa with those of the lowlands. Moreover, as in the Andes, the highlands of the Pantepui region also underwent vertical shifting of their vegetation belts during the climatic changes of the Pleistocene (Rull, 2005). The Pantepui is situated to the east of the Orinoco basin, on the northwest of the Guiana Shield, and is characterized by table mountains or tepuis. These tepuis have flat and wide summits, with elevations ranging from 1500 to 3000 m, and vertical walls that separate them from the surrounding lowlands (Briceño & Schubert, 1990; Berry *et al.*, 1995; Huber, 1995; Rull, 2005). Thus, vegetation shifts in the tepuis during the Pleistocene might have had a direct influence on the diversification of their biota, as occurred in the Andes. Moreover, different events of marine transgressions during the Plio-Pleistocene (Nores, 1999, 2000, 2004) may have vicariated some taxa between Amazonia and the Pantepui, as well as between the Andes and the Chocó. Lastly, the final closing of the Isthmus of Panama during the Pliocene (Coates *et al.*, 1992), may have contributed to the diversification of some taxa to Central and Mesoamerica.

MATERIAL AND METHODS

Recognition of diagnosably distinct taxa, habitat characterization, and molecular sampling

In order to understand the evolutionary history of any group a first step is to delimit basal taxonomic units (Cracraft, 1997). This was done by consulting all relevant literature, and examining the skins housed in the American Museum of Natural History (AMNH) ornithology collection, which includes individuals of all recognized species and subspecies included in this study.

Ecological habitat of each species was characterized according to their reproduction grounds dividing them into vegetation zones (Table 1) following Fjeldså & Krabbe (1990), and Hooghiemstra *et al.* (2006). Forested vegetation was divided into tropical lowland or wet forest (sea level to 1000–1200 m); subandean or lower montane forest (800–to 2300 m); Andean or upper montane forest (2300–3300 m); *subpáramo* belt, (3200–3600 m), with a lower part dominated by shrub and dwarf forest, and an upper part characterized by dwarf shrub vegetation. Open vegetation in the Andes is dominated by *páramo* (3500 to ca. 4200 m). However, many hummingbirds are found in open zones within forested vegetation, which includes borders or secondary growth (Fjeldsa & Krabbe, 1990). Other open or semi-open vegetation in the lowlands includes the dry forest and plains of the Chaco, and the Cerrado of eastern Brazil.

Molecular sampling included 124 individuals representing all diagnosably distinct taxa within *Doryfera, Schistes* and *Colibri*. Most samples were from fresh tissues (Table 1), but sequences from 42 skins (toe pads, Table 1) were used to increase sampling. Following McGuire *et al.* (2007) and McGuire *et al.*(2009), sequences from *Florisuga, Topaza* and the hermits *Phaethornis, Glaucis*, and *Threnetes* were used to test the monophyly of the three ingroup genera, while *Aerodramus vanikorensis* was used as a deeper outgroup (Hackett *et al.*, 2008). Sequences for species other than mangoes were obtained from GenBank (Table 1).

DNA extraction, amplification, and sequencing

DNA extraction from both skin and tissue samples were performed with the DNeasy kit (Qiagen, Valencia CA, USA), adding DTT to the incubation buffer and incubating overnight in the case of skins. The mitochondrial cytochrome *b* (cyt *b*) and ND2 genes were sequenced for all samples, using general primers designed by Sorenson *et al.*, (1999) in the case of tissues, and specifically designed primers for amplifying fragments of 200 - 350 bp, with 30 - 50 bp of overlapping between adjacent fragments in the case of skins (Table 2).

Amplifications were conducted using GoTaq Polymerase (Promega), and GoTaq Hot Start Polymerase (Promega) for skins. Negative controls were used during all amplifications to discard contamination. 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 in a 3730 Automated DNA Sequencer (Perkin-Elmer, ABI) following standard protocol.

Phylogenetic analyses

Sequences were edited using Sequencher 4.5 (Gene Codes Corporation), and the incongruence length difference (ILD) test (Farris *et al.*, 1995) was performed to assess incongruence of phylogenetic signal between both mitochondrial genes. Maximum Parsimony (MP), Maximum Likelihood (ML), and Bayesian Inference (BI) analyses were performed for the combined data set. MP was performed in PAUP* v. 4.0b10 (Swofford, 2002), using PAUPRat (Nixon, 1999), with 200 iterations, 10% of perturbed characters, uniform weighting, random addition, and TBR as the branch-swapping algorithm. Five independent ratchet replicates were conducted to ensure that the searches had converged on the shortest tree. GARLI (Zwickl, 2006) was used to perform two independent search replicates of ML, using the GTR+I+G model of substitution, estimating base frequencies and the proportion of invariant sites. The starting tree topology was generated via a stepwise-addition of taxa, and the analysis was automatically terminated when no significant improvements of topology (0.01 lnL) were found after 2 M generations. Support for the nodes for both the MP and ML analyses was assessed by non-parametric bootstrapping (Felsenstein, 1985) in PAUP* v. 4.0b10 (Swofford, 2002), via an heuristic search, TBR branch swapping, 100 replicates with 10 random stepwise addition replicates. BI was performed in MrBayes v. 3.1 (Huelsenbeck & Ronquist, 2001), using partitioned likelihood so that parameters could vary independently for each gene, using the best fit model of substitution parameters calculated in MrModeltest v. 2.3 (Nylander, 2004). Analyses ran using one cold and three incrementally heated Markov chains for 10 M generations, sampling trees every 1000 generations, for a total of 10,000 trees, 10 % of which were discarded as burn-in. All sampled trees obtained after burn-in from two simultaneous analyses were used to compute the 50% consensus trees with posterior probabilities for each node. MP, ML, and BI analyses were conducted via the CIPRES portal v 2.2 (Miller *et al.*, 2010).

Dating of divergence times

Divergence dates between lineages and their associated error were estimated through a relaxed clock as implemented in BEAST v 1.5.2 (Drummond & Rambaut, 2007), using a reduced matrix containing only two individuals per basal taxonomic unit of *Colibri, Doryfera,* and *Schistes*, plus one individual each of *Topaza, Florisuga*, *Phaethornis*, *Glaucis*, *Threnetes*, the swifts *Apus*, *Hemiprocne*, and *Aegothelus cristatus* as outgroup. The model for the analysis was selected in BEAUti using the GTR+I+G model of nucleotide substitution, which corrects for saturation and among-site rate variation, estimating base frequencies and mean substitution rates, with a relaxed, uncorrelated lognormal clock, using a random starting tree and a Yule process as the tree prior category. In order to assign calibrations to internal nodes, I used the data provided by Brown & Mindell (2009), who summarized the available studies which have proposed divergence dates for the split between hummingbirds and swifts and within swifts. Three independent analyses were run based on the reported mean ages, plus the lower- and upper-bound estimated dates reported by Brown & Mindell (2009), in order to provide a very conservative bracket for the estimated dates. Thus, the priors for the split between swifts and hummingbirds were 55, 71.5, and 89 Mya, and that between swifts (*Apus apus*) and tree swifts (*Hemiprocne*) were 31, 34, and 57 Mya. For all the priors, I used normal distributions with a1.0 My standard deviation. Furthermore, the estimated age of the fossil *Eurotrochilus inexpectatus* (Mayr, 2003, 2004, 2007), a stem taxon which has been described as the sister group to the Trochilidae crown-group, was used to put a constraint on the hummingbird node at 32 Mya. Chains ran for 10 M generations sampling trees every 1000 generations. Results were summarized via TreeAnotator v 1.5 after a 1000 burn-in, using the maximum clade credibility option as target tree type, and mean heights for node heights.

RESULTS

Taxonomy and basal taxonomic units

The taxonomy within this group has changed considerably over the years. At one time *Doryfera* was placed within the Phaethornithinae (Cory, 1918; Peters, 1945; Meyer De Schauensee, 1970), until it was demonstrated that it belonged to the Trochilinae and was part of the monophyletic "mangoes" group (Bleiweiss *et al.*, 1994; Bleiweiss *et al.*, 1997; McGuire *et al.*, 2007; McGuire *et al.*, 2009). *Schistes* was merged with the genus *Augastes* by Schuchmann (1999), following Ruschi (1963), based mostly on plumage similarities, and some behavioral and ecological characters. However, no molecular level study has included both genera to test this hypothesis. In this analysis, we only included *Schistes*, which McGuire *et al*. (2007) and McGuire *et al.* (2009) found to belong to the mangoes.

After reviewing the specimens at the AMNH collection and relevant literature, 16 different basal taxonomic units were identified (Table 3; description in Supplementary 1): five for *Doryfera*, three for *Schistes*, and eight for *Colibri*. These results indicate that the diversity within this clade of mangos is greater than currently recognized at the biospecies level.

Molecular phylogeny

Sequences for the cytochrome *b* (1072 bp.), and ND2 (1024 bp.) genes were manually aligned, translated to confirm the correct reading-frame, and checked for the presence of stop codons. The results of the ILD test rejected incongruence between the two genes ($p > 0.05$). 792 out of the 2096 characters were parsimony informative. In the MP analysis, the five ratchet replicates yielded 274, 288, 286, 286, and 290 trees respectively, all of 2836 steps. The strict consensus of all the MP trees is presented in supplementary S2. For the ML search, GARLI calculated the following 6 nucleotide rates (AC = 0.41, AG = 23.50, AT = 1.29, CG = 0.85, CT = 11.73, GT = 1.0), four equilibrium state frequencies (ACGT = 0.3271 0.4001 0.0815 0.1913), four discrete gamma distributed rate categories, with an alpha parameter =1.2388, and the invariant (invariable) site category parameter =0.4934. The final lnL score of both analysis was = -15859.15. Finally, for the BI analysis, the GTR+I+G model of substitution was selected by the AIC criterion in MrModeltest v 2.3 for each of the individual genes, and the arithmetic mean of both simultaneous runs had a final Bayes factor =-16007.19.

The topologies resulting from the MP, ML and BI analyses all largely agree with one another. The ML tree, along with bootstrap support and posterior probabilities show that hermits (*Phaethornis, Glaucis, Threnetes*) + *Topaza* are the sister group of a clade that includes the three genera of mangoes of this study + *Florisuga mellivora* in the case of the ML and BI results (Fig. 2). However, the clade of the mangos + *Florisuga mellivora* had very poor support using BI (0.52 posterior probability). *Doryfera*, *Colibri*, and *Schistes* form a well-supported clade, and *Doryfera* is sister to *Schistes* + *Colibri*.

The individuals included in this study represent 16 taxonomic units. Of these, 15 were identified as distinct in the molecular phylogeny (Fig. 2). Our results identified four distinct species-level taxa within *Doryfera*, distributed in two clades (Fig. 2) that correspond to each of the traditionally recognized biological species, *D. ludovicae* and *D. johannae.* Within the *johannae* species-group, the molecular analysis recovers two well-supported clades (Fig. 2) comprising *Doryfera johannae* and *D. guianensis*. *D. johannae* is found in the wet tropical lowland forest of the eastern slopes of the east Andes and adjacent lowlands, between 800-1200 m, whereas *D. guianensis* is distributed in the upper tropical-subtropical forests of the tepuis (Schuchmann, 1999). These two species are divided by dry vegetation of the Llanos and the Orinoco River to the north and to the west (Fig. 1). Within the *ludovicae* species-group, the analyses find two well-supported clades (Fig. 2), corresponding to *D. veraguensis* and *D. ludovicae*. *D. veraguensis* was recognized as a separate species by Cory (1918), but Peters (1945) treated it as conspecific with *D. ludovicae.* These two species have disjunct distributions, as *D. ludovicae* is distributed from extreme E Panama to Bolivia, throughout the E Andes, and Cordilleras Central and Occidental of Colombia (Fig. 1) in humid subandean or premontane forests ranging from 2400 to 2850 m (Fjeldsa & Krabbe, 1990; Schuchmann, 1999), whereas *D. veraguensis* of the Central American highlands is found in humid forests at altitudes averaging 2400 m (Schuchmann, 1999).

Within *Schistes*, the three basal taxonomic units were recovered as reciprocally monophyletic lineages in the molecular phylogeny. *S. albogularis* was recognized by Cory (1918) as a separate species, until Peters (1945) merged it with *S. geoffroyi*, although recently Ridgely & Greenfield (2001) suggested that *S. albogularis* might indeed be a different species. *S. geoffroyi* and *S. chapmani* form a clade that is sister to *S. albogularis* (Fig. 2). These three species are found in the humid subandean or premontane forest, usually at 2500-2800 m (Fjeldsa & Krabbe, 1990). *S. geoffroyi* and *S. chapmani* are distributed on the east slope of the Central Andes and are divided by the Apurimac River Valley. *S. albogularis* is distributed on the west slope of the Andes of Ecuador and Cordillera Occidental of Colombia (Fig. 1), thus it is separated from the other two species by the open woodland, dry forest and arid scrub of the Cauca Valley.

Finally, within *Colibri* there are four major clades that correspond to each of the nominal biological species for the genus: *C. serrirrostris*, *C. coruscans*, *C. delphinae*, and *C. thalassinus*. *C. serrirostris* is sister to the other three clades. *C. delphinae* is sister to the *coruscans*-species group, and together these two are sister to the *thalassinus* species-group (Fig. 2). Within this genus, two widespread species, *Colibri delphinae* and *C. serrirostris,* are monotypic. *C. serrirostris* is found in dry semi-open habitat in the southern Brazilian uplands and the Chaco, reaching the temperate slopes of the eastern Andes in Bolivia and N Argentina at altitudes from 1500 to 3600 (Fjeldsa & Krabbe, 1990). *C. delphinae* is usually found in the humid subandean forests and lower mountain slopes of semi-open types (Schuchmann, 1999). Within this species, a proposed subspecies from Bahia, eastern Brazil (*C. d. greenwalti*) is not diagnosably distinct (Schuchmann, 1999). Within the *coruscans* species-group, two subspecies are currently recognized: *C. germanus* and *C. coruscans*. Our results show that the two are diagnosably distinct in plumage and that they form reciprocally monophyletic, unrelated clades in the molecular phylogeny. This finding is not new, as *C. germanus* was considered to be a separate species from *C. coruscans* by Cory (1918), until Peters (1945) merged them. Moreover, our results show that *C. rostratus* described by Phelps & Phelps (1952), which is also diagnosably distinct in plumage (Table 3, S1), forms a separate taxon that is sister to *C. germanus* (Fig. 2). *C. coruscans* and *C. rostratus* are found in open vegetation on the Andean slopes and highland grasslands of the *subpáramo* and *páramo* at heights of 2000-4500 m (Fjeldsa & Krabbe, 1990; Schuchmann, 1999). These two species are divided by the Caquetá River Valley, whereas *C. rostratus* and *C. germanus* are divided by the dry savanna vegetation of the Llanos and the Orinoco River valley (Fig. 1). Finally, within the *thalassinus* species-group, the four currently recognized subspecies are diagnosably distinct, but only three of them were recovered as reciprocally monophyletic groups in the molecular phylogeny, as individuals of *C. crissalis* and *C. cyanotus* are part of the same clade (Fig. 2). All these species are found in humid subandean and Andean forest, in areas of open vegetation, from 1200 to 3000 m. Further sampling is required for *C. thalassinus*, as the populations from Honduras have been described as being diagnosably distinct from those of Mexico (Peters, 1945).

Divergence times among clades

Table 4 shows the mean values resulting from the calibration of nodes A, B, and C of Figure 3 along with the 95% confidence intervals (CI), whereas the range of values reported are the upper- and lower-bound means for each node. The ages obtained for the upper- and lower-bound estimates should not be interpreted as confidence intervals, but rather extremely conservative estimates. Results from the BEAST analysis suggest that the diversification of this clade of mangos began *ca*. 25.4 Mya (Fig. 3, node 1, Table 4). The split between *Doryfera* and the rest of the mangos took place *ca.* 20 Mya (14-26.4 Mya 95% CI; Fig. 3, node 2), while *Colibri* and *Schistes* diverged from each other around 17.9 Mya (12.3-32.8 Mya 95% CI; Fig. 3, node 6).

The split between the two major clades of *Doryfera* took around 11.4 Mya (6.5-17.2 Mya 95% CI; Fig. 3, node 3). *D. ludovicae* split from *D. veraguensis* around 4.5 Mya (1.8-7.8 Mya 95% CI; Fig. 3, node 5), while *D. johannae* diverged from *D. guianensis* between 3.8 and 4.4 Mya, with a mean of 4 Mya (Fig. 3, node 4). Within *Schistes* the two main clades split around 11.8 Mya (6.6-18.3 Mya 95% CI; Fig. 3, node 7), while *S. geoffroyi* and *S. chapmani* split *ca*. 2.5 Mya (1.1-4.1 Mya 95% CI; Fig. 3, node 8). Finally, within *Colibri*, *C. serrirostris* diverged from the remainder of the clade around 12 Mya (7.6-16.6 Mya 95% CI; Fig. 3, node 9), while the *thalassinus* species-group split from the *delphinae-coruscans* species-group around 9 Mya (5.8-12.7 Mya 95% CI; Fig. 3, node 11). Within the *thalassinus* species-group, *C. cyanotus* split from the *C. thalassinus-C. cabanidis* clade at around 5.8 Mya (3.2-8.6 Mya 95% CI; Fig. 3, node 12), while these latter two taxa split around 4.9 Mya (2.6-7.6 Mya 95% CI; Fig. 3, node 13). Finally, *C. delphinae* and the *coruscans* species-group split *ca*. 7.5 Mya (4.5-11 Mya 95% CI; Fig. 3, node 14), and within the *coruscans* species-group *C. coruscans* split from the *C. germanus*-*C. rostratus* clade between *ca*. 2.5 Mya (1.1-4.4 Mya 95% CI; Fig. 3, node 15), whereas these two split around 0.7 Mya (0.2-1.2 Mya 95% CI; Fig. 3, node 16).

DISCUSSION

Recognition of basal taxonomic units

Our results indicate that diversity within this group of mangoes has been underestimated, and the recognition of these phylogenetic species allows a better understanding of the diversification history and biogeographic relationships of this group. Moreover, most of these species are divided by geographical disjunctions such as river valleys, or extended areas of vegetation that have been recognized as efficient barriers to dispersal (Cracraft, 1985). These disjunctions further advance the idea that these species have been isolated and constitute independent basal taxonomic units.

Spatial and temporal patterns of diversification

The calibrations used in this study were derived from two sources: a consensus of divergence dates from different studies [mtDNA and DNA-DNA hybridization data, (Brown & Mindell, 2009)], and the results from recent fossil findings (Mayr, 2003, 2004, 2007). The accuracy of the calibration process can greatly affect estimates of rate variation, and thus the estimation of divergence events (Ho & Phillips, 2009; Smith, 2009; Smedmark *et al.*, 2010). In order to account for the uncertainty pertaining to data derived from previous analyses, probabilistic calibration priors were used, which are more appropriate in dealing with uncertainty than point calibrations (Drummond *et al.*, 2006). Thus, a normally distributed (symmetric) prior on the ages of the calibrated nodes was used, with the highest probability around the mean, which allows for a bidirectional distribution of the uncertainty during the estimation (Ho & Phillips, 2009). The resultant divergence dates using the priors from the reported means as well as from the upper- and lower-bound estimates from Brown & Mindell (2009) are not very different from each other, and they all fall within the 95% CI calculated for the means. However, the ages derived from the upper- and lower-bound confidence intervals should only be interpreted as a very conservative estimate of the ages for each node, and not as a CI in themselves. Although the 95% CI range is given for each of the dated node (Table 4), the conclusions and comparisons throughout the biogeogaphic discussion are drawn from the mean age, as it represents the set of trees with the highest posterior density (Drummond & Rambaut, 2007), and as such is the date encompassing the interval with the highest posterior credibility. This dating approach constitutes the current best and transparent approach to the temporal diversification of this group of birds given available data.

Divergence of ***Doryfera***, ***Schistes***, and ***Colibri***

The split between this subclade of mangoes and its sister group took place around 25.4 Mya (Fig. 3, node 1), whereas that between *Doryfera* and the clade that contains *Schistes* and *Colibri* occurred ~20 Mya (Fig. 3, node 2), and between *Colibri* and *Schistes* ~17.9 Mya (Fig. 3, node 6). All these events took place before the eastern Cordillera of Bolivia had attained half of its current altitude (Kennan *et al.*, 1997; Lamb & Hoke, 1997; Gregory-Wodzicki, 2000; Garzione *et al.*, 2008), and the highest elevations would have been *ca*. 1000 m (Hartley, 2003). This is consistent with the McGuire *et al.* (2007) data that suggest that the common ancestors of the three most-basal hummingbird clades (topazes, hermits, and mangoes) had lowland distributions. Thus, the ancestor of this subclade of mangos must have been distributed either in the lowlands, or along the low-altitude slopes of the Andes.

Generic patterns of divergence

Doryfera

Doryfera has two main clades: the *johannae* species-group, which is distributed in the tropical lowlands and the tepuis, and the *ludovicae* species-group, which is mainly distributed at higher altitudes along the dense, wet subandean forest. The split between these two clades took place *ca*. 11.4 Mya (Fig. 3, node 3). This split is consistent with a vicariance hypothesis, as it constitutes a disjunction between sister taxa that are allopatrically distributed in lower tropical forests and mid montane wet forests, and temporally, it coincides with the beginning of the uplift of the eastern Cordillera of Bolivia (Vandervoort *et al.*, 1995; Hartley, 2003, Garzione *et al.*, 2008; Graham, 2009; Hoorn *et al.*, 2010).

The split between *D. johannae* and *D. guianensis* took place around 4 Mya (Fig. 3, node 4). This split represents the first diversification event into the Pantepui region within mangoes. Authors such as Chapman (1931), Mayr & Phelps (1967), Cook (1974), and Haffer (1974), suggested that the tepuis were colonized from the northern Andes, as many species of plants and animals from these mountains have been found in the summits of the tepuis (Mayr & Phelps, 1967; Huber, 1988). Furthermore, Chapman (1931), Cook, (1974), and Haffer (1974), proposed that dispersal between these two areas occurred recently, related perhaps to the climatic oscillations of the Pleistocene, which might have connected these two regions through the expansion of vegetation. In contrast, authors such as Braun *et al.* (2005), Brumfield & Edwards (2007), and Mauck & Burns (2009), proposed that these climatic events are too recent to explain distributions in the tepuis, and suggested that some species distributed in this region could be derived from relictual taxa that were at some point widespread across Northern South America. In the case of *D. guianensis*, the hypothesis of a north Andean ancestor does not hold, as its sister taxon, *D. johannae*, is distributed in the tropical lowlands. It is also clear that the split predated the climatic events of the Pleistocene. The vicariance between these two species might be explained by the marine incursions of the Pliocene, *ca*. 5 Mya, along the Amazon, Branco, and Orinoco Rivers that isolated two large islands from the rest of the tropical lowlands, one in southern Venezuela, and the other one in Guiana and northern Brazil (Nores, 1999, 2000). To better understand diversification in the Pantepui region, further sampling of *D. guianensis* is needed, as most individuals of this species in the present analysis belong to the Gran Sabana subcenter of endemism (Cracraft, 1985), with only one individual from the Duida subcenter (Cracraft, 1985).

Speciation between *D. veraguensis* and *D. ludovicae* occurred around 4.5 Mya (Fig. 3, node 5). *D. veraguensis* is distributed from W Panama to Costa Rica, whereas *D. ludovicae* occurs from extreme E Panama to Bolivia. This speciation event may be related to the episodes of marine incursions during the Plio-Pleistocene from the Pacific and the Caribbean into the lowlands of northern South America, that isolated the rainforests of the Chocó lowlands from the dry habitats of the north (Nores, 2000, 2004), thus vicariating these two species. The final closing of the Isthmus of Panama *ca* 3.5 Mya (Coates *et al.*, 1992) served as a bridge to allow the dispersion of *D. veraguensis* to Panama and Costa Rica.

Schistes

The genus *Schistes* consists of two main clades: one contains *S. albogularis*, while the other one contains *S. geoffroy*i and *S. chapmani* (Fig. 2). *S. albogularis* is distributed in the western slope of the Ecuadorian Andes, and Cordilleras Central and Occidental of Colombia, while *S. geoffroy*i and *S. chapmani* are distributed to the east of the Andes (Fig 1). Thus, the split of these two clades around 11.8 Mya (Fig. 3, node 7), constitutes a cis/trans Andean vicariance event, and it took place during the time of the uplift of the Cordillera Oriental of Colombia. This uplift separated the rain forest area of the Amazon basin from the Chocó and the Magdalena Valley (Hoorn *et al.*, 1995; Hooghiemstra *et al.*, 2006). The vicariance between these two clades coincides temporarily with the cis/trans Andean splitting of other groups as in *Pyrilia* [*Pyrilia* = *Gypopsitta* (Banks *et al.*, 2008), in Ribas *et al.* 2005]. *S. chapmani* and *S. geoffroyi* split around 2.5 Mya (Fig. 3, node 8), around the same time as the split between the parrots *Hapalopsittaca peruviana* and *H. melanotis* (~1 Mya), two taxa that share the same distributions and, like *S. chapmani* and *S. geoffroyi,* are divided by the Apurimac River Valley (this thesis).

Colibri

The split between *C. serrirostris* and the remainder of the genus occurred at around 12 Mya (Fig. 3, node 9), which is contemporary to the split of the two main clades of the genus *Doryfera*, and just like in the latter, it might have been related to beginning of the uplift of the eastern Cordillera of Bolivia (Hartley, 2003), as the Andean populations of *C. serrirostris* are distributed along the Andes of Argentina and Bolivia.

Differentiation between the Andean and the Serra do Mar populations of *C. serrirostris* began around 0.5 Myr (Fig. 3, node 10). *C. serrirostris* is distributed from semi-open areas of the Subandean forests of Bolivia and N Argentina, to the open and semi-open habitats of the Chaco in Bolivia and Paraguay, and the Cerrado. Because all the species of *Schistes* and *Colibri* are associated with the Andes, it is reasonable to assume that the ancestor of *C. serrirostris* was also Andean. The current distribution of this species from the Andes to the coast of Brazil may be due to dispersion of these populations from the open vegetation of the Andean slopes into the open environments of the lowlands during the climatic oscillations of the Pleistocene. During glacial periods, the lowest line of the subandean forest descended to altitudes near current distribution of the lowlands (Hooghiemstra *et al.*, 2000; Hooghiemstra *et al.*, 2006). Because *C. serrirostris* inhabits open areas within the Andean forests, this habitat preference may have allowed this species to easily disperse through the dry, semi-open areas of Bolivia, Paraguay, and Brazil.

Within the *coruscans* species-group, *C. coruscans* split from the clade containing *C. rostratus* and *C. germanus* around 2.5 Mya (Fig. 3, node 15), while *C. germanus* and *C.*

rostratus diverged at *ca*. 0.7 Mya (Fig. 3, node 16). Thus, diversification in the Guianas is recent and may be linked to the climatic oscillations of the Pleistocene, as suggested by Chapman, (1931), Cook, (1974), and Haffer, (1974). Furthermore, as the sister group to this species, *C. rostratus*, is distributed in the northern Andes of Colombia and Venezuela, it is possible that the ancestor of *C. germanus*-*C. rostratus* was distributed along the Northern Andes, as suggested by Chapman (1931), Mayr & Phelps (1967), Cook (1974), and Haffer (1974), and were later split during the climatic oscillations of the Pleistocene, due to vicariance as a result of the vertical shifting and expansion of the vegetation of the Tepuis, similar to the vegetation belts in the Andean *páramos* (Rull, 2005). Thus, it is possible that the ancestor of *C. germanus* first reached the lowlands adjacent to the Andes during the glacial periods of the Pleistocene, when the Subandean forest belt was maximally depressed, and from there made it to the Guianas. Later, during the interglacial, this species could have come to occupy the tepui slopes.

Within the *thalassinus* species-group, *C. cyanotus* from Bolivia, Peru, Ecuador, Cordillera Oriental of Colombia, and the Andes of eastern Venezuela diverged from the clade containing *C. thalassinus* of Mesoamerica (Honduras, Nicaragua, Guatemala, and Mexico), and *C. cabanidis* from Panama and Costa Rica at about 5.8 Mya (Fig. 3, node 12). As in *D. veraguensis*, this split may be related to the isolation of the Chocó lowlands from the dry habitats of the north.

General biogeographic trends

My results indicate that the biogeographic history of this group of mangoes has been shaped by Earth history through the uplift of the Andes, which vicariated species from the tropical lowlands from those of the newly created montane environments, as well as cis/trans Andean taxa. Moreover, the marine transgressions of the Plio-Pleistocene that isolated the tropical lowlands of the Amazonia from the Pantepui to the east could be the reason of the vicariance between these areas. Furthermore, the marine transgressions of the northern Andes isolated the lowlands north of Ecuador, Colombia and Panama from the surrounding areas, causing the vicariance between the Andean and Choco/Central America areas. The final closure of the Isthmus of Panama later acted as a bridge for these species to disperse into Central and Mesoamerica. Finally, the climatic oscillations of the Pleistocene allowed some populations of *C. serrirostris* to reach the open, dry areas of the Chaco lowlands, and later disperse to other open areas of Paraguay and Brazil. Thus, our study suggests that biodiversity in both lowlands and highlands can be understood through Earth history.

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FIGURE LEGENDS

Figure 1. Distribution of species included in this study. a) distribution of the species in the genus *Doryfera*; b) distribution of the species in the genera *Schistes* and *Colibri* ; b, c)and *Colibri*; distribution of the rest of the species in the genus *Colibri*.

Figure 2. ML Phylogram of the genera *Doryfera*, *Schistes*, and *Colibri*. Voucher numbers correspond to those on Table 1. Each species group (see text) is depicted inside a rectangle. Within the *thalassinus* species-group, individuals from the diagnosably distinct group *C. crissalis*, which are nested along the individuals from *C. cyanotus* (see text) are marked with three asterisks (***). Vertical bars to the right of the tree depict vegetation zones in which the species are distributed. Highland taxa clades are presented in orange, while lowland taxa are presented in green. Bootstrap values are depicted above branches, posterior probabilities bellow. For both statistics, only values above 70 are presented.

Figure 3. Chronogram obtained through a relaxed clock in BEAST for the genera *Doryfera*, *Schistes* and *Colibri*. Numbers on nodes correspond to those on Table 4. Units on scale correspond to Mya. Blue horizontal lines depict confidence intervals presented on Table 4. Color lines represent major geological events related to the diversification of the group.

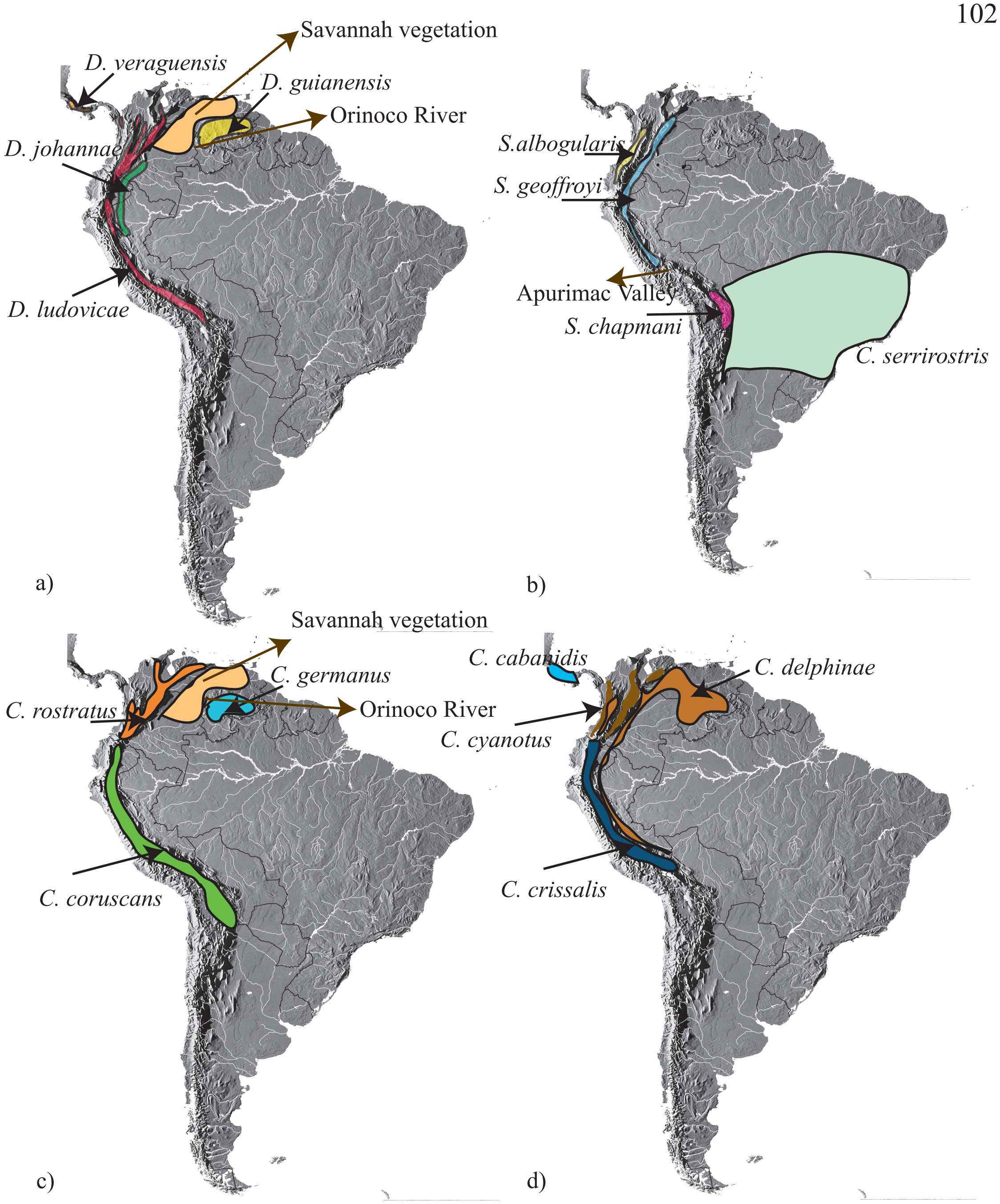

Savannah vegetation
D. veraguensis
D. guianensis
Orinoco River
D. johannae
D. ludovicae
a)
S.albogularis
S. geoffroyi
Apurimac Valley
S. chapmani
C. serrirostris
b)
Savannah vegetation
C. germanus
C. rostratus
Orinoco River
C. coruscans
c)
C. cabanidis
C. delphinae
C. cyanotus
C. crissalis
d)

Figure 1

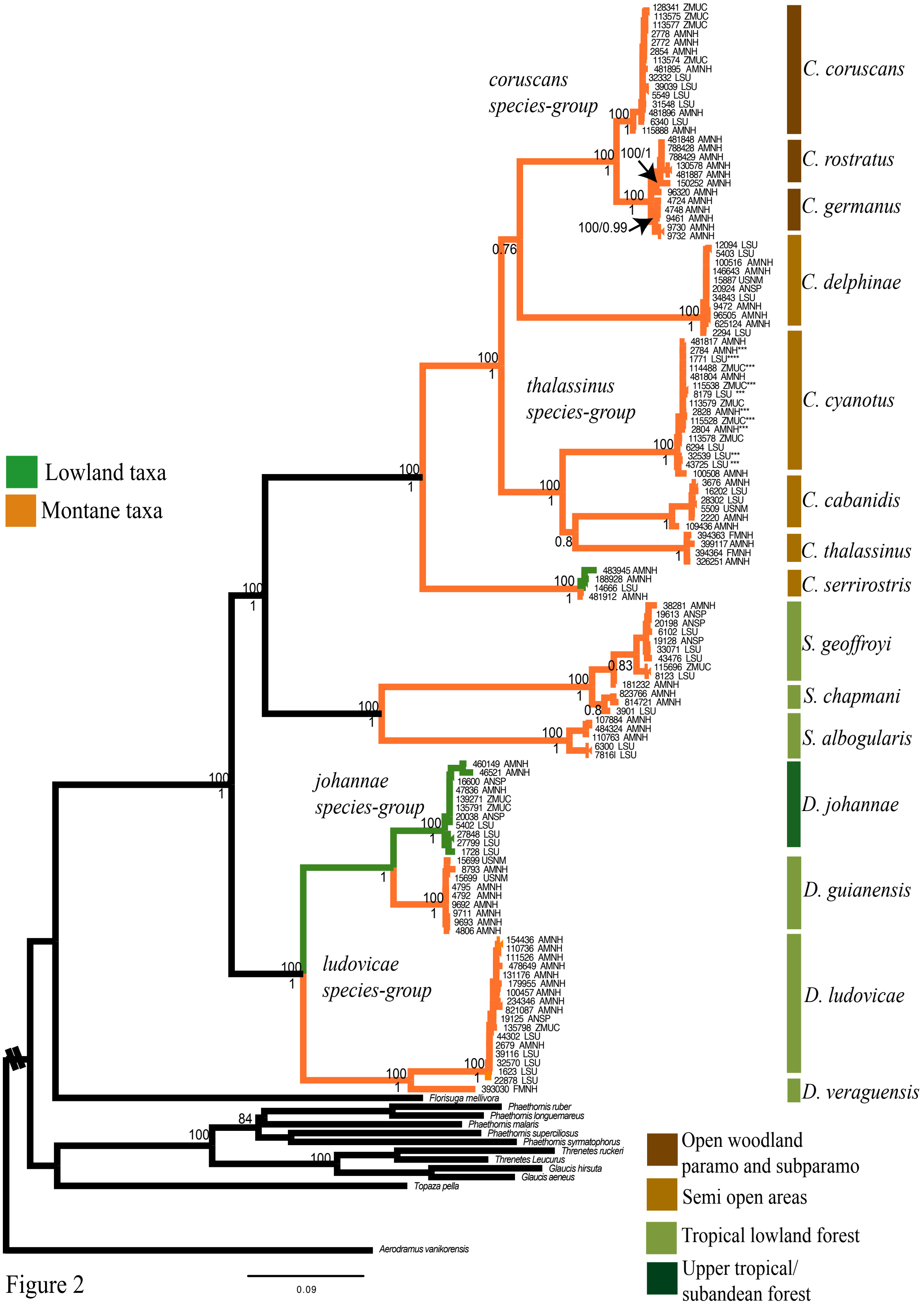
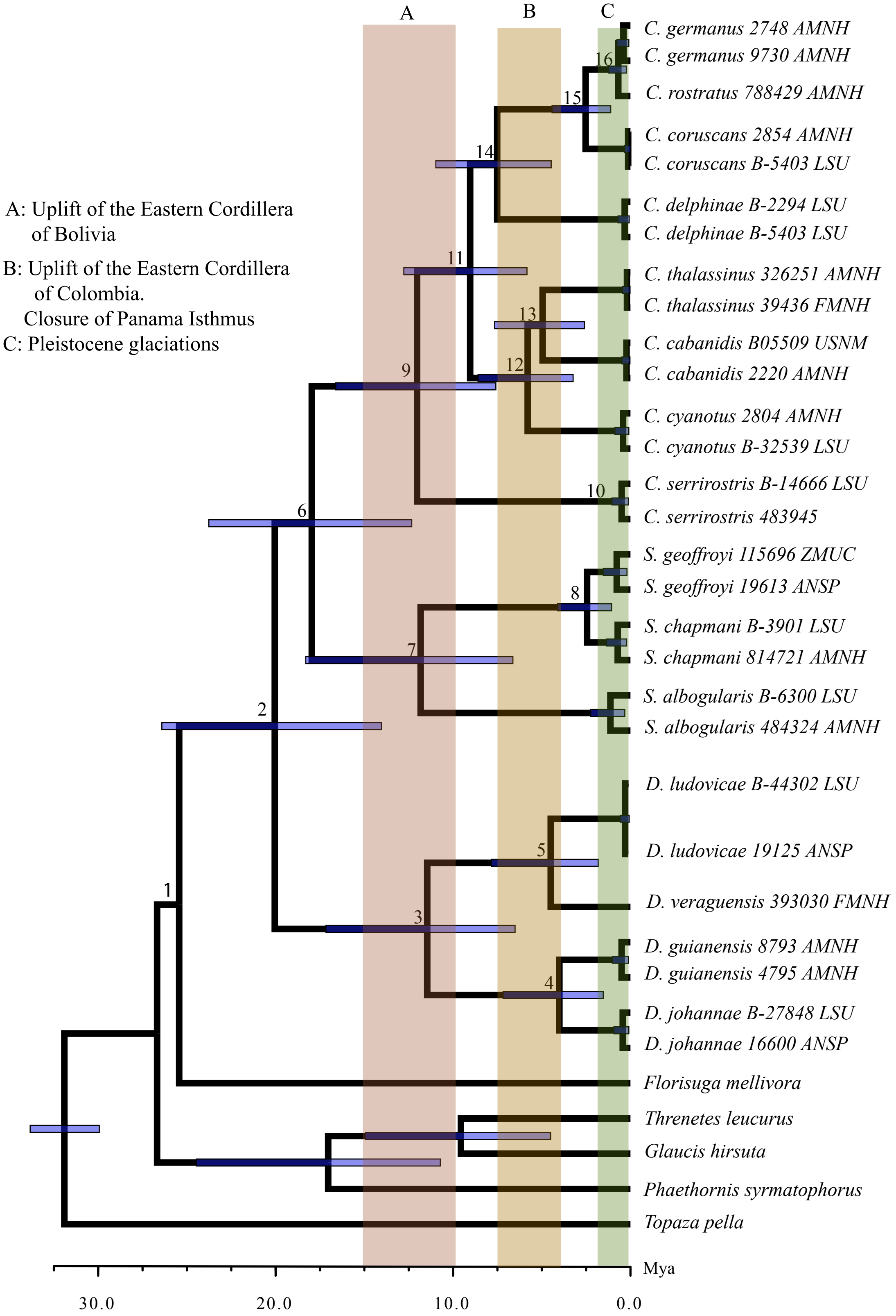

coruscans species-group
128341 ZMUC
113575 ZMUC
113577 ZMUC
2778 AMNH
2772 AMNH
2854 AMNH
113574 ZMUC
481895 AMNH
32332 LSU
39039 LSU
5549 LSU
31548 LSU
481896 AMNH
6340 LSU
115888 AMNH
100
1
100
1
100/1
481848 AMNH
788428 AMNH
788429 AMNH
130578 AMNH
481887 AMNH
150252 AMNH
96320 AMNH
4724 AMNH
4748 AMNH
9461 AMNH
9730 AMNH
9732 AMNH
100
1
100/0.99
0.76
12094 LSU
5403 LSU
100516 AMNH
146643 AMNH
15887 USNM
20924 ANSP
34843 LSU
9472 AMNH
96505 AMNH
625124 AMNH
2294 LSU
100
1
100
1
thalassinus species-group
481817 AMNH
2784 AMNH***
1771 LSU****
114488 ZMUC***
481804 AMNH
115538 ZMUC***
8179 LSU ***
113579 ZMUC
2828 AMNH***
115528 ZMUC***
2804 AMNH***
113578 ZMUC
6294 LSU
32539 LSU***
43725 LSU ***
100508 AMNH
100
1
100
1
3676 AMNH
16202 LSU
28302 LSU
5509 USNM
2220 AMNH
109436 AMNH
1
0.8
394363 FMNH
399117 AMNH
394364 FMNH
326251 AMNH
1
100
1
483945 AMNH
188928 AMNH
14666 LSU
481912 AMNH
100
1
100
1
Lowland taxa
Montane taxa
38281 AMNH
19613 ANSP
20198 ANSP
6102 LSU
19128 ANSP
33071 LSU
43476 LSU
115696 ZMUC
8123 LSU
0.83
181232 AMNH
823766 AMNH
814721 AMNH
3901 LSU
100
1
0.8
107884 AMNH
484324 AMNH
110763 AMNH
6300 LSU
7816I LSU
100
1
100
1
100
1
johannae species-group
460149 AMNH
46521 AMNH
16600 ANSP
47836 AMNH
139271 ZMUC
135791 ZMUC
20038 ANSP
5402 LSU
27848 LSU
27799 LSU
1728 LSU
100
1
1
15699 USNM
8793 AMNH
15699 USNM
4795 AMNH
4792 AMNH
9692 AMNH
9711 AMNH
9693 AMNH
4806 AMNH
100
1
ludovicae species-group
100
1
154436 AMNH
110736 AMNH
111526 AMNH
478649 AMNH
131176 AMNH
179955 AMNH
100457 AMNH
234346 AMNH
821087 AMNH
19125 ANSP
135798 ZMUC
44302 LSU
2679 AMNH
39116 LSU
32570 LSU
1623 LSU
22878 LSU
393030 FMNH
100
1
100
1
Florisuga mellivora
Phaethornis ruber
Phaethornis longuemareus
Phaethornis malaris
Phaethornis superciliosus
Phaethornis syrmatophorus
Threnetes ruckeri
Threnetes Leucurus
Glaucis hirsuta
Glaucis aeneus
Topaza pella
84
100
100
Aerodramus vanikorensis
0.09
C. coruscans
C. rostratus
C. germanus
C. delphinae
C. cyanotus
C. cabanidis
C. thalassinus
C. serrirostris
S. geoffroyi
S. chapmani
S. albogularis
D. johannae
D. guianensis
D. ludovicae
D. veraguensis
Open woodland paramo and subparamo
Semi open areas
Tropical lowland forest
Upper tropical/ subandean forest

Figure 2



A: Uplift of the Eastern Cordillera
of Bolivia

B: Uplift of the Eastern Cordillera
of Colombia.
Closure of Panama Isthmus
C: Pleistocene glaciations

Figure 3

Table 1

Voucher number	Species	Habitat	Area of endemism	Locality	
B15699 USNM	*D. guianensis*	Upper tropical forest	Gran Sabana	Guyana	Mount Roraima
B18966 USNM	*D. guianensis*	Upper tropical forest	Gran Sabana	Guyana	Kopinang Village
4795 AMNH	*D. guianensis*	Upper tropical forest	Gran Sabana	Venezuela	Bolivar, Cerro Guanay CAMP 1
4792 AMNH	*D. guianensis*	Upper tropical forest	Gran Sabana	Venezuela	Bolivar, Cerro Guanay CAMP 1
9692 AMNH	*D. guianensis*	Upper tropical forest	Gran Sabana	Venezuela	Bolivar, Cerro Guanay CAMP 1
4806 AMNH	*D. guianensis*	Upper tropical forest	Gran Sabana	Venezuela	Bolivar, Cerro Guanay CAMP 1
9711 AMNH	*D. guianensis*	Upper tropical forest	Gran Sabana	Venezuela	Bolivar, Cerro Guanay CAMP 1
9693 AMNH	*D. guianensis*	Upper tropical forest	Gran Sabana	Venezuela	Bolivar, Cerro Guanay CAMP 1
8793 AMNH	*D. guianensis*	Upper tropical forest	Duida	Venezuela	Amazonas, Sierra Tapiropecó Tamacuari
20038 ANSP	*D. johannae*	Lowland forest	Napo	Ecuador	Sucumbios
135791 ZMUC	*D. johannae*	Lowland forest	Napo	Ecuador	Napo, km 13 Ministerio Rd
139271 ZMUC	*D. johannae*	Lowland forest	Napo	Ecuador	Nangaritza Valley, 5 km SW Las Orquideas Zamora Chinchipe
16600 ANSP	*D. johannae*	Lowland forest	Napo	Ecuador	Morona Santiago

B-5402 LSU	*D. johannae*	Lowland forest	Napo	Peru	San Martín, 20 km by road NE Tarapoto on road to Yurimanguas
B-27848 LSU	*D. johannae*	Lowland forest	Napo	Peru	Loreto, Ca 77 km WNW Contamana
B-27799 LSU	*D. johannae*	Lowland forest	Napo	Peru	Loreto, Ca 77 km WNW Contamana
460149 AMNH *	*D. johannae*	Lowland forest	Napo	Colombia	Meta, Mt. Macarena
46521 AMNH *	*D. johannae*	Lowland forest	Cordillera Oriental	Colombia	Bogotá
47836 AMNH *	*D. johannae*	Lowland forest	Cordillera Oriental	Colombia	Bogotá
B-1728 LSU	*D. johannae*	Lowland forest	Central Peruvian	Peru	Pasco, Santa Cruz, about 9 Km SSE Oxapampa
393030 FMNH	*D. veraguensis*	Humid forest	Central American Highlands	Costa Rica	San José
B-22878 LSU	*D. ludovicae*	Subandean forest	Southern Peru	Bolivia	La Paz, Prov. B Saavedra 83 km by road E Charazani, Cerro Asunta Plata
B-39116 LSU	*D. ludovicae*	Subandean forest	Southern Peru	Bolivia	Cochabamba, Prov Chaparé, San Onofre ca 43 Km W Villa Tunari
2679 AMNH	*D. ludovicae*	Subandean forest	Southern Peru	Bolivia	La Paz, Nor Yungas,
B-32570 LSU	*D. ludovicae*	Subandean forest	Northern Peru	Peru	Cajamarca,

					Quebrada las Palmas, near the Rio Elena
234346 AMNH *	*D. ludovicae*	Subandean forest	Northern Peru	Peru	La Lejia
B-1623 LSU	*D. ludovicae*	Subandean forest	Central Peru	Peru	Pasco, Santa Cruz, about 9 Km SSE Oxapampa
821087 AMNH *	*D. ludovicae*	Subandean forest	Central Peru	Peru	Huanuco, Cerros del Sira
179955 AMNH*	*D. ludovicae*	Subandean forest	Northern Ecuador	Ecuador	Oyacachi
131176 AMNH *	*D. ludovicae*	Subandean forest	Meridian Andes	Venezuela	Sierra Nevada, Mérida
100457 AMNH *	*D. ludovicae*	Subandean forest	Meridian Andes	Venezuela	Mérida, Sierra Nevada
478649 AMNH *	*D. ludovicae*	Subandean forest	Cordillera Oriental, Colombia	Colombia	Bogotá
154436 AMNH *	*D. ludovicae*	Subandean forest	Cordillera Central Colombia	Colombia	Medellín, Central Andes
110736 AMNH *	*D. ludovicae*	Subandean forest	Cordillera Central Colombia	Colombia	Antioquia, Central Andes
111526 AMNH *	*D. ludovicae*	Subandean forest	Cordillera Central Colombia	Colombia	Salento, W Quindio, Central Andes
B-44302 LSU	*D. ludovicae*	Subandean forest	Northern Peru	Peru	San Martín, Ca 22 Km ENE Florida
135798 ZMUC	*D. ludovicae*	Subandean forest	Southern Ecuador	Ecuador	Napo, km 13 Ministerio Rd
19125 ANSP	*D. ludovicae*	Subandean forest	Southern Ecuador	Ecuador	Zamora Chinchipé
110763	*S. albogularis*	Subandean forest	Cordillera Occidental	Colombia	Antioquia

AMNH *					
107884 AMNH *	*S. albogularis*	Subandean forest	Cauca Valley	Colombia	San Antonio, Valle del Cauca
484324 AMNH *	*S. albogularis*	Subandean forest	Cordillera Occidental	Colombia	W Cordillera
B-6300 LSU	*S. albogularis*	Subandean forest	Cordillera Occidental	Ecuador	Pichincha, W slope of W Andes near Mindo
B-7816 LSU	*S. albogularis*	Subandean forest	South Ecuador	Ecuador	El Oro, 9.5 Km road to Piñas
19128 ANSP	*S. geoffroyi*	Subandean forest	Southern Ecuador	Ecuador	Zamora Chinchipé
B-43476 LSU	*S. geoffroyi*	Subandean forest	Northern Peru	Peru	San Martín, Ca 22 Km ENE Florida
20198 ANSP	*S. geoffroyi*	Subandean forest	Southern Ecuador	Ecuador	Sucumbios
19613 ANSP	*S. geoffroyi*	Subandean forest	Southern Ecuador	Ecuador	Napo
B-6102 LSU	*S. geoffroyi*	Subandean forest	Southern Ecuador	Ecuador	Morona-Santiago West Slope of Cordillera del Cutucu
115696 ZMUC	*S. geoffroyi*	Subandean forest	Northern Peruvian	Peru	Amazonas, Cordillera Colan
38281 AMNH *	*S. geoffroyi*	Subandean forest	Cordillera Oriental	Colombia	Bogotá
B-8123 LSU	*S. geoffroyi*	Subandean forest	Central Peru	Peru	Pasco, Cushi
B-33071 LSU	*S. geoffroyi*	Subandean forest	Northern Peru	Peru	Cajamarca, C 3 Km NNE San José de Lourdes
181232 AMNH *	*S. geoffroyi*	Subandean forest	Northern Peru	Peru	Cajamarca, Chaupé

B-39101 LSU	*S. chapmani*	Subandean forest	Southern Peru	Bolivia	Cochabamba, Chapare, Sn Onofre ca 43 Km W Villa Tunari
823766 AMNH *	*S. chapmani*	Subandean forest	Southern Peru	Bolivia	Rio Vanimayo: Yungas de Totora: 30 km N. Mte Punco
814721 AMNH *	*S. chapmani*	Subandean forest	Southern Peru	Bolivia	La Paz, Rio Zongo
481912 AMNH *	*C. serrirostris*	Subandean forest/dry-open areas	Austral Andean	Argentina	Tucumán
B-14666 LSU	*C. serrirostris*	Dry forest and savannah	Chaco Center	Bolivia	Santa Cruz, Serranía de Huanchaca, 21 Km SE Catarata Arcoiris
483945 AMNH *	*C. serrirostris*	Savannah	Serra do Mar	Brazil	Sao Paulo, Anhembi
188928 AMNH *	*C. serrirostris*	Subtropical forest and savannah	Serra do Mar	Brazil	Serra Itatiaia, Alto Itatiaia
113578 ZMUC	*C. cyanotus*	Subandean /Andean forest /open types	Southern Ecuador	Ecuador	Zamora Chinchipé near Chinapinza, Cordillera del Condor
100508 AMNH *	*C. cyanotus*	Subandean /Andean forest /open types	Meridian Andes	Venezuela	Mérida, Páramo de los Conejos
481804 AMNH *	*C. cyanotus*	Subandean /Andean forest /open types	Meridian Andes	Venezuela	Sierra de Mérida
B-6294 LSU	*C. cyanotus*	Subandean /Andean forest /open types	Cordillera Occidental	Ecuador	Pichincha, W Slope of W Andes, on

					road from Quito to Mindo
481817 AMNH *	*C. cyanotus*	Subandean /Andean forest /open types	Cordillera Oriental	Colombia	Bogotá
113579 ZMUC	*C. cyanotus*	Subandean /Andean forest /open types	Southern Ecuador	Ecuador	Loja, Guachanama, Celica mts
B-43725 LSU	*C. crissalis*	Subandean /Andean forest /open types	Northern Peru	Peru	San Martín, Ca 22 Km ENE Florida
B-32539 LSU	*C. crissalis*	Subandean /Andean forest /open types	Northern Peru	Peru	Cajamarca, Quebrada las Palmas
B-8179 LSU	*C. crissalis*	Subandean /Andean forest /open types	Northern Peru	Peru	Piura, Playa Pampa ca 8 km NW Cushi on trail to Chaglla
B-1771 LSU	*C. crissalis*	Subandean /Andean forest /open types	Central Peru	Peru	Pasco, Santa Cruz about 9 km SSE Oxapampa
115528 ZMUC	*C. crissalis*	Subandean /Andean forest /open types	Southern Peru	Bolivia	Cochabamba, Coca-pata
115538 ZMUC	*C. crissalis*	Subandean /Andean forest /open types	Northern Peru	Bolivia	Cochabamba, Pujyani, Coca-pata
114488 ZMUC	*C. crissalis*	Subandean /Andean forest /open types	Austral Andean	Bolivia	La Paz, Inquisivi
2784 AMNH	*C. crissalis*	Subandean /Andean forest /open types	Austral Andean	Bolivia	Sta Cruz, Prov. Caballeros, Parque Nacional Amboro
2828 AMNH	*C. crissalis*	Subandean /Andean forest /open types	Austral Andean	Bolivia	Sta Cruz, Prov. Caballeros, Parque Nacional Amboro
2804 AMNH	*C. crissalis*	Subandean /Andean forest	Austral Andean	Bolivia	Sta Cruz, Prov.

		/open types			Caballeros, Parque Nacional Amboro
394363 FMNH	*C. thalassinus*	Humid forest of open type vegetation	Mesoamerican Highlands	Mexico	Michoacán
394364 FMNH	*C. thalassinus*	Humid forest of open type vegetation	Mesoamerican Highlands	Mexico	Michoacán
399117 AMNH *	*C. thalassinus*	Humid forest of open type vegetation	Mesoamerican Highlands	Guatemala	Quetzaltenango
326251 AMNH *	*C. thalassinus*	Humid forest of open type vegetation	Mesoamerican Highlands	Honduras	Copán, La Libertad
109436 AMNH *	*C. cabanidis*	Humid forest of open type vegetation	Cordillera Occidental	Colombia	Cauca, Cerro Munchique, W Popayan
3676 AMNH	*C. cabanidis*	Humid forest of open type vegetation	Central American Highlands	Costa Rica	Cartago, 3Km North of Villa Mills-La Georgina
B-16202 LSU	*C. cabanidis*	Humid forest of open type vegetation	Central American Highlands	Costa Rica	San José, Cordillera Talamanca, cerro de la muerteLa Georgina, Km 95 Pan American Hwy
B-28302 LSU	*C. cabanidis*	Humid forest of open type vegetation	Central American Highlands	Panama	Chiriquí, Dist. Boquete, paso de respingo, cerro punta-boquete trail
B05509 USNM	*C. cabanidis*	Humid forest of open type vegetation	Central American Highlands	Panama	Cerro Hornito, Fortuna Reserva,
2220 AMNH	*C. cabanidis*	Humid forest of open type vegetation	Central American Highlands	Costa Rica	San José, Cordillera Talamanca, cerro de la muerteLa

					Georgina, Km 95 Pan American Hwy
B-2294 LSU	*C. delphinae*	Humid forest of open type vegetation	Central American Highlands	Panama	Darién, Cana on E Slope Cerro Pirré
B-12094 LSU	*C. delphinae*	Andean forest /open type vegetation	Northern Ecuador	Ecuador	Pichincha, Mindo
B-5403 LSU	*C. delphinae*	Andean forest /open type vegetation	Northern Peru	Peru	San Martín, 20 km by road NE Tarapoto on road to Yurimanguas
100516 AMNH *	*C. delphinae*	Andean forest /open type vegetation	Meridian Andes	Venezuela	Sierra de Mérida
146643 AMNH *	*C. delphinae*	Andean forest /open type vegetation	Meridian Andes	Venezuela	Sierra de Mérida
96505 AMNH *	*C. delphinae*	Andean forest /open type vegetation	Cordillera Oriental	Colombia	Bogotá
B15887 USNM	*C. delphinae*	Humid forest of open type vegetation	Gran Sabana	Guyana	Mount Roraima
9472 AMNH	*C. delphinae*	Humid forest of open type vegetation	Gran Sabana	Venezuela	Bolivar, Auyan Tepui
20924 ANSP	*C. delphinae*	Humid forest of open type vegetation	Gran Sabana	Guyana	Potaro-Siparuni, Guyana
B10798 NMNH	*C. delphinae*	Humid forest of open type vegetation	Gran Sabana	Guyana	North Side Acari Mountains
B-34843 LSU	*C. delphinae*	Humid forest of open type vegetation	North Peruvian	Peru	Cajamarca, Cordillera del Condor, Picorana
115888 AMNH *	*C. coruscans*	Open woodlands, subpáramo, páramo	Cordillera Central	Colombia	
B-6340 LSU	*C. coruscans*	Open woodlands,	Northern Ecuador	Ecuador	Pichincha,

		subpáramo, páramo			Yanacocha, N slope Volcan pichincha
113574 ZMUC	*C. coruscans*	Open woodlands, subpáramo, páramo	Central Ecuador	Ecuador	Loja, Guachanama, Celica mts.
481896 AMNH *	*C. coruscans*	Open woodlands, subpáramo, páramo	Austral Andean	Argentina	Marimara, Jujuy
B-31548 LSU	*C. coruscans*	Open woodlands, subpáramo, páramo	Austral Andean	Bolivia	Santa Cruz, Prov Florida
2854 AMNH	*C. coruscans*	Open woodlands, subpáramo, páramo	Austral Andean	Bolivia	Santa Cruz, Prov Caballeros, Parque Nacional Amboro
481895 AMNH *	*C. coruscans*	Open woodlands, subpáramo, páramo	Austral Andean	Argentina	Marimara, Jujuy
113577 ZMUC	*C. coruscans*	Open woodlands, subpáramo, páramo	Southern Peru	Peru	NW Arequipa, Chuquibamba
2778 AMNH	*C. coruscans*	Open woodlands, subpáramo, páramo	Southern Peru	Bolivia	La Paz, Bautista Savaedra, near Wakella
2772AMNH	*C. coruscans*	Open woodlands, subpáramo, páramo	Southern Peru	Bolivia	La Paz, Bautista Savaedra
B-39039 LSU	*C. coruscans*	Open woodlands, subpáramo, páramo	Southern Peru	Bolivia	Cochabamba, San Onofre, Prov. Chapare
B-32332 LSU	*C. coruscans*	Open woodlands, subpáramo, páramo	Central Peru	Peru	Cajamarca , Quebrada Lanchal
128341ZMUC	*C. coruscans*	Open woodlands, subpáramo, páramo	Southern Ecuador	Ecuador	Morona Santiago, Rio Upano
B-5549 LSU	*C. coruscans*	Open woodlands, subpáramo, páramo	Northern Peru	Peru	San Martín, 15 km by trail NE jirillo on trail to Balsapuerto

113575 ZMUC	*C. coruscans*	Open woodlands, subpáramo, páramo	Southern Ecuador	Ecuador	Zamora Chinchipé, Cordillera del Cóndor, Chinapinza
9461 AMNH	*C. germanus*	Upper tropical forest/ open type	Gran Sabana	Venezuela	Bolivar, Auyan Tepui
4724 AMNH	*C. germanus*	Upper tropical forest/ open type	Gran Sabana	Venezuela	Bolivar, Auyan Tepui
4748 AMNH	*C. germanus*	Upper tropical forest/ open type	Gran Sabana	Venezuela	Bolivar, Auyan Tepui
9730 AMNH	*C. germanus*	Upper tropical forest/ open type	Duida	Venezuela	Amazonas, Cerro Yavi
9732 AMNH	*C. germanus*	Upper tropical forest/ open type	Duida	Venezuela	Amazonas, Cerro Yavi
130578 AMNH *	*C. rostratus*	Open woodlands, subpáramo, páramo	Cordillera Oriental	Colombia	Bogotá
481887 AMNH *	*C. rostratus*	Open woodlands, subpáramo, páramo	Santa Marta	Colombia	Santa Marta
788429 AMNH *	*C. rostratus*	Open woodlands, subpáramo, páramo	Cordillera Oriental	Colombia	Boyacá, 5 K. N. Miraflores
481848 AMNH *	*C. rostratus*	Open woodlands, subpáramo, páramo	Meridian Andes	Venezuela	Mérida, Sierra de La Culata
788428 AMNH *	*C. rostratus*	Open woodlands, subpáramo, páramo	Cordillera Oriental	Colombia	Cundinamarca, La Mesa
150252 AMNH *	*C. rostratus*	Open woodlands, subpáramo, páramo	Guajiran	Venezuela	Caracas
96320 AMNH *	*C. rostratus*	Open woodlands, subpáramo, páramo	Meridian Andes	Venezuela	Sierra de Mérida
	Florisuga mellivora		AY830485		
	Topaza pella		AY830528	FJ588450	

Phaethornis longuemareus	EU042580	EU442350
Phaethornis superciliosus	GU167254	
Phaethornis ruber	AY830515	
Phaethornis malaris	AY830514	
Phaethornis syrmatophorus	EU042583	EU167028
Glaucis hirsuta	AY830486	
Glaucis aeneus	EU042234	FJ588451
Threnetes ruckeri	AY830602	AY150659
Threnetes leucurus	AY830526	
Aerodramus vanikorensis	AY294506	AY2944444
Apus apus	AY294532	AY294470
Hemiprocne comata	AY294545	AY294483
Aegotheles cristatus	NC_011718	NC_011718

Table 2 List of primers used during the amplification and sequencing of skin samples.

Colibri			
F1N CND2	CATACCCCGAAAATGATGGT	F1N CYTB	GCAAATCCCACCCCCTAYTAAA
R1N CND2	GTGGGGTGRTTGAGTTGAGT	R1N CYTB	GGAYTACTCCYGTRTTTCAGGTC
F2N CND2	TCCACACTWYTACTCTTCTCAAGYA	F2N CYTB	GGACGAGGCTTCTACTAYGGC
R2N CND2	GTYTGRTTAAGYCCCAYTCACCC	R2N CYTB	GGCAAAGAAYCGRGTTAGTGT
F3 CND2	CCYRCCCTACTCACCACAAT	F3 CCYTB	YGGYCARACCCTTGTRGAAT
R3 CND2	CATTTGGGYAAGAATCCAGT	R3 CCYTB	TTRGCYGGRGTRAAGTTTTCT
F4 CND2	CCYRCACTTAATGCAGCCCTR	F4N CYTB	CCCCYTACTAACCCTRGCAA
R4 CND2	GGGGACAGRGGAAGAAGGAGRG	R4 CYTB	GGTGCTRATGAGGGGRAAKAG
Doryfera			
F1 CND2	CATACCCCGAAAATGATGGT	F1 DCYTB	GCAAATCCCACCCCCTAYTAAA
R1 DND2	GGGAATCAGAAGTGGAAYGG	R1 DCYTB	GGAGGATTACTCCTGTGTTTCAA
F2 DND2	ACTCRGGRCAATGAGACAT	F2 DCYTB	CTSCACATTGGACGAGGRTT
R2 DND2	TCCCAGGTGTGAGATTGATG	R2 DCYTB	GTTGTTGGAGCCRGTTTCGT
F3 DND2	CCGCACTAGGRGGATGRATR	F3 DCYTB	ATTCTTTGCCCTCCACTTCC
R3 DND2	GCGGAGGYRGTTATYTCTTG	R3 DCYTB	TGCRAATARGAAGTATCATTCTGG
F4 DND2	TRTCAYTRGCAGGTCTRCCC	F4 DCYTB	CGGRGACCCAGAAAACTTCA
Schistes			
F1CND2	CATACCCCGAAAATGATGGT	F1CCYTB	GCAAATCCCACCCCCTAYTAAA
R1 SND2	GGTTAGGGAGGAACCTTGGA	R1 SCYTB	CCCGTGTTTCAAGTTTCTTTG
F2 SND2	ATCACCCCACATCATCCCTA	F2 SCYTB	GGACGAGGGTTCTACTACGG
R2 SND2	GCTGGTCGTGATGCAGTAGA	R2 SCYTB	CGGTTTCGTGGAGGAAAGT
F3 SND2	CAAATCCGAAAAGTCCTAGCC	F3 SCYTB	AGGTGGATTTTCAGTCGACAA
R3 SND2	AGCGGAAGCGGTTATTTCTT	R3 SCYTB	GTGTGGGGGTGTGACTAAGG
F4 SND2	AAACGCAGCCCTAATAATAACA	F4 SCYTB	GCAATATTTTCCCCCAACCT
R4 SND2	GGGGACAGGGGAAGAAGGAGGG	R4 SCYTB	ATYYGGCCGATGATGAATGG

Table 3. Identified basal taxonomic units

Species	**Distribution**	**Map**
Doryfera ludovicae	Bolivia to extreme E Panama	Fig. 1a
D. veraguensis	W Panama to N Costa Rica	Fig. 1a
D. johannae	NE Peru to Cordillera Oriental, Colombia	Fig. 1a
D. guianensis	S Guyana, S Venezuela, N Brazil	Fig. 1a
Schistes geoffroyi	E Peru to N Venezuela	Fig. 1b
S. albogularis	W Ecuador to W and C Cordilleras of Colombia	Fig. 1b
S. chapmani	Central Bolivia	Fig. 1b
Colibri. serrirostris	N Argentina, Bolivia, C Paraguay, SE Brazil	Fig. 1b
C. germanus	S Venezuela, E Guyana, N Brazil	Fig. 1d
C. coruscans	NW Argentina to Ecuador	Fig. 1d
C. rostratus	Colombia and NW Venezuela	Fig. 1d
C. thalassinus	N Nicaragua to C Mexico	---
C. cabanidis	W Panama and Costa Rica	Fig. 1d
C. crissalis	Andes of NW Argentina, Bolivia and Peru	Fig. 1d
C. cyanotus	Andes of Ecuador, Colombia and Venezuela	Fig. 1d
C. delphinae	Bolivia to Venezuela, Trinidad, Guyana, NC Brazil Guatemala and Belize	Fig. 1c

Table 4. Diversification dates and confidence intervals obtained during the relaxed clock analysis. Nodes A and B are fixed, whereas nodes1 to 16 correspond to those of Fig. 3.

Node	Lower-bound[1]	Mean[2]	95% CI [3]	Upper bound[4]
A	55	71.5		89
B	31	34		57
C	32	32		32
1	23.2	25.4		32.2
2	18.1	20	14-26.4	23
3	10.7	11.4	6.5-17.2	13
4	3.8	4	1.5-7.8	4.4
5	4.1	4.5	1.8-7.8	5.2
6	16	17.9	12.3-23.8	20.7
7	10.5	11.8	6.6-18.3	13.8
8	2.3	2.5	1.1-4.1	2.8
9	10.9	12	7.6-16.6	14
10	0.5	0.5	0.1-1	0.59
11	8.1	9	5.8-12.7	10.5
12	5.2	5.8	3.2-8.6	7
13	4.4	4.9	2.6-7.6	6
14	6.7	7.5	4.5-11	8.6
15	2.4	2.5	1.1-4.4	2.9
16	0.7	0.7	0.2-1.2	0.8

1 Mean divergence dates obtained using the lower-bound CI reported by Brown & Mindell (2009) as a prior.

2 Mean divergence dates obtained using the mean reported by Brown & Mindell (2009) as a prior.

3 95% CI for the divergence dates using the reported mean as a prior.

4 Mean divergence dates obtained using the upper-bound CI rerported by Brown &Mindell (2009) as a prior.

SUPPLEMENTARY S1.

Description of each of the basal taxonomic units recognized in the analysis.

D. ludovicae: Frontlet glittering pale green, crown and nape dark coppery-bronze, shading to bronzy green on back; uppertail-coverts blue, tinged grey-blue distally; tail black, narrowly tipped with dull grey; underparts dull, dark greenish bronze, darker and greener on throat..

D. veraguensis: Smaller than *D. ludovicae* and more dichromatic; male darker, duskier green below, darker bronze on crown and nape providing increased contrast with frontlet;

D. johannae: Frontlet violet, rest of upper underparts dark bronzy green, tinged dark bronze on nape, uppertail coverts blue with duller tips, tail blue-black; underparts blue-black glossed with bluish green on throat and breast.

D. guianensis: Paler ventral coloring than in *D. johannae*, less intensely violet crown in male, and shorter bill.

Schistes geoffroyi: Above bronzy –green becoming coppery on rump; throat iridescent golden green, broken pectoral band white, patch on each side of throat glittering violet, rest of underparts green, undertail coverts white; tail rounded, central rectrices green, rest bronze, with green, with darkish blue subterminal band, tipped white.

S. albogularis: Similar to *S. geoffroyi*, but lateral throat patches more violet-blue, unbroken white pectoral band across chest, lower back and central rectrices dark green, undertail coverts shinning bronze green.

S. chapmani: Uniform colored crown like in *S. geoffroyi*, lateral throat patches without white, less white on belly.

Colibri delphinae: Dull greyish brown, glossed with green on the back; uppertail-coverts dusky, broadly edged with cinnamon; tail bronze-green with greenish black subterminal band, narrow ochraceus to greyish tip; violet patch from bellow eye to auriculars; lores and bread malar stripe buffy white, center of throat glittering green, to blue at lower edge; bill black, feet dark grey.

C. serrirostris: shinning green, with long, decurved bill; lower upperparts yellow-green with a blue shimmer; ear coverts, subocular and postauricular regions spotted violet blue. Rectrices glittering green, with broad steel-blue subterminal band; undertail coverts pure white. The upper mandible is sometimes serrated.

C. coruscans: Slightly decurved bill; upperparts metallic bluish green, bluish violet ear plumes, elongated and erectile; chin bluish violet, rest of underparts green with blue belly; tail double-lobed, metallic green with steely blue subterminal band.

C. germanus: Similar to *C. coruscans*, but with forecrown, underparts and tail bluer.

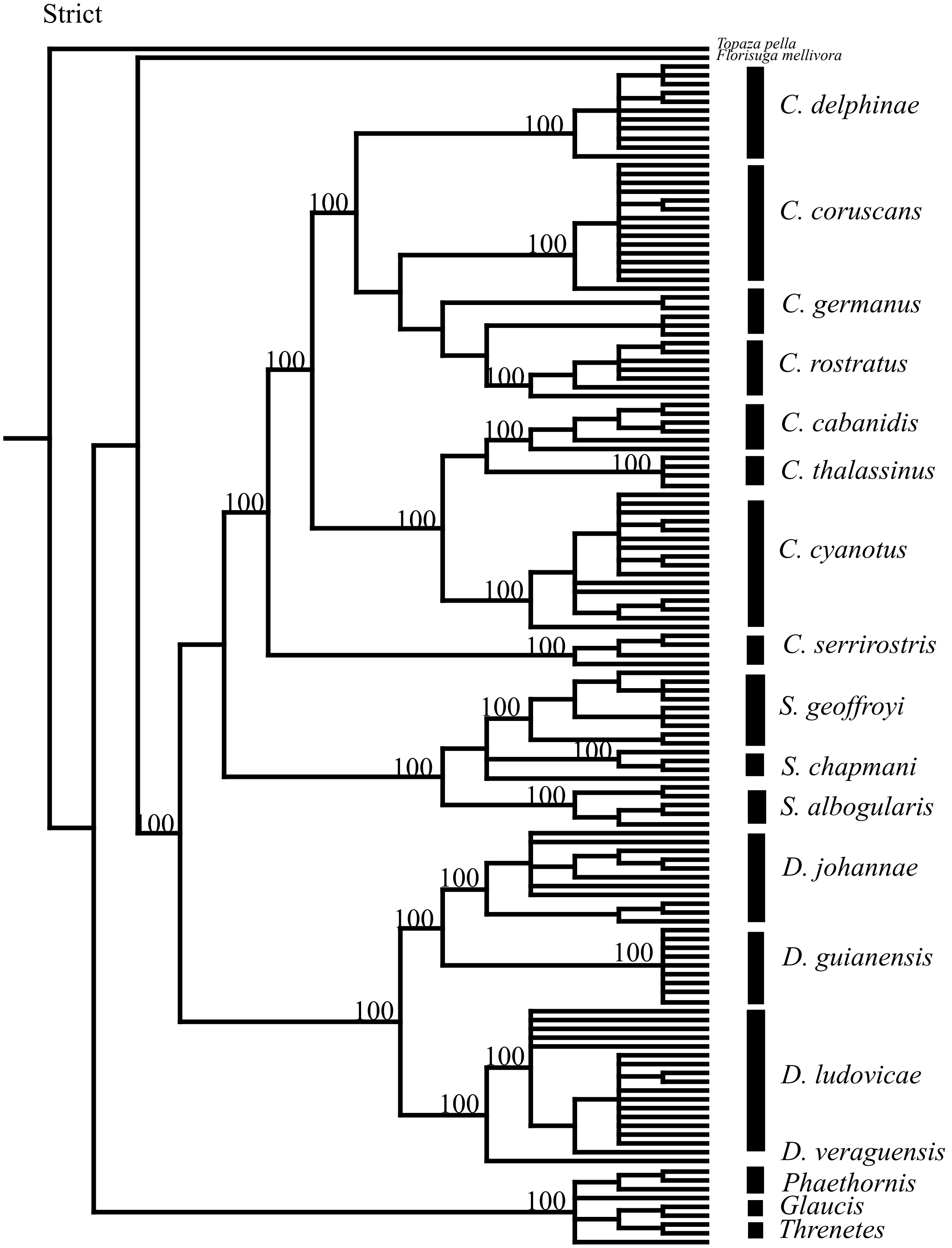
C. rostratus: Similar to *C. germanus*, with longer bill and tail.

C. thalassinus: Plumage mostly a rather bluish green, with subterminal blue-black band on tail and broad violet patch from bellow eye to auriculars; feathers of throat and chest glittering green with darker centers; undertail coverts edged with buff; bill and feet black; violet blue patch on chest; sometimes presents a blue chin; bill slim.

C. cabanidis: No violet blue patch on chest, although sometimes shows some blue on chest.

C. cyanotus: No blue on chest, and greener plumage on the back.

C. crissalis: Paler underparts than *C. cyanotus*, and little or no green in the undertail coverts



S2 Strict consensus tree for the complete set of trees obtained by PAUPRat (see text). Bootstrap values are above branches.

CHAPTER 4

Phylogeny and Biogeography of Thripophagini Ovenbirds (Aves, Synallaxinae, Furnariidae)

INTRODUCTION

In a recent study Moyle *et al.* (2009) introduced the name of 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). The group includes approximately 600 species of Neotropical birds primarily distributed in South America throughout a broad range of habitats. Numerous studies have confirmed their monophyly (Sibley & Ahlquist, 1985, 1990; Irestedt *et al.*, 2001; Irestedt *et al.*, 2002; Chesser, 2004). Within the infraorder, the Furnariidae—or ovenbirds—comprise 236 recognized species (Sibley & Ahlquist, 1990, Moyle *et al.*, 2009) and have been described by Sibley & Ahlquist (1990) as being one of the most diverse avian groups. Within the Furnariida, the subfamily Synallaxinae is of great interest as it is said to have the highest diversification rate within the family (Irestedt *et al.*, 2009).

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 (Fig. 1a), whereas species of *Thripophaga* (Fig. 1a), *Xenerpestes* (Fig. 1a), and *Cranioleuca* (Fig. 1b, c, d) 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, *Acrobatornis, Limnoctites* (Fig 1b)*, Roraima* (Fig. 1b)*,* and *Metopothrix* (Fig. 1a) occur in isolated areas of the South American lowlands.

Irestedt *et al.* (2009) suggested that the radiation of Synallaxinae ovenbirds took place during the last 15 Mya, 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 the precipitation patterns (Hooghiemstra *et al.*, 2000, Hoorn *et al.*, 2010). Many authors suggest that these changes might have had a strong influence on the diversification of Andean groups (Bates & Zink, 1994; Bleiweiss, 1998; Perez-Eman, 2005; Cadena *et al.*, 2007; Chaves *et al.*, 2007). Some other authors directly link the orogenesis of the Andes to the origin of highland taxa from lowland ancestors and their subsequent diversification (Almeida *et al.*, 2007; Ribas *et al.*, 2007; this thesis). Because of its diversity and distribution, the tribe Thripophagini can be used to test the idea that Earth history played an important role in the origin and diversification of Andean groups. Thus, in this study we reconstruct the phylogeny and estimate the time of divergence of this group of ovenbirds, using sequences from two mitochondrial genes.

MATERIALS AND METHODS

Study group and recognition of diagnosably distinct taxa

The Thripophagini tribe is comprised of a heterogeneous array of taxa, both in terms of morphology and ecology (Remsen, 2003). 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 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 throughout the years, and to this day, there are doubts about the taxonomic status of some of the species. Many of the biological species within the tribe have two or more recognized subspecies. Rather than using biospecies as terminal taxa in this study, we first assessed which of the subspecies-level taxa were diagnosably distinct, as the use of basal taxonomic units is essential for understanding temporal and spatial patterns of diversification within any group (Cracraft, 1997). To do this, fixed external plumage were examined for all available skin specimens of Thripophagini from the ornithology collection at the American Museum of Natural History (AMNH). Guided by these results, hypotheses of phylogenetic species limits were tested with independent DNA data in a phylogenetic analysis.

Habitat characterization and ancestral charcter-state reconstruction

In order to correlate the current habitat distribution with the biogeographic history of this group, 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–to 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 ca. 4200 m), whereas open vegetation in the lowlands was divided into swamps, woodlands, dry Chaco, and Pampas (Table 1). Furthermore, we reconstructed the ancestral character-states for the geographic distribution on the ML phylogeny using the parsimony option in the Trace Character History feature in Mesquite v. 2.72 (Maddison & Maddison, 2009). 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

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). Extraction was performed using the DNeasy kit (Qiagen, Valencia CA, USA), and the complete cytochrome *b* (cyt *b*) and the subunit 2 of the NADH (ND2) 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 protocol.

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 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 10 independent parsimony replicates. Branch support was estimated through non-parametric bootstrapping (Felsenstein, 1985) in PAUP v. 4.0b10 (Swofford, 2002), via an heuristic search, TBR branch swapping, 1000 replicates with 10 random stepwise addition sequence replicates. Maximum Likelihood (ML) was performed using GARLI (Zwickl, 2006), with the 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 of topology were found after 2 M 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 M generations, with trees being sampled every 1000 generations, keeping 9,000 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*, *Synalaxis azarae*, and *Hellmayrea gullaris* were used as outgroups (Moyle et al. 2009). All analyses were run on the CIPRES portal v. 2.2 (Miller *et al.*, 2010).

Divergence time estimates

Because the split between New Zealand and Antarctica has been suggested as being responsible for the split between *Acanthisitta* and the rest of the passerine birds (Barker *et al.*, 2002; Ericson *et al.*, 2002; Barker *et al.*, 2004), Irestedt *et al.* (2009) used this event to calculate divergence dates within the Furnariides. According to their results, the ovenbird-woodcreeper radiation started to diverge at *ca.* 33 Mya, while the Synallaxines started to diverge at *ca*. 19 Mya. I used their results to estimate divergence times within the Thripophagini using BEAST (Drummond & Rambaut, 2007). In order to account for the uncertainty of using results from a previous analysis, which carry with 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 gullaris* and the rest of the clade were 13.7, 16.38, and 21.5 Mya (node B, Table 2), whereas the priors for the node that splits *Asthenes* + *Schizoeaca* from the rest of the group were 13.4, 15.63, and 20.3 (node C, Table 2). In all cases a normal distribution prior with a standard deviation of 1.0 My 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 was used, containing only one or two individuals per basal taxonomic unit, plus *Leptasthenura* as 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. A10 M chain length was used, and the resulting trees after a 1000 burn-in 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

Recognition of basal taxonomic units

After reviewing the skins housed in the AMNH ornithology collection, as well as the literature (no specimens from *C. henricae* were available), I was able to distinguish 49 basal taxonomic units (Table 3; descriptions and distributions are presented in Supplementary 1), and 35 were included in the molecular analysis (Table 1). These results show that taxonomic diversity in this group of ovenbirds has been substantially underestimated. Irestedt *et al.* (2009) noted that the amount of morphological variation found within the ovenbirds might be due to convergent evolution rather than to common ancestry, which may explain why traditional classifications have been unable to accurately reflect the relationships within this group.

Phylogenetic analyses

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

The 10 replicates of the MP searches yielded between 165 and 184 MP trees of 1791 steps each, and the majority consensus of them is presented in Supplementary 2. 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 AIC criterion. The arithmetic mean of the Bayes factor for the two simultaneous BI analyses was lnL -11898.28. The ML analysis had a final score of lnL= -11769.9675, and Fig. 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 it was nested within *C. henricae*, whereas in the MP and BI analyses it was not, and was sister to the clade of *C. pyrrophia* + *C. striaticeps*. Nevertheless, both in the case of the relationships between *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). Although *Xenerpestes* has three diagnosably distinct taxa, only one, *X. singularis*, was included in this analysis. 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 should be renamed to reflect its different taxonomic position (Fig. 2). 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*, and the latter therefore, should be considered as part of *Limnoctites* instead of *Cranioleuca*. Both *L. rectirostris* and *L. sulphurifera* are distributed in the Pampean-Uruguayan area of endemism (Fig. 1b), which is a wet area in southern Brazil, Uruguay, and eastern Argentina (Cabrera, 1971, 1973; Cabrera & Willink, 1973). Further sampling is needed to clarify the boundaries of the genus *Thripophaga*, as Vaurie (1980) and Irestedt *et al.*(2009) suggested that it might not form a monophyletic group.

Excluding *C. gutturata* and *L. sulphuriphera* that are not closely related to the other species of *Cranioleuca* (Fig. 2)*,* the reminder of the species in this genus form a well-supported monophyletic group. *Cranioleuca* can be partitioned into four clades, A through D (Fig. 2). Clade A contains the following basal taxa: C. *marcapatae, C. weskei, C. discolor,* and *C. albiceps.* Fjeldså & Krabbe (1990) proposed to treat the biospecies *C. marcapatae* and *C. albiceps* as conespecific, following Remsen (1984) and the results by

García-Moreno et al. (1999). However, these two taxa are diagnosably distinct for plumage, geographically separated (Fig. 1b), and form two separate clades in the molecular phylogeny (Fig. 2), so there is no reason for treating them as one single taxon. The biospecies *C. albiceps* has two basal taxonomic units, *C. albiceps* and *C. discolor* (Peters 1951), but they were not recovered as different clades in the molecular phylogeny. The same was true for the diagnosably distinct taxa within the biospecies *C. marcapatae: C. marcapatae* and C. *weskei* (Remsen, 1984), which were recovered as part of the same clade (Fig. 2).

Clade B is unique in that it is the only one containing species found solely in Amazonia (Fig. 1d). *C. vulpecula* was considered to be a subspecies of the biospecies *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. The results from our molecular phylogeny confirm that they 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 *C. albicapilla*, *C. albigula*, *C. pyrrhophia*, *C. rufipennis*, *C. striaticeps*, *C. henricae,* and *C. obsoleta*. Within it, the biospecies C. *albicapilla* contains two described subspecies (Fig. 1b), *C. albicapilla* and *C. albigula* (Cory & Hellmayr, 1925; Peters, 1951), which are diagnosably distinct for plumage, and are sister groups in the molecular phylogeny (Fig. 2). This clade is sister to the one formed by the *pyrrhophia* species-group, which contains C. *pyrrhophia*, *C. striaticeps, C. rufipennis, C. henricae*, and *C. obsoleta.* 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. In our analyses, the position of *C. obsoleta* varied among the different analyses and was not supported in any of them. However, this species is diagnosably distinct for plumage. Thus, there is a need to include more samples of *C. obsoleta,* as having only one individual could be the cause for this lack of resolution. On the other hand, the biospecies *C. pyrrhophia* has three described subspecies: *C. pyrrhophia*, *C. striaticeps*, and *C. rufipennis* (Cory & Hellmayr, 1925; Peters, 1951). Each of them is diagnosably distinct for plumage, and they have disjunct distributions (Fig. 1c). Sibley & Ahlquist (1990) and Maijer & Fjeldsa (1997) proposed that *C. henricae*, the biospecies *C. pyrrhophia,* and *C. obsoleta* form a "superspecies," a claim that was supported by the results of García-Moreno et al. (1999). Our results show that *C. pyrrhophia* and *C. striaticeps* belong to separate clades (Fig. 2), although there is one individual of *C. striaticeps* nested within *C. pyrrhophia*. Moreover, within *C. striaticeps*, we found one individual originally identified as *C. albicapilla* (ZMUC 126990) that, because of its distribution (Cochabamba; Table 1), is most likely a misidentified individual of *C. striaticeps*, as *C. albicapilla* does not reach Bolivia (Fig. 1b, Remsen, 2003). *C. striaticeps* and *C. henricae* are paraphyletic on the gene tree (Fig. 2), and within *C. henricae*, we found two individuals of *C. debilis* (22647 LSU, 22894 LSU). C. *debilis, C. cisandina,* and *C. curtata* are considered to be subspecies of the biospecies *C. curtata* (Peters 1951), which is part of clade D. *C. henricae* is diagnosably distinct in plumage from C. *debilis*, *C. rufipennis*, and *C. striaticeps*. However, according to Claramunt (personal communication) there is reason to believe that *C. henricae* might be a hybrid between *C. rufipennis* and *C. debilis*, as *C. henricae* has some intermediate morphological features between *C. rufipennis* and *C. debilis*. These two species are allopatric (Fig. 1c), with *C. rufipennis* found in the arid woodlands of La Paz and NW Cochabamba, and *C. debilis* in the humid montane forests of Bolivia (the Yungas), reaching south to Santa Cruz, but it may be possible that at some point, they may come in contact. *C. rufipennis* was not sampled in the molecular phylogeny, but given that *C. henricae* is paraphyletic for mtDNA with respect to *C. striaticeps*, and the individuals of *C. debilis* are nested within *C. henricae*, this lends support to the idea that *C. henricae* could in fact be an hybrid. There is a need to conduct a detailed morphological and phylogeographic analysis of *C. henricae*, in order to clarify its status.

Clade D contains *C. semicinerea*, *C. demissa*, *C. cardonai*, *C. dissita*, *C. erythrops, C. rufigenis*, *C. griseigularis*, *C. antisiensis*, *C. palamblae*, *C. curtata, C. debilis*, *C. cisandina*, *C. baroni*, *C. capitalis*, and *C. zaratensis*. The biospecies *C. demissa* has two described subspecies (Fig. 1c), *C. demissa,* from the tepuis of the Duida subcenter of endemism (Cracraft, 1985), and *C. cardonai* (Phelps & Dickerman, 1980), from the tepuis of the Gran Sabana subcenter of endemism (Cracraft, 1985). Both are diagnosably distinct for plumage and 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 reminder of the group. *C. 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 reminder of the group is divided into two clades. The first contains *C. erythrops* and *C. rufigenis*, and the other *C. antisiensis, C. cisandina*, and *C. baroni* (Fig. 2). The biospecies *C. erythrops* is described as having three subspecies: *C. erythrops*, *C. rufigenis*, and *C. griseigularis* (Cory & Hellmayr, 1925; Peters, 1951), all of them which are diagnosably distinct based on plumage, and with disjunct distributions (Fig. 1c). However, *C. griseigularis* was not recovered as a separate species in the molecular phylogeny, as the two individuals included (Table 1) were nested within *C. erythrops*. As already mentioned, *C. cisandina*, *C. curtata*, and *C. debilis* (Fig. 1c) are basal taxa currently classified as subspecies of the biospecies *C. curtata* (Peters 1951), even though Cory & Hellmayr (1925) recognized *C. cisandina* as a separate species. Only C. *cisandina* was included in the molecular phylogeny. The biospecies *C. antisiensis* is described as having two subspecies, *C. antisiensis* and *C. palamblae* (Cory & Hellmayr,1925), each of them diagnsably distinct for plumage, and with allopatric distributions (Fig. 1c). However, the results of the molecular phylogeny show that the individuals from both basal taxa are nested in the same clade. Finally, the biospecies *C. baroni* has three described subspecies (Fig. 1c), *C. baroni*, *C. capitalis* (Cory & Hellmayr,1925; Peters, 1951), and *C. zaratensis*, which was described by Koepcke (1961a). Although each of these taxa is diagnosably distinct for plumage, they were not recovered as different clades in the molecular phylogeny (Fig. 2). Fjeldså & Krabbe (1990) proposed that the biospecies *C. pyrrhophia* may form a superspecies with *C. antisiensis* and the biospecies *C. baroni*, and that *C. curtata* should be treated as conspecific with C. *erythrops*. Neither of these arguments is supported by the results (Fig. 2), as *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 for mtDNA with respect to each other, each is diagnosably distinct for plumage. *C. baroni* and *C. antisiensis* have been previously reported as being conspecific by Koepcke (1961b) and Fjeldsa & Krabbe (1990), although Cory & Hellmayr (1925), as well as Peters (1951) considered them as separate species. Remsen (2003) noted that these two species had "clearly distinct populations at the extreme of their ranges." However, *C. baroni* and *C. antisiensis* are in fact allopatric, with *C. baroni* found in N and C Peru in semi-arid woodlands, whereas *C. antisiensis* is found from S Ecuador to N Peru in montane or subandean humid forests, so there is no reason for considering them as conspecific. The results of the molecular phylogeny (Fig. 2) show that some individuals identified as *C. antisiensis* were nested within *C. baroni* (391887 FMNH, 391884 FMNH, 3597 LSU). However, the distributions of these specimens in central Peru (Table 1) suggest that these are individuals from *C. capitalis* (3597 LSU) and *C. zaratensis* (391887 FMNH, 391884 FMNH), respectively, 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 (Figure 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 as repoted 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 CI reported by Irestedt *et al.* (2009) as priors are highly congruent with the results from the 95% CI for the repoted mean (Table 3). This congruence suggests that the conservative estimation of the divergence dates is similar to the confidence intervals recovered when using the mean. Throughout the biogeogaphic discussion only the mean dates are used, as they represent the set of trees the highest posterior density (Drummond & Rambaut, 2007), and as such is the date with the highest posterior credibility. According to the results, the subtribe Thripophagini diverged from the Synallaxini around 13.3 Mya (11.4-15.1 Mya 95% CI; node 1, Fig. 3). The clade of *Metopothrix* and *Xenerpestes* diverged *ca.* 11.2 Mya (9.3-13.1 Mya 95% CI; node 2, Fig. 3), whereas the split between *S. nortoni* and the rest of the Thripophagini took place around 8.4 Mya (6.7-11.4 Mya 95% CI; node 4, Fig. 3), and the split leading to *C. gutturata* and the rest of the clade took place around 5.8 Mya (4.5-7 Mya 95% CI; node 5, Fig. 3). *Roraima* split from the rest of the tribe *ca.* 5.6 Mya (4.3-6.6 Mya 95% CI; node 6, Fig. 3), while the next split gave origin to the *Limnoctites* + *Thripophaga* + *Cranioleuca* clade, and it occurred around 5.1 Mya (4.1-5.3 Mya 95% CI; node 8, Fig. 3). Within *Cranioleuca* the split between clade A and the rest of the genus occurred at 4.4 Mya (3.4-5.3 Mya 95% CI; node 9, Fig. 3), clade B split from clades C + D around 3.4 Mya (2.7-4.2 Mya 95% CI; node 11, Fig. 3), and clades C and D split around 2.8 Mya (2.2-3.5 Mya 95% CI; node 14, Fig. 3).

DISCUSSION

Spatial and temporal patterns of diversification

The split between the tribes Synallaxini and Thripophagini took place around 13.3 Mya (node 1, Fig. 3), 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 middle to late Miocene (Graham, 2009). The ancestral character state reconstruction for the node leading to the Thripophagini was recovered as equivocal (Fig. 4), due to poor sampling of Synallaxini and the widespread distributions of some thripophagine taxa. Because of the low altitude of the Andes at that time, 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 (node 3, Fig. 3). *Metopothrix* is distributed in the lowlands of the Napo area of endemism (Fig. 1a), whereas *X. singularis* is distributed along the eastern slope of the Andes of Ecuador and N Peru, in the humid montane forest (Fig. 1a). The split between these two allopatric species coincides in time to active uplift of the northern Andes (Hoorn *et al.*, 1995; Hooghiemstra *et al.*, 2006; Graham, 2009), so their vicariance might be related to this event. It can be postulated that uplift created new environments while at the same time creating ecological barriers altitudinally between newly vicariated species. The next clade to split was that of

Siptornis nortoni, which is distributed along the E slope of the Andes of N Peru (Fig. 1a). This split took place *ca*. 8.4 Mya (node 4, Fig. 3). It is possible the origin of this deep lineage is also related to Andean uplift.

Roraima adusta is distributed in the Pantepui region (Fig. 1b). The reconstruction of the ancestral character-state for the node leading to *R. adusta* is equivocal (Fig. 4). *C. gutturata* is the sister-group to the remainder of the thripophagines, including *R. adusta* (Fig. 2), and is distributed in the tropical forest, *varzea*, and *tierra firme* of the Amazon basin (Fig. 1b). *R. adusta* diverged around 5.4 Mya (node 6, Fig. 3). Although some authors have suggested that the tepuis were recently colonized from the northern Andes (Chapman, 1931; Mayr & Phelps, 1967; Cook, 1974; Haffer, 1974), likely 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 most likely distributed in the surrounding lowlands of the Pantepui. However, the actual mechanism by which its ancestor was vicariated from the lowlands to the Pantepui is not clear.

The split leading to the clade of *Limnoctites* + *Thripophaga* + *Cranioleuca* took place *ca*. 5.1 Mya (node 8, Fig. 3). Once more, the reconstruction of the ancestral state of this node was equivocal (Fig. 4). 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 (node 9, Fig. 3). Both species of clade A, *C. albiceps* and *C. marcapatae*, are distributed in the upper montane or Andean forest of Peru and Bolivia respectively (Fig. 1b). However, the reconstruction of the ancestral character state leading to this clade is equivocal (Fig. 4). Because the closest genera to *Cranioleuca*—*Tripophaga* and *Limnoctites*—are distributed in the lowlands (Fig. 1a, b), one can infer that the ancestor of *Cranioleuca* was also distributed in the lowlands, and that this split may be explained by a vicariance event due to the uplift of the Andes. As the eastern Bolivian cordillera gained almost half of its current height in the last 6-10 Mya (Graham, 2009), it is possible that the ancestor of *Cranioleuca* was distributed along the slopes of the Andes at lower altitudes, and was uplifted along with the Andes. *C. albiceps* split from *C. marcapatae* between 1.2 and 1.9 Mya, with a mean of 1.5 Mya (node 10, Fig. 3). These two species are separated by the Apurimac River Valley, and their divergence is more or less contemporary to the hummingbirds *Schistes chapamani* and *S. geoffroyi* (~2.5 Mya; this thesis)*,* and the parrots *Hapalopsittaca peruviana* and *H. melanotis* (~1 Mya; this thesis), which have the same distribution and are divided by this same barrier. The divergence of these three pairs of disjunct species at about the same time suggests that the formation of this valley may be associated with vicariance of all three pairs.

Clade B is the only one within *Cranioleuca* that is composed entirely of Amazonian species (Fig. 1d). *C. muelleri* inhabits *várzea* forests*, C. vulpina* is found in *várzea* 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-waters tributaries" (Zimmer, 1997). This clade was isolated in Amazonia between 2.3 and 3.7 Mya, with a mean of around 2.8 Mya (node 12, Fig. 3). Campbell *et al*. (2006) and Ribas *et al*. (in review) have suggested that this was the time when the Amazon drainage was established, so the isolation of this clade may have been related to this event.

Clades C and D split *ca*. 2.8 Mya (node 14, Fig 3). 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 vicariated these two clades.

Within clade C, the divergence between *C. pyrrhophia, C. striaticeps, C. henricae*, and *C. obsoleta* of the Austral Andes and the Pampas, on the one hand, and *C. albicapilla,* and *C. albigula* from central and southern Peru, on the other, was initiated around 1.7 and 2.7 Mya, with a mean at *ca*. 2.1 Mya (node 15, Fig. 3). As in the case of *C. marcapate*/*C. albiceps*, the Andean species of the two subclades within clade C are divided by the Apurimac river valley, and their divergence is contemporary to that of the other pairs of species that share this distribution (the parrots *H. melanotis* and *H. peruviana*, and the hummingbirds *S. chapmani* and *S. geoffroyi*). Thus, the split between *C. albicapilla* + *C. albigula* and the clade including *C. pyrrhophia, C. striaticeps*, *C. henricae*, and *C. obsoleta* serves as further evidence to suggest that the formation of the Apurimac river valley was a major biogeographic event. The clade of *C. pyrrhophia, C. striaticeps*, *C. henricae*, and *C. obsoleta* diverged around 1.1 Mya (node 17, Fig. 3). *C striaticeps* is allopatric to C. *pyrrhophia* (Fig. 1c), with *C. striaticeps* found in the dry woodlands of the Bolivian Andes, and *C. pyrrhophia* distributed in the dry areas of the Chaco and the Pampas. Speciation 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 (Hoogimestra *et. al.*, 2000). As dry vegetation is present in both species' distributions, 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, vicariating *C. striaticeps* from *C. pyrrophia*. No biogeographical inferences of *C. henricae* and *C. obsoleta* can be drawn at this time, until their taxonomic status has been resolved.

Within group D (Fig. 3), the clade containing *C. cardonai, C. 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 (node 19, Fig. 3). The split between *C. semicinerea* of the dry Caatinga forest in east Brazil and *C. cardonai* and *C. demissa* of the humid montane forests of the Pantepui (Fig. 1c) took place around 1.9 Mya (node 20, Fig. 3). 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 (Hooghimestra *et. al*., 2000). Once in the Pantepui, the ancestor of *C. cardonai* + *C. 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 vicariance between *C. cardonai* of the Gran Sabana, and *C. demissa* of the Duida*. C. dissita* split from the rest of the clade *ca.* 0.7 Mya (node 21, Fig. 3). *C. dissita* is distributed on Isla Coiba, in the Veragua Archipelago of Panama (Fig. 1d). 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 speciated this taxon, and the reconstruction of the ancestral character state is equivocal for this node (Fig. 4). Finally, the next split divided the reminder of clade D into two groups: *C. erythrops* (W Ecuador) + *C. rufigenis* (Central America) from *C. baroni, C. cisandina* and *C. antisiensis* from the Andes (Fig. 1b). This split took place around 1.8 Mya (node 23, Fig. 3). At this point 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. *C. erythrops* from W Ecuador, and *C. rufigenis* from west Panama and Costa Rica (Fig. 1b) diverged from each other around 1.1 Mya (node 24, Fig. 3), after the Isthmus of Panama was already in place (Coates *et al*., 1992). The clade that contains *C. cisandina, C. antisiensis* and *C. baroni* diverged around 0.7 Mya (node 25, Fig 3), so each of the species within it is very recent (Fig. 3). *C. cisandina, C. antisiensis* and *C. baroni* have allopatric distributions (Fig. 1c), with *C. cisandina* and *C.*

antisiensis distributed in humid montane forests at lower altitudes than *C. 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 (Fig. 4). The difference in habitat between the humid montane *C. cisandina, C. antisiensis* and the upper montane, drier *C. baroni* may be an indication that the vicariance between these taxa was probably related to vegetation changes during the climatic oscillations of the Pleistocene (Hooghiemstra *et al*., 2000).

CONCLUSIONS

The use of basal taxonomic units has allowed us to better understand the diversity, evolutionary relationships, and history of this complex and diverse group. The results of this study indicate that Earth history is probably strongly linked to the diversification of this group, 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.

Finally, and in order to have a clearer picture of the evolution and biogeography of this very diverse and biogeographically complex tribe of birds, there is a need for further phylogeographic studies to establish the species limits within the complex formed by *C. antisiensis*, *C. baroni*, and *C. cisandina*, as well as to clarify the species status of *C. henricae*.

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FIGURE LEGENDS

1. Distribution of the taxa within Thripophagini.

a) Distribution of *Metopothrix, Xenerpestes, Siptornis* and *Tripophaga.*

b) Distribution of *Roraima, Limnoctites* and part of the genus *Cranioleuca. C. gutturata*, which needs to be renamed, as well as *Cranioleuca sulphurifera* (= *Limnoctites sulphurifera*) are included here (see text).

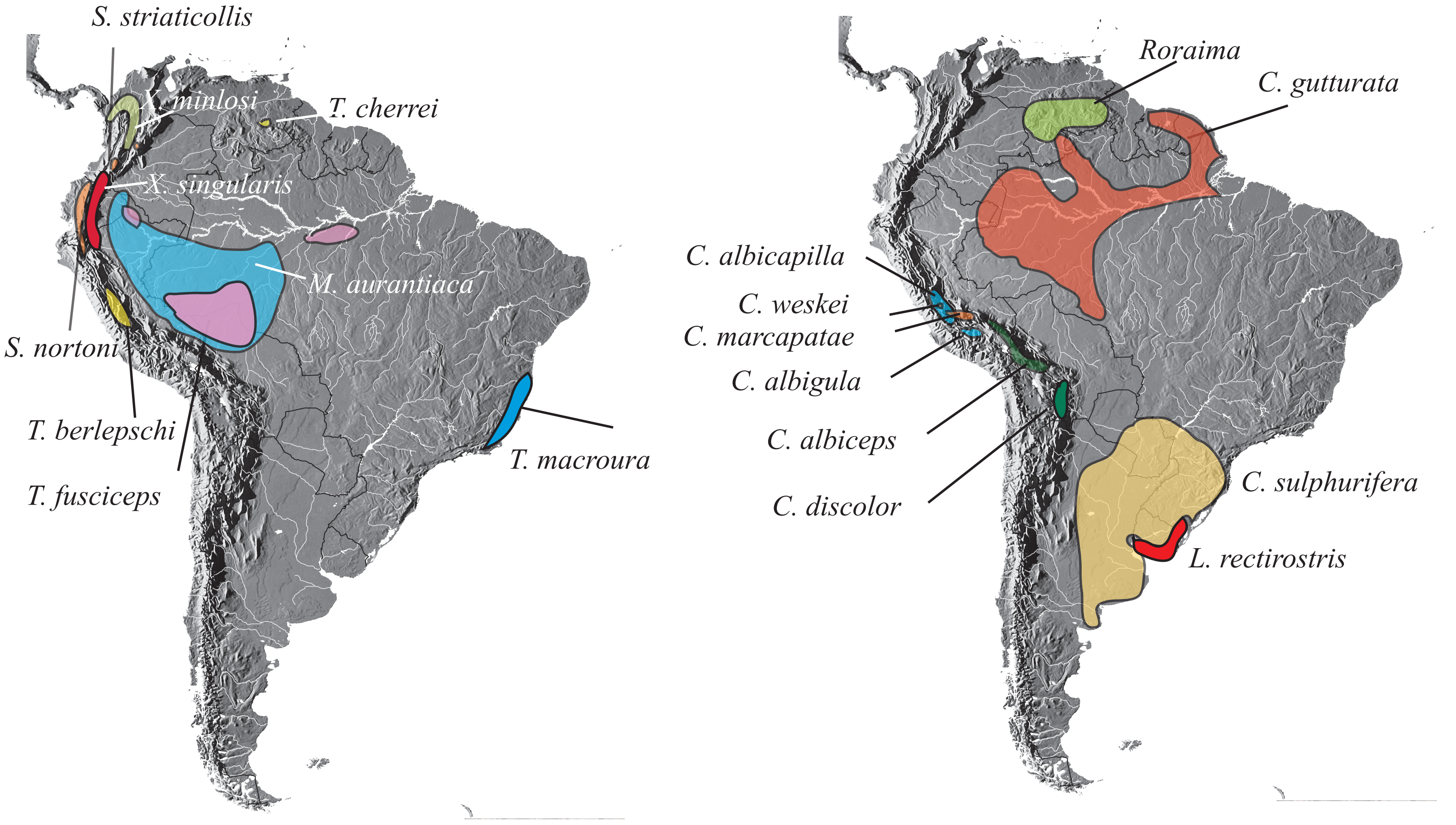
c) Distribution of part of the species of the genus *Cranioleuca*.

d) Distribution of part of the species of *Cranioleuca*,

2. ML phylogram of the tribe Thripophagini. Bootstrap support values are depicted above branches, while posterior probabilities are below. Voucher numbers correspond to those on Table 1. Individuals of *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).

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

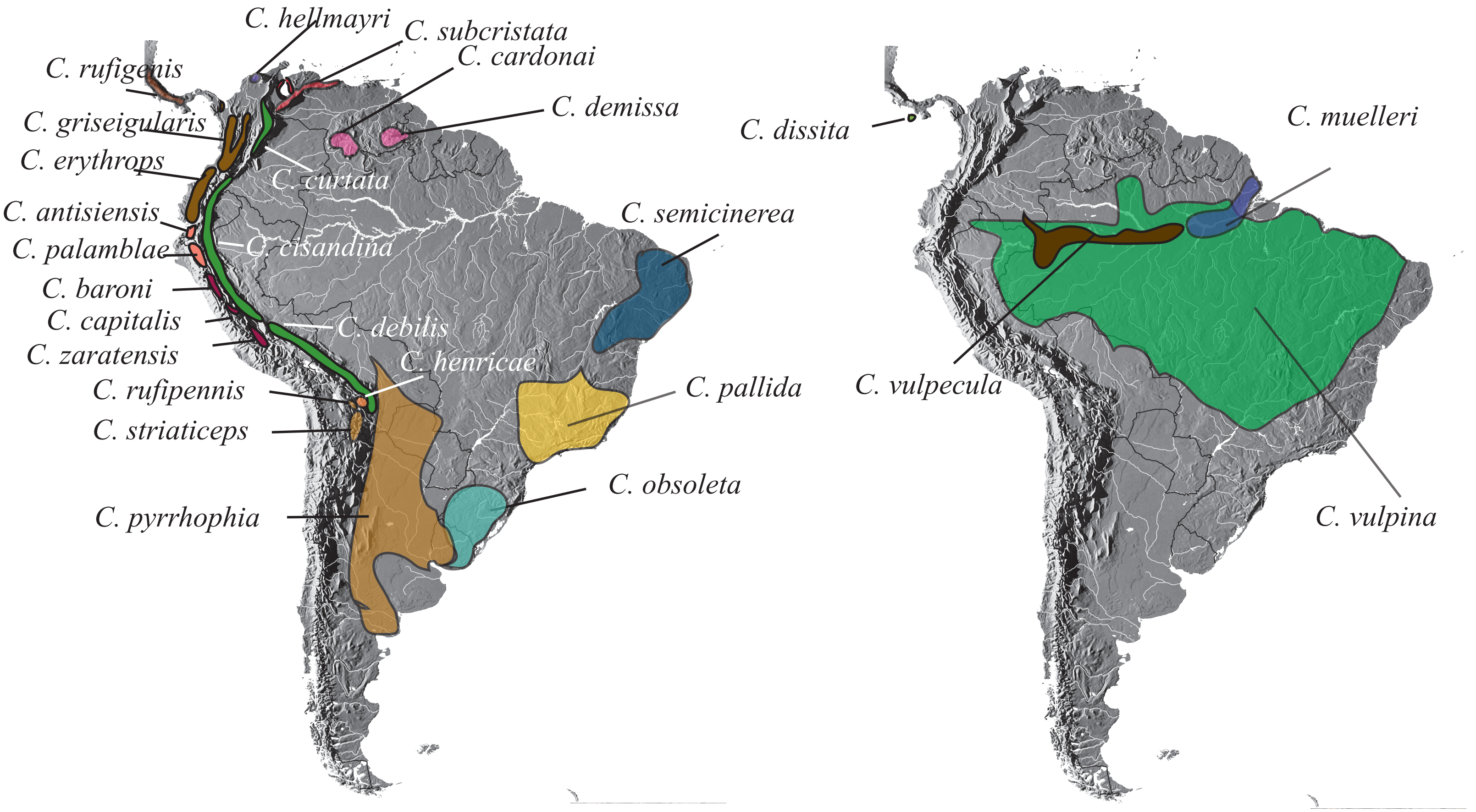
4. Ancestral character-state reconstruction for the area of distribution of the species within Thripophagini. Colored circles (other than gray) represent the different areas (see legend), whereas gray circles represent equivocal reconstructions.



a) *Metopothrix, Xenerpestes, Siptornis,Thripophaga*

b) *Roraima, Limnoctites, Cranioleuca*

Figure 1



c) *Cranioleuca*

d) *Cranioleuca*

Figure 1

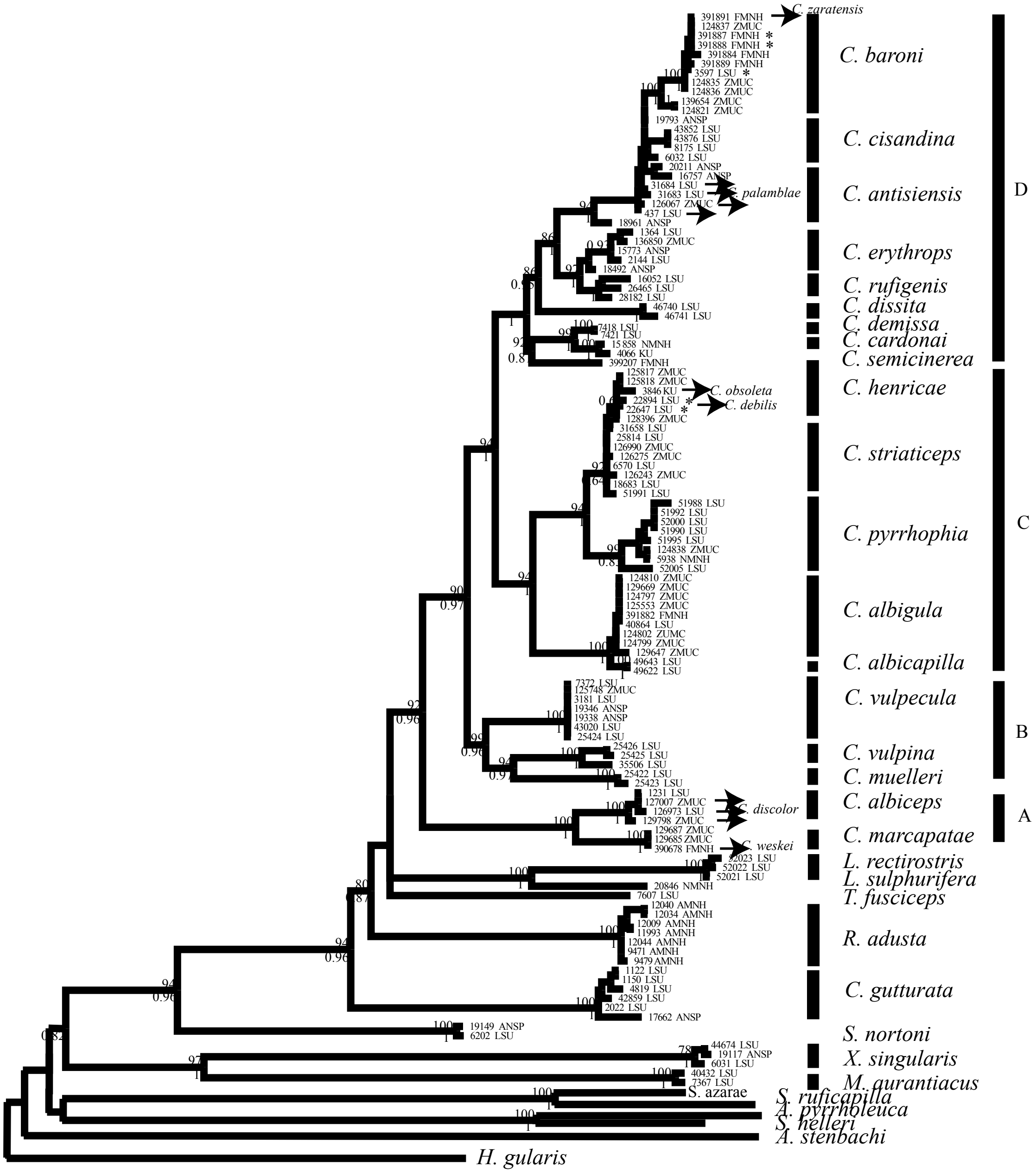

C. zaratensis
391891 FMNH
124837 ZMUC
391887 FMNH *
391888 FMNH *
391884 FMNH
391889 FMNH
3597 LSU *
124835 ZMUC
124836 ZMUC
139654 ZMUC
124821 ZMUC
C. baroni
19793 ANSP
43852 LSU
43876 LSU
8175 LSU
6032 LSU
C. cisandina
20211 ANSP
16757 ANSP
31684 LSU
31683 LSU
126067 ZMUC
437 LSU
C. palamblae
C. antisiensis
18961 ANSP
1364 LSU
136850 ZMUC
15773 ANSP
2144 LSU
18492 ANSP
C. erythrops
16052 LSU
26465 LSU
28182 LSU
C. rufigenis
46740 LSU
46741 LSU
C. dissita
7418 LSU
7421 LSU
C. demissa
15858 NMNH
4066 KU
C. cardonai
399207 FMNH
C. semicinerea
125817 ZMUC
125818 ZMUC
3846 KU
C. obsoleta
22894 LSU *
22647 LSU *
C. debilis
128396 ZMUC
C. henricae
31658 LSU
25814 LSU
126990 ZMUC
126275 ZMUC
6570 LSU
126243 ZMUC
18683 LSU
51991 LSU
C. striaticeps
51988 LSU
51992 LSU
52000 LSU
51990 LSU
51995 LSU
124838 ZMUC
5938 NMNH
52005 LSU
C. pyrrhophia
124810 ZMUC
129669 ZMUC
124797 ZMUC
125553 ZMUC
391882 FMNH
40864 LSU
124802 ZUMC
124799 ZMUC
129647 ZMUC
C. albigula
49643 LSU
49622 LSU
C. albicapilla
7372 LSU
125748 ZMUC
3181 LSU
19346 ANSP
19338 ANSP
43020 LSU
25424 LSU
C. vulpecula
25426 LSU
25425 LSU
35506 LSU
C. vulpina
25422 LSU
25423 LSU
C. muelleri
1231 LSU
127007 ZMUC
126973 LSU
129798 ZMUC
C. discolor
C. albiceps
129687 ZMUC
129685 ZMUC
390678 FMNH
C. weskei
C. marcapatae
52023 LSU
52022 LSU
52021 LSU
L. rectirostris
20846 NMNH
L. sulphurifera
7607 LSU
T. fusciceps
12040 AMNH
12034 AMNH
12009 AMNH
11993 AMNH
12044 AMNH
9471 AMNH
9479 AMNH
R. adusta
1122 LSU
1150 LSU
4819 LSU
42859 LSU
2022 LSU
17662 ANSP
C. gutturata
19149 ANSP
6202 LSU
S. nortoni
44674 LSU
19117 ANSP
6031 LSU
X. singularis
40432 LSU
7367 LSU
M. aurantiacus
S. azarae
S. ruficapilla
A. pyrrholeuca
S. helleri
A. stenbachi
H. gularis
D
C
B
A
100
100
94
86
86
0.63
0.93
97
92
0.8
100
99
100
0.6
97
0.64
94
99
0.81
94
100
94
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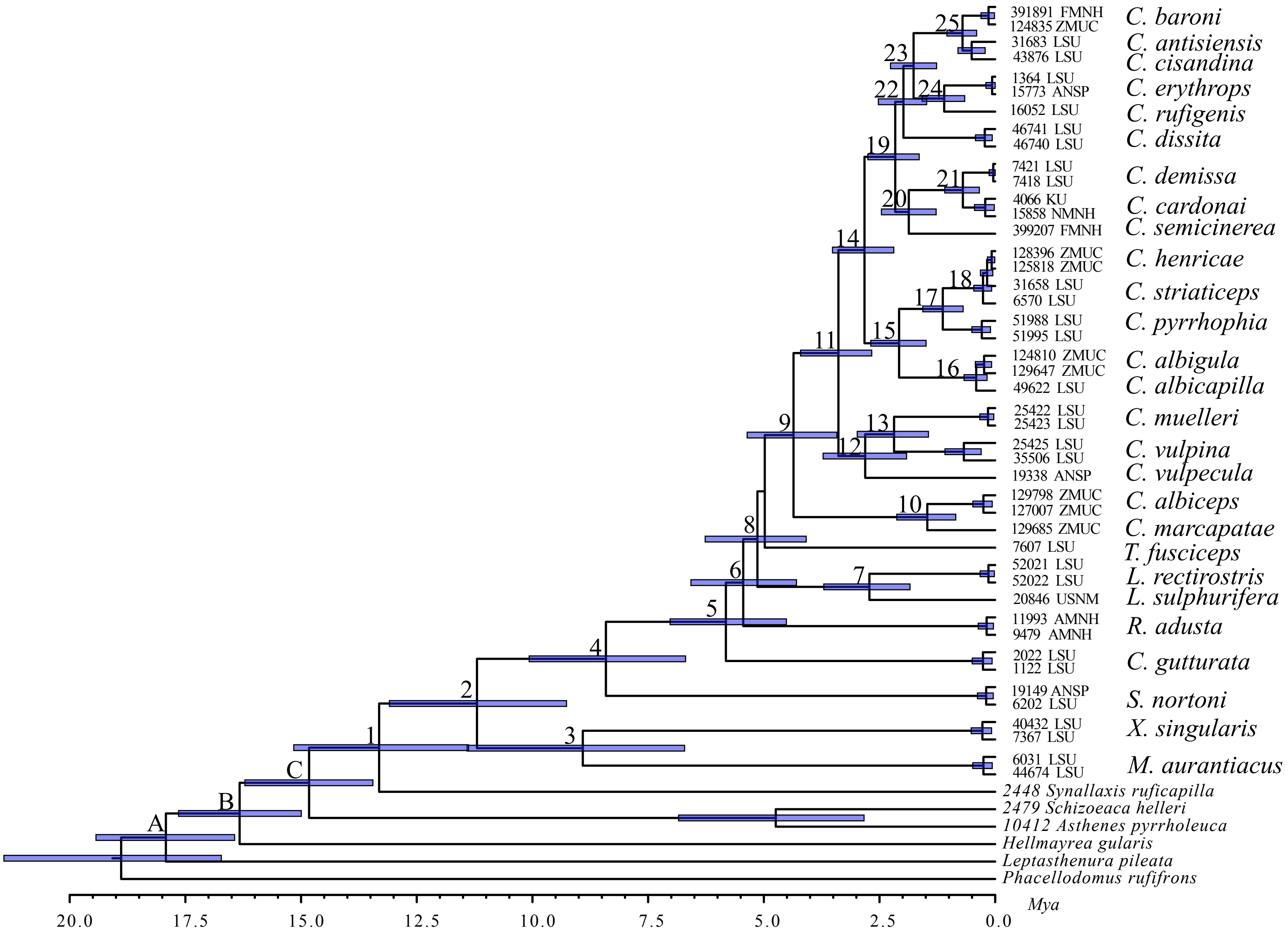
Figure 2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C
B
A
391891 FMNH
124835 ZMUC
C. baroni
31683 LSU
C. antisiensis
43876 LSU
C. cisandina
1364 LSU
15773 ANSP
C. erythrops
16052 LSU
C. rufigenis
46741 LSU
46740 LSU
C. dissita
7421 LSU
7418 LSU
C. demissa
4066 KU
15858 NMNH
C. cardonai
399207 FMNH
C. semicinerea
128396 ZMUC
125818 ZMUC
C. henricae
31658 LSU
6570 LSU
C. striaticeps
51988 LSU
51995 LSU
C. pyrrhophia
124810 ZMUC
129647 ZMUC
C. albigula
49622 LSU
C. albicapilla
25422 LSU
25423 LSU
C. muelleri
25425 LSU
35506 LSU
C. vulpina
19338 ANSP
C. vulpecula
129798 ZMUC
127007 ZMUC
C. albiceps
129685 ZMUC
C. marcapatae
7607 LSU
T. fusciceps
52021 LSU
52022 LSU
L. rectirostris
20846 USNM
L. sulphurifera
11993 AMNH
9479 AMNH
R. adusta
2022 LSU
1122 LSU
C. gutturata
19149 ANSP
6202 LSU
S. nortoni
40432 LSU
7367 LSU
X. singularis
6031 LSU
44674 LSU
M. aurantiacus
2448 Synallaxis ruficapilla
2479 Schizoeaca helleri
10412 Asthenes pyrrholeuca
Hellmayrea gularis
Leptasthenura pileata
Phacellodomus rufifrons
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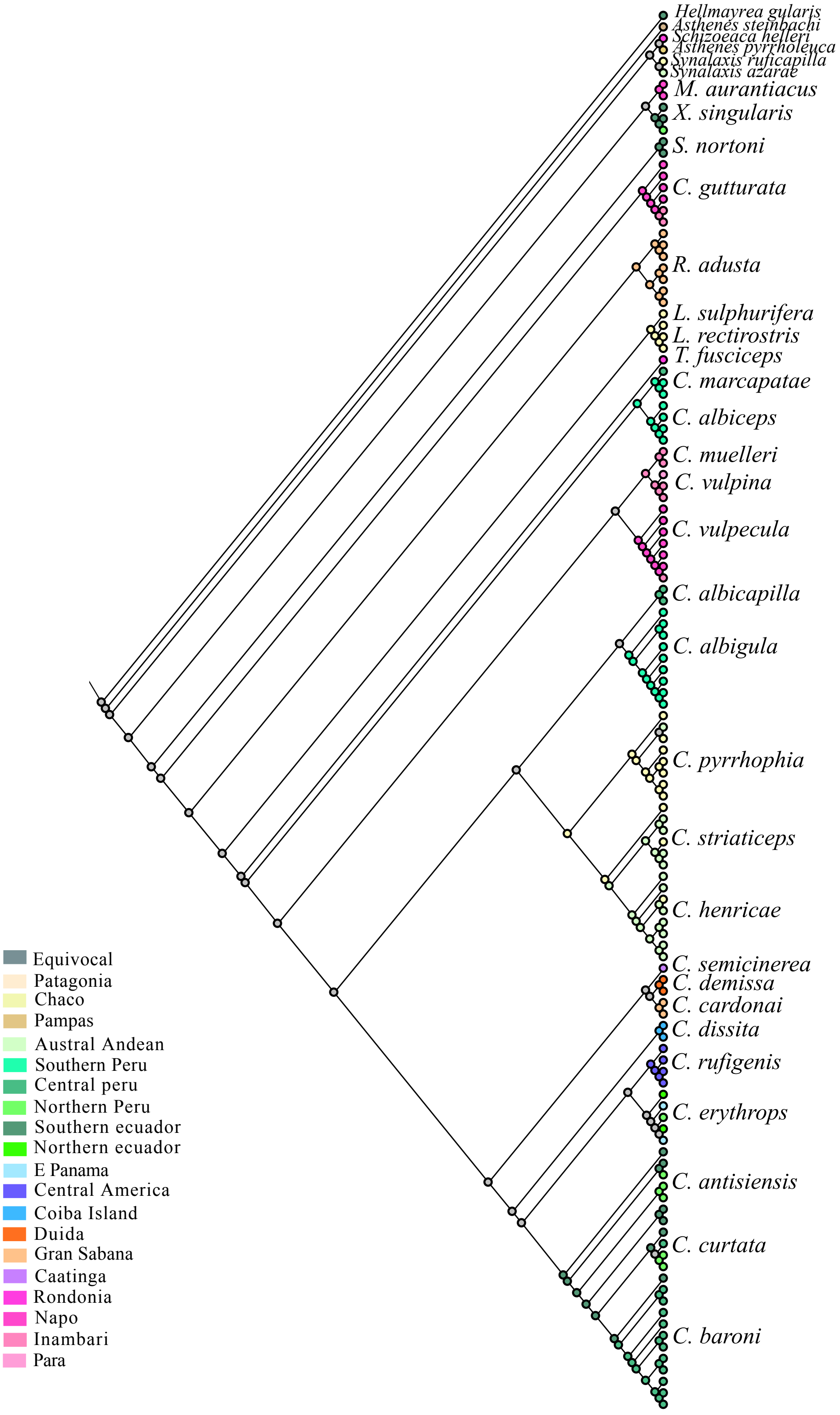
Figure 3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S. nortoni
C. gutturata
R. adusta
L. sulphurifera
L. rectirostris
T. fusciceps
C. marcapatae
C. albiceps
C. muelleri
C. vulpina
C. vulpecula
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C. albigula
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C. striaticeps
C. henricae
C. semicinerea
C. demissa
C. cardonai
C. dissita
C. rufigenis
C. erythrops
C. antisiensis
C. curtata
C. baroni
Equivocal
Patagonia
Chaco
Pampas
Austral Andean
Southern Peru
Central peru
Northern Peru
Southern ecuador
Northern ecuador
E Panama
Central America
Coiba Island
Duida
Gran Sabana
Caatinga
Rondonia
Napo
Inambari
Para

Figure 4

Table 1. List of taxa included in this study

Voucher no.	**Species**	**Habitat**	**Area of endemism**	**Country**	**Locality**
19117 ANSP	*X. singularis*	Lower montane/subandean forest	Southern Ecuador	Ecuador	Zamora Chinchipé, Panguri; ca. 12 km NE San Francisco del Vergel
6031 LSU	*X. singularis*	Lower montane/subandean forest	Southern Ecuador	Ecuador	Morona Santiago, W Slope Cordillera del Cutucú,
44674 LSU	*X. singularis*	Lower montane/subandean forest	Northern Peru	Peru	San Martín, Ca 24 KM ENE Florida
40432 LSU	*M. aurantiacus*	Tropical lowland forest	Napo	Peru	Loreto, Amazonas, I Resaro, 78 km NE Iquitos, 80 m
7367 LSU	*M. aurantiacus*	Tropical lowland forest	Napo	Peru	Loreto, ca 86 km SE Juanjui on E bank upper Rio Pauya
19149 ANSP	*S. nortoni*	Lower montane/subandean forest	Southern Ecuador	Ecuador	Zamora Chinchipé, Panguri; ca. 12 km NE San Francisco del Vergel
6202 LSU	*S. nortoni*	Lower montane/subandean forest	Southern Ecuador	Ecuador	Morona Santiago, W Slope Cordillera del Cutucú, S trail from Logroño
17662 ANSP	*C. gutturata*	Tropical lowland forest	Napo	Ecuador	Morona Santiago
1122 LSU	*C. gutturata*	Tropical lowland forest	Inambari	Bolivia	La Paz, Rio Beni, ca 20 Km by river N Puerto Linares
1150 LSU	*C. gutturata*	Tropical lowland forest	Inambari	Bolivia	La Paz, Rio Beni, ca 20 Km by river N Puerto Linares
42859 LSU	*C. gutturata*	Tropical lowland forest	Napo	Peru	Loreto, ca 54 Km NNW mouth of Rio Morona, on east bank

4819 LSU	*C. gutturata*	Tropical lowland forest	Napo	Peru	Loreto, S Rio Amazonas, ca 10 Km SSW mouth Rio Napo on E Bank
2022 LSU	*C. gutturata*	Tropical lowland forest	Napo	Peru	Pasco, Km 41 on Villa Rica, Puerto Bermudez highway
12009 AMNH	*R. adusta*	Montane forest	Gran Sabana	Venezuela	Bolivar
11993 AMNH	*R. adusta*	Montane forest	Gran Sabana	Venezuela	Bolivar
12044 AMNH	*R. adusta*	Montane forest	Gran Sabana	Venezuela	Bolivar
9471 AMNH	*R. adusta*	Montane forest	Gran Sabana	Venezuela	Bolivar, Auyan Tepui
12034 AMNH	*R. adusta*	Montane forest	Gran Sabana	Venezuela	Bolivar
12040 AMNH	*R. adusta*	Montane forest	Gran Sabana	Venezuela	Bolivar
9479 AMNH	*R. adusta*	Montane forest	Gran Sabana	Venezuela	Bolivar
52023 LSU	*L. rectirostris*	Fresh water marshses	Pampas	Uruguay	Cerro Largo, Sierra de los Rios, Arroyo Sarandi, Paso Montaraz
52022 LSU	*L. rectirostris*	Fresh water marshses	Pampas	Uruguay	Rivera, Estancia Trinidad, COFUSA
52021 LSU	*L. rectirostris*	Fresh water marshses	Pampas	Uruguay	Rocha, Arroyo sauce del Peñon
B20846 NMNH	*L. sulphurifera*	Fresh water marshses	Pampas	Uruguay	Rocha
7607 LSU	*T. fusciceps*	Tropical lowland forest	Rondonia	Bolivia	Beni, Cercado 6 km by rd SE Trinidad
390678 FMNH	*C. weskei*	Andean/upper montane forest	Central Peru	Peru	Junin, Cordillera Vilcabamba, headwaters Rio Pomureni
129685	*C. marcapatae*	Andean/upper montane	Southern	Peru	Puno, 5 km from Soqapata, Carabaya

ZMUC		forest	Peru		
129687 ZMUC	*C. marcapatae*	Andean/upper montane forest	Southern Peru	Peru	Puno, 5 km from Soqapata, Carabaya
1231 LSU	*C. albiceps*	Andean/upper montane forest	Southern Peru	Bolivia	La Paz, Ca 1 km S Chuspipata
127007 ZMUC	*C. discolor*	Andean/upper montane forest	Southern Peru	Bolivia	Cochabamba, Pujyani, Cocapata 3860 m
129798 ZMUC	*C. discolor*	Andean/upper montane forest	Southern Peru	Bolivia	Cochabamba, Sivingani, Ayopaya Range
126973 ZMUC	*C. discolor*	Andean/upper montane forest	Southern Peru	Bolivia	Cochabamba, Coca-pata 4050 m
25422 LSU	*C. muelleri*	Tropical lowland forest	Inambari	Brazil	Amazonas, Rio Solimoes, Ilha Marchantaria, ca 15 km S Manaus
25423 LSU	*C. muelleri*	Tropical lowland forest	Inambari	Brazil	Amazonas, Rio Solimoes, Ilha Marchantaria, ca 15 km S Manaus
25425 LSU	*C. vulpina*	Tropical lowland forest	Inambari	Brazil	Amazonas, Rio Solimoes, Ilha Marchantaria, ca 15 km S Manaus
25426 LSU	*C. vulpina*	Tropical lowland forest	Inambari	Brazil	Amazonas, Rio Solimoes, Ilha Marchantaria, ca 15 km S Manaus
35506 LSU	*C. vulpina*	Tropical lowland forest	Para	Brazil	Mato Grosso: Island do Ludovico on rio Teles Pires, 32 Km NE
19338 ANSP	*C.vulpecula*	Tropical lowland forest	Napo	Ecuador	Napo, Río Napo/Aguarico 150 m
19346 ANSP	*C.vulpecula*	Tropical lowland forest	Napo	Ecuador	Napo, Río Napo/Aguarico 150 m
25424 LSU	*C.vulpecula*	Tropical lowland forest	Inambari	Brazil	Amazonas, Rio Solimoes, Ilha Marchantaria, ca 15 km S Manaus
3181 LSU	*C.vulpecula*	Tropical lowland forest	Napo	Peru	Loreto, Isla Ronsoco, Rio Napo opposite Libertad, 80 km N Iquitos
43020	*C.vulpecula*	Tropical lowland forest	Napo	Peru	Loreto, River island in Rio Marañon at mouth

LSU					of rio Morona
125748 ZMUC	*C. vulpecula*	Tropical lowland forest	Napo	Ecuador	Napo, Río Napo/Aguarico 150 m
7372 LSU	*C.vulpecula*	Tropical lowland forest	Napo	Peru	Loreto, Amazonas, I Pasto, 80 km NE Iquitos, 80 m
399207 FMNH	*C. semicinerea*	Tropical forest/woodlands	Caatinga	Brazil	Pernambuco, Taquaritinga
B15858 NMNH	*C. cardonai*	Montane forest	Gran Sabana	Guyana	Mount Roraima
4066 KU	*C. cardonai*	Montane forest	Gran Sabana	Guyana	N slope of Mount Roraima
7418 LSU	*C. demissa*	Montane forest	Duida	Venezuela	Amazonas, Cerro de la Neblina Camp VII, 1800 m
7421 LSU	*C. demissa*	Montane forest	Duida	Venezuela	Amazonas, Cerro de la Neblina Camp VII, 1800 m
46740 LSU	*C. dissita*	Tropical lowland forest	Coiba Island	Panama	Veraguas, Isla Coiba, Playa Hermosa, old airstrip
46741 LSU	*C. dissita*	Tropical lowland forest	Coiba Island	Panama	Veraguas, Isla Coiba, Playa Hermosa, old airstrip
26465 LSU	*C. rufigenis*	Lower montane/subandean forest	Central America	Panama	Chiriquí, Dist Gualaca, Cordillera Central
28182 LSU	*C. rufigenis*	Lower montane/subandean forest	Central America	Panama	Chiriquí, Dist Gualaca, Cordillera Central
16052 LSU	*C. rufigenis*	Lower montane/subandean forest	Central America	Costa Rica	Heredia, Finca La Fortuna, 4 km SE Virgen del Socorro
1364 LSU	*C. griseigularis*	Lower montane/subandean forest	Eastern Panama	Panama	Darién, Ca. 9 Km NW Cana, on slopes of Cerro Pirre

2144 LSU	*C. griseigularis*	Lower montane/subandean forest	Eastern Panama	Panama	Darién, About 6 km NW Cana
15773 ANSP	*C. erythrops*	Lower montane/subandean forest	Northern Ecuador	Ecuador	Carchi
18492 ANSP	*C. erythrops*	Lower montane/subandean forest	Northern Ecuador	Ecuador	Manabi
136850 ZMUC	*C. erythrops*	Lower montane/subandean forest	Northern Ecuador	Ecuador	Pichincha, Tandayapa, 1600 m
18961 ANSP	*C. antisiensis*	Lower montane/subandean forest	Southern Ecuador	Ecuador	Loja
16757 ANSP	*C. antisiensis*	Lower montane/subandean forest	Southern Ecuador	Ecuador	Loja
31683 LSU	*C. palamblae*	Lower montane/subandean forest	Northern Peru	Peru	Cajamarca, El Espino
31684 LSU	*C. palamblae*	Lower montane/subandean forest	Northern Peru	Peru	Cajamarca, El Espino
437 LSU	*C. palamblae*	Lower montane/subandean forest	Northern Peru	Peru	Piura, Cruz Blanca, 33rd km SW Huancabamba
126067 ZMUC	*C. palamblae*	Lower montane/subandean forest	Southern Ecuador	Ecuador	Azuay, St. Isabel to Girón, 1750 m

20211 ANSP	*C. cisandina*	Lower montane/subandean forest	Northern Ecuador	Ecuador	Sucumbios, Cascada de San Rafael
6032 LSU	*C. cisandina*	Lower montane/subandean forest	Southern Ecuador	Ecuador	Morona Santiago, West slope of Cordillera del Cutucu
8175 LSU	*C. cisandina*	Lower montane/subandean forest	Central Peru	Peru	Pasco, Cushi
43852 LSU	*C. cisandina*	Lower montane/subandean forest	Northern Peru	Peru	San Martín, Ca 24 KM ENE Florida
43876 LSU	*C. cisandina*	Lower montane/subandean forest	Northern Peru	Peru	San Martín, Ca 24 KM ENE Florida
19793 ANSP	*C. cisandina*	Lower montane/subandean forest	Southern Ecuador	Ecuador	Zamora Chinchipé, Cord. del Condor; above Chinapinza
124821 ZMUC	*C. baroni*	Andean/upper montane forest (dry)	Central Peru	Peru	Pasco, upper Huallaga, Pariamarca
139654 ZMUC	*C. baroni*	Andean/upper montane forest (dry)	Central Peru	Peru	Ancash,Cordillera Blanca, Gague, Huaraz
124835 ZMUC	*C. baroni*	Andean/upper montane forest (dry)	Central Peru	Peru	Ancash,Cordillera Blanca, Quebrada Pucavado
391889 FMNH	*C. baroni*	Andean/upper montane forest (dry)	Central Peru	Peru	Ancash, Yungay Morococha
391888 FMNH	*C. baroni*	Andean/upper montane forest (dry)	Central Peru	Peru	Ancash, Yungay Morococha
124837 ZMUC	*C. baroni*	Andean/upper montane forest (dry)	Central Peru	Peru	Ancash,Cordillera Blanca, Rurichinchay

124836 ZMUC	*C. baroni*	Andean/upper montane forest (dry)	Central Peru	Peru	Ancash,Cordillera Blanca, Quebrada Pucavado
391884 FMNH *	*C. antisiensis* (zaratensis)	Andean/upper montane forest (dry)	Central Peru	Peru	Oyon, Lima
391887 FMNH *	*C. antisiensis* (zaratensis)	Andean/upper montane forest (dry)	Central Peru	Peru	Oyon, Lima
391891 FMNH	*C. zaratensis*	Andean/upper montane forest (dry)	Central Peru	Peru	Oyon, Lima
3597 LSU *	*C. antisiensis* (capitalis)	Andean/upper montane forest (dry)	Central Peru	Peru	Huanuco, Quebrada Huaunash, 4 km by road NW Nuevas Flores
49622 LSU	*C. albicapilla*	Andean/subparamo (dry)	Central Peru	Peru	Junin, Lampa, ca 39 KM ENE Huancayo
49643 LSU	*C. albicapilla*	Andean/subparamo (dry)	Central Peru	Peru	Junin, Lampa, ca 39 KM ENE Huancayo
129647 ZMUC	*C. albigula*	Andean/subparamo (dry)	Southern Peru	Peru	Cusco, Quelcamachay, Santa Teresa, La Convención
391882 FMNH	*C. albigula*	Andean/subparamo (dry)	Southern Peru	Peru	Urubamba, Cuzco, Peru
124797 ZMUC	*C. albigula*	Andean/subparamo (dry)	Southern Peru	Peru	Apurimac, Abancay, 3200 m
124802 ZMUC	*C. albigula*	Andean/subparamo (dry)	Southern Peru	Peru	Apurimac, 7 Km S Cotaruse
124799 ZMUC	*C. albigula*	Andean/subparamo (dry)	Southern Peru	Peru	Apurimac, Abancay, 3200 m
124810 ZMUC	*C. albigula*	Andean/subparamo (dry)	Southern Peru	Peru	Cusco, Chainapuerto
125553 ZMUC	*C. albigula*	Andean/subparamo (dry)	Southern Peru	Peru	Cusco, Calca, 4150 m
129669 ZMUC	*C. albigula*	Andean/subparamo (dry)	Southern Peru	Peru	Cusco, Mantanay Urubamba

40864 LSU	*C. albigula*	Andean/subparamo (dry)	Southern Peru	Peru	Cusco, Mantanay ca 11 K NW Urubamba
124838 ZMUC	*C. striaticeps*	Andean/upper montane forest (dry)	Austral Andean	Bolivia	Cochabamba, 10 Km SW Aiquile
126243 ZMUC	*C. striaticeps*	Andean/upper montane forest (dry)	Austral Andean	Bolivia	Chuquisaca, Palmarcito
18683 LSU	*C. striaticeps*	Andean/upper montane forest (dry)	Austral Andean	Bolivia	Santa Cruz, Cordillera, Estancia Pereforación, ca 130 km E Charagua
31658 LSU	*C. striaticeps*	Andean/upper montane forest (dry)	Austral Andean	Bolivia	Santa Cruz, El Tambo, 14 km SE Comarapa
6570 LSU	*C. striaticeps*	Andean/upper montane forest (dry)	Austral Andean	Bolivia	Santa Cruz, 2.5 km N Tambo
126275 ZMUC	*C. striaticeps*	Andean/upper montane forest (dry)	Austral Andean	Bolivia	Potosí, Parinolqui Pampa
126990 ZMUC *	*C. albicapila (striaticeps)*	Andean/upper montane forest (dry)	Austral Andean	Bolivia	Cochabamba, Cassay Vinto Coca-pata. 4050 m
B05938 NMNH	*C. pyrrhophia*	Semi-humid to arid Chaco	Chaco center	Argentina	Corrientes, Argentina
25814 LSU	*C. pyrrhophia*	Semi-humid to arid Chaco	Chaco center	Paraguay	Alto Paraguay, Madrejón
51988 LSU	*C. pyrrhophia*	Semi-humid to arid Chaco	Pampas	Uruguay	Cerro Largo, Rio negro, Paso Mazangano
52000 LSU	*C. pyrrhophia*	Semi-humid to arid Chaco	Pampas	Uruguay	Colonia, Conchillas, Estancia el Topadro
51990 LSU	*C. pyrrhophia*	Semi-humid to arid Chaco	Pampas	Uruguay	Rio Negro, Isla de Lobos
51992 LSU	*C. pyrrhophia*	Semi-humid to arid Chaco	Pampas	Uruguay	Rivera, Rio negro, Paso Mazangano
51991 LSU	*C. pyrrhophia*	Semi-humid to arid Chaco	Pampas	Uruguay	Alto Paraguay, Madrejón

51995 LSU	*C. pyrrhophia*	Semi-humid to arid Chaco	Pampas	Uruguay	Durazno, Estancia San José
52005 LSU	*C. pyrrhophia*	Semi-humid to arid Chaco	Pampas	Uruguay	Rio Negro, Isla de Lobos
125817 ZMUC	*C. henricae*	Andean/upper montane forest (dry)	Southern Peru	Bolivia	La Paz, Inquisiví, 2350 m
128396 ZMUC	*C. henricae*	Andean/upper montane forest (dry)	Southern Peru	Bolivia	La Paz/ Cochabamba
125818 ZMUC	*C. henricae*	Andean/upper montane forest (dry)	Southern Peru	Bolivia	La Paz, Inquisiví, 2350 m
22647 LSU *	*C. debilis*	Lower montane/subandean forest	Southern Peru	Bolivia	La Paz, Prov. B. Saavedra, 83 km by road E Charzani, Cerro Asunta
22894 LSU *	*C. debilis*	Lower montane/subandean forest	Southern Peru	Bolivia	La Paz, La Paz, Prov. B. Saavedra, 83 km by road E Charzani
3846 KU	*C. obsoleta*	Tropical woodlands	Chaco center	Paraguay	San Rafael National Park, Parabel
10390 AMNH	*Asthenes steinbachi*	Lower montane/subandean forest (dry)	Patagonia	Argentina	Neuquen
10412 AMNH	*Asthenes pyrrholeuca*	Lower montane/subandean forest (dry)	Patagonia	Argentina	Neuquen, Departamento Anelo
2479 AMNH	*Schizoeaca helleri*	*Paramo* and elfin forest	Rondonia	Bolivia	Franz Tamayo, Tojoloque, near Queara
2448 AMNH	*Synallaxis ruficapilla*	Tropical lowland forest	Chaco center	Argentina	Misiones, San Ignacio
2771 AMNH	*Synalaxis azarae*	Lower montane/subandean	Austral Andean	Bolivia	Bautista Saavedra

		forest		
18799 AMNH	*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; LSU: 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[1]	Mean[2]	95% CI[3]	Upper-bound[4]
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

1 Mean divergence dates obtained using the lower-bound CI reported by Irestedt et al., 2009 as a prior.

2 Mean divergence dates obtained using the mean reported by Irestedt et al., 2009 as a prior.

3 95% CI for the divergence dates using the reported mean as a prior.

4 Mean divergence dates obtained using the upper-bound CI rerported by Irestedt et al., 2009 as a prior.

Table 3. Diagnosably distinct units within the Tripophagini tribe and their distribution

Genus Metopotrhix	
Metopothrix aurantiacus	SE Colombia, E Ecuador, E Peru, N Bolivia, Beni, and W Amazon in Brazil
Genus *Xenerpestes*	
Xenerpestes singularis	E slope of Andes in Ecuador and N Peru.
X. minlosi	Caribbean lowlands of Colombia in NW Santander and W Boyaca
X. umbraticus	E Panama in Darien, W Colombia, and NW Ecuador
Genus *Siptornis*	
Siptornis striaticollis	E Andes of Colombia, in Cundinamarca, and Rio Magdalena valley.
S. nortoni	E Ecuador and extreme north Peru, north of Cajamarca.
Genus *Roraima*	
Roraima adusta	Tepuis of SE Venezuela, N Brazil, W Guyana.
R. obscurodorsalis	Cerro Paraque in SE Venezuela.
R. duidae	Mt Duida, Cerro Huachamacari and Serrania Paru.
(New Genus)	
Cranioleuca gutturata	widely distributed in the Amazon basin; absent from upper Rio Negro drainage.
Genus *Limnoctites*	
Limnoctites rectirostris	Extreme SE Brazil, Uruguay, and extreme E Argentina.
L. sulphuriphera	E Argentina, extreme S Brazil, and Uruguay.

Genus *Thripophaga*

Thripophaga fusciceps	N Bolivia, in Beni, La Paz, and Cochabamba.
T. dimorpha	SE Peru and E Ecuador.
T. obidensis	Lower Amazonia of Brazil
T. cherrei	Known from only one site in S. Venezuela.
T. macroura	SE Brazil, S of Bahia through Minas Gerais and Espirito Santo to N Rio de Janeiro.

Genus *Cranioleuca*

Cranioleuca marcapatae	Cusco, Peru.
C. weskei	Cordillera Vilcabamba, Peru.
C. obsoleta	SE Brazil and NE Argentina.
C. albiceps	La Paz, Bolivia, and Puno, Peru.
C. discolor	Cochabamba and Santa Cruz, Bolivia.
C. vulpina	Goiaz, Mato Grosso, and Amazonas, Brazil.
C. reiseri	NE Brazil, in Piaui, Pernambuco and Bahia.
C. vulpecula	NE Peru, W Brazil, and NE Bolivia, on the lower Rio Beni.
C. muelleri	N Brazil, on the north bank of the lower Amazon.
C. curtata	E Andes of Colombia, form SE Santander S to Huila.
C. cisandina	W Caqueta, E Ecuador and N Peru at least to Pasco.
C. debilis	C Peru, S from Ayacucho to C Bolivia to W Santa Cruz.
C. hellmayri	Santa Marta Mountains, Colombia.
C. baroni	Andes of N and C Peru.
C. capitalis	Andes of C Peru, in E Huanaco and Pasco.

C. zaratensis	Andes of WC Peru, in Lima.
C. antisiensis	Andes of SW Ecuador, at N Azuay, El Oro, and Loja.
C. palamblae	Andes of N Peru, from Piura to N Lambayeque.
C. erythrops	Subtropical zone of the Andes of W Ecuador.
C. rufigenis	Mountains of Costa Rica and W Panama.
C. griseigularis	Extreme E Panama and W and C cordilleras of Colombia.
C. dissita	Coiba Island, Panama.
C. demissa	Tepuis of Gran Sabana in Venezuela, Guyana and Brazil.
C. cardonai	Tepui region of S Venezuela in Duida.
C. semicinerea	NE and SC Brazil, south to Bahia and extreme N. of Minas Gerais.
C. albicapilla	Temperate zones of C Peru.
C. albigula	Cusco and Apurimac, Peru.
C. pyrrhophia	S Bolivia, W Paraguay and Argentina south to the Rio Negro; Uruguay.
C. striaticeps	C Cochabamba, W Santa Cruz, Bolivia..
C. rufipennis	La Paz (Tilotilo) and NW Cochabamba, Bolivia.
C. henricae	Rio Cotacajes drainage in La Paz, and Cochabamba, Bolivia

Supplementary 1.

Description and distribution of each basal taxonomic unit within Thripophagini

Genus Metopotrhix

Metopothrix aurantiacus: Small warbler- like; Gray-olive upperparts; bright orange forehead; bright yellow foreface and throat; bright orange legs; wing coverts with yellow edges; pale yellow underparts. From SE Colombia, north to Putumayo, E Ecuador, mainly in Napo, E Peru, south to Madre de Dios, N Bolivia, Beni, and W Amazon in Brazil, east to middle Rio Purus.

Genus *Xenerpestes*

Xenerpestes singularis: Olive-gray upperparts; rufous forehead; white superciliary band; creamy underparts with gray streaking. Locally along E base of Andes in Ecuador, north to Napo, and N Peru, near Carmen in N Cajamarca and NW of Rioja in N San Martin.

X. minlosi: Not included in phylogenetic analysis. Warbler-like furnarid. Gray face; creamy superciliary band; olive-buff lores; dark gray line behind eye; blackish crown; dark gray wing-coverts with two white wingbars; bend of wing yellow; dark fuscous remiges; slightly rounded dark gray tail; underparts creamy white, with some grayish flecking on breast. Caribbean lowlands of Colombia E to middle Magdalena Valley, in NW Santander and W Boyaca.

X. umbraticus: Not included in phylogenetic analysis. Darker underparts, wings and tail than *X. minlosi*. E Panama in Darien, W Colombia, and NW Ecuador, in Esmeraldas, NW Pichincha.

Genus *Siptornis*

Siptornis striaticollis: Distinct warber-like bill; rufous-brown upperparts; chestnut crown; dark lores; white postocular stripe and incomplete eye-ring; rufous chestnut wing coverts and tail; brownish gray underparts; throat and chest streaked with white. West slope of E Andes of Colombia, in Cundinamarca, and around head of Rio Magdalena valley.

S. nortoni: Throat and chest more conspicuously streaked than in *S. striaticollis*. E Ecuador and extreme north Peru, north of Cajamarca.

New Genus

(Cranioleuca) gutturata: Dark olive-brown upperparts; rufous-chestnut crown; buff superciliary band; Ochre-yellow chin; underparts buff, specked with blackish on breast, with darker speckles on belly. S Venezuela, in the S of Bolivar and Amazonas, SE Colombia, E Ecuador, E Peru, N Bolivia, south to La Paz and Cochabamba, French Guiana, Surinam and Amazonia of Brazil, south of Rondonia, and east to the lower Rio Tocantins; absent from upper Rio Negro drainage.

Genus ***Roraima***

Roraima adusta: Chestnut upperparts, with sides of neck and nape brighter, extending to form a superciliary band; black-brown crown and auriculars; white throat; rest of underparts streaked with buff and dark brown. Tepuis of SE Venezuela, in Mt Roraima and associated Tepuis in SE Bolivar, N Brazil, in Mt Roraima, and W Guyana in Mt Tewk-quay.

R. obscurodorsalis: Not included in the phylogenetic analysis. Cerro Paraque in SE Venezuela. Overall darker than R. *adusta*. Cerro Paraque in SE Venezuela.

R. duidae: Not included in the phylogenetic analysis. Brighter upperparts than those of R. *adusta*, but with less rufous on nape. Mt Duida, Cerro Huachamacari and Serrania Paru.

Genus *Limnoctites*

Limnoctites rectirostris: Brownish-gray upperparts; white superciliary band; rufous wings and tail; protruding bare shafts from graduated tail; whitish underparts, with buffy flanks and undertail coverts. Extreme SE Brazil, in Rio Grande do Sul, Uruguay and extreme E Argentina, in Entre Rios, and northern Buenos Aires.

Limnoctites sulphuriphera: Considered first as part of *Synalaxis* and then of *Cranioleuca*. Olive-brown upperparts; contrasting with rufous greater and median wing-coverts; buffish-white superciliary band, rest of face white with gray steaks; yellow throat patch; whitish underparts, with fine grayish streaks on breast. E Argentina, in SE Cordoba, S Santa Fe, and S Corrientes S to Rio Negro and S Buenos Aires, extreme S Brazil in Rio Grande do Sul, and Uruguay.

Genus *Thripophaga*

Thripophaga fusciceps: Olive-brown upper and underparts; buff superciliary band and frontlet; rufous wings and tail. N Bolivia, in Beni, La Paz, and Cochabamba.

T. dimorpha: Not included in the phylogenetic analysis. Larger than *T. fusciceps*. Disjunctly in SE Peru and E Ecuador and adjacent Peru.

T. obidensis: Not included in the phylogenetic analysis. Darker and browner than *T. fusciceps*. Disjunctly in lower Amazonia of Brazil.

T. cherrei: Olive-brown upperparts; paler underparts; breast and sides of neck with distinct buffy-white streaking; white superciliary band; orange-rufous chin patch; chestnut wings and rufous-chestnut tail. Known from only one site in S Venezuela.

T. macroura: Not included in the phylogenetic analysis. Rufous-brown upperparts; crown and back streaked with buff; buffy-white superciliary band; bright cinnamon tail; orange-rufous chin patch; dull brown underparts streaked with white. Locally in SE Brazil, S of Bahia through Minas Gerais and Espirito Santo to N Rio de Janeiro.

Genus *Cranioleuca*

Cranioleuca marcapatae: Rufous mantle and tail, olive-gray rump; rufous crown outlined by black, white narrow superciliary band; sides of head and nape grayish; white throat; underparts buffy gray. Cusco, Peru.

C. weskei: Cordillera Vilcabamba, Peru. Similar to C. *marcapatae* but with white crown.

C. obsoleta: Olive-brown upperparts; white superciliary band; rufous wing-coverts and tail; buffy-olive underparts, palest on throat. Cordillera Vilcabamba, Peru.

C. albiceps: Rufous mantle and tail; white or buff crown, outlined by black; dark-gray superciliary band and sides of head; olive-brown nape and rump; white chin, and dull olive-brown underparts. La Paz, Bolivia, and Puno, Peru.

C. discolor: Similar to *C. albiceps* but with intense buff crown. Cochabamba and Santa Cruz, Bolivia.

C. vulpecula: reddish-rufous crown and upperparts; dull buff supercilium; brown lores and superciliary band; white throat; breast streaked in white and brown, with darker belly; brown franks and undercoverts. E Ecuador, NE Peru, SW Amazonian Brazil, and NE Bolivia.

C. vulpina: Rufous upperparts; narrow white superciliary band, gray cheeks with paler streaking; buffy-gray underparts, palest on throat with light streaked effect on chest. Goiaz, Mato Grosso, and Amazonas, Brazil.

C. reiseri: Not included in the phylogenetic analysis. Similar to *C. vulpina* but with brighter rufous upperparts, paler and buffier below, no streaked chest. Northeastern Brazil, in the states of Piaui, Pernambuco and Bahia.

C. muelleri: Dark olive-brown upperparts, wings and tail; rufous crown; narrow buff superciliary band; white-buffy underparts; dark olive edged feathers, becoming uniform olivaceous on flanks. northern Brazil, on the north bank of the lower Amazon from the Rio Jamunda to Macapa.

C. curtata: Not included in the phylogenetic analysis. Brown face with pale superciliary band; faint pale streaks on auriculars; forehead brown, dark chestnut crown; brown back and dark gray breast; reddish uppertail coverts; graduated tail; chestnut-red wings, with dark tips on remiges. E Andes of Colombia, form the W Slope of SE Santander S to Huila.

C. cisandina: Overall darker than *C. curtata*. E Andes of S Colombia, S from W Caquetá, E Ecuador and N Peru at least to Pasco.

C. debilis: Not included in the phylogenetic analysis. Similar to *C. cisandina*, with paler crown and back and underparts, and solid chestnut forecrown. Andes from C Peru, S from Ayacucho and Cusco, and S to C Bolivia, S to W Santa Cruz.

C. hellmayri: Not included in the phylogenetic analysis. Similar to *C. cisandina,* but with pale iris, rufous crown streaked with black, whiter superciliary band, and more streaks on sides of head. Santa Marta Mountains, Colombia.

C. baroni: Back gray-brown or olive-gray, paler on rump and upper-tail coverts; dark gray-brown face with conspicuous white superciliary band; red-brown forehead streaked with black, covering white supraloral spots; rufous crown; reddish-brown wings, with dark tips on remiges; white throat and upper breast, brownish-gray lower breast and sides, with buff-whitish streaks, narrower and fainter on belly. Andes of north and central Peru, from Central Cajamarca and S Amazonas, S to la Libertad, Ancash and WC Huanuco.

C. capitalis: Similar to *C. baroni*, but with white shaft spots on sides of neck and breast. Andes of C Peru, in E Huanaco and Pasco.

C. zaratensis: Not included in phylogenetic analysis. Smaller than *C. capitalis*. Andes of WC Peru, in Lima.

C. antisiensis: White superciliary band and dark postocular stripe; buff-brown face buff-brown with few faint streaks; rufous crown; brown back; uppertail coverts with rufous tips; pale grayish underparts. Andes of SW Ecuador, at N Azuay, El Oro, and Loja.

C. palamblae: Not included in phylogenetic analysis. Similar to *C. antisiensis*, with a whiter superciliary band, auriculars with white streaks. Andes of N Peru, from Piura and Cajamarca, S to N Lambayeque.

C. erythrops: Rufous crown and face; olive-brown upperparts; rufous wings; dull olive-brown underparts. Subtropical zone of the Andes of western Ecuador.

C. rufigenis: Similar to *C. erythrops*, with more extensive rufous facial area, and rufous central rectrices. Mountains of Costa Rica and W Panama.

C. griseigularis: Similar to *C. erythrops*, with brighter central rectrices and grayer breast.

C. dissita: Rufous upperparts, narrow white superciliary band, gray cheeks, lightly streaked; reddish underparts. Extreme E Panama in Cerro Pirre, Cerro Tacarcuna, Cerro Mali, and western and central cordilleras of Colombia, from Antioquia to Quindio. From Coiba Island, Panama.

C. demissa: Rufous-chestnut crown, and grayish superciliary band; olive brown upperparts with contrasting rufous-chestnut wings and tail; grayish-white underparts.

C. cardonai: Similar to *C. demissa*, with olivaceous brown underparts. Venezuela, in Tepuis of Sierra Parima in Amazonas, Mt Roraima, and Tepuis of Gran Sabana region, in SE Bolivar; extreme WC Guyana, and extreme N Brazil, in Mt Roraima.

C. semicinerea: Gray head and neck, with faint whitish superciliary band; rufous upperparts and pale-gray underparts. Northeast and south-central Brazil, Ceara and Alagoas south to S Bahia and extreme n. Minas Gerais.

C. albicapilla: Cream-white crown buffier on nape; narrow white postocular stripe; rest of upperparts brownish-olive, with contrasting rufous wing coverts and tail; pale underparts. Temperate zones of central Peru, in departments of Junin, Huancavelica (Anco), and Ayacucho (Valley of Rio Pampas).

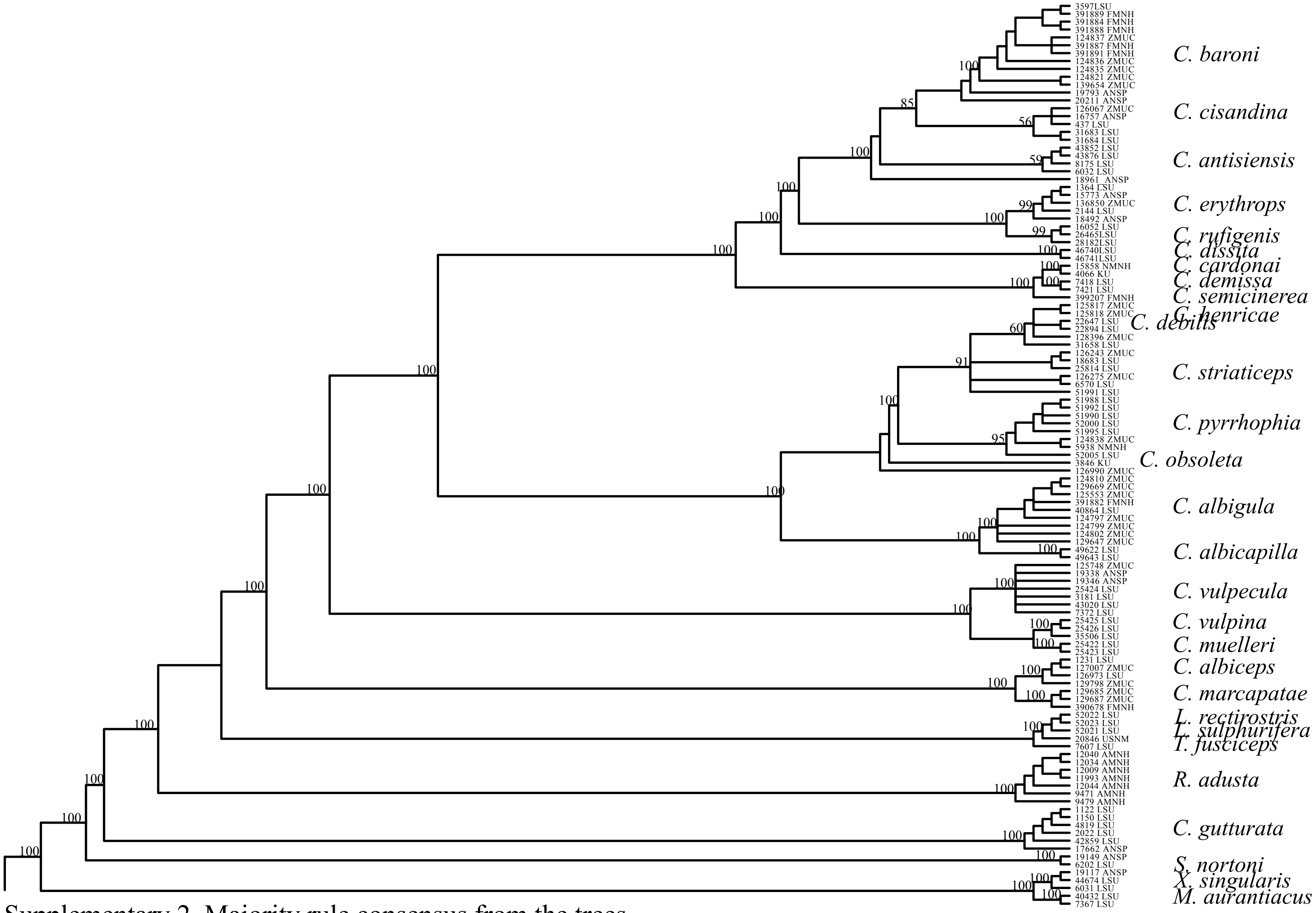
C. albigula: Similar to *C. albicapilla*, with buffier crown and ochre underparts. Cusco and Apurimac, Peru.

C. pyrrhophia: Brownish-gray upperparts with contrasting rufous wing-coverts and tail; crown streaked buff and black, lined by a white superciliary and a black postocular line; otherwise mostly brownish gray above; whitish underparts. Southern Bolivia in departments of Santa Cruz (Guanaco) and Tarija; western Paraguay; the greatest part of Argentina south to the Rio Negro; Uruguay; extreme SE Brazil, in Rio Grande do Sul.

C. striaticeps: Similar to *C. pyrrhophia*, but with browner upperparts, with more streaking on crown. Andes of C and S Bolivia, in C Cochabamba, W Santa Cruz, Chuqisaca, Tarija.

C. rufipenis: Similar to *C. striaticeps* but smaller in size, with narrower streaks on crown; browner upper parts, and rufous outer secondaries. Bolivian Andes in La Paz and NW Cochabamba.

C. henricae: Whitish lores; black patch in front of eye; white superciliary band; dull fuscous postocular band; rest of face grayish-brown with faint buff streaks; forehead blackish with thin rufous streaks, crown rufous, some thin dark streaks extending to anterior crown; back brownish olive, becoming more tawny on rump and more rufescent on uppertail-coverts; wings mostly rufous-chestnut; tail graduated; throat whitish or dingy white; underparts pale grayish-olive, darker on undertail coverts. Rio Cotacajes drainage in La Paz, and Cochabamba, Bolivia.



Supplementary 2. Majority rule consensus from the trees obtained during the MP ratchet search. Bootstrap support is shown above branches.

CHAPTER 5

Understanding the Origin and Diversification of Andean Taxa Through a Select Group of Birds

INTRODUCTION

Many biogeographical studies have sought to explain the origin and diversification of Andean taxa (Chapman, 1917, 1926; Vuilleumier, 1969; Terborgh, 1971; Vuilleumier & Monasterio, 1986; Fjeldså, 1987; Gerwin & Zink, 1989; Arctander & Fjeldså, 1994; Ramsen & Graves, 1995a, 1995b; Garcia-Moreno *et al.*, 1998, 1999a, 1999b; Dingle *et al.*, 2006; Fjeldsa & Rahbek, 2006; Brumfield & Edwards, 2007; Cadena *et al.*, 2007; Ribas *et al.*, 2007; Sedano & Burns, 2009). Most studies have invoked long distance dispersion, range expansion, and ecological factors to explain the diversity found in the Andes. Disjunct distributions between Andean taxa and their sister-groups [e.g: tropical lowlands for *Heliodoxa* hummingbirds (Gerwin & Zink, 1989) and *Leptopogon* flycatchers (Bates and Zink 1994); Central America for the rodent genus *Akodon* (Patton & Smith, 1992) and *Buarremon* brush-finches (Cadena *et al.*, 2007); southern-temperate South America for the high Andean coot species (Fjeldså, 1985); southeastern coasts of South America for some *Thamnophilus* species (Brumfield & Edwards, 2007) and *Ithomiola* butterflies (Hall, 2005)] may suggest that long-distance dispersion is responsible for the origin of these montane groups, although the exact way in which these groups diversified into the Andes is still highly debated. On the other hand, many authors have recognized the influence of the uplift of the Andes and the climatic oscillations of the Plio-Pleistocene on the diversification of Andean biota (Bates & Zink, 1994; Bleiweiss, 1998; Cadena *et al.*, 2007; Chaves *et al.*, 2007; Koscinski *et al.*, 2008; Cossios *et al.*, 2009), yet few have directly linked the origin of Andean taxa to Earth history (Van Der Hammen & Cleef, 1986; Bates & Zink, 1994; Bleiweiss, 1998; Almeida *et al.*, 2007; Ribas *et al.*, 2007; this thesis). Furthermore, some studies have proposed ecological factors to be responsible for structuring current patterns of distribution along the Andes (Terborgh, 1971; Ramsen & Graves, 1995a, 1995b; Brumfield & Edwards, 2007), whereas other studies propose that ecological interactions may be too young to account for current patterns of distribution (Flanagan *et al.*, 2004; De Chaine & Martin, 2006; Cadena, 2007).

Because of the Andes' extensive latitudinal span and complexity, there is no one single cause of origin of diversification that can explain the diversity found in them. This summary of previous work explores different patterns of origin and diversification that have given raise to some of the diversity found throughout this mountain chain. Although there are claims that speciation may be clade-specific (Cracraft, 1988; Bush, 1994; Eberhard & Bermingham, 2005), a comparison of spatio-temporal patterns from different groups—with different evolutionary histories, ecological requirements, and dispersal abilities—may offer an opportunity to find common processes that have contributed to the origin and speciation of Andean taxa. An obvious caveat in such a comparison is the uncertainty related to using divergence dates obtained from multiple studies, as well as to the uncertainty relative to the calibrations used to obtain divergence dates for the groups included in this dissertation. Calibration priors for the parrots *Hapalopsittaca*, the hummingbirds *Doryfera*, *Schistes*, and *Colibri*, and the ovenbirds within the Thripophagini tribe were taken from the results of previous studies. 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), with a normal distribution prior that allows for a conservative bidirectional distribution of the uncertainty during the estimation (Ho & Phillips, 2009). In this summary, the mean ages obtained in BEAST (Drummond & Rambaut, 2007) for these groups will be used throughout the biogeographic discussion (the 95% confidence interval ranges for all nodes are reported in each individual chapter). This mean age represents the highest posterior credibility and thus the set of trees with the highest posterior probability (Drummond & Rambaut, 2007).

ORIGIN OF ANDEAN TAXA

Biogeographic patterns between Central America and the Andes

Chapman (1917) proposed that the majority of Andean species might have been derived from contiguous areas, namely the Guianan highlands, the Central American highlands, and the temperate lowlands of southern South America. *Chlorospingus ophthalmicus, Buarremon bruneinucha, B. torquatus,* and the genera *Myioborus*, *Myadestes*, and *Cyanolyca* are among the Andean taxa having Central American sister- groups and thus may have a Mesoamerican origin. The *Chlorospingus ophthalmicus* complex originated in Central America, as evidenced by the fact that the basal clade of the complex is distributed in Mexico, whereas the sister group to the clade is endemic to Central America, and later dispersed to the Andes, around 4.7 Mya (Weir *et al.*, 2008). The sister group to the genus *Myioborus*, as well as the most basal species, *M. pictus*, are distributed in Northern and Central America (Perez-Eman, 2005). Within *Myioborus miniatus*, the Central America gene lineages are separated by very short internodes, which suggests that these populations expanded rapidly across the region, a pattern also found in *Buarremon bruneinucha*, another taxon with a northern origin that expanded its range southward to colonize the Andes (Cadena *et al.*, 2007). Moreover, genetic distances in both *Myoborus miniatus* and *B. bruneinucha* suggest that these two groups colonized South America almost simultaneously after the final closure of the Isthmus of Panama (Perez-Eman, 2005; Cadena *et al.*, 2007). The genus *Myadestes* is another example of a taxon with a Central American origin that diversified into the Andes just after the closing of the Isthmus of Panama (Miller *et al.*, 2007).

Biogeographical patterns from the Andes to South and Central America

Although the genus *Cyanolyca* had a Mesoamerican origin and later in its evolutionary history colonized the Andes, *C. cucullata* reinvaded Mesoamerica, most likely after the final closure of the Isthmus of Panama (Bonaccorso, 2009). Dispersion from the Andes to Central America, Mesoamerica, and the lowlands of South America is found in other groups with Andean origins. For instance, the origin of the Neotropical genus *Tangara* is reconstructed as being north Andean (Burns & Naoki 2004). From the northern Andes, *Tangara* later diversified into in the Central Andes, the South American lowlands (Amazonia and Atlantic Forest), and the Central American Highlands (Chiriqui-Darien Highlands). In *Aulacorhynchus prasinus*, another group of northern Andean origin, dispersion to Central America is proposed to have taken place after the closing of the Isthmus of Panama (Puebla-Olivares *et al.*, 2008), just as in *Colibri*, *Doryfera*, and

Cranioleuca (this thesis). Within *Doryfera*, the split between *D. ludovicae*, which is distributed from extreme E Panama to Bolivia, and *D. veraguensis* from W Panama to Costa Rica, occurred around 4.5 Mya, whereas the split between the Andean *Colibri cyanotus* from the clade that contains *C. thalassinus-C. cabanidis* from Central and Mesoamerica, took place *ca*. 5.8 Mya. Within *Cranioleuca*, *C. erythrops* from western Ecuador and *C. rufigenis* from western Panama and Costa Rica diverged from each other around 1.1 Mya. Thus, in *Cyanolyca*, *Aulacorhynchus prasinus*, and *Cranioleuca,* dispersion from South America to Central and Mesoamerica occurred after the closure of the Isthmus of Panama, at a time when montane forests were continuous throughout this region (Bonaccorso, 2009). Although the split between South and Central America taxa of *Doryfera* and *Colibri* predated the final closing of the Isthmus, the actual dispersion of these species to Central and Mesoamerica may have taken place after the Isthmus was already in place.

Biogeographic patterns between the lowlands and the Andes

There has been a lack of attention to montane-lowland biogeographical patterns throughout the Andes, even though these patterns provide the basis for asking whether the origin of some Andean groups is related to the uplift of the Andes (Ribas *et al.*, 2007). Following is a discussion of some taxa that exemplify this pattern: the parrot genera *Hapalopsittaca* and *Pionus*, the hummingbirds *Doryfera* and *Colibri*, and some ovenbirds within the tribe Thripophagini.

Origin of Hapalopsittaca

Hapalopsittaca is an exclusively Andean parrot genus with restricted distributions in the temperate humid montane forests (Fjeldsa & Krabbe, 1990), whereas its sister group, *Pyrilia* [*Pyrilia* = *Gypopsitta* (Banks *et al.*, 2008), in Ribas *et al.* (2005)] is distributed in the adjacent lowland forests of South and Central America, east and west of the Andes (Collar, 1999). The genus *Hapalopsittaca* represents a phylogenetic and biogeographic pattern connecting high montane biotas to the lowlands (this thesis). *Hapalopsittaca* + *Pyrilia* belong to the "amazons and allies" clade (Tavares *et al.*, 2006), and their sister group (*Triclaria, Pionopsitta, Pionus, Amazona, Alipiospsitta* and *Graydidascalus*) contains mainly lowland species, with the exception of *Pionus*, which has lowland and highland groups. These distributions lead to the inference that the ancestral character-state of the branch leading to *Pyrilia* +*Hapalopsittaca* was lowland. Moreover, the montane *Hapalopsittaca* is allopatric relative to the lowland *Pyrilia*, and the time of this split (~12.1-12.9 Mya, Fig 1) is consistent with the hypothesis of vicariance by Andean uplift as a cause of this highland/lowland disjunction. The ancestor of *Hapalopsittaca* was likely distributed along the Andean cordilleras when its elevation was similar to that of some of the extant species of *Pyrilia*. That ancestor was then uplifted to higher altitudes as the result of final uplift of this mountain range (this thesis). This hypothesis is consistent with the fact that by *ca.* 14 Mya the eastern cordillera of Bolivia was about 30% of its modern elevation (Gregory-Wodzicki, 2000; Garzione *et al.*, 2008), whereas to the north, the Cordillera Oriental of Colombia had not exceeded more than 40% of its current altitude by 5 Mya (Gregory-Wodzicky, 2000; Graham, 2009).

Origin of Doryfera, *Schistes,* and *Colibri*

McGuire *et al.* (2007) found high likelihood support (0.999) for a lowland ancestral character-state for the common ancestor of the three most basal clades of hummingbirds (topazes, hermits, and mangoes). Thus, I explored what events could account for diversification into the Andes of the clade that contains the genera *Doryfera, Schistes,* and *Colibri* (McGuire *et al.*, 2007; McGuire *et al.*, 2009).

The split between *Doryfera* and the clade that contains *Schistes* and *Colibri* took place around ~20 Mya (Fig 2), whereas that between *Colibri* and *Schistes* around ~17.9 Mya (Fig 2). The timing of these splits is consistent with data from McGuire *et al.* (2007) that suggest that the common ancestor of topazes, hermits, and mangoes had a lowland distribution, as the splits took place when the eastern cordillera of Bolivia (Kennan *et al.*, 1997; Lamb & Hoke, 1997; Gregory-Wodzicki, 2000; Hartley, 2003; Garzione *et al.*, 2008) and the northern Andes (Gregory-Wodzicki, 2000; Graham, 2009) had not attained half of their current altitude.

The split between the two main clades of *Doryfera*—the *johannae* species-group, distributed in the tropical lowlands and the tepuis, and the *ludovicae* species-group, distributed at higher altitudes along the dense, wet subandean forest—took place *ca.* 11.4 Mya (Fig 2). This split constitutes a disjunction between sister-taxa that are allopatrically distributed in lower tropical forests and mid montane wet forests, and it coincides temporally with the beginning of the uplift of the eastern cordillera of Bolivia (Vandervoort *et al.*, 1995; Hartley, 2003). Furthermore, the split between *C. serrirostris* and the remainder of the genus *Colibri* also occurred at around 12 Mya (Fig. 2). Because the highland populations of *C. serrirostris* are distributed along the Andes of Argentina and Bolivia, this split may have also been related to the beginning of the uplift of the eastern cordillera of Bolivia (Vandervoort *et al.*, 1995; Hartley, 2003).

Origin of the tribe Thripophagini

The split between the tribes Synallaxini and Thripophagini took place *ca*. 13.3 Mya (Fig. 3). The phylogeny of the tribe Synallaxini is poorly understood at present, and like the tribe Thripophagini, they have a wide distribution across South America. Thus, it is not possible to accurately reconstruct the ancestral distribution leading to the Synallaxini and Thripophagini. However, because the split between these two groups occurred at a time when the eastern cordillera of the Central Andes was about 30% of its current elevation (Gregory-Wodzicki, 2000; Garzione *et al.*, 2008), and the northern Andes had attained only half of their present elevation by middle to late Miocene (Gregory-Wodzicki, 2000; Graham, 2009), it may be plausible to infer that the common ancestor of Thripophagini was distributed in the lowlands or low montane forests (this thesis).

Divergence between *Metopothrix* of the lowlands of the Napo area of endemism and *Xenerpestes singularis* of the humid montane forest of the eastern slope of the Andes of Ecuador and N Peru took place around 11.2 Mya (Fig. 3). The split between these allopatric groups coincides spatio-temporally with the active uplift of the northern Andes (Hoorn *et al.*, 1995; Hooghiemstra *et al.*, 2006; Graham, 2009). The split between *Siptornis nortoni*—from the E slope of the Andes of N Peru, and the reminder of the clade took place *ca*. 8.4 Mya (Fig. 3). Because of this timing, this speciation event might also be associated with a vicariance event related to the uplift of the Andes, as in the case of the split between *Metopothrix* and *Xenerpestes.*

Within *Cranioleuca*, the divergence between *C. albiceps* + *C. marcapatae* and the remainder of the genus occurred at ~4.3 Mya (Fig. 3). *C. albiceps* is distributed in the upper montane forest of Peru, whereas *C. marcapatae* is found in the upper montane forest and Bolivia. The sister-group to *Cranioleuca* contains *Thripophaga* + *Limnoctites*, both distributed in the lowlands. Thus it is possible that the ancestor of *Cranioleuca* was also distributed in the lowlands, and that the split leading to this genus constitutes another example of lowland-highland vicariance event related to the uplift of the Andes (this thesis).

General biogeographic trends between the lowlands and the Andes

The summary of the biogeographical patterns of *Hapalopsittaca*, *Doryfera*, *Colibri*, and the ovenbirds within the tribe Thripophagini suggests that geological events have directly contributed to the origin of avian taxa in high montane environments through vicariance from lowland sister-groups.

Of the lowland-montane diversification events, those between *Hapalopsittaca* and *Pyrilia* (this thesis), the two main clades of *Doryfera* (this thesis), *C. serrirostris* and the remainder of *Colibri* (this thesis), *Metopothrix* and *Xenerpestes*, and *Siptornis nortoni* and the remainder of the Thripophagini clade (this thesis), are seemingly contemporaneous events. On the other hand, the split that gave rise to *Cranioleuca* occurred much later in time (*ca.* 4.3 Mya) but is contemporary with the first lowland-highland disjunction within the parrot genus *Pionus* (Ribas *et al.*, 2007), whose vicariance has been suggested to be an example of montane origin due to Andean uplift. These two episodes of vicariance between lowland-montane pairs coincide with the two most active periods of mountain building in the Andes, which according to Hoorn *et al.* (2010) took place during the late middle Miocene (~12 Mya) and early Pliocene (~4.5 Mya).

DIVERSIFICATION WITHIN ANDEAN TAXA

Several mechanisms have been implicated in the diversification within Andean, such as tectonics (Chapman, 1926; Cracraft, 1985; Garcia-Moreno *et al.*, 1998; Garcia-Moreno *et al.*, 2001; Perez-Eman, 2005; Fjeldså & Rahbek, 2006; Cadena *et al.*, 2007; Chaves *et al.*, 2007; Sedano & Burns, 2009), vegetation shifts initiated by climatic oscillations of the Pleistocene (Van Der Hammen & González, 1963; Van Der Hammen *et al.*, 1973; Hooghiemstra, 1984; Van Der Hammen & Cleef, 1986; Van Der Hammen, 1989; Hooghiemstra & Van Der Hammen, 2004; Hooghiemstra *et al.*, 2006), competition and predation (Terborgh, 1971; Terborgh & Weske, 1975; Remsen & Graves, 1995a,b; Navas, 2003; Buckley & Roughgarden, 2005; Brumfield & Edwards, 2007), parapatric speciation along elevational gradients (Endler, 1977; Hall, 2005), and rapid radiation as a response to newly created habitats (Vuilleumier, 1970; von Hagen & Kadereit, 2001; Kadereit & von Hagen, 2003; Bell & Donoghue, 2005; Hughes & Eastwood, 2006). Multiple studies have falsified the hypothesis of parapatric speciation as an explanation for the diversity of the Andes, including those by Patton & Smith (1992) for *Akodon* mice, Arctander & Fjeldså (1994) for *Scytalopus*, Hillis (1985) for the Andean Lizard *Pholidobolus*, and Dingle *et al.* (2006) for *Henicorhina* wrens. Moreover, Cadena (2007), Sorenson et al. (2003), Flanagan et al. (2004), and De Chaine & Martin (2006) suggested that ecological interactions cannot explain Andean diversification as they are too recent and thus would only have played a small part in the evolutionary history of taxa. Here I review diversification within different groups of Andean birds in order to find common patterns.

Divergence within Hapalopsittaca

The split between the central and northern Andean clades of *Hapalopsittaca*, located at the Marañón Valley, took place between 8.6 and 9.2 Mya (Fig. 1). Montario *et al.* (2005) provided evidence that major canyon incision in the Cordillera Blanca took place between 5 and 8 Mya, and Picard *et al.* (2008) proposed that the Andes of Central Peru were uplifted above 2000-2500 m by the late Miocene. Thus, this increase in elevation may be related to north-south vicariance in *Hapalopsittaca*, and an arid Marañón Valley may subsequently have acted as a barrier between these two species (this thesis).

The origin of the north Andean clade of *Hapalopsittaca* took place around 3.1-3.4 Mya (Fig. 1). Because both the Ecuadorian Andes (Coltorti, 2000) and the Cordillera Oriental of Colombia (Gregory-Wodzicky, 2000; Graham, 2009) were experiencing their final uplift at this time, this event may have isolated the ancestor of H. *amazonina, H. theresea*, and *H. velezi* in the Cordillera Oriental from the ancestor of *H. pyrrhops* and *H. fuertesi* in northern Ecuador and the Central Cordillera of Colombia (this thesis).

Within *Hapalopsittaca*, there appears to be a spatio-temporal link between the expansion and isolation of the highland vegetation belts and speciation of the northernmost species. During the Pleistocene, *páramo* vegetation changed from being isolated on the mountain tops during the interglacials to being widely distributed downslope during the glacial periods (Van Der Hammen & González, 1963; Simpson, 1975; Hooghiemstra, 1984; Hooghiemstra & Cleef, 1995; Mommersteeg, 1998; Hooghiemstra *et al.*, 2000; Hooghiemstra & Van Der Hammen, 2004; Hooghiemstra *et al.*, 2006). From 2.2-1.0 Mya BP the *páramo* formed continuous areas that may have allowed the ancestral populations of *H. velezi*, *H. amazonina*, and *H. theresae* to expand to the Cordilleras Central, and Oriental of Colombia, as well as to the Venezuelan Andes. During later warm climatic conditions, the *páramo* was fragmented into small islands (Simpson, 1975; Hooghiemstra *et al.*, 2000; Hooghiemstra & Van Der Hammen, 2004), causing the vicariance of this ancestral population into the three species we find today (this thesis, Fig. 1).

Divergence within Schistes and Colibri

There are two main clades within *Schistes* (Fig 2): *S. albigularis* and *S. geoffroyi* + *S. chapmani*. The split of these two clades constitutes a cis/trans (east/west) Andean vicariance event since *S. albigularis* is distributed along the western slope of the Ecuadorian Andes, as well as the Cordilleras Central and Occidental of Colombia, whereas *S. geoffroyi* and *S. chapmani* occur only on the eastern slopes of the eastern Andes from Venezuela to Bolivia. This east-west split could be explained by the uplift of the Cordillera Oriental of Colombia, which separated the slopes of the eastern Andes and the rain forest area of the Amazon basin from the western slopes of the Andes, the Chocó, and the Magdalena Valley (Hoorn *et al.*, 1995; Hooghiemstra *et al.*, 2006). The origin of these cis/trans Andean clades is contemporary with the split of cis/trans Andean taxa in the lowland genus *Pyrilia* (Ribas *et al.*, 2005).

Within *Colibri*, the *coruscans* species-group includes the species *C. coruscans*, *C. rostratus,* and *C. germanus*. *C. rostratus* from the northern Andes of Colombia and Venezuela, and *C. germanus* from the Pantepui, are sister-groups and diverged at *ca*. 0.7 Mya (Fig. 2). It is possible that the ancestor of the *C. germanus*-*C. rostratus* clade was distributed along the Northern Andes, as suggested by Chapman (1931), Mayr & Phelps (1967), Cook (1974), and Haffer (1974), and that climatic oscillations of the Pleistocene initiated vicariance resulting in these two species. The ancestor of *C. germanus* might have first reached the lowlands adjacent to the Andes during the glacial periods of the Pleistocene, and when the subandean forest belt was maximally depressed, it may have reached the Guianas. Later, during the interglacial, this species could have dispersed to the tepuis slopes as the vegetation belts shifted upslope (Rull, 2005). Thus, speciation of *C. germanus* is not spatio-temporally congruent with that of *D. guianensis*, which took place earlier (*ca*. 4.5 Mya, Fig. 2) and whose ancestor was distributed in the tropical lowlands (this thesis).

Divergence within Cranioleuca

Cranioleuca cisandina, C. antisiensis, and *C. baroni* diverged from one another around 0.7 Mya (Fig. 3). *C. cisandina* and *C. antisiensis* are distributed in the humid montane forests at lower altitudes than *C. baroni*, which is found in the dry upper montane or Andean forests. The differences in habitat among these three species, as well as their relative young age, may be an indication that their vicariance might have been related to the vegetation changes during the climatic oscillations of the Pleistocene (Hooghiemstra *et al*., 2000; Hooghiemstra *et al.*, 2006; Weng *et al.*, 2007).

Diversification within other groups

Within the Andean species of *Tangara*, speciation appears to have taken place between the late Miocene and the Pliocene (Burns & Naoki, 2004). During this time, Andean tectonics and climatic changes may have provided this, and other groups, with plenty of opportunities for speciation as a result of the isolation caused by fragmentation and isolation of Andean habitats (Hooghiemstra & Van der Hammen, 1998). Moreover, Burns & Naoki (2004) suggested that most species within *Tangara* were allopatrically speciated, with sympatric and parapatric patterns originating later on, from secondary dispersion.

According to Perez-Eman (2005), the lack of phylogenetic resolution among upper-montane species of *Myioborus* implies that once in South America, these taxa became isolated relatively quickly in different mountain ranges. He further proposed that once isolated, these lineages were allopatrically speciated through the uplift of the Andes or by the shifting of altitudinal vegetation belts during the glacial-interglacial periods. Within Andean species of the *Buarremon torquatus* complex, the relationships among many gene lineages are unresolved, which points to a rapid differentiation similar to that of

Myioborus (Perez-Eman, 2005). It would be worth investigating whether this rapid speciation pattern is found within other Andean groups, and whether these bursts of speciation took place at the same time, in order to find if common processes were involved.

Dispersion from the highlands to the lowlands

The clade of *Cranioleuca pyrrhophia, C. striaticeps*, and *C. henricae* diverged around 1.1 Mya (Fig. 3). The reconstruction of the ancestral character-state for this clade shows that it was distributed in the highlands (this thesis). *C striaticeps* is found in the dry woodlands of the Bolivian Andes, whereas C. *pyrrhophia* is distributed in the dry areas of the Chaco and the Pampas. Speciation of C. *pyrrhophia* may have been related to the shifting of the upper montane forest to altitudes that correspond to those of the current montane and tropical lowland forest during the glacial cycles of the Pleistocene (Hoogimestra *et. al*, 2000; Hooghiemstra *et al.*, 2006; Weng *et al.*, 2007). As the habitat of both species consists of dry, open vegetation, the descent of the vegetation during glacial cycles may have served as a dry corridor that allowed the common ancestor of these species to reach lower altitudes. During interglacials this connection might have been lost, causing the vicariance between *C. striaticeps* + *C. henricae* and *C. pyrrophia*. This scenario is similar to that of *Colibri serrirostris* (Fig. 2), which is distributed in the upper and lower dry montane forests of the Andes of Bolivia and Argentina, as well as in the dry, open lowlands of Bolivia, and the Cerrado of Brazil. The ancestral character-state of the clade leading to *Colibri* is also reconstructed as being highland (this thesis). As there is a spatio-temporal coincidence in the separation between the Andean and Cerrado populations of *Colibri serrirostris,* and that of *Cranioleuca pyrrophia*, it may be possible that divergence in both groups was related to the same vegetation shifts caused by the Pleistocene climatic cycles.

BIOGEOGRAPHIC BARRIERS THROUGHOUT THE ANDES

The Magdalena and Cauca River Valleys

The Magdalena River Valley separates the Cordillera Oriental from the Cordillera Central of Colombia, whereas the Cauca River Valley separates the Cordillera Central from the Cordillera Occidental. In *Buarremon bruneinucha*, distinct western and eastern Andean clades were recovered, with no signs of gene flow between the Cordillera Oriental and the Cordilleras Central and Occidental of Colombia (Cadena *et al.*, 2007). The two separate lineages of *B. bruneinucha* suggest two things: first, that the range expansion by this species followed two separate routes, one through the east and one through the west, and second, that the Magdalena River Valley is an efficient barrier preventing gene flow between highland populations (Cadena *et al.*, 2007). In the case of *Hapalopsittaca*, the current distributions of the clade formed by H. *amazonina, H. theresae*, and *H. velezi* might imply that the Magdalena Valley was not an efficient barrier for the dispersion of these taxa, as *H. amazonina* and *H. theresea* are distributed in the Cordillera Oriental of Colombia and Venezuela, whereas *H. velezi* is found in the Cordillera Central. However, the current distribution of this clade may be explained by the vegetation shifts during the glacial periods of the Pleistocene —when the upper vegetation belts migrated downslope and formed continuous areas between the cordilleras— allowing the ancestral populations of this clade of *Hapalopsittaca* to expand to the Central Cordillera of Colombia and to the Venezuelan Andes. During the interglacials, warm climatic conditions fragmented continuous vegetation at high altitudes into small islands (Simpson, 1975; Hooghiemstra & Van Der Hammen, 2004), resulting in the differentiation of the three current species —*H. amazonina*, *H. velezi*, and *H. theresea* (this thesis).

In contrast to the Magdalena Valley, the Cauca River Valley is not as efficient a barrier in preventing gene flow, perhaps due to its higher elevation in comparison to that of the Magdalena. This higher altitude may have allowed for increased connectivity between cordilleras during the climatic oscillations of the Pleistocene, when vegetation belts were shifted up and downslope (Hooghiemstra & Van Der Hammen, 2004). Several studies have documented close affinities between taxa from the Cordillera Central and Cordillera Occidental (Cuervo *et al.*, 2005; Cadena *et al.*, 2007; *Schistes*, this thesis), which suggests that this pattern may be common among many different taxa.

The Marañon River Valley

The Marañon River Valley is considered as one of the most important geographical barriers for Andean birds (Vuilleumier, 1969; Cracraft, 1985; Weir, 2009). Within *Myadestes*, the split between both diagnosably distinct populations of *M. ralloides* north and south of the valley took place around 3.0 Mya (Miller et al., 2007). The split within *M. ralloides* postdates that between the central and northern Andean clades of *Hapalopsittaca*, which took place around 8.6 and 9.2 Mya (this thesis). *Cyanolyca turcosa* (Ecuador) and *C. viridicyanus* (Peru and Bolivia) are also separated by this barrier, but no dates are proposed for their split (Bonaccorso, 2009). The difference of divergence times between pairs of species at either side of this valley indicates that different events are responsible for their vicariance, which should be further investigated.

The Apurimac River Valley

The Apurimac River Valley is recognized as one of the major geological features of the Andes, constituting a barrier to dispersion for highland birds along this mountain chain (Cracraft, 1985; Weir, 2009). Some of the many pairs of species that are separated by it include *Hapalopsittaca pyrrhops* and *H. fuertesi*, whose speciation took place around 1.0 Mya (this thesis, Fig 1); *Schistes geoffroyi* and *S. chapmani*, which split around 2.5 Mya, (this thesis, Fig. 2); *Cranioleuca albiceps* and *C. marcapatae*, which speciated around 1.5 Mya; *C. albicapilla* + *C. albigula* and (*C. pyrrhophia, C. striaticeps*, *C. henricae*, and *C. obsoleta*) which split at *ca*. 2.1 Mya (this thesis, Fig. 3); and *Chlorospingus cinereocephalus* and *C. peruvianus*, which diverged *ca*. 3.5 Mya (Miller, 2007). The divergence of these pairs of disjunct species between 1.0 and 3.5 Mya suggests that the formation of the Apurimac Valley, or a climatic event that took place around the same time as these splits may have been responsible for their vicariance. Further studies will be needed to clarify this.

CONCLUSIONS

There is no trivial explanation for the origin and diversification of Andean taxa. However, as I have presented in this summary, some common spatio-temporal patterns for the origin and diversification of different taxa do suggest some common biogeographical processes. Some biogeographic patterns link montane taxa in the Andes to either Central America or to South American lowlands. Those Central American taxa that have dispersed to the Andes seem to have done so after the final closure of the Isthmus of Panama, perhaps as a result of the expansion of the montane forests across the Isthmus. On the other hand, the origin of Andean taxa whose closest relatives are in the South American lowlands can be explained through vicariance from lowland sister-groups mediated by the uplift of the Andes. Thus, in these cases geological events appear to be responsible for originating diversity throughout montane environments.

Once in the Andes, diversification of montane taxa can be explained by tectonic events that created canyons and valleys that are associated with vicariant distributions, and by climatic oscillations during the Pleistocene, which caused cyclic altitudinal shifts of the vegetation, as well as the expansion and contraction of montane vegetation belts. Thus, many spatio-temporal patterns of evolution within the groups of birds included in this study can be linked to Earth history, both in terms of the uplift history of the Andes and the climatic events of the Pleistocene.

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