

Papéis Avulsos de Zoologia

Museu de Zoologia da Universidade de São Paulo

Volume 54(7):69-79, 2014

Aceito em: 28/04/2014

Publicado em: 09/05/2014

www.mz.usp.br/publicacoes

www.revistas.usp.br/paz

www.scielo.br/paz

ISSN impresso: 0031-1049

ISSN on-line: 1807-0205

TAXONOMY AND BIOGEOGRAPHY OF *STEPHANOXIS* SIMON, 1897 (AVES: TROCHILIDAE)

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ABSTRACT

After the description in the 19th century of two hummingbird species currently allocated to the genus *Stephanoxis*, Peters (1945) merged both taxa into a single species without providing any rationale. Here we re-evaluate the taxonomy and species limits of the representatives of this genus based on an extensive number of specimens. We demonstrate these taxa are better treated as full species under both the Biological and Phylogenetic Species Concepts due to their well-defined range and plumage patterns and reciprocally diagnosability. They have distinct, allopatric distributions segregated by a 160 km gap between the Serra do Mar, to the east, and Serra de Paranapiacaba, to the west, in the state of São Paulo. *Stephanoxis* species have ranges which are congruent with other montane bird species' suggesting shared vicariance events during preterit interglacial periods.

KEY-WORDS: Apodiformes; Atlantic forest; Montane forest; Serra do Mar; Serra de Paranapiacaba; Species limits.

INTRODUCTION

The Plovercrest *Stephanoxis lalandi* (Vieillot, 1818), as currently recognized, is a small (2.2-3.4 g, 8.5-9.0 cm) sexually dimorphic crested hummingbird which ranges from the state of Espírito Santo south to

Rio Grande do Sul, in Brazil, to eastern Paraguay and Misiones and Corrientes, in Argentina (Schuchmann, 1999). The two subspecies representative of the genus are endemic to the Atlantic forest and inhabit forested and semi-open highlands, up to 2,900 m in Serra do Caparaó, Minas Gerais state, Brazil (Sick, 1997), but

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<http://dx.doi.org/10.1590/0031-1049.2014.54.07>

can occasionally be found near sea level in the states of Santa Catarina and Rio de Janeiro, Brazil (Sick, 1997; Naka *et al.*, 2002; Mallet-Rodrigues *et al.*, 2010).

The first description of a species of Plovercrest was that of Vieillot (1818: 427), *Trochilus Lalandi*, based on a pair from “Brésil” (restricted to Rio de Janeiro by Pinto [1978]) that were originally part of P. A. Delalande’s collection. Vieillot left no doubt regarding the identification of his specimens, for which the long bright green crest, flanked with smaller bright golden-green feathers, are mentioned. He also described the diagnostic blue coloration of the throat, neck and chest, as well as the grey belly and sides of the body. The female, housed at the Muséum National d’Histoire Naturelle (currently CG 2001.966) was considered smaller and crestless. A few years later, J. Gould, who possessed an undescribed hummingbird from “Rio Grande” (Rio Grande do Sul), Brazil, in his collection, dedicated this new species to G. Loddiges and named it after him (although he did not publish his finding at that time). Vigors (1831: 12) acknowledged this act and first introduced the name *Trochilus Loddigesii* Gould, based on a male (currently BMNH 193.11.14.26), while highlighting the differences between Gould’s hummingbird species and Vieillot’s *T. Lalandei* (sic), from which it differed in having a purple crest, grey throat and black chest and abdomen.

Simon (1897) initially described *Stephanoxis* as a *nomen novum* due to a complex scenario created by previous unavailable names given by other authorities. Both *Cephallepis* Loddiges (1831) and *Cephalolepis* Cabanis & Heine (1860), to which Vieillot’s and Gould’s species were later allocated, were pre-occupied. Therefore, to satisfy taxonomic arrangements, Simon included *T. Lalandi* and *T. Loddigesii* within *Stephanoxis*. Cory (1918: 306), in his embracing reference work, presented a short *Stephanoxis* synonymy, misspelling genera and changing its authority (an evident *lapsus calami*), to which he assigned O. Salvin’s name. It was Peters (1945) who first depicted these issues, although with no intended intention of including all synonyms (see below).

The relationship of these two taxa to other hummingbird genera was not well resolved (*e.g.*, Willis, 1992), although they were sometimes considered closely related to *Klais* Reichenbach (Schuchmann, 1999). Phylogenetic hypotheses of the family, based on Bayesian and maximum-likelihood molecular analyses, did not include *Stephanoxis* (McGuire *et al.*, 2007, 2009). Nonetheless, these latter authors suggested the genus be embedded within the “Emerald clade” complex according to size, plumage patterns, soft-part coloration, and positions within linear se-

quences of reference works, such as Peters’ (1945). This viewpoint has been recently elucidated and corroborated with the inclusion of *Stephanoxis* on the aforementioned phylogenies, which were augmented with the inclusion of other taxa. The genus proved to be sister to *Anthocephala* Cabanis & Heine, therefore, within the Emeralds (McGuire *et al.*, 2014).

Early on, the two taxa were recognized as distinct species by most authors (*e.g.*, Salvin, 1892; Ihering & Ihering, 1907; Cory, 1918; Pinto, 1938). However, Peters (1945), without any reasoned argument, considered *Stephanoxis loddigesii* as a subspecies of *S. lalandi*, a treatment that has been followed ever since (*e.g.*, Pinto, 1978, Schuchmann, 1999; Grantsau, 2010). As no taxonomic revision has been done since these taxa were described, we here present (1) a taxonomic revision of this complex based on extensive specimen examinations, as well as (2) its updated distribution. We then discuss the biogeography of the genus suggesting a recurrent, but novel, interpretation of the role of glacial cycles in the diversification of endemic bird taxa in south-eastern Brazilian Atlantic forests, as well as the topography and barriers in the areas where these taxa are distributed.

METHODS

We personally examined 173 specimens available in nine collections worldwide (see acknowledgements), 112 pertaining to *Stephanoxis l. lalandi* and 61 to *S. l. loddigesii* (Appendix), including the holotypes and paratypes of both taxa. In addition, we analysed 518 photographs (accessed until 23 January 2014) of both taxa available in Wiki Aves (www.wikiaves.com.br), a free tool for online publication of photos and sounds of Brazilian birds. We only included photographs in which it was possible to evaluate diagnosable features, and used coordinates of the closest municipal centre, as given in Wiki Aves, to construct the most updated distribution map. Coordinates of specimens were acquired via ornithological gazetteers (Paynter, 1985; Paynter & Taylor, 1989, 1991).

Colour characters were scored using the Smith (1975) colour catalogue. In the “Results” section, colours are numbered according to these scores. Every specimen was tested under the diagnostic characters proposed for both taxa. Measurements of bill length, wing chord and tail were taken with the aid of a 0.01 mm precision digital calliper and were limited to specimens with unspoiled traits. A Mann-Whitney test was performed after normality and homogeneity of variances were examined to determine whether signifi-

cant differences exist between taxa, using a significance level of 0.05. Tests were run with SPSS 13.0 (SPSS, 2004). Taxonomic decisions were based on colour patterns found in plumage and morphometric data.

RESULTS

Plumage coloration

We found several differences between taxa and sexes. The main five exclusive and unequivocal diagnostic features between males of either taxon are the coloration of the crest, auricular region, chin, throat, and abdomen. Although the abdomen coloration was scored equally for both taxa, it does differ slightly, between violet-blue in *S. l. lalandi* and blackish violet-blue in *S. l. loddigesii* (Fig. 1, Table 1). *Stephanoxis l. lalandi* males also have large terminal Smoke Gray (44) tips to the rectrices, except for the Dark Green central pair. These become increasingly shorter towards the centre of the tail, culminating in an entirely black (Blackish 82) tip in the second rectrices. In contrast, *S. l. loddigesii* individuals always have white tipped rectrices, which also become shorter towards the inner rectrices. The coloration of the back and upper tail also differs between taxa, for both sexes, between Dark Green (262) in *S. l. lalandi* and Yellowish Olive-Green (5) in *S. l. loddigesii*. In addition, only in *S. l. lalandi* is there a black (Blackish 82) sub terminal band on all rectrices except for the first pair. In *S. l. loddigesii* both the first and second pairs of the rectrices lack this dark band (Fig. 1). Within males of each taxon, there is little individual variation, and most seems to be related to the specimens' age or iridescence of feathers. In contrast, females of both taxa are very similar to each other, generally green in the back and with whitish (Pearl Gray 81) underparts, but can be diagnosed by the distinct coloration of the back and crown (Table 1). Both sexes also share a white spot behind the eye and have the same soft parts coloration, such as Dusky Brown (19) tarsi. None of the characters cited above show overlap or signs of hybridization.

Measurements

We measured 108 specimens, 21 (19.4%) of which corresponded to *S. l. loddigesii*. There was overlap between taxa for all measurements and they cannot therefore be diagnosed morphometrically. However, medians of all features are significantly longer in *S. l. loddigesii* (Table 2).

Range

Stephanoxis l. lalandi is found in the south-eastern Brazilian Atlantic Forest from south-western Espírito Santo south to the high elevations in São Paulo's northern coastal mountains, as well as in the states of Minas Gerais and Rio de Janeiro; it is thus endemic to Brazil. *Stephanoxis l. loddigesii* ranges from Serra de Paranapiacaba in south-western São Paulo south to Paraná, Santa Catarina and Rio Grande do Sul states, as well as in adjacent forests of eastern Argentina and Paraguay, where commonly found below 500 m (Fig. 2).

DISCUSSION

There are a number of authors who mentioned plumage variations especially regarding the coloration of the crest as well as of the long feathers of the occiput. This is clearly exemplified by Elliot's (1874: 262) conclusions based on three specimens of *Cephaelis beskii* Pelzeln, a junior synonym of *S. lalandi*: "It differs from the common species in having the crest a bluish metallic green, instead of bright green... The crest, (...) is a shiny black, with a kind of greenish gloss..." We suggest these differences and variations are individual and should be ascribed to the nature of iridescent feathers, inherent to most hummingbird species (Schuchmann, 1999).

Although *S. loddigesii* tends to have larger dimensions compared to *S. lalandi*, there is much overlap within morphometric measurements. However, there are no signs of intergradation in plumage patterns or

TABLE 1: Differences in body coloration between *Stephanoxis* taxa.

		<i>S. l. lalandi</i>	<i>S. l. loddigesii</i>
1	Crest	Parrot Green (160)	Spectrum violet (72)
2	Auricular region	Dark Neutral Gray (83)	Sepia (Dark Drab 119A)
3	Chin and throat	Spectrum violet (72)	Sepia (Dark Drab 119A)
4	Abdomen	Spectrum violet (72)	Blackish (Spectrum violet 72)
5	Back	Dark green (262)	Yellowish Olive-Green (5)
6	Crown (females)	Dark green (262)	Yellowish Olive-Green (5)

coloration, which are geographically separate and can be used to determine either taxon unequivocally. We did not detect intermediate individuals, supporting a supposed lack of gene flow. These populations are segregated by at least 160 km at the closest proximity to each other in São Paulo (Fig. 2) and show no contact zones. Because plumage patterns and coloration are diagnostic in both sexes, we warrant specific status to *S. lalandi* and *S. loddigesii* under the Phylogenetic Species Concept (Nelson & Platnick, 1981; Cracraft, 1985). In addition, body adornments commonly assumed to be important for sexual selection in males

(crest, throat colouration) differ between *Stephanoxis* populations, the differences of which are determined not only by colouration, but by a clear geographic pattern as well. These observations are even more evident than in pairs of some hummingbird taxa which are undoubtedly considered as separate species, such as the Emeralds Violet-capped *Thalurania glaukopis* / Fork-tailed Woodnymph *Thalurania furcata*, warranting specific status to *Stephanoxis* subspecies also under the Biological Species Concept (Mayr, 1942, 2000). Their synonymy is given below according to Dubois' (2000) suggestions:

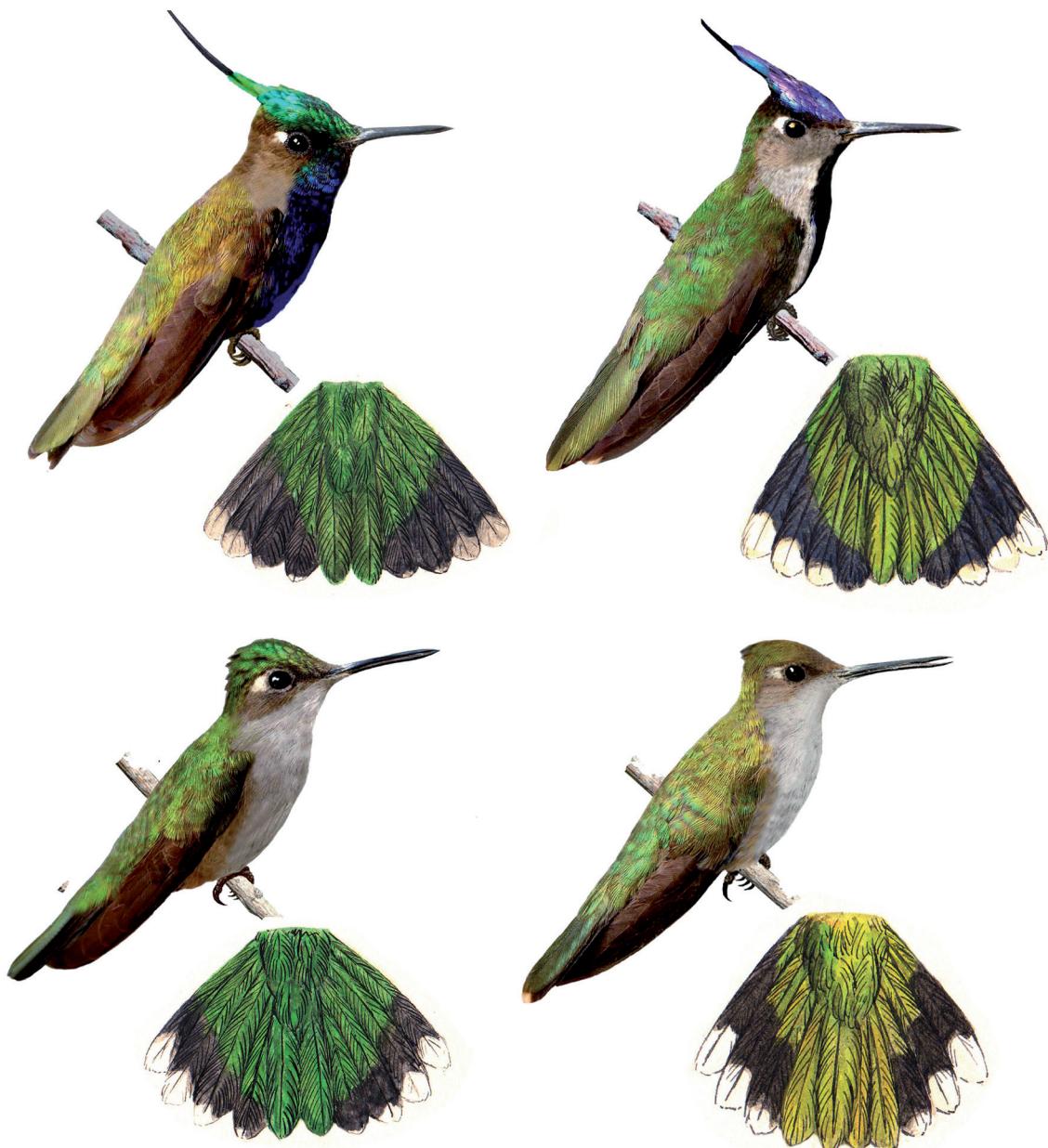


FIGURE 1: *Stephanoxis lalandi* (left) and *Stephanoxis loddigesii* (right). Males above, females below. Plate by Rolf Grantsau.

TABLE 2: Results of Mann-Whitney U tests performed between *Stephanoxis* taxa.

	Taxa	N	U	P
Bill length	<i>lalandi</i>	75	13	0.000
	<i>loddigesii</i>	19		
Wing chord	<i>lalandi</i>	78	488	0.005
	<i>loddigesii</i>	21		
Tail	<i>lalandi</i>	78	426.5	0.002
	<i>loddigesii</i>	20		

Stephanoxis lalandi (Vieillot, 1818)

English name: Green-crested Plovercrest.

Portuguese name: beija-flor-de-topete-verde.

Trochilus Lalandi Vieillot, 1818: 427, plate G 36. Brésil.

Trochilus lalandei: VIGORS, 1831: 12.

Ornismya delalandii Lesson 1830-32: 48, plate 23.

Cephalepis lalandi Bonaparte 1850: 83.

Cephalepis delalandi: GOULD, 1854: 80, plate 208.

Cephalepis delalandii: REICHENBACH, 1854: 12.

Cephalepis beskii: ELLIOT, 1874: 262.

Cephallepis beskii: MULSANT, 1876: 222.

Orthorhynchus Delalandii Reichenbach, 1855: 9.

Cephalolepis delalandi Cabanis & Heine, 1860: 61.

[Emendation of *Cephallepis* Loddiges].

Cephalolepis beskii: PELZELN, 1868: 58.

Bellona delalandii Verreaux & Verreaux, 1866: 75.

Stephanoxis Delalandei Simon, 1897: 40. [New name for *Cephallepis* Loddiges and *Cephalolepis* Cabanis & Heine, both pre-occupied].

Stephanoxis lalandei: HARTERT, 1900: 213.

Stephanoxis lalandi: CORY, 1918: 306.

Stephanoxis lalandi lalandi [subspecies]: PETERS,

1945: 30.

Diagnosis: Males diagnosed by a green crest (1), grey auriculars (2), violet-blue chin, throat (3) and abdomen (4) and, as in females, dark green back (5) and crown (6) (Table 1, Fig. 1).

Stephanoxis loddigesii (Gould, 1831)

English name: Purple-crested Plovercrest.

Portuguese name: beija-flor-de-topete-roxo.

Trochilus Loddigesii GOULD in Vigors, 1831: 12. Rio Grande.

Cephalepis loddigesii Bonaparte, 1850: 83.

Cephalepis loddigesii: REICHENBACH, 1854: 12.

Orthorhynchus loddigesii Reichenbach, 1855: 9.

Orthorhynchus loddigesii: BURMEISTER, 1856: 352.

Cephalolepis loddigesii Cabanis & Heine, 1860: 61. [Emendation of *Cephallepis* Loddiges].

Bellona loddigesii Verreaux & Verreaux, 1866: 75.

Cephallepis loddigesii Mulsant & Verreaux, 1874-77: 291.

Stephanoxis Loddigesii Simon, 1897: 40. [New name for *Cephallepis* Loddiges and *Cephalolepis* Cabanis & Heine, both pre-occupied].

Stephanoxis loddigesii: HARTERT, 1900: 214.

Stephanoxis lalandi loddigesii [subspecies]: PETERS, 1945: 31.

Cephalolepis apirati BERTONI & BERTONI in Bertoni, 1901: 55.

Diagnosis: Males diagnosed by a violet-blue crest (1), brownish auriculars (2), chin and throat (3), blackish violet-blue abdomen (4) and, as in females, yellowish green back (5) and crown (6) (Table 1, Fig. 1).

Nomenclature

Vigors (1831) described *Trochilus Loddigesii* Gould, while acknowledging that the name was dedicated to Loddiges by J. Gould, to whose collection the type specimen belonged. According to article 50.1.1 of the International Code of Zoological Nomenclature (ICZN, 1999), hereafter the Code, "...if it is clear from the contents that some person other than an author of the work is alone responsible both for the name or act and for satisfying the criteria of availability other than actual publication, then that other person is the author of the name or act." This statement deems *Stephanoxis loddigesii* (GOULD in Vigors, 1831) both available and valid, satisfying the criteria of Articles 8 (what constitutes published work) and 10 – 12 (provisions and requirements conferring availability) of the Code. In the same publication, Loddiges (1831: 12) states that this "...species belonged to a genus which he [himself] had distinguished among the Trochilidae by the name of *Cephallepis*..." However, this new genus-group name was pre-occupied, leading Simon (1897) to provide a substitute name (*nomen novum*) for the genus (see also Cory, 1918; Peters, 1945). Namely, *Cephallepis* was already in use (Rafinesque & Gill, 1810) while *Cephalolepis* was an attempt by Cabanis & Heine to amend Loddiges's genus; Cabanis & Heine, however, failed to realize its previous applications (Dumeril & Bibron, 1844; Agassiz, 1847). It is unclear to us why Peters (1945) considered *Cephalolepis apirati* BERTONI & BERTONI in Bertoni (1901) an emendation, since the author explicitly mentioned the etymology of this genus was

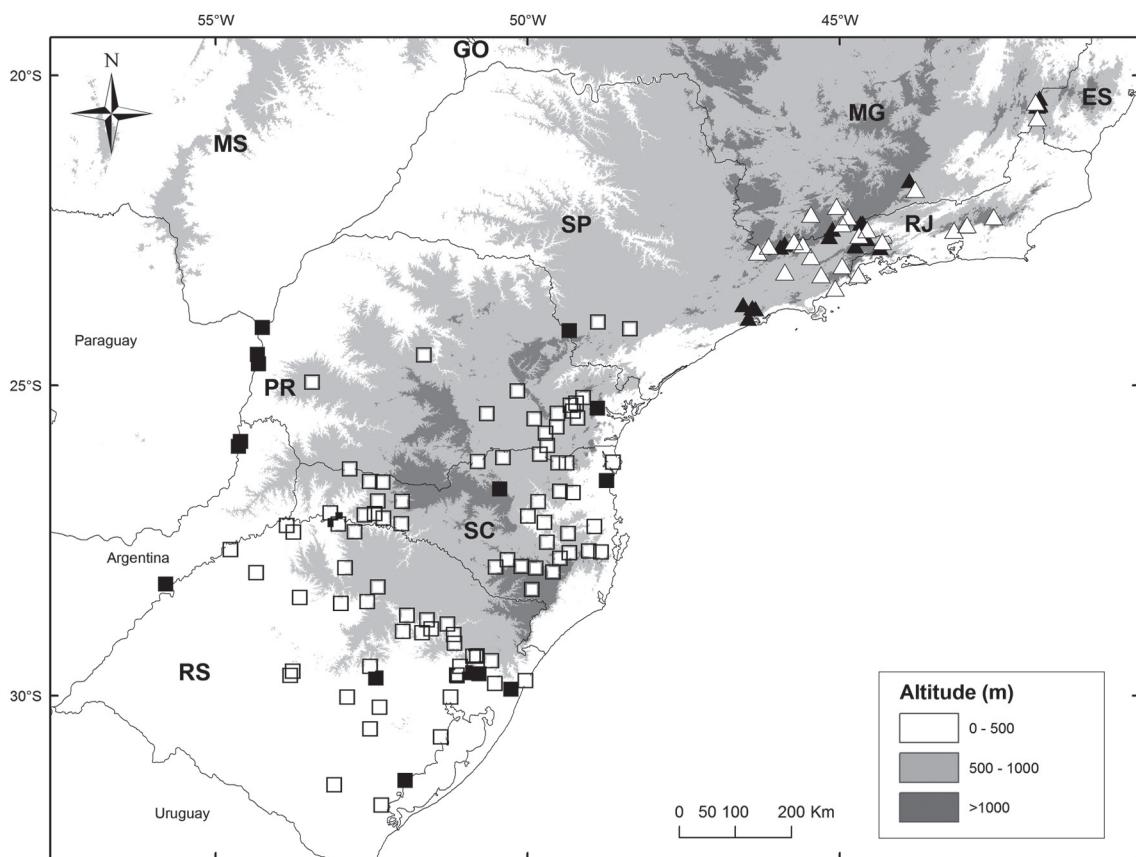


FIGURE 2: Distribution of *Stephanoxis lalandi* (triangles) and *S. loddigesii* (squares). Black symbols: skins, white symbols: photographs.

unknown. He did consider, however, that *Cephaloepis apirati* could be a variation of Vieillot's *Trochilus Delandi* (sic). It is, in fact, a synonym of *Stephanoxis loddigesii*.

Biogeography

The Serra do Mar has long been known to be an area of endemism for Atlantic forest vertebrates (e.g., Müller, 1973; Kinsey, 1982; Cracraft, 1985; Stattersfield et al., 1998; Costa et al., 2000), including passerine birds (Silva et al., 2004). Müller was the first to propose a "Paulista" centre, suggesting that the vertebrate fauna in northern São Paulo is more closely related to the northern Atlantic forest than to the southern Serra de Paranapiacaba. This was corroborated by Costa et al. (2000), who came to the same conclusion, using a parsimony analysis of endemism with primates and small mammals, even though their grids were arbitrarily defined at a rough scale of 275 × 275 km. Nevertheless, this pattern was not recovered by Silva et al. (2004), who used the same biogeographic method to identify areas of ende-

mism for passerine birds with 1 × 1 degree quadrats (ca. 110 km²). The latter authors concluded there are four areas of endemism within the Atlantic forest, one consisting of the south-eastern portion of the domain, from the states of Espírito Santo south to northern Santa Catarina, which includes the Serra do Mar and Serra de Paranapiacaba in a single area.

Recently, the use of ecological niche models under paleoclimates and phylogeographic analyses have allowed the re-evaluation of some traditional hypotheses based on empirical species ranges and past and current disposition of forests and terrains. This includes the role of forest refugia in the diversification of Neotropical birds (e.g., Haffer 1967, 1969). Carnaval & Moritz (2008), modelling the spatial range of the coastal Brazilian Atlantic forest under different climatic scenarios, suggested the existence of stable forest refugia north and south of the São Francisco River, namely the Pernambuco and Bahia refuges, respectively. The high levels of endemism south of the Doce River could not, however, be explained as this region was predicted to bear less historical stability.

Despite the existence of two Plovercrest species, there are at least three other pairs of montane sister

taxa with similar distributions in south-eastern Brazil, *i.e.* populations centred in northeast and south-western São Paulo segregated by a kilometric gap between the Serra do Mar (just north of the Baixada Santista) and Serra de Paranapiacaba. These include the Mouse-coloured Tapaculo *Scytalopus speluncae* / *Scytalopus* sp. nov. (Mata *et al.*, 2009), the Buff-throated *Poospiza lateralis* / Gray-throated Warbling-Finch *Poospiza cabanisi* (Assis *et al.*, 2007), and the Brown-breasted Pygmy-Tyrant *Hemitriccus o. obsoletus* / *Hemitriccus o. zimmeri* (Straube & Di Giacomo, 2007: 61). There are also at least three species that have the same distribution pattern but that show no apparent break in plumage or voice consistency. These are the Gray-bellied Spinetail *Synallaxis cinerascens*, Serra do Mar Tyrannulet *Phylloscartes difficilis* and Great Pampa-Finch *Embernagra platensis*. Furthermore, Cabanne *et al.* (2007) revealed a cryptic genetic diversity within the Lesser Woodcreeper *Xiphorhynchus f. fuscus*, which has a large genetic distance observed in northern and southern São Paulo, exhibiting a range remarkably similar to *Stephanoxis* spp.

We followed the scenario in which Carnaval & Moritz's (2008) and Carnaval *et al.* (2009) proposed that historical refuges south of the Doce River had existed and were less stable, but not absent (see also Maldonado-Coelho, 2012). Silva *et al.* (2012) systematically tested in how many vertebrate components the Brazilian Atlantic Forest could be divided by analysing existing empirical data. They found a marked east-west differentiation on the southerly portion of this domain, which may be credited either to the uplift of the Serra do Mar and Serra da Mantiqueira, recent population expansions within those forests (Cabanne *et al.*, 2008; D'Horta *et al.*, 2011) or local topography that suffered contrasting modifications across time, making the southern Atlantic forest of Brazil unsuitable for an exuberant forest on several occasions. Since the Atlantic forest is composed of a complex mosaic of vegetation and topography with potential for vertical migration (Por, 1992), we suggest *Stephanoxis*, *Scytalopus*, *Hemitriccus* and *Poospiza* may have evolved in cool and humid refuges (perhaps in higher elevations) during glacial periods. Other ecologically plastic species which were able to survive in expanding and retracting forests may have occupied surrounding habitats, therefore remaining phenotypically stable due to free genetic flow. Only older, true highland lineages, which supposedly remained isolated in mountaintops, are obviously morphologically distinguished at present. The ancestral populations of both lineages of *Stephanoxis* may have expanded northward during cooler and humid events.

This follows a pattern similar to that observed for the Paraná pine *Araucaria angustifolia* (see Hueck, 1953, 1972; Behling, 1998, 2002), several other bird taxa (Vasconcelos & Rodrigues, 2010; Freitas *et al.*, 2012), a rodent (Gonçalves *et al.*, 2007) and bees (Silveira & Cure, 1993), although not necessarily in the same time cycles. It seems probable that during one (or more) warmer and drier cycles, a population retracted southward and another moved to lower latitudes, becoming trapped in these south-eastern highlands, leading to vicariance. Although the barrier between both species is located in São Paulo, it is possible that the real vicariant barrier occurred elsewhere and that subsequent population expansions led to the current gap between the Serra do Paranapiacaba/Serra do Mar. A similar pattern was recently recognized in eastern Brazil for another highland hummingbird genus (Vasconcelos *et al.*, 2012).

We predict several more species occurring in this region may show recent populational expansions between extreme latitudes in São Paulo. This viewpoint is in accordance with phylogeographies of *X. f. fuscus* and *Pyriglena leucoptera*, Atlantic forest endemic bird species found from sea level to montane forests (Cabanne *et al.*, 2008; Maldonado-Coelho, 2012). We strongly suggest more phylogeographic studies be developed within those areas, which could account for overlooked biogeographic patterns. Although unsurprising to recently witness the discovery of a new area of endemism on the under-studied north-western Brazilian Amazonia (Borges & Silva, 2012), how exciting would it be to suggest a novel insight into the biogeography of the scientifically best known rain forest of Brazil?

RESUMO

*Após a descrição no século XIX de duas espécies de beija-flores atualmente alocados no gênero *Stephanoxis*, ambos os táxons foram considerados subespécies por Peters (1945), sem que o autor fornecesse qualquer justificativa para tal decisão taxonómica. Com base em um expressivo número de exemplares nós reavaliarmos a taxonomia e o limite de espécies dos representantes deste gênero, e demonstramos que ambos são mais bem tratados como espécies plenas sob os Conceitos Biológico e Filogenético de Espécie devido aos bem definidos padrões de plumagem e de distribuição geográfica, assim como pela distinta reciprocidade monofilética. Ambos os táxons são separados por cerca de 160 quilômetros entre a Serra do Mar, a leste, e a Serra de Paranapiacaba, a oeste, dentro do Estado de São Paulo. A distribuição das duas espécies de*

Stephanoxis é congruente com as de outras espécies de aves montanas, o que sugere eventos vicariantes compar-tilhados durante períodos interglaciais pretéritos.

PALAVRAS-CHAVE: Apodiformes; Florestas montanas; Mata Atlântica; Serra do Mar; Serra de Paranapiacaba; Limite de espécies.

ACKNOWLEDGEMENTS

We thank the staff and curators of the institutions which allowed us to examine *Stephanoxis* specimens: Museu de Zoologia da Universidade de São Paulo (MZUSP), British Museum of Natural History (BMNH), American Museum of Natural History (AMNH), Muséum National d'Histoire Naturelle (MNHN), Museu de História Natural “Capão da Imbuia” (MHNCL), Coleção Rolf Grantsau (SG), Museu de História Natural de Taubaté (MNHT), Museu de Biologia Professor Mello Leitão (MBML) and Coleção do Departamento de Zoologia da Universidade Federal de Minas Gerais (DZUFMG). Gláucia Del-Rio constructed the map; Jeremy Dickens improved the English, and Vitor Piacentini and two anonymous reviewers for their helpful critics to the manuscript. Thanks to Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for the concession of grants (Rede BioM.A. 35/2012) and fellowship to LFS, and Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA/ICMBio-SISBIO) for collecting permits.

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APPENDIX

Material analysed

Skins

Stephanoxis lalandi – 112: **BRAZIL:** (2♂ MBML 655, MBML 659). **Espírito Santo:** Caparaó (1♀ MBML 657). **Minas Gerais:** As Macieiras, Caparaó (3♂ AMNH 316658, AMNH 316659, AMNH 316660); Campos São Domingos, Caparaó (3♀ AMNH 316642, AMNH 316645, AMNH 316646; 1♂ AMNH 316644); Casa das Macieiras, Caparaó (1♀ AMNH 316661); Casa Queimada, Caparaó (1 undetermined AMNH 316639; 1♀ AMNH 316640); Gruta da Pedra Menina, Caparaó (1 undetermined AMNH 316652; 4♂ AMNH 316647, AMNH 316648, AMNH 316649, AMNH 316650); Parque Estadual do Ibitipoca, Lima Duarte (1♀ DZUFMG 3027); Taperinha, Camanducaia (1♂ DZUFMG 5633); Serra do Juncal, Sertão do Cantagalo, Gonçalves (1♂ DZUFMG 5759); Várzea da Congonha, Caparaó (4♂ AMNH 316653, AMNH 316654, AMNH 316655, AMNH 316656). **Minas Gerais/Rio de Janeiro:** Alto Itariaya (3♂ AMNH 188933, AMNH 188934, AMNH 188935). **Rio de Janeiro:** (1 undetermined MZUSP 1730; 1♀ MNHN 2.001.966); Itatiaia (5♂ SG 2565, SG 2566, SG 2567, SG 2568, SG 2569); Macieiras, Parque Nacional do Itatiaia (8♂ AMNH 188936, MZUSP 34155, MZUSP 34156, MZUSP 34159, MZUSP 34161, MZUSP 34311, MZUSP 34312, MZUSP 78715); Ponte Maromba, Itatiaya (1♂ AMNH 188937); Quilômetro 10, Parque Nacional do Itatiaia (1♂ MZUSP 36326); Quilômetro 16, Parque Nacional do Itatiaia (4♂ MZUSP 34121, MZUSP 34157, MZUSP 34158, MZUSP 34160, MZUSP 34313); Teresópolis (2♀ AMNH 146924, MBML 658; 1♂ MBML 656). **Rio de Janeiro/São Paulo:** Serra da Bocaina, Confluência RJ/SP (1♀ MZUSP 27182; 5♂ MZUSP 27183, MZUSP 27184, MZUSP 27185, MZUSP 27186, MZUSP 27187). **São Paulo:** Campo Grande (8♀ SG 910, SG 911, SG 945, SG 946, SG 1438, SG 1451, SG 2415, SG 3248; 18♂ MHNT 5027, SG 835, SG 860, SG 862, SG 899, SG 1018, SG 1429, SG 1450, SG 3240, SG 3241, SG 3242, SG 3243, SG 3246, SG 3247, SG 4311, SG 6577, SG 6578, SG 6579); Campos do Jordão (4♂ MHNT 2454, MZUSP 5928, MZUSP 5929, MZUSP 5930); Catuçaba, São Luiz do Paraitinga (2♀ MHNT 3940, MHNT 4141; 2♂ MHNT 2630, MHNT 3065); E. E. Bananal (1♂ MZUSP 78308); Pilar (1♂ MZUSP 10484); Piquete, Pico dos Marins (2♀ DZUFMG 3464, MHNT 2962; 1♂ MHNT 4298); Rio Grande da Serra (4♀ SG 5845, SG 5901, SG 5902, SG 5998; 8♂ SG 4240, SG 5894, SG 5896, SG 5928, SG 6000, SG 6001, SG 7516, SG 7530); São Bernardo (1♂ MZUSP 3136); São José do Barreiro (1♂ MHNT 7516).

Stephanoxis loddigesii – 61: **BRAZIL:** (1 undetermined BMNH 1933.11.14.29; 1♀ BMNH 1933.11.14.28; 1♂ BMNH 1933.11.14.27). **São Paulo:** Itararé (1♀ MZUSP 4253; 2♂ MZUSP 4255, MZUSP 4256). **Paraná:** Corvo, Serra da Graciosa (1♀ AMNH 318309; 1♂ AMNH 318308); Faz. Capivari, Campina Grande do Sul (1♂ MHNCI 2978); Guayra, Rio Paraná (1♂ AMNH 318312); Margem do Rio Iraí, Quatro Barras (1♂ MHNCI 4999); P. F. Caxambu, Castro (1♂ MHNCI 2430); Porto Britania, Rio Paraná (1♀ AMNH 318311); Porto Mendes, Rio Paraná (1♀ AMNH 318310); Rio do Salto, Cascavel (1♂ MHNCI 3998); UHE-Segredo, Foz Rio dos Touros, Pinhão (1♂ MHNCI 3855); Umbará, próximo ao rio Iguaçu (1♂ MZUSP 51072). **Santa Catarina:** Campo Comprido, Catanduvas (1♂ MHNCI 3435); Ilha Redonda (1♂ AMNH 314200); Ouro Verde, Serra de Lucindo (1♀ AMNH 314193; 2♂ AMNH 314191, AMNH 314192); Salto Pirahy, Joinville (1♀ AMNH 314190; 2♂ AMNH 314188, AMNH 314189); Vila da Montanha, Urubici (1♂ MZUSP 82504). **Rio Grande do Sul:** (1♂ BMNH 1933.11.14.26); Canela, Gramado (2♀ SG 7251, SG 7642; 4♂ SG 7640, SG 7641a,b, SG 7643); Conceição do Arroio (1♂ AMNH 314197); Novo Hamburgo, Dois Irmãos (1♂ SG 8948); Santa Cruz (1♀ AMNH 314196; 2♂ AMNH 314194, AMNH 314195); Sapu-ranga (2♀ AMNH 314198, AMNH 314199); São Lourenço (1♀ AMNH 321827; 2♂ MZUSP 3848, MZUSP 3849); Taquara do Novo Mundo (3♂ AMNH 38346, AMNH 485054, BMNH 1887.3.22.1551). **ARGENTINA:** **Misiones:** Arroyo Uruguay, km 10 (1♀ AMNH 793798; 7♂ AMNH 769780, AMNH 769781, AMNH 769782, AMNH 769783, AMNH 769824, AMNH 769832, AMNH 769833); Arroyo Uruguay, km 30 (1 undetermined AMNH 769779; 2♀ AMNH 769830, AMNH 769831; 2♂ AMNH 769778, AMNH 769822); Puerto Segundo (1♂ AMNH 154189). **Corrientes:** Cnia Garabí, Ea. Rincón de las Mercedes (1♂ AMNH 793797).

Photographs

Stephanoxis lalandi: **Espírito Santo:** Dores do Rio Preto. **Minas Gerais:** Caparaó, Camanducaia, Extrema, Itamonte, Lima Duarte, Passa Quatro, Pedralva, São Lourenço. **Rio de Janeiro:** Itatiaia, Nova Friburgo, Paraty, Petrópolis, Teresópolis. **São Paulo:** Areias, Bananal, Campos do Jordão, Cunha, Pindamonhangaba, São Bento do Sapucaí, São José dos Campos, São Luiz do Paraitinga, Ubatuba.

Stephanoxis loddigesii: **São Paulo:** Itapeva, Ribeirão Grande. **Paraná:** Almirante Tamandaré, Bocaiúva do Sul, Campo do Tenente, Campo Largo, Cascavel, Colombo, Contenda, Curitiba, Iratí, Lapa, Manoel Ribas, Ponta Grossa, Porto Amazonas, São José dos Pinhais. **Santa Catarina:** Abelardo Luz, Águas Mornas, Alfredo Wagner, Arvoredo, Bom Retiro, Canoinhas, Capão Alto, Chapecó, Concórdia, Doutor Pedrinho, Irineópolis, Lages, Laurentino, Mafra, Nova Trento, Painel, Palmitos, Petrolândia, Ponte Serrada, Rancho Queimado, Rio dos Cedros, Rio Negrinho, São Bento do Sul, São Domingos, São Francisco do Sul, São Joaquim, São Lourenço do Oeste, Seara, Taió, Urubici, Urupema, Vidal Ramos, Vitor Meireles, Xanxeré. **Rio Grande do Sul:** Alecrim, Alpestre, Anta Gorda, Antônio Prado, Cachoeira do Sul, Canela, Capão da Canoa, Caxias do Sul, Colorado, Cotiporã, Derrubadas, Encruzilhada do Sul, Ernestina, Flores da Cunha, Giruá, Gramado, Itara, Morro Reuter, Nonoi, Nova Prata, Novo Hamburgo, Pantano Grande, Passo Fundo, Pejuçara, Pelotas, Piratini, Porto Alegre, Santa Maria, Santo Antônio da Patrulha, São Francisco de Paula, Sarandi, Serafina Corrêa, Sinimbu, Tapes, Tenente Portela, Veranópolis.