Research paper

A phantom on the trees: Integrative taxonomy supports a reappraisal of rear-fanged snakes classification (Dipsadidae: Philodryadini)

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ABSTRACT

The Neotropics harbour a spectacular amount of biodiversity, but many of these species remain to be discovered and placed into the tree of life. In the neotropical snake genus *Philodryas*, the systematics of these rear-fanged snakes has been controversial and debated in recent years. Here, we combine published datasets with new morphological (scale microdermatoglyphics, osteology, pholidosis and genital features) and molecular (mitochondrial and nuclear) data to reassess the phylogenetic positioning of rear-fanged snakes within the tribe Philodryadini. We identified putative synapomorphies and pronounced morphological variation in hemipenial features. Our results suggested a need to reclassify many species in order to clarify some relationships within the *Philodryas* radiation. We also redefined Philodryadini by resurrecting three genera and naming a newly discovered species.

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1. Introduction

The Neotropical region is famous for its spectacular biodiversity (Pimm et al. 2010, 2014; Scheffers et al. 2012). However, the paucity of knowledge of this diversity underscores our inadequate understanding of the tree of life despite a recent surge of new species descriptions (Costello et al. 2012). This underestimation problem is the combined result of incompletely sampled regions and of collected specimens that are waiting to be described as new species (Hortal et al. 2015). The number of recognised species is expected to increase up to 250% for some groups of terrestrial vertebrates (Fouquet et al. 2007; Funk et al. 2012; Milá et al. 2012).

With more than 750 currently recognised species, the Neotropical family Dipsadidae Bonaparte 1838 (*sensu* Vidal et al. 2007) is a major radiation of snakes (Zaher et al. 2019). They range from small fossorial forms to large-bodied terrestrial and highly-adapted arboreal ones, including both harmless and "mildly venomous" species (Weinstein et al. 2011). Molecular data have led to significant improvements in the alpha taxonomy and understanding of higher-level relationships of these snakes in recent years (see Grazziotin et al. 2012). In contrast, morphology-based species delimitation in this group has been challenging, especially for taxa with conserved morphological characters such as some secretive and rare enigmatic species (Myers 2011; Myers & McDowell 2014; Smaga et al. 2019), because they have required multiple lines of evidence to achieve satisfactory delimitation results. Even with the application of molecular data, researchers have had difficulties accommodating some unusual taxa, leading to the

erection of new names, synonymies, or redefinitions in the higher-level relationships of snakes (Pyron et al. 2016; Zaher et al. 2009, 2018). Consequently, many of the phylogenetic relationships and species compositions of these clades remain doubtful, under-estimated, and/or unresolved (Pyron et al. 2015; Streicher & Wiens 2016, 2017). The elucidation of this poorly known branch of the tree of life represents a systematic problem that necessitates an inte-grative approach involving natural history, morphology, molecular genetics, and biogeography (Rodrigues 2005; Padial et al. 2010).

Most of the Neotropical xenodontine snake tribes (Caaete-boiini, Conophiini, Echinantherini, Hydrodynastini, Psomophiini, Saphenophiini, Tropidodryadini) were raised by Zaher et al. (2009) due to unstable interrelationships between well-established tribes. Among Racer snakes of the Philodryadini Cope, new arrangements were needed to maintain the monophyly of tribe. Zaher et al. (2009) stated: "a more detailed phylogenetic analysis of the newly extended genus *Philodryas* may show the necessity of a partition of the latter with some of the generic names synonymized here being applicable to the recovered monophyletic subunits."

2. Brief taxonomic history for neotropical racer snakes

Wagler (1830) erected the genera *Chlorosoma* and *Philodryas* to accommodate *Coluber viridissimus* Linnaeus, 1758 and *Coluber olfersii* Lichtenstein, 1823, respectively. Fitzinger (1843) was the first author to follow the scheme proposed by Wagler. Duméril et al. (1854) synonymized *Philodryas* Wagler, 1830 with *Dryophylax* Wagler, 1830 and described *Dryophylax aestivus* Dumeril, Bibron & Dumeril, 1854. Later, Günther (1858) rejected the synonymy and included all *Dryophylax* species in the genus *Philodryas*: *Philodryas aestiva* (Dumeril, Bibron & Dumeril, 1854), *Philodryas olfersii* (Lichtenstein, 1823), *Philodryas schottii* Fitzinger, 1826, *Philodryas serra* (Schlegel, 1837), *Philodryas viridissima* (Linnaeus, 1758). Girard (1858) described *Callirhinus patagoniensis* from Argentina. Steindachner (1870) described *Philodryas nattereri* from Mato Grosso (Brazil). *Philodryas psammophidea* Günther, (1872) and *Philodryas baroni* Berg, (1895) were described from Tucuman (Argentina). *Philodryas bolivianus* Boulenger, (1896) was described and in the same publication included accounts for *Philodryas burmeisteri* Jan, 1861 [= *Philodryas trilineata* (Burmeister, 1861)], *Philodryas elegans* (Tschudi, 1845), *Philodryas vitellinus* Cope, 1878 transferring *Philodryas dorsalis* to the genus *Ialtris* Cope, 1862. This generic arrange-ment remained unmodified until Peters & Orejas-Miranda (1970) revised this genus. Thomas & Dixon (1977) recognized the genus *Tropidodryas* Fitzinger, 1843 as distinct from *Philodryas* based on hemipenial morphology and microdermatoglyphics of *Philodryas serra* (Schlegel, 1837) and *Philodryas pseudoserra* Amaral, 1938 [= *Tropidrodryas striaticeps* (Cope, 1870)]. Thomas et al. (1977) removed *Philodryas borelli* Peracca from the synonymy of *P. psammophidea*. Later, Thomas & Johnson (1984) placed *P. borelli* in the synonymy of *Philodryas varia* Jan, 1861.

Machado (1993) described the genus *Xenoxybelis* to accommo-date *Oxybelis argenteus* Daudin, 1803 and stated that, based on evidence from hemipenial morphology, it should be allocated to the tribe Alsophiini Jenner 1983. Ferrarezzi (1994) summarized the characters redefining the composition of Philodryadini Cope, 1866. Despite recognizing the paraphyletic nature of this tribe, he included the genera *Ditaxodon* Hoge, 1958, *Philodryas* Wagler, 1830, *Platyinion* Amaral, 1923, *Pseudablabes* Boulenger, 1896, and *Tropi-dodryas* Fitzinger, 1843 without any mention of tribal allocation for *Xenoxybelis*. Lobo & Scrocchi (1994) described the osteology of *Philodryas patagoniensis* (Girard, 1858) and performed a phyloge-netic analysis of eleven species using ten morphological characters, but their inferred topologies were inconclusive and poorly

supported. Thomas & Fernandes (1996) synonymized the mono-typic genus *Platyinion* Amaral, 1923 with *Philodryas*.

Zaher's (1999) study, which was also based on hemipenial morphology, partially agrees with Machado's (1993) statement of diagnosability regarding *Xenoxybelis*, but he recommended the inclusion of *Xenoxybelis* as a member of the *P. olfersii* group. In Vidal et al. (2000) phylogenetic trees, *Xenoxybelis* is the sister taxon of *P. viridissima*. Pinou et al., (2004), based primarily on data provided by Vidal et al. (2000), found *P. olfersii* to be the sister species of *Xenoxybelis argenteus*. Prudente et al. (2008) provided new data on morphological variation in *Xenoxybelis boulengeri* and pointed out that some evidence supports the inclusion of species allocated to *Xenoxybelis* with *Philodryas*. Zaher et al. (2009) included in their analysis three previously unsampled species of *Philodryas* as ter-minals (*P. aestiva*, *P. patagoniensis* and *Philodryas mattogrossensis* Koslowsky, 1898), but they did not use the sequences generated by Vidal et al. (2000). Zaher et al. (2009) recovered *Philodryas* as par-aphyletic with respect to *Xenoxybelis* and *Pseudablabes* Boulenger, 1896 and, therefore, they proposed the synonymy of both genera with *Philodryas* to ensure monophyly of the group, and redefined the Philodryadini tribe to encompass *Philodryas (sensu lato)* and *Ditaxodon* Hoge, 1958. These authors also provided diagnostic characters for the tribe Philodryadini mainly based on hemipenial morphology.

Vidal et al. (2010) improved the sampling compared to previous studies by including *P. psammophidea*, which resulted in *Philodryas* becoming paraphyletic and accepted the synonymization of *Pseu-dablabes* with *Philodryas*. Although *Philodryas* was paraphyletic with respect to *Xenoxybelis*, these authors recommended the recognition of the later genus (because it is morphologically distinctive), pending further studies with denser taxonomic and character sampling. Based on a supermatrix representing more than 760 terminals, Pyron et al. (2011) retrieved *Philodryas* as polyphyletic and recovered, *Xenoxybelis boulengeri* as the sister species to *P. baroni*. Grazziotin et al. (2012) obtained strong support for *Philodryas* monophyly, in agreement with Zaher et al. (2009). In an expanded analysis, Pyron et al. (2013) retrieved a monophyletic *Philodryas*, which contrasted with the polyphyletic tree recovered by Figueroa et al. (2016).

In the present study, we incorporate new data for previously unsampled taxa in the Philodryadini tribe, which allowed us to improve the phylogenetic relationships among genera of the tribe. We also update the nomenclatural arrangements applied in the last decade, thereby improving the recent changes in the classification of these rear-fanged snakes (Table 1).

3. Material and methods

3.1. Taxon sampling and data acquisition

3.1.1. Fieldwork and morphological comparisons

This work was divided into two main stages. First, curatorial work by the first author in the herpetological collection of the Universidade Federal do Acre, Rio Branco (UFAC-RB), Acre, Brazil in 2007 revealed two enigmatic specimens of snakes. Subsequent comparisons with relevant literature suggested that they did not fit with any known genus. Consequently, the senior author and col-laborators (see acknowledgments) performed fieldwork between 2008 and 2014 (sampling weekly or biweekly) in the region where the first specimens were found in order to obtain natural history information, photos of live specimens, and tissue samples. Geographic coordinates were taken in the field with GPS using Datum WGS84.

From 2014 onwards, we studied a variety of distinct phenotypic character systems based on eight specimens at the Museu Nacional,

Table 1
Recent taxonomic arrangements in the genus Philodryas.

Zaher et al. 2008	Zaher et al. (2009)	Vidal et al. (2010)
Philodryas aestiva (Duméril, Bibron & Duméril, 1854)	*Philodryas aestiva* (Duméril, Bibron & Duméril, 1854)	*Philodryas aestiva* (Duméril, Bibron & Duméril, 1854)
Philodryas arnaldoi (Amaral, 1932)	**Philodryas argentea** (Daudin, 1803)	*Philodryas arnaldoi* (Amaral, 1932)
Philodryas baroni Berg, 1895	*Philodryas arnaldoi* (Amaral, 1932)	*Philodryas agassizii* (Jan, 1863)
Philodryas chamissonis (Wiegmann, 1835)	**Philodryas agassizii** (Jan, 1863)	*Philodryas baroni* Berg, 1895
Philodryas cordata Donnelly & Myers, 1991	*Philodryas baroni* Berg, 1895	*Philodryas chamissonis* (Wiegmann, 1835)
Philodryas hoodensis (Van Denburgh, 1912) = currently *Pseudalsophis hoodensis* (Van Denburgh, 1912)	**Philodryas boulengeri** (Procter, 1923) = **secondary homonymy of Philodryas boulengeri** (Werner, 1909)	*Philodryas cordata* Donnelly & Myers, 1991
Philodryas laticeps Werner, 1900	*Philodryas chamissonis* (Wiegmann, 1835)	*Philodryas laticeps* Werner, 1900
Philodryas livida (Amaral, 1923)	*Philodryas cordata* Donnelly & Myers, 1991	*Philodryas livida* (Amaral, 1923)
Philodryas mattogrossensis Koslowsky, 1898	*Philodryas laticeps* Werner, 1900	*Philodryas mattogrossensis* Koslowsky, 1898
Philodryas nattereri Steindachner, 1870	*Philodryas livida* (Amaral, 1923)	*Philodryas nattereri* Steindachner, 1870
Philodryas olfersii (Lichtenstein, 1823)	*Philodryas mattogrossensis* Koslowsky, 1898	*Philodryas olfersii* (Lichtenstein, 1823)
Philodryas patagoniensis (Girard, 1858)	*Philodryas nattereri* Steindachner, 1870	*Philodryas patagoniensis* (Girard, 1858)
Philodryas psammophidea Günther, 1872	*Philodryas olfersii* (Lichtenstein, 1823)	*Philodryas psammophidea* Günther, 1872
Philodryas simonsii Boulenger, 1900	*Philodryas patagoniensis* (Girard, 1858)	*Philodryas simonsii* Boulenger, 1900
Philodryas tachymenoides (Schmidt & Walker, 1943)	*Philodryas psammophidea* Günther, 1872	*Philodryas tachymenoides* (Schmidt & Walker, 1943)
Philodryas trilineata (Burmeister, 1861)	*Philodryas simonsii* Boulenger, 1900	*Philodryas trilineata* (Burmeister, 1861)
Philodryas varia (Jan, 1863)	*Philodryas tachymenoides* (Schmidt & Walker, 1943)	*Philodryas varia* (Jan, 1863)
Philodryas viridissima (Linnaeus, 1758)	*Philodryas trilineata* (Burmeister, 1861)	*Philodryas viridissima* (Linnaeus, 1758)
	Philodryas varia (Jan, 1863)	**Xenoxybelis argenteus** (Daudin, 1803)
	Philodryas viridissima (Linnaeus, 1758)	**Xenoxybelis boulengeri** (Procter, 1923)

Pyron et al. (2011)	Grazziotin et al. (2012)	Wallach et al. (2014)
Pseudablabes agassizii (Jan, 1863)	*Philodryas aestiva* (Duméril, Bibron & Duméril, 1854)	*Philodryas aestiva* (Duméril, Bibron & Duméril, 1854)
Philodryas aestiva (Duméril, Bibron & Duméril, 1854)	**Philodryas agassizii** (Jan, 1863)	*Philodryas agassizii* (Jan, 1863)
Philodryas arnaldoi (Amaral, 1932)	*Philodryas argentea* (Daudin, 1803)	*Philodryas argentea* (Daudin, 1803)
Philodryas baroni Berg, 1895	*Philodryas arnaldoi* (Amaral, 1932)	*Philodryas arnaldoi* (Amaral, 1932)
Philodryas chamissonis (Wiegmann, 1835)	*Philodryas baroni* Berg, 1895	*Philodryas baroni* Berg, 1895
Philodryas cordata Donnelly & Myers, 1991	*Philodryas chamissonis* (Wiegmann, 1835)	*Philodryas boliviana* Boulenger, 1896
Philodryas laticeps Werner, 1900	*Philodryas cordata* Donnelly & Myers, 1991	*Philodryas chamissonis* (Wiegmann, 1835)
Philodryas livida (Amaral, 1923)	**Philodryas georgeboulengeri** Grazziotin, Zaher, Murphy, Scrocchi, Benavides, Zhang & Bonnatto, 2012	*Philodryas cordata* Donnelly & Myers, 1991
Philodryas mattogrossensis Koslowsky, 1898	*Philodryas laticeps* Werner, 1900	*Philodryas georgeboulengeri* Grazziotin, Zaher, Murphy, Scrocchi, Benavides, Zhang & Bonnatto, 2012
Philodryas nattereri Steindachner, 1870	*Philodryas livida* (Amaral, 1923)	*Philodryas laticeps* Werner, 1900
Philodryas olfersii (Lichtenstein, 1823)	*Philodryas mattogrossensis* Koslowsky, 1898	*Philodryas livida* (Amaral, 1923)
Philodryas patagoniensis (Girard, 1858)	*Philodryas nattereri* Steindachner, 1870	*Philodryas mattogrossensis* Koslowsky, 1898
Philodryas psammophidea Günther, 1872	*Philodryas olfersii* (Lichtenstein, 1823)	*Philodryas nattereri* Steindachner, 1870
Philodryas simonsii Boulenger, 1900	*Philodryas patagoniensis* (Girard, 1858)	*Philodryas olfersii* (Lichtenstein, 1823)
Philodryas tachymenoides (Schmidt & Walker, 1943)	*Philodryas psammophidea* Günther, 1872	*Philodryas patagoniensis* (Girard, 1858)
Philodryas trilineata (Burmeister, 1861)	*Philodryas simonsii* Boulenger, 1900	*Philodryas psammophidea* Günther, 1872
Philodryas varia (Jan, 1863)	*Philodryas tachymenoides* (Schmidt & Walker, 1943)	*Philodryas simonsii* Boulenger, 1900
Philodryas viridissima (Linnaeus, 1758)	*Philodryas trilineata* (Burmeister, 1861)	*Philodryas tachymenoides* (Schmidt & Walker, 1943)
Xenoxybelis argenteus (Daudin, 1803)	*Philodryas varia* (Jan, 1863)	*Philodryas trilineata* (Burmeister, 1861)
Xenoxybelis boulengeri (Procter, 1923)	*Philodryas viridissima* (Linnaeus, 1758)	*Philodryas varia* (Jan, 1863)
		Philodryas viridissima (Linnaeus, 1758)

Figueroa et al. (2016)	Uetz et al., 2019	**PRESENT STUDY**
Philodryas aestiva (Duméril, Bibron & Duméril, 1854)	*Philodryas aestiva* (Duméril, Bibron & Duméril, 1854)	**Pseudablabes agassizii** (Jan, 1863)
Philodryas agassizii (Jan, 1863)	*Philodryas agassizii* (Jan, 1863)	**Pseudablabes arnaldoi** (Amaral, 1932)
Philodryas argentea (Daudin, 1803)	*Philodryas amaru* Zaher, Arrendondo, Valencia, Arbeláez, Rodrigues & Altamirano-Benavides, 2014	**Pseudablabes patagoniensis** Girard, 1858
Philodryas baroni Berg, 1895	*Philodryas argentea* (Daudin, 1803)	**Chlorosoma dunupyana sp. nov.**
Philodryas chamissonis (Wiegmann, 1835)	*Philodryas arnaldoi* (Amaral, 1932)	**Chlorosoma laticeps** (Werner, 1900)
Philodryas georgeboulengeri Grazziotin, Zaher, Murphy, Scrocchi, Benavides, Zhang & Bonnatto, 2012	*Philodryas baroni* Berg, 1895	**Chlorosoma viridissimum** (Linnaeus, 1758)
Philodryas mattogrossensis Koslowsky, 1898	*Philodryas boliviana* Boulenger, 1896	*Philodryas aestiva* (Duméril, Bibron & Duméril, 1854)
Philodryas nattereri Steindachner, 1870	*Philodryas chamissonis* (Wiegmann, 1835)	*Philodryas amaru* Zaher, Arrendondo, Valencia, Arbeláez, Rodrigues & Altamirano-Benavides, 2014
Philodryas olfersii (Lichtenstein, 1823)	*Philodryas cordata* Donnelly & Myers, 1991	*Philodryas baroni* Berg, 1895
Philodryas patagoniensis (Girard, 1858)	*Philodryas erlandi* Lönnberg, 1902	*Philodryas boliviana* Boulenger, 1896
Philodryas psammophidea Günther, 1872	*Philodryas georgeboulengeri* Grazziotin, Zaher, Murphy, Scrocchi, Benavides, Zhang & Bonnatto, 2012	*Philodryas chamissonis* (Wiegmann, 1835)
Philodryas trilineata (Burmeister, 1861)	*Philodryas laticeps* Werner, 1900	*Philodryas cordata* Donnelly & Myers, 1991

Table 1 (*continued*)

Zaher et al. 2008	Zaher et al. (2009)	Vidal et al. (2010)
Philodryas viridissima (Linnaeus, 1758)	*Philodryas livida* (Amaral, 1923)	*Philodryas erlandi* Lönnberg, 1902
	Philodryas mattogrossensis Koslowsky, 1898	*Philodryas livida* (Amaral, 1923)
	Philodryas nattereri Steindachner, 1870	*Philodryas mattogrossensis* Koslowsky, 1898
	Philodryas olfersii (Lichtenstein, 1823)	*Philodryas nattereri* Steindachner, 1870
	Philodryas patagoniensis (Girard, 1858)	*Philodryas olfersii* (Lichtenstein, 1823)
	Philodryas psammophidea Günther, 1872	*Philodryas psammophidea* Günther, 1872
	Philodryas simonsii Boulenger, 1900	*Philodryas simonsii* Boulenger, 1900
	Philodryas tachymenoides (Schmidt & Walker, 1943)	*Philodryas tachymenoides* (Schmidt & Walker, 1943)
	Philodryas trilineata (Burmeister, 1861)	*Philodryas trilineata* (Burmeister, 1861)
	Philodryas varia (Jan, 1863)	*Philodryas varia* (Jan, 1863)
	Philodryas viridissima (Linnaeus, 1758)	***Xenoxybelis argenteus*** (Daudin, 1803)
		Xenoxybelis boulengeri (Procter, 1923)

Universidade Federal do Rio de Janeiro (MNRJ), Rio de Janeiro, Brazil. Specifically, on each specimen, we examined traditional external features (colour pattern, meristic and morphometric data), cranial osteology, microdermatoglyphics of dorsal scales, soft anatomy, and male genitalia (= hemipenes). Our detailed anatomical examinations of these specimens established that they do not fit the diagnosis or definition of any previously recognized snake genus, but share at least two evidently derived characters (= putative synapomorphies)—presence of well-developed calyces on the hemipenial lobes and sulcus spermaticus bifurcating on the central region of hemipenial body, outside capitulum—with advanced snakes of the superfamily Colubroidea Oppel, 1811 (sensu Zaher et al. 2009).

3.2. Molecular data

3.2.1. DNA extraction, PCR protocols, alignment and editing of sequences

Liver tissues were obtained from nine specimens and preserved in 95% ethanol. These included three voucher specimens of unnamed species (CORBIDI 19094, MNRJ 25242 and UFAC-RB 554), two *Philodryas argentea* (MNRJ 16783 and UFAC-RB 530), two *P. viridissima* (MNRJ 26648 and MNRJ 26660), one *Philodryas laticeps* (MNRJ 23683), and one *Philodryas georgeboulengeri* (MNRJ 26161). We extracted mitochondrial and nuclear DNA using the saline method of Miller et al. (1988). To amplify each target gene for sequencing, we set up 25 μL PCR reactions consisting of 12.5 μL of Promega Green Master Mix 2X, 0.4 μL each primer (10 μM each), 10 μL of molecular biology grade water, and 1 μL of purified DNA template (~10 ng). We used the following thermocycler profile for all PCRs: 94 °C for 30 s × 1 cycle, [94 °C for 30 s, 50 °C for 45 s, 72 °C for 1:00 × 35 cycles, and 72 °C for 10:00 × 1 cycle. All successful PCRs, which showed only the correct-sized bands in 2% agarose gels, were subsequently purified using the 20% PEG method (see Jennings 2016). Purified PCR products were sequenced in forward and reverse directions on an ABI capillary sequencer.

To evaluate the phylogenetic position of the new snake species within the Colubroidea, we sequenced the same four mitochondrial (12S, 16S, *Cytb*, and ND4) and two nuclear (*c-mos* and BDNF) genes used in previous comparable studies (e.g., Zaher et al. 2009; Grazziotin et al. 2012). We PCR-amplified and sequenced these genes using the primers 12S-L1091, 12S-H1557.mod, 16Sar, 16Sbr, c-mos S77, and *c-mos* S78 found in Zaher et al. (2009) and primers cytb 703Botp.mod, cytb MVZ16p.mod, ND4-NAD4, ND4-Leu, BDNFF, and BDNFR from Grazziotin et al. (2012). However, we modified these primers by tailing them with M13-forward (−21) and M13-reverse (−29) sequencing primers in order to facilitate the sequencing of PCR products (Supplementary Table 1; see Jennings (2016) for more information about the use of M13 primer tails). All sequences were deposited in GenBank under accessions:

MK287602−MK287616 and MK282799−MK282826. Alignments were performed using Clustal W with default parameters in the program MEGA 7.0 (Kumar et al. 2016).

3.3. Inferring phylogenetic relationships

We searched for sequences of Caenophidian snakes in GenBank using Blast software (https://blast.ncbi.nlm.nih.gov/Blast.cgi). This exercise confirmed that most of the available similar sequences belong to members of the subfamily Xenodontinae Bonaparte, 1845 (sensu Grazziotin et al. 2012). We included 24 terminals for the outgroup of our phylogenetic analyses with representative terminals from all currently recognized tribes of the Xenodontinae Bonaparte, 1845 (sensu Grazziotin et al. 2012) and the colubrid *Mastigodryas boddaerti* (Sentzen, 1796) (Supplementary Table 2) with at least two molecular markers shared by at least three species in order to avoiding "paraphyly of singletons", thus, allowing include ND4 marker which is available for few species of *Philodryas* (see Figueroa et al., 2016). The only exception being Eutrachelophiini Myers & McDowell 2014, for which, as far as we know, there is no tissue sample preserved in collections (but see Zaher & Prudente 2020). A concatenated dataset was generated in Sequence Matrix (Vaidya et al. 2011).

We analysed our data using Bayesian inference and maximum likelihood methods, both implemented in the CIPRES Science Gateway V. 3.3 (Miller et al. 2010). For the Bayesian analyses, we used the MrBayes 3.2.1 package (Ronquist et al. 2012) with four independent runs and four Markov chains of 10 million generations each, sampling every 10,000 generations. We used a single partition for RNA, whereas protein-coding sequences were partitioned by codon position using Partition Finder 2 (Lanfear et al. 2016). We used the Bayesian information criterion for model selection (Sullivan & Joyce 2005). Convergence and stationarity were assessed using Tracer 1.5 (Rambaut et al. 2018), ESS>200 was maintained for model parameters, and we combined runs in LogCombiner 1.8 (with a 10% burn-in) allowing us to summarize the results in a maximum clade credibility tree in TreeAnnotator 1.8 (Drummond et al. 2012). For ML, we used RAxML v.8 (Stamatakis 2014) with partitions restricted to GTR-based models and using GTRGAMMA for bootstrapping, with rapid bootstrap analysis and 1000 bootstrap iterations. In all analyses, we unlinked parameters of substitution rates and nucleotide frequencies between partitions. The resulting topologies were visualized in FigTree 1.4 (available from http://tree.bio.ed.ac.uk/software/figtree/).

3.4. Terminology and techniques for phenotypic dataset

Terminology for cephalic shields follows Peters (1964) and ventral and subcaudal counts follow Dowling (1951). The sex of each specimen was determined through a ventral incision at the

base of the tail to check for the presence of hemipenes. We defined mature individuals through inspection of convoluted deferent ducts in males and occurrence of vitelogenic follicles, eggs or pleated glandular uterus in females (Shine 1988, 1994). We follow Köhler's (2012) nomenclature for definition of colour tones. We obtained morphometric measurements with an analog caliper (Mitutoyo®) to the nearest 0.1 mm under a Stemi 2000C (Zeiss) stereomicroscope, except for snout—vent length (SVL) and tail length (TLL), which we measured with a flexible ruler to the nearest 1 mm. We measured cephalic shields on the right side of the head. The superficial layers of the dorsal scales of the specimens were sampled from three distinct regions of the body (anterior, medial and posterior) and separately stored in 70% ethanol. We removed layers with the aid of forceps. Samples were affixed with double-faced carbon tape in metal plates, they were sputter coated using an ELMITECH K550 and examined and imaged on a JEOL JSM 6460 LV scanning electron microscope under 500x—10,000× magnifications and 20 kV at the Scanning Electron Microscopy laboratory of the Museu Nacional/UFRJ. Terminology for micro-ornamentation descriptions follows Price (1982) and Price & Kelly (1989). We investigated two portions of the dorsal scales (basal and mid-apical) each of which displayed their own features. We prepared hemipenes from the specimens UFAC-RB 421, UFAC-RB 345, CORBIDI 19094, according to procedures described in Pesantes (1994), but replacing potassium hydroxide with distilled water (Passos et al. 2016). We immersed everted and fully expanded hemipenes in 70% alcoholic solution with Alizarin Red for approximately 10 min to stain calcified structures (Uzzell 1973). We inflated the organs with a solution of liquid petroleum jelly with green pigments to obtain contrast for photographs. Terminology for hemipenes descriptions follows Dowling & Savage (1960), as augmented by Zaher (1999) and Zaher et al. (2014).

We used one entire specimen (UFAC-RB 451) and the partially damaged specimen (UFAC-RB 262, see below) to study visceral topology and gross morphology, making a ventral incision to expose all visceral organs. Two specimens (UFAC-RB 357, mature female and MNRJ 25242, immature female) were scanned on a Skyscan 1173 in-vivo high-resolution μ-CT scan at the Universidade de São Paulo, Brazil. Specimens were scanned at 40 kV and 533 μA and rendered in three dimensions using CTVox for Windows 64 bits version 2.6. Skull terminology followed Cundall & Irish (2008).

4. Results

The phylogenetic analyses resulted in a well-resolved tree with most nodes having high posterior probabilities (PP) > 0.95 and high bootstrap values (BS) > 70 and moderate support values between 50 and 70. Both topologies were almost identical, except for some relations between tribes that do not interfere in our result. These results confirmed the relationships of many tribes as well as monophyly of most genera (Fig. 1).

4.1. Phylogenetic relationships of rear-fanged snakes

We recovered the tribe Tropidodryadini Zaher et al., 2009 (Clade E) as the sister-group of the tribe Philodryadini Cope, 1886 (Clade F) with maximum support (Fig. 1). Four major clades were found into Philodryadini. The first (Clade D) comprises *Philodryas agassizii* + *P. patagoniensis* (Fig. 1). The second clade is comprised exclusively by the Amazonian species of the genus *Xenoxybelis* Machado, 1993, which was recovered with maximum support (Clade C). The third clade contains our new sequence data and the newly sampled *P. laticeps* Werner, 1900 was recovered as the sister species of *P. viridissima* with moderate support. Our new taxon was recovered in a maximally supported clade with

P. viridissima + *P. laticeps* in both analyses (Clade B). The fourth (Clade A) comprises all remaining species of *Philodryas* Wagler, 1830 (Fig. 1).

The classification of groups must reflect their phylogenetic affinities. We therefore adopted many actions to ensure that our results reflect our current knowledge of the phylogeny based in the following Taxon Name Criteria (TNC) from Vences et al. (2013): i) we have recovered an unknown taxon as a clade in an explicit phylogenetic analysis; ii) we have robust clade support for this taxon; iii) we have performed a relatively dense taxon sampling; and iv) we have easily detected its phenotypic diagnosability using several putatively non-correlated phenotypic systems (e.g., scales, bones, viscera and genitalia).

Following the TNC's from Vences et al. (2013), we also observed that these taxa were recovered in distinct clades with many putative morphological synapomorphies, they are geographically restricted to rainforests (Atlantic Forest and Amazonia), and they exhibited morphological and behavioural adaptations for an arboreal lifestyle. Thus, we decided to resurrect three genera (see below). Given the controversial relationships of *P. viridissima* recovered by previous studies (see Discussion), and based on the support from both morphological and molecular evidence, a new generic assignment becomes necessary to better reflect the relationships among taxa.

4.2. Systematic account

Order Squamata Oppel, 1811
Family Dipsadidae Bonaparte, 1838
Subfamily Xenodontinae Bonaparte, 1838

4.2.1. Genus Pseudablabes Boulenger, 1896 status revalidated

We searched for a less inclusive available name that included the clade D and we found that the names *Pseudablabes* Boulenger, 1896 and *Callirhinus* Girard, 1858 met such requirements. The type species of the genus *Pseudablabes* is *Eirenis agassizii* Jan, 1863 and the type species of *Callirhinus* is *C. patagoniensis* Girard, 1858. *Callirhinus* has priority over *Pseudablabes* following the provisions given in the article 23 (ICZN 1999), but is preoccupied by *Callirhinus* Blanchard, 1850. We therefore propose the resurrection of the genus *Pseudablabes* for the clade containing *Pseudablabes agassizii* (Jan, 1863) (Fig. 1D) and *Pseudablabes patagoniensis* (Girard, 1858) **comb. nov.** We tentatively include *Pseudablabes arnaldoi* (Amaral, 1932) **comb. nov.** in this genus based on overall external similarities (e.g., colour pattern, pholidosis and general habitus), but mainly by sharing unique similarities of hemipenial morphology (Fig. 2).

The unique combination of features assigned herein to this genus include (hereafter the putative apomorphies followed by '*'): head, body, and tail uniformly reticulated gray or brown, with anteriormost edge of ventrals being green coloured*; lack of deep body calyces on the proximal half of the asulcate surface of the hemipenial body*; lateral enlarged spines; distal rows of middle sized spines disposed in a typical "V-shape" configuration on the asulcate surface of the hemipenial body*; diameter of the middle of the hemipenes larger than both proximal and distal extremities; dorsal scale rows reducing anterior-posteriorly from 19 to 13 or uniformly in 13—13 in *Pseudablabes agassizii*; low number of ventral scales (130—184); seven supralabials; body with dorsolateral stripes and short tail.

4.2.2. Genus Chlorosoma Wagler, 1830 status revalidated

We searched for a less inclusive available name for this taxon and found that the name *Coluber viridissimus* Linnaeus, 1758 represents the type species of the genus *Chlorosoma* Wagler, 1830. Consequently, here, we formally propose the resurrection of the
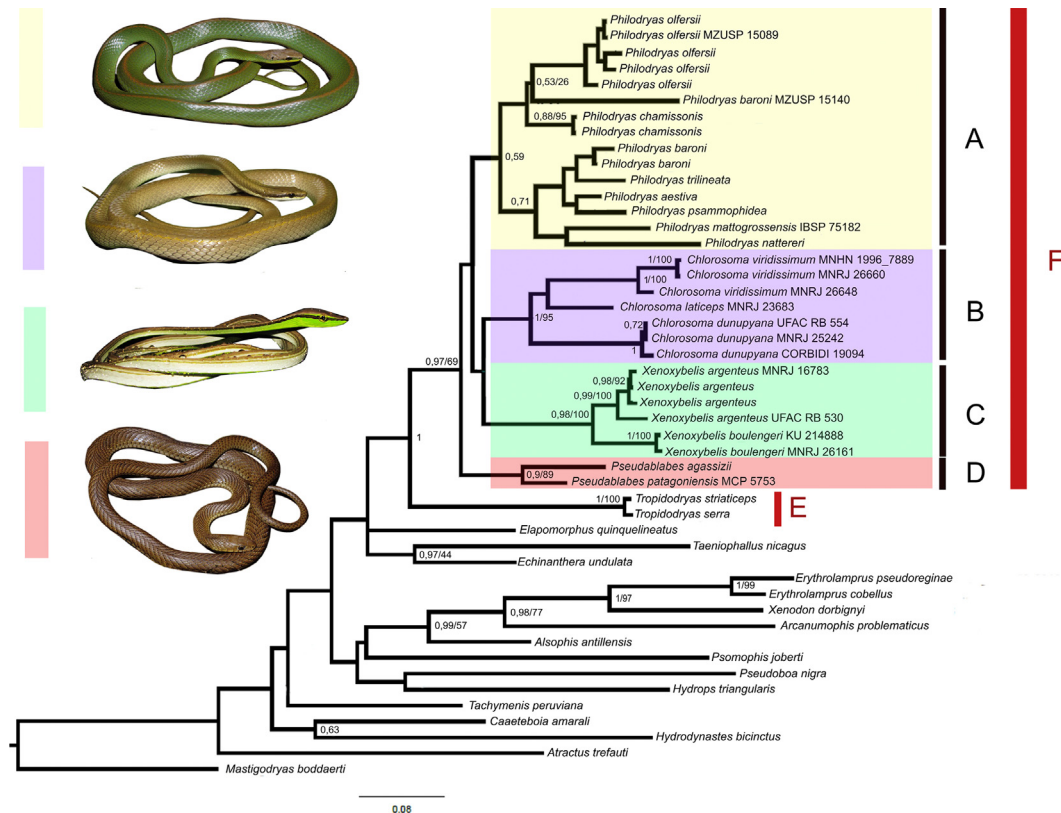
Fig. 1. Phylogenetic relationships of Xenodontinae snakes estimated under a Bayesian framework based on six genes. Posterior probabilities and bootstrap values are separated by slash respectively. Clade A: *Philodryas*; Clade B: *Chlorosoma viridissimum* + *C. laticeps* and *C. dunupyana*; Clade C: *Xenoxybelis*; Clade D *Pseudablabes*; Clade E: Tropidodryadini; Clade F: Philodryadini.

genus *Chlorosoma* for the clade containing *Chlorosoma viridissimum* (Linnaeus, 1758) (Fig. 3) and *Chlorosoma laticeps* (Werner, 1900) **comb. nov.**

The unique combination of features assigned herein to this genus include (hereafter the putative apomorphies followed by '*'): head, body, and tail uniformly green, except for the gular region and anteriormost ventrals being white coloured (yellow in life in the *C. laticeps*; Fig. 3)*; lack of well-defined longitudinal rows of large and deep body calyces on the distal half of the asulcate surface of the hemipenial body*; lateral enlarged spines reduced to middle sized spines; distal rows of middle sized spines disposed in a typical "V-shape" configuration on the asulcate surface of the hemipenial body; * diameter of the half portion of the hemipenes larger than both proximal and distal extremities (Zaher et al. 2008); dorsal scale rows reducing anterior-posteriorly from 19 to 17 to 13—11; high number of ventral scales (204—218); body with slight lateral compression more pronounced in the extremities and belly laterally angulated.

4.2.3. Genus Xenoxybelis Machado, 1993 status revalidated

This genus can be diagnosed by a unique combination of the following characters: mid-dorsal scales smooth in 17 rows (with posterior reduction) without apical pits; head presenting snout complex frontally projected and eyes laterally displaced, resulting in complete stereoscopic vision*; body elongation with 189—207 ventrals and 174—209 subcaudals in both sexes; dorsal surface of body with conspicuous dorsolateral stripes originating at the snout, passing by the eye and extending to the tail*; ventral surface of body with midline or paired ventral stripes*; maxillae with 17—21 subequal teeth followed by a diastema with 2—3 enlarged and

grooved teeth*; dorsal surface of tongue with conspicuous dorsolateral stripes*; hemipenes bilobed and semicapitated with semicentrifugal orientation of the sulcus spermaticus; hemipenes with large spines on its proximal region and with distal spinulated calyces on the sulcate side of capitulum, while asulcate side is mostly naked with a median papillate crest between two rows of body calyces, and two rows of lateral large spines (Procter 1924; Machado 1993; Prudente et al. 2008).

This genus contains *Xenoxybelis argenteus* (Daudin, 1803) and *Xenoxybelis boulengeri* (Procter, 1923) (Fig. 4). *Xenoxybelis boulengeri* was described as *Oxybelis boulengeri* by Procter, (1923). Machado (1993) proposed the genus *Xenoxybelis* to accommodate the sharp-nosed snakes. Zaher et al. (2009) retrieved a paraphyletic *Philodryas* and therefore proposed the synonymy of *Pseudablabes* and *Xenoxybelis*. This action implied in the combination *Philodryas boulengeri* for the taxon formerly known as *Xenoxybelis boulengeri*. Grazziotin et al. (2012) realised that *P. boulengeri* Werner, 1909 was a junior synonym of *P. mattogrossensis* Koslowsky, 1898 and thus, *P. boulengeri* (Procter 1923) represented a secondary homonym. To solve this problem, they proposed the replacement name *P. georgeboulengeri*. However, with the resurrection of the genus *Xenoxybelis* the replacement name is not necessary for *Xenoxybelis boulengeri* (Procter, 1923).

4.2.4. A new species of arboreal rear-fanged snakes

We describe herein a new species very divergent from open forest with bamboo. We have three options based on our phylogenetic tree: 1- leave the *Philodryas* genus as it is, ignoring all the contrary evidences; 2- present a new classification proposal including a new genus for the species that we describe here; 3-
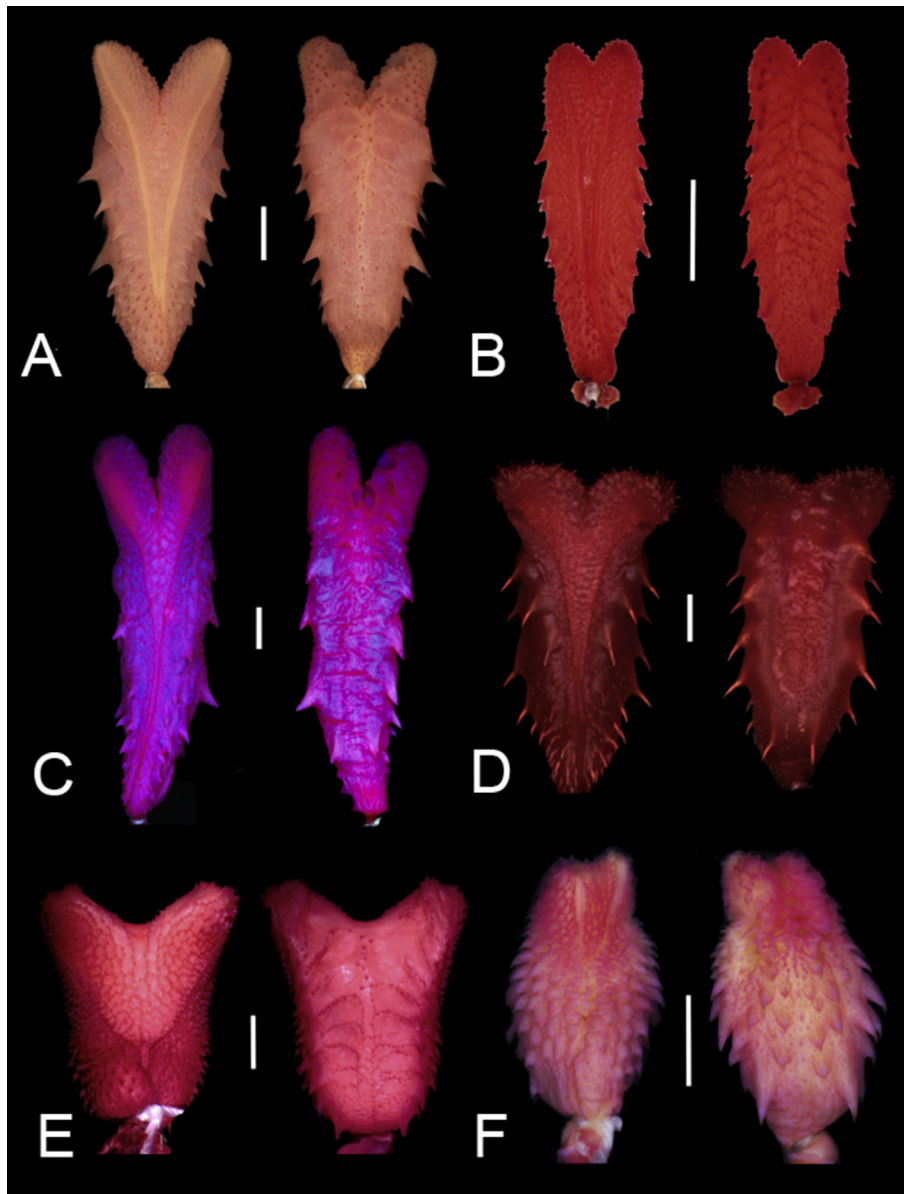
Fig. 2. Hemipenial morphology of some Philodryadini species showing the asulcated and sulcated views. (A) MNRJ 3239 *Philodryas aestiva* from Brasília, Distrito Federal, Brazil. (B) MNRJ 14847 *Pseudablabes agassizii* from João Pinheiro, Minas Gerais, Brazil. (C) MCP 14396 *Pseudablabes arnaldoi* from Arvorezinha, Rio Grande do Sul, Brazil. (D) MNRJ 13391 *Pseudablabes patagoniensis* from Mburucuya, Corrientes, Argentina. (E) MNRJ 8443 *Philodryas olfersii* from Uraçu, Goiás, Brazil. (F) CORBIDI 11237 *Philodryas simonsii* from Caylloma, Arequipa, Peru.

present a new classification proposal, resurrecting three monophyletic and already known genera. The latter option seems more sensible and appropriate for the moment. For this reason, we describe here the third species of *Chlorosoma*. Our criteria for promoting a new classification scheme, combines some ideas pointed out in Vences et al. (2013) with improvements of diagnoses of all recognized genera into broad evolutionary sense. Both clusters of species (i.e., *Pseudablabes*, *Chlorosoma*, and *Xenoxybelis*), exhibit distinct levels of phenotypic and behavioural adaptations for terrestrial and arboreal lifestyle, respectively; which differ broadly from all other species currently allocated in the genus *Philodryas* (terrestrial to semi-arboreal; see discussion). Operationally, our action facilitates the comprehension and recognition of the tribe from a systematic and ecological point of view and provides new insights on the hemipenial evolution likely related to arboreality.

5. *Chlorosoma dunupyana* sp. nov.

urn:lsid:zoobank.org:act:AF20EBF3-91DB-4049-A6E7-882CFB7E6A74

Taeniophallus brevirostris: (non Peters 1863) Silva et al., 2012:169.

Holotype: UFAC-RB 345, an adult male from Parque Zoobotânico of Universidade Federal do Acre, Rio Branco, Acre, Brazil, 9°57′26″ S, 67°52′25″ W, 164 m above sea level (hereafter asl), collected on 15 October 2009 by N.M. Venâncio.

Paratypes: MNRJ 27152 (formerly UFAC-RB 210), an adult male from Segundo Distrito (this region encompasses the urban area of Rio Branco city at the right bank of Rio Acre), Rio Branco, Acre, Brazil, collected on December 1998 by N. Ishi. UFAC-RB 262, an adult female from Parque Ambiental Chico Mendes, Rio Branco, Acre, Brazil, 10°02′11.0″ S, 67°47′43.1″ W, 157 m asl, collected on 17
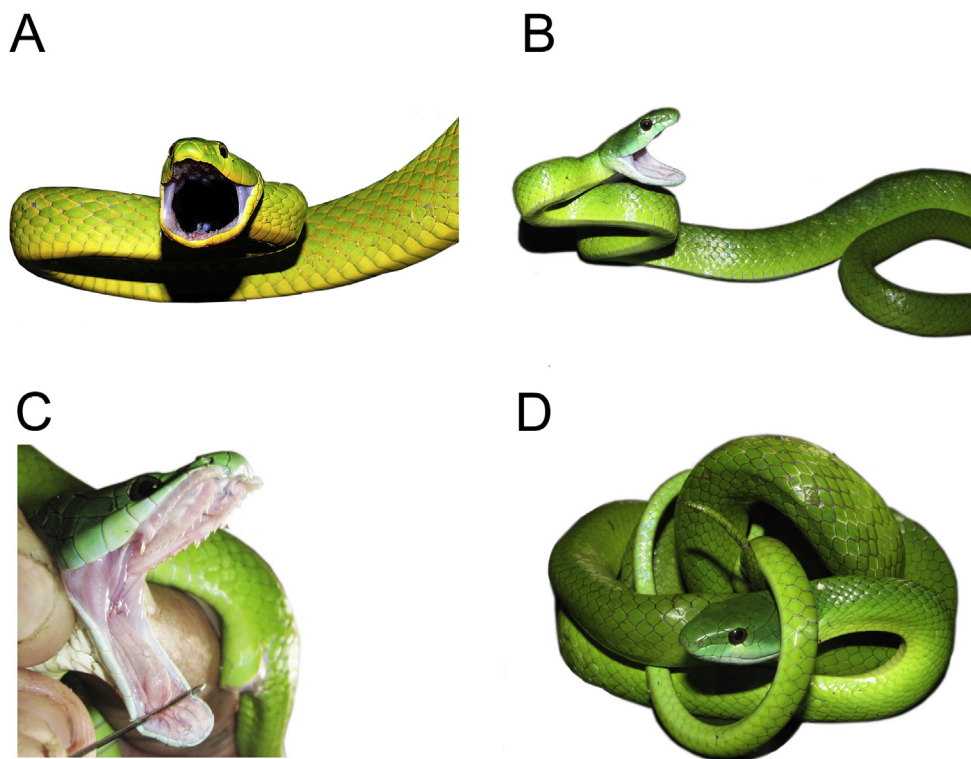
Fig. 3. Live specimens of *Chlorosoma*: (A) *C. laticeps* Photo: Arthur Abegg. (B—D) *C. viridissimum* (UFAC-RB 359) from Rio Branco, Acre, Brazil.
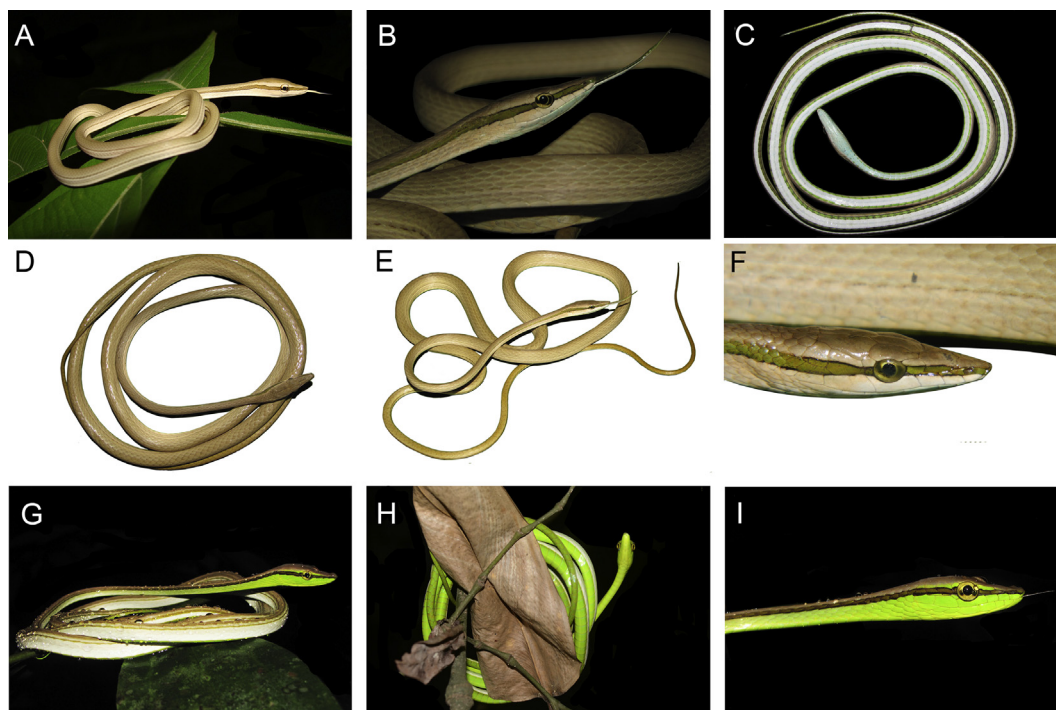

Fig. 4. Live specimens of *Xenoxybelis* species. (A) UFAC-RB 319 juvenile *Xenoxybelis argenteus* (B-F) UFAC-RB 640 adult male *Xenoxybelis argenteus* from Senador Guiomard, Acre, Brazil. (G and I) UFAC-RB 639 adult male *Xenoxybelis boulengeri* from Porto Velho, Rondônia, Brazil. (H) MNRJ 26161 *Xenoxybelis boulengeri* from Boca do Acre, Amazonas, Brazil.

November 2005 by M.B. Souza. MNRJ 27153 (formerly UFAC-RB 346), an adult female from type locality collected on 29 November 2009 by P.R Melo-Sampaio. UFAC-RB 357, an adult female from Chácara de Jesus, km 4 of Quixadá road, Rio Branco, Acre,

Brazil, 9°54′42.8″ S, 67°46′02.6″ W, 173 m asl, collected on 3 September 2011 by P.R. Melo-Sampaio, J.M.L. Maciel, C.M.B. Oliveira, P.L.A. Elias, M.O. da Cunha and R.S. Moura. MNRJ 27154 (formerly UFAC-RB 421), a subadult male from type locality,

collected on 30 March 2012 by M.B. Souza and J.S. Araújo. UFAC-RB 554, a subadult male from type locality collected on 22 October 2014 by P.R. Melo-Sampaio and J.M.L. Maciel. UFAC-RB 649 (PRMS 466 field number), a subadult female from type locality collected on 27 November 2018 by P.R. Melo-Sampaio, R. Mustafa and M.B. Souza. MNRJ 25242, a subadult female from type locality collected on 13 May 2015 by P.R. Melo-Sampaio, E. Lima, J. Costa and J.N. Caruta. CORBIDI 19094 (GCI-084 field number), an adult male from Nuevo Mundo camp, La Convención, Cusco, Peru 11°32′26.8″ S, 73°08′34.8″ W; 333 m asl, collected on 7 October 2017 by G. Chávez.

5.1. Comparisons

Chlorosoma dunupyana differs from all species in the Philodryadini tribe by dorsal coloration being a yellowish cream to smoke gray (vs. uniform green in remaining *Chlorosoma* and some *Philodryas*, uniform gray or pale brown with green stripes in *Xenoxybelis*, dark striped on brown dorsum in many *Philodryas*), small size <650 mm total length (vs. minimum >800 mm in *Chlorosoma* and *Xenoxybelis*), dorsal scale rows in 17/17/15 (vs. 19/19/13 in other *Chlorosoma*, 21/21/17, 19/19/15 or 13/13/13 in *Philodryas* and *Pseudablabes*), hemipenes unilobed with calyces restricted to capitulum and lacking of the lateral row of enlarged spines (vs. bilobed hemipenes with calyces extending to proximal region of the hemipenial body and presence of lateral rows of enlarged spines in Philodryadini), and by molecular data.

5.2. Definition and diagnosis

Chlorosoma dunupyana is a gracile dipsadid snake characterized by the following unique combination of characters: unilobed hemipenes*, with capitulum restricted to a distal region of hemipenial body*; four enlarged spines adjacent to capitulum and few rows of spines throughout body, sulcus spermaticus bifurcating to the half of organ, with enlarged calyces restricted to capitulum*; pupil round; maxillary teeth with two grooved teeth; 17 dorsal scales at mid-body reducing to 15 posteriorly; six to seven supralabials, third and fourth contacting the eye; nine to ten infralabials, first four contacting first pair of chinshields; nasal entire; postoculars two; temporals $1 + 1$ or $1 + 2$; dorsal scales smooth with a single apical pit; 188—194 ventrals; cloacal plate divided; 118—130 paired subcaudals.

5.3. Hemipenial morphology

Organs in situ (entirely retracted; $n = 3$) extend to subcaudals 5—8. Fully everted and almost maximally expanded hemipenes ($n = 3$) renders a unilobed, unicapitate, and unicalyculate; organ ellipsoid with proximal (base of the hemipenial body with spinules) and distal (capitulum) regions narrowed than most of hemipenial body; lobe cylindrical and slightly attenuate; lobular region entirely covered by well-defined shallow (compared to Philodryadini) calyces, constituting a conspicuous capitulum; lobes covered with spinulate calyces connected to below and above series, resulting a faveolate pattern; spinules gradually replaced by papillae toward apices of capitulum; capitular groove well defined on the asulcate side and laterally, and indistinct on the sulcate side; capitulum varying from 30 to 40% length of hemipenial body; hemipenial body elliptical with few irregularly distributed hooked spines; lateral region of the organ lacking a regular row of enlarged spines; largest hooked spines adjacent to capitular groove on the asulcate side and lateral region of the organ; hemipenial body scattered with irregularly distributed medium-sized hooked spines; medium-sized spines more scarce and spaced on the sulcate side; sulcus spermaticus bifurcates at about the half length of

the organ with each branch centrifugally oriented, running centrolinearly to the tip of lobe; sulcus spermaticus margins relatively narrow at level of division and very expanded above capitular crotch; sulcus spermaticus bordered by few spinules or papillae from the base of organ to apices of the lobes; proximal region of hemipenial body narrowed and separated and covered by small spines and spinules; proximal region entirely delimited by a conspicuous nasal constriction on both sides of organ; basal naked pocket absent; proximal region of hemipenes with longitudinal plicae and dispersed spinules (Fig. 5).

5.4. Microdermatoglyphics of dorsal scales

The basal portion is lamellate and imbricate with denticulate smooth borders, not exceeding 6 μm from each other; denticulations triangular, usually higher than wide, rarely exceeding 0.6 μm high, presenting "U" or "V" shaped gaps; cell surface with slightly distinct pores. Mid-apical portion also with layers of lamellate and imbricate cells posteriorly oriented; cell borders with long, narrow and triangular denticulations (about 5 μm high) notably embedded in the adjacent cell at the level of the denticulations, with no depression between each denticulation; denticulations arranged in longitudinal rows, with surface presenting lateral grooves separated by a central prominent crest that extends from each denticulation tip to the adjacent denticulation lateral border; larger pores are present between denticulations (Fig. 6).

5.5. Cranial osteology

Skull deeply ossified (except for dorsolateral portions of nasals), long, limited anteriorly by premaxilla, anterolaterally by maxillae and posteriorly by exoccipitals. In lateral view, the skull height slightly increases towards the middle portion of the parietal, slightly decreasing in width until reaching the exoccipitals. The palatomaxillary arc and snout elements are visible ventrally. The maxilla, lower jaw, palatine, and pterygoid support a row of teeth longitudinally disposed (Fig. 7).
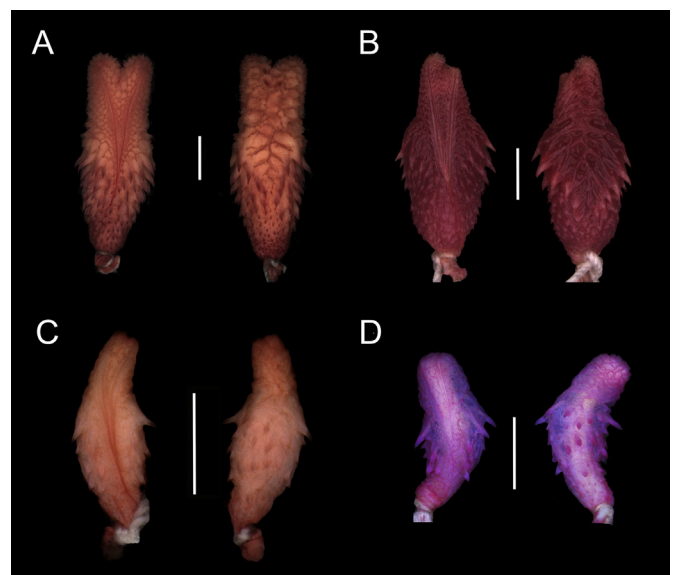

Fig. 5. Hemipenial morphology of all *Chlorosoma* species showing asulcated and sulcated views (A) MNRJ 23683 *Chlorosoma laticeps* from Linhares, Espírito Santo, Brazil. (B) MNRJ 26648 *Chlorosoma viridissimum* from Rio Branco, Acre, Brazil. (C) UFAC-RB 421 *Chlorosoma dunupyana* paratype from type locality. (D) CORBIDI 19094 *Chlorosoma dunupyana* paratype from La Convención, Cusco, Peru.
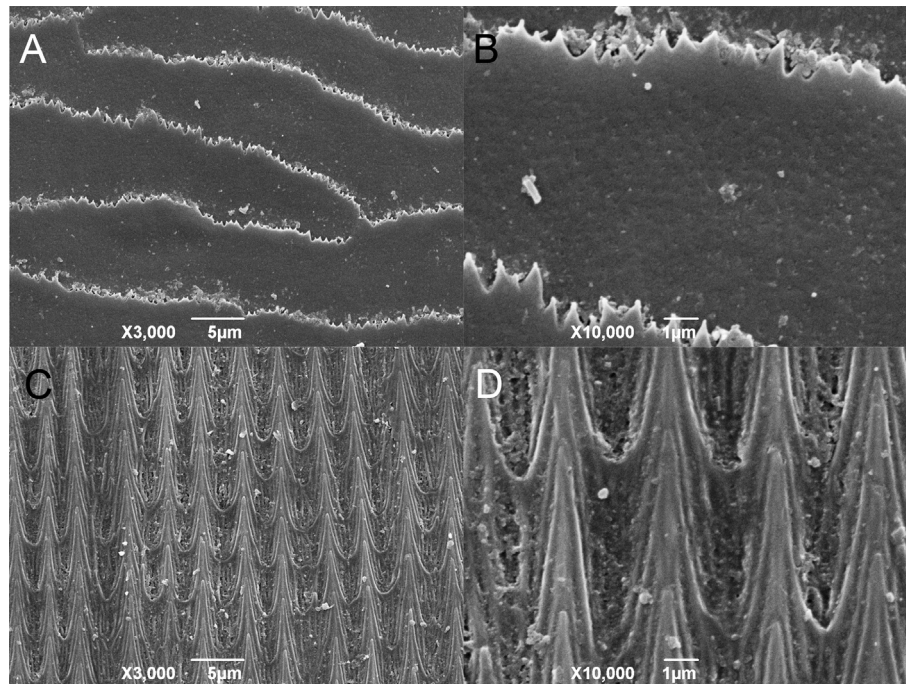
Fig. 6. Microdermatoglyphies of the dorsal scales of the paratype of *Chlorosoma dunupyana* (UFAC-RB 346) from Parque Zoobotânico, Rio Branco, Acre, Brazil. General view (1, X600), basal (2, X3000) and apical (3, X3000) portions, and detailed view of the apical portion (4, X10000).

Premaxilla: small, toothless, on the anterior edge of skull. Nasal process present, tapered towards the nasal, slightly concave in its anterior lamina, not contacting the nasals dorsally. Anteroventral lamina slightly projects anteriorly in a rounded process and expands laterally as the dorsally flattened maxillary processes of the premaxilla; anteriorly, the premaxilla is approximately triangular. Ventrally, the premaxilla displays two or three foramina, expanding posteriorly into bifurcated septomaxillar processes that contact each vomer in its anterior medial portions, but not in contact with the septomaxillaries. **Septomaxillae:** well developed, forming the nasal cavity floor. Dorsally, each septomaxilla expands anteriorly towards the premaxilla overlapping the anterior wings of the vomer. Anterior borders in dorsal view are slightly rounded, with two anteriorly directed processes: (1) in anterolateral position, (2) might be present or absent, slightly more developed, anterior to the ascending lateral flange of the septomaxilla. The ascending lateral flange connects ventrally to the lateral wing of vomer to form the *fenestra vomeronasalis*, which is circular. The lateral flanges expand dorsally inflecting medially, tapering or not in its dorsal end in its dorsal portion towards the nasals. Each septomaxilla also expands posteriorly to connect dorsally to the posterior and most ventral portion of the nasal septum, and also to the ventral-anterior process of the frontal, by a posterolateral process slightly inflected anteriorly, representing the only connection of the prokinetic joint attaching to the braincase. This posterior process rests on the posterior and dorsally developed process of the vomer.

Nasals: slightly triangular or trapezoidal in dorsal view with convex dorsal lamina, anteriorly in skull between the premaxilla and frontals, forming the roof of the nasal cavity. Each nasal is pierced by a well-developed foramen, which constitute the foramen for the *apicalis nasi* nerve (*sensu* Oelrich 1956). Each nasal develops ventrally into a nasal septum situated vertically to longitudinal line of contact between nasals, forming the nasal cavity inner wall. The nasals do not reach the lateral processes of prefontrals. **Vomers:** well-developed premaxillary processes present, a lateral process, and a laterally flattened and well-developed posterior process present. The anterior process of the vomer tapers anteriorly to attach to the lateral edge of the septomaxilla process of the premaxilla. Ventrally, the posterior and medial edges of the anterior process develop into a medial process that slightly occludes the *fenestra vomeronasalis*. The lateral processes are convex posteriorly and form the posterior wall of the *fenestra vomeronasalis*. It contacts the ventral lamina of the septomaxilla throughout most of its ventral lamina. The posterior and ventral portion of lateral wall of the posterior process is pierced by a large foramen. In ventral view, the posterior processes slightly inflect medially. **Frontals:** trapezoidal dorsally, enlarged medially and slightly tapered laterally. Anterior and posterior edges slightly convex, lateral edge concave, and medial suture straight. A short anterolateral process is present and contacts the prefrontals anterolaterally. The posterior lateral portion of the dorsal lamina of the frontal is often pierced by one or two foramina. The medial frontal pillars are present and fused to the subolfactory process. The anterior ventral lamina of each frontal develops an anterior process to attach to the septomaxilla. **Prefrontals:** rectangular in dorsal view, contact the frontal in its posterolateral portion and the maxillary ventrally. The lateral descending lamina of prefrontal is enlarged anteriorly and posteriorly, and its ventral portion is pierced by the large lacrymal foramen, and dorsal to it, a small foramen. Its medial-ventral portion expands medially towards the palatine to form a short process that does not contact the palatines. Anterior lamina of prefrontal is marked by a deep recess dorsally to the lachrymal foramen. **Postorbitals:** small and slender, each postorbital delimits the orbital cavity posteriorly. They attach to the parietal through an anterior-laterally hollow. **Parietals:** anterior edge concave, sutured to the frontals, with or without a slightly small projection that fits into their medial suture. The parietal exhibits short anterolateral projections articulating with postorbital bone. Posteriorly, the parietal is sutured to the supraoccipitals and posterolaterally to the prootics. It is also pierced by a pair of small medial foramens. The parietal descends lateroventrally to fuse to the lateral edges of the parabasisphenoid through a medial folding.
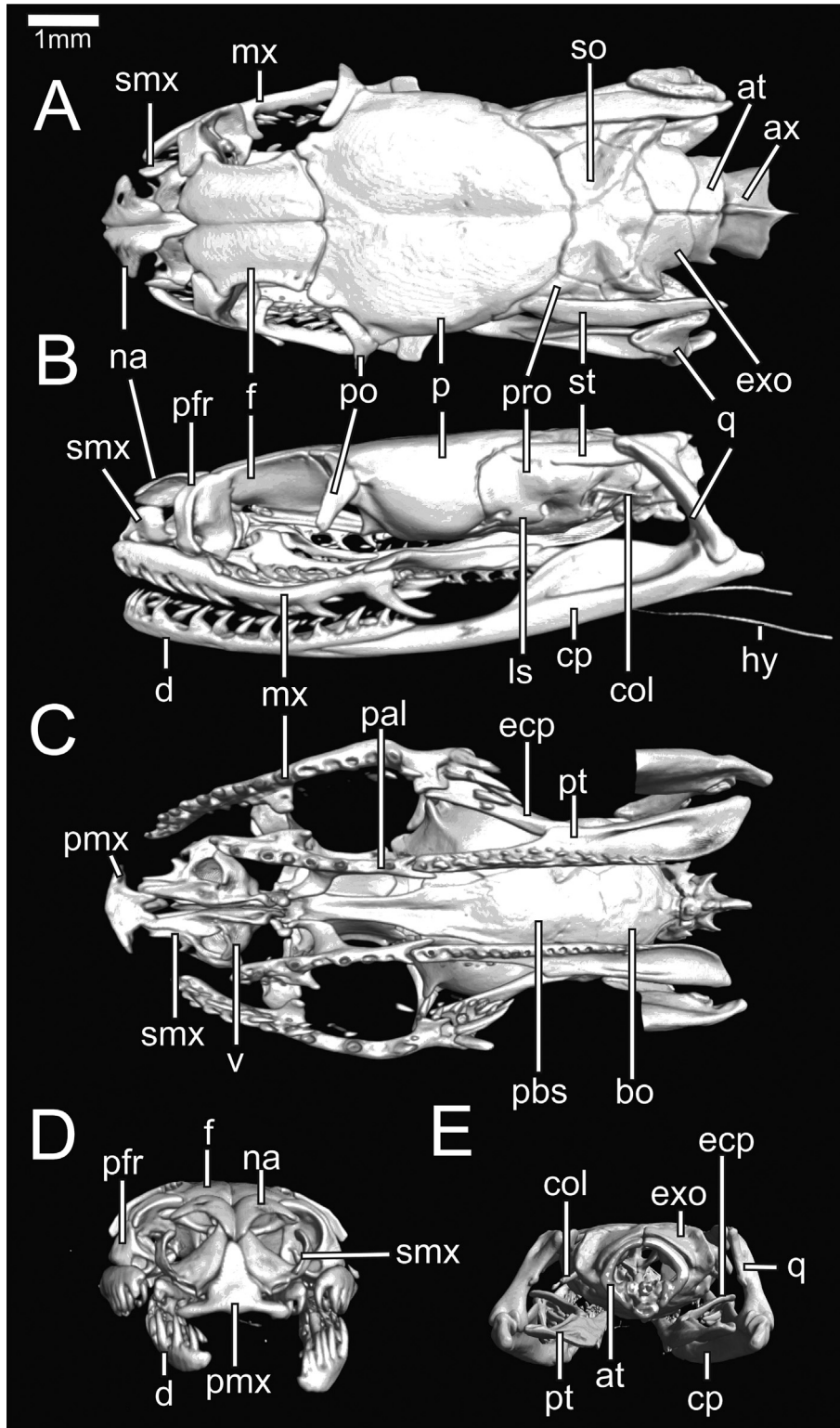
Fig. 7. Dorsal (A), lateral (B), ventral (C) views of skull and anterior (D) and posterior (E) views of mandible of the paratype of *Chlorosoma dunupyana* (UFAC-RB 346). Abbreviations are as follows: pmx = premaxilar, ns = nasal, smx = septomaxillar, pfr = prefrontal, pal = palatine, pso = presubocular, mx = maxillar, po = postorbital, pbs = parabasisphenoid, bo = basioccipital, p = parietal, pp = parietal process, st = supratemporal, ecp = ectopterygoid, pro = prootic, exo = exorbital, q = quadrate, at = atlas, ax = axis, d = dentary, hy = hyoid, col = columella, v = vomer.

The posterior internal pillars are present and well-developed. **Supraoccipital:** heptagonal and in the dorsal-posterior region of the skull. It contacts the parietal anteriorly, prootics laterally, and exoccipitals posteriorly. Its dorsal surface presents two oblique crests, splitting the supraoccipital into three triangular shaped regions: two lateral regions, with concave surface and pierced or by a single foramen; and a posterior region slightly concave posteriorly in a region that is pierced by a pair or a single foramen.

Exoccipitals: elongate in dorsal view and in the posterior edge of skull, comprising the dorsal edge of the *foramen magnum*. Each exoccipital contacts the basioccipital ventrally and prootic laterally and articulates to the atlas posteriorly. Dorsally, each exoccipital presents a posterolateral and well-developed crest which may be pierced or not by a pair of foramens posteriorly, and a single foramen anteriorly. This crest also descends lateral-ventrally, ending in the lateral limits of the skull in ventral view, where it is pierced by two foramina that open internally; the large opening for the vagus nerve, immediately posterior to the *fenestra ovalis*; the reduced hypoglossal nerve foramen. Three small additional foramina perforate the posterior lateral lamina of each exoccipital, located one dorsal to the other, and ventral do the atlantal process. The ventralmost foramen might represent the second opening for the hypoglossal nerve. The lateral-ventral wall of the exoccipital forms the *fenestra ovalis* together with the prootics. The posterior dorsal limits of the exoocipital develop into well-developed atlantal processes of the exoccipitals, covering the anteriormost portion of the atlas. **Basioccipital:** hexagonal, in the mid-posterior portion of the braincase; the basioccipital contributes to the posterior portion of the braincase floor, as well as the median portion of occipital condyle, articulating to the ventral element of the atlas. In contact with the parabasisphenoid complex in an anterior centrally concave suture, anterolaterally to the prootics and posteriorlaterally to the exoccipitals. Its ventral surface may be pierced or not by a foramen located posteriorly in its ventral surface. The dorsal surface of the basioccipital is slightly concave and pierced by three posterior foramina. **Parabasisphenoid complex:** elongate, slightly tapering anteriorly, and ending anteriorly into a bifurcate tip or triradiate with lateral tips slightly longer than de medial one. The thin anteroposterior region of the parabasisphenoid complex expands into a short median wall that supports the subolfactory processes of the frontals. Its posterior-ventral surface is slightly convex, pierced by a pair of foramina, which most likely represent the posterior Vidian foramen. The dorsoposterior surface of the parabasisphenoid complex is notched by a well-developed *sella turcica*, posteriorly followed by a dorsal wall that slightly projects over the this region, and then extends posteriorly forming the posteriormost region of the dorsal surface of the parabasisphenoid complex. This area is pierced by a pair of foramina. Another foramen is formed together with the parietal in its posterolateral edge and might represent the foramen for dorsal constrictor branch of trigeminal nerve. **Prootics:** irregular and contacting the parietal throughout all its anterior edge, the parabasisphenoid and basioccipital ventrally, the supraoccipital dorsoposteriorly, and the exoccipital lateral-posteriorly. Each prootic presents a short dorsal and lateral process to support the supratemporal. A laterosphenoid splits the foramen for the maxillary branch of trigeminal nerve, located more anteriorly, and the posterior foramen, the foramen for the mandibular branch of trigeminal nerve, slightly larger than the former. The foramen for the facial nerve pierces the posterior internal pillar. Two additional foramina are present immediately bellow the foramen for the mandibular and maxillary branches, being relatively smaller than the formers. The posterior region of the prootics opens to the insertion of *columela auris*.

Optic capsule: without a statolithic mass. The acoustic nerve passes through a pair of foramina that pierce the internal wall of the prootics. A small foramen ventral to both acoustic foramina open externally into the large foramen for the mandibular branch of trigeminal nerve. An endolymphatic foramen is present. A medial opening for the *recessus scalae timpani* is present, located anterior to the internal opening for the vagus nerve. A small foramen perforates the anterodorsal medial wall of the optic capsule, opening into the anteriormost semicircular canal.

Maxillaries: curved at the marginal line of skull, limiting the lateral edge of anterior and medial portion of skull. Each maxilla extends from the level of the anterior limit of the septomaxillae, until reaching the ectopterygoid slightly posterior to the level of the palatine and pterygoid contact. The medial surface of each maxilla is concave, exhibiting a medial palatine process that supports the descending wall of the prefrontal and an ectopterygoid process, located on its posterior region. The ventrolateral margins of maxilla support a series of 12−15 curved posteriorly teeth, followed by toothless area equivalent to three to four interspaces among previous teeth. Posterior to the toothless area there is a pair of enlarged teeth notched by an evident posterior groove forming rear-fang. **Palatines:** elongate, shorter than the maxilla, extending anteriorly from the level of the lateral processes of the vomer, until reaching the pterygoids posteriorly into a forked edge (the medial longer than the lateral). An anterior process at the level of the 3rd−6th tooth develops dorsal-laterally, also giving support to the descending wall of the prefrontal. A medial process (the choanal process of the palatine) develops at the level of the 6th−7th tooth, projecting dorsally and anteriorly and then folding ventrally. This process does not contact any skull element. The ventral surface of the palatine supports a longitudinal series of eight or nine teeth extending until the posterior portion of bone. **Ectopterygoids:** elongate, forked anteriorly, with its lateral projection supported by the maxilla, on the level of the fang, and the medial process supported by the posterior maxillary process. The posteriormost edges of the ectopterygoids attach to the pterygoid through a lateral flattened posterior portion, at the level of its 10−13th tooth. **Pterygoids:** elongated extending through over half of skull total length. Each pterygoid is posteriorly to the palatine with its posterior end about three times larger than the anterior one, fitting to the palatines anteriorly, and receiving the ectopterygoid posterior process dorsally. The ventral surface of the pterygoid is laterally curved and supports a row of 12−17 teeth. The pterygoidal teeth are slightly smaller than the palatine ones.

Columela auris: small and paired bone inserted in the *fenestra ovalis*, crossing the such region towards the quadrate. The μCT images show that the collumela does not attach to the quadrate, ending bluntly in this path. This suggests that the collumela is connected to the quadrate by a columellar cartilage. **Supratemporals:** elliptical placed posterior-laterally to the braincase. Each supratemporal extend over most of the prootic length, and exceeding the posterior limits of the skull, reaching the level of the atlas. Its medial surface attaches to the dorsolateral surface of the prootic, and attaches to the quadrates in its posterior medial surface. **Quadrates:** articulating slightly obliquely to the skull. Its proximal portion articulates with the supratemporal while its distal end slightly enlarges to articulate to the glenoid cavity of retroarticular process, forming the quadrate-articular articulation. The medial surface of each quadrate with a short posterior oblique process. Its distal medial lamina is perforated by a small foramen, located in a recess dorsal to its articulatory head with the compound bone. **Dentaries:** each dentary curve medially in its anterior end towards the opposite dentary. The medial surface of the dentary receives the elongate anterior process of the splenial, above the Meckel's groove, which extends from the level of the 8th teeth. The posterior portion of the dentary forks into a dorsal and ventral portion. The dorsal contacts the anterior tip of the angular in its medial surface, and the ventral attaches to the splenial in its medial surface, and to the angular in ventral-lateral view. The compound bone also attaches to the forked end of the dentary, touching the ventral surface of its the posterior dorsal process. The dorsal edge of the dentary supports a row of 17−19 teeth. **Splenials:** triangular, deeply tapered anteriorly, at the medial surface of the mandible. Its

anterior end fits to dentary through a long and tapering process that reaches the level of the ninth tooth, while its posterior end contacts the angular. Its posteromedial surface is pierced by a single milohyoid foramen. **Angulars:** triangular, at the medial surface of the mandible, with a long and tapering projection oriented posteriorly, and a dorsal process that extends above the splenial until reaching the dentary dorsally. It attaches do the compound bone posteriorly, also in contact with the dentary anteriorly in its dorsal and ventral processes, and the splenial anteriorly. The dorsal process of the angular originates at level of the 12th dentary tooth. Its medial surface is pierced by a single mylohyoid foramen. **Compound bone:** elongated representing largest bone of mandible. and connected to the skull through the glenoid cavity in its posterior end. The anterior portion projects as a tapering process, inserting onto the dentary and extending until the level of 12−13th dentary tooth. The surangular crest forms a deep mandibular fossa on its medial portion, and more posteriorly, the short retroarticular process short extends posteriorly and slightly ventrally, being and pierced by foramen on its ventral lamina. The foramen for the facial nerve VII is present, anterior to the retroarticular process, ad posterior to the glenoid cavity. A short mid-ventral process is present, projecting from the medial posterior lamina of the quadrate, projecting ventral into a short rod-shaped process. **Atlas:** slightly dorsoventrally compressed, and lacking a neural spine and ribs associated to it. The neural arches are paired and non-fused lateral elements, not contacting each other dorsally. Both elements expand posteriorly and dorsolaterally to form short processes that do not articulate to the axis. A short transversal process is present. The intercentrum I (*sensu* Holman 2000) is ventral to the neural arches, not fused to them, being roughly triangular in anterior view, tapering ventrally. **Axis:** composed by a centrum, a neural arch, a spinal process, an odontoid process, a condyle, a cotyle, and an intercentrum II and III. No ribs are associated. A short lateral anterior process develops anteriorly to articulate to the atlas, in the ventral surface of the neural arches. The neural spine is poorly developed, dorsally projected, and slightly anteriorly and posteriorly projected. A postzygapophysis articulate to the prezygapophyseal articular facet of the first trunk vertebrae. A transverse process develops posteriorly. The Intercentrum II is roughly triangular or rounded in shape, being pierced by three small foramina, located at the anteriormost edge of its lateral surface. The Intercentrum III is pointed (*sensu* Holman 2000), pierced by two foramina, dorsal to its anterior limit. The odontoid process tapers anteriorly. Its dorsal surface is pierced by a pair of foramina located at the lateral end of a crest present at this region. **Anterior trunk vertebrae:** bearing a neural spine that runs along its entire dorsal surface, except for the anteriormost portion of the vertebrae and slightly exceeding the posterior limits of the vertebrae. The zygosphene articulate with the zygantral articular facet. The postzygapophysis articulate through the postzygapophyseal articular facet to the prezygapophyseal articular facet of the posterior vertebrae. A prezygapophysis develops laterally into a prezygapophyseal accessory process that articulates with through the oval prezygapophyseal articular facet to the vertebrae anterior to it. The centrum is notched by a single foramen visible in lateral view. The synapophysis are composed by both the diapophysis and parapophysis. Ventral to the vertebrae, a well-developed hemal keel runs through most of the vertebral extension, posteriorly developing into a well-developed hypapophysis, truncated in lateral view. The condyle and cotyle are oval, rounded and slightly flattened dorsal-ventrally. **Ribs:** long, curved and articulate to the synapophyses of their respective vertebrae through a diapophysis + parapophysis; tuberculiform process is present and oriented posterior and medially; a single foramen in the median line of the ventral lamina of the rib head is present; a lateral

foramen is absent. **Hyoid**: "Y-shaped", with a short lingual process that starts at the level of the posterior process of the basioccipital, expanding posteriorly into well-developed cornua that exceed the limit of the 7th trunk vertebrae.

5.6. Visceral anatomy

Heart at 23.8% (SVL), the mid-ventral line of the body cavity, being relatively small in size (1.8%); right atrium twice longer than the left, projecting more anteriorly, and posteriorly over the lateral border of the ventriculum; Left atrium limited posteriorly by the ventriculum anteriormost border, not overlapping it; posterior end of ventriculum slightly oriented to the right; ventriculum elongate and tapering at its posterior end, twice longer than the right atrium; systemic arches joint posterior to the heart (1.4%). Thyroid gland short, ellipsoidal, anterior to the heart, with a slight gap from the heart; two pairs of thymus are located at both sides of the thyroid; the trachea extends up to the anterior tip of the heart, where the parenchyma slightly enlarges to constitute the cardiac lung in the middle of the heart length (at the anteriormost border of the ventricle), extending dorsal to the posteriormost part of the heart; the right lung is unicameral, bearing faviform parenchyma (*sensu* Wallach 1998), with posterior limit uncertain due to damage by tissue removal for DNA sampling; a vestigial and small left lung (0.5%) connects to the trachea but does not bear its own left bronchus. The posterior tip of the left lung is slightly posterior (21%) to the ventricular apex (20%). The parenchyma continues forward to the heart, on the wall of the trachea, with discrete trabeculae extending about half-heart length anterior to the heart; the liver is the longest organ in the body (27.8%), light red in colour (preserved specimen) and located on the right side of the body cavity, separated from the heart by a short gap (7%); the right liver extends more posteriorly than the left one (1.4% posterior asymmetry). The pancreas is large (1.2%), oval and creamish white, attached to the anterior end of the duodenum; the gall bladder is oval, anterior to the pancreas, in the left side of pyloric region, in contact with the spleen laterally, and to the pancreas posteriorly; the pancreas, spleen and gall bladder are in the anterior part of the second half of the body; the testicles are in the anterior part of the last third of the body cavity, a quite long gap (20%) from the gall bladder, lying slightly anterior to the kidneys (0.8%), being ovoid in shape. The specimen examined bears thickened and coiled efferent ducts; the adrenals are light orange in colour, dorsoposteriorly to each of the testes, small and slightly elongated; the kidneys are the last paired organs in the body cavity (4.2% distance from the vent), being ellipsoidal, deeply lobed and elongated. The right kidney is longer (4.2%) than the left (3.2%), and is located more anterior than the left one, although no gap is found between them. Its medial surface is slightly concave. A rectal caecum is absent.

5.7. Description of the holotype

An adult male, dorsals in 17/17/15 rows; dorsal scale rows reducing to 16 at level of scale 116 (right) and 118 (left) respectively; posterior reducing to 15 scales rows at level of ventral scale 125; dorsals above tail in 6/6 rows; hemipenes extends to level of tenth subcaudal; the muscle retractor extends to level of 24th subcaudal vertebra; 190 ventrals, angulated; 121 subcaudals paired; anal plate divided; terminal spine as large as adjacent subcaudal; supralabials 7/7 with 3 and 4 touching the orbit; infralabials 10/10 with first five in contact with anterior genials; two pairs of chinshields (genials); 5/6 infralabials in contact with second pair of genials; gulars in 5/5 rows; four preventrals; nasals entire; preoculars 1/1; loreals 1/1; post-oculars 2/2; temporals in

1 + 2+2/1 + 2+2 rows; teeth 14 + 2/14 + 2 being the last two enlarged, sulcated and separated by diastema. SVL 347 mm; TTL 160 mm; mid-body diameter 4.9 mm.

Head length 126 mm; head width 5.7 mm; eye diameter 2.1 mm; body diameter 6 mm; rostral subhexagonal width 2/2 mm, 1/1 mm long; internasals 1.2 mm long, 1.5 mm wide; internasal suture sinistral; rostral not visible from above; head distinct of the body; snout rounded in dorsal view, truncated in lateral view; canthus rostralis well defined; head depressed in lateral view with orbital region slightly pronounced; rostrorbital distance 3.3 mm; interorbital distance 4.2 mm; nasal-orbit distance 2.4 mm; postorbital-quadrate distance 6.2 mm; head height 3.8 mm; prefrontal 1.4 mm long, 2.1 mm wide, rectangular; supraocular length 2.7 mm, 1.4 mm long, slightly concave above the eye; frontal subpyramidal 3.6 mm long, 2.3 mm wide anterior and 1.8 mm posterior; parietal 4.8 long, 2.9 mm wide; nasal entire 1.4 mm long, 0.7 mm high; loreal 1 mm long, 0.6 mm high; preocular not in contact with frontal 1.5 mm height, 0.7 mm length; eye diameter 2.1 mm; postoculars rectangulars and subequals slightly wide than long; anterior temporals two times long than wide; sixth supralabial enlarged and elongated in the lower line of postocular; triangular symphysial; anterior genials two times longer than wide, posterior genials four times longer than wide; height of midbody 6.1 mm.

Dorsum of head beige (smoke gray) with black suture between the cephalic shields. Interparietal suture black. Irregular black interparietal stripe extending from the anterior portion of parietal scales, into the first occipital scale, immediately after the parietals; center of the frontal and parietal shields with diffuse and smoky greenish pigment; background of the head beige into the dorsal portion of supralabials; black lateral stripe beginning in the medial portion of rostral shield and extending to the end of supralabials; stripe with tenue black pigments on the nasals, loreal, lower portion of preorbital, lower postocular, anterior and posterior temporals; conspicuous stripe on the dorsal margin of supralabials completely black; sixth and seventh supralabials with black spots, extending more ventrally; gular region cream immaculate; venter and tail cream with some dark sutures (Fig. 8).

Dorsum of body beige (smoke gray), except by the three first cream scale rows, starting from 30th ventral; dorsal scales mostly beige; paravertebral region delimited by two thin stripes yellow-green formed by the depigmentation of lateral margins of the eightieth rows from each side; vertebral stripe with 2.5 scales wide; paravertebral lines more conspicuous after 40th scale into 150th ones.

5.8. Meristic and morphometric variation

Total length ranging from 241 to 640 mm in females, 420—555 mm in males; TL/TTL 41.8—51.6% in females, 47—50% in males; usual colubroid pattern complement of head scales; supralabials usually 7/7 but may be 6/6 in some specimens due fusion of two last scales, with third and fourth supralabials contacting the eye; infralabials 9/9 or 10/10, first four contacting anterior chinshields; postoculars 2/2; temporals 1 + 2 with the anterior scale larger (sometimes 1 + 1); ventrals 188—194 in males, 188—192 in females (there is no apparent secondary sexual dimorphism); subcaudals 122—130 in males, 112—126 in females; dorsal scales smooth without apical pits; dorsal scales in 17/17/15 rows; 8—14 maxillary teeth plus one or two postdiastemal grooved teeth; dorsal colouration uniformly beige with lime green narrow paravertebral stripes starting in the first quarter of body, bordering the edges of seventh and eighth dorsal scale rows. Paratypes MNRJ 27152 and UFAC-RB 554 have an entire cloacal plate. Males are generally darker than females (Fig. 9).

5.9. Natural history

Chlorosoma dunupyana is a diurnal species that feeds on small treefrogs (*Scinax ictericus* Duellman & Wiens 1993) as checked in the stomach content of the paratype MNRJ 25242. It is very active both on the ground and on trees searching for prey items in the early morning. During the sunset, the species is found climbing shrubs, palm leaves and trees to sleep. Three specimens were found coiled in branches in height ranging from 4 to 8 m (Fig. 10). An adult female (UFAC-RB 357) was collected in September 2011 and her oviduct contained mature eggs. The new species is found syntopically with the arboreal snakes *Chlorosoma viridissimum* (Linnaeus, 1758) and *Xenoxybelis argenteus* (Daudin, 1803) in forest fragments in Rio Branco, Acre, Brazil with a disjunct population in the lower Urubamba river (one of the longest Peruvian rivers and one of the first Andean tributaries of the great Amazon basin) Cusco, Peru, typically occurring in bamboo forest surrounded by open areas (Fig. 11). The paratype CORBIDI 19094 was also found active in the afternoon (26 °C air temperature) foraging between bamboo branches at a height of two meters above the ground, showing no aggressive behaviour and only trying to escape at the time of capture.

5.10. Etymology

From the Panoan speakers Katukina/Kashinawa Indigenous words *dunu* (= snake) + *pyanã* (= venomous) (see Souza et al. 2002), used herein in reference to well-developed Duvernoy's gland and rear-fang in the posterior portion of maxillary of the newly discovered snake.

6. Discussion

6.1. Generic assignment for Coluber viridissimus Linnaeus, 1758

Amaral (1929b:104) employed the genus *Chlorosoma* in reference to other species of *Philodryas* (e.g., *P. olfersii*), explicitly arguing that the first genus has priority over *Philodryas* due to pagination precedence (Amaral 1929c: 212). Amaral (1929a: 42) mentioned for the first time the name *Chlorosoma viridissimum* when he synonymized *Philodryas affinis* Müller, 1928 with the former. Later, Amaral (1932) also included under this generic allocation the new species *Chlorosoma arnaldoi*. However, Parker (1932) pointed out that the first mention of both genotypes (*P. olfersii* and *Chlorosoma viridissimum*) were joined in a single genus *Philodryas* for the first time by Günther (1858), who acted under principle of first reviewer (ICZN 1999). Following Peters & Orejas-Miranda (1970), the combination in genitive masculine as *Philodryas viridissimus* was employed by all subsequent authors until the early 90's when Donnelly & Myers (1991) clarified the gender of the genus *Philodryas*, rendering a genitive feminine owing to Wagler's (1830) original spelling. We noted an important lapse in synonymic list of Wallach et al. (2014) where information about type-species of the genus *Chlorosoma* is missing. We also noticed that spelling related to gender of genus-group names that must be appreciated. Following Article 30.1.2 of ICZN (1999), we apply to the genus *Chlorosoma* the rule that implies when Greek nouns transliterated without change into Latin as the whole or part of a name are neuter in gender. Thus, the Greek word Χλωρος (*chloros* = green) with suffix "σωμα" (*soma* = body) when combined in a genus the specific epithet should be also neuter, so the correct spelling is *Chlorosoma viridissimum*, which contemplates the idea of the green snake (grüne Schlange) of Wagler (1830) and re-establishes the correct binomium used by Amaral (1929a, b, c).
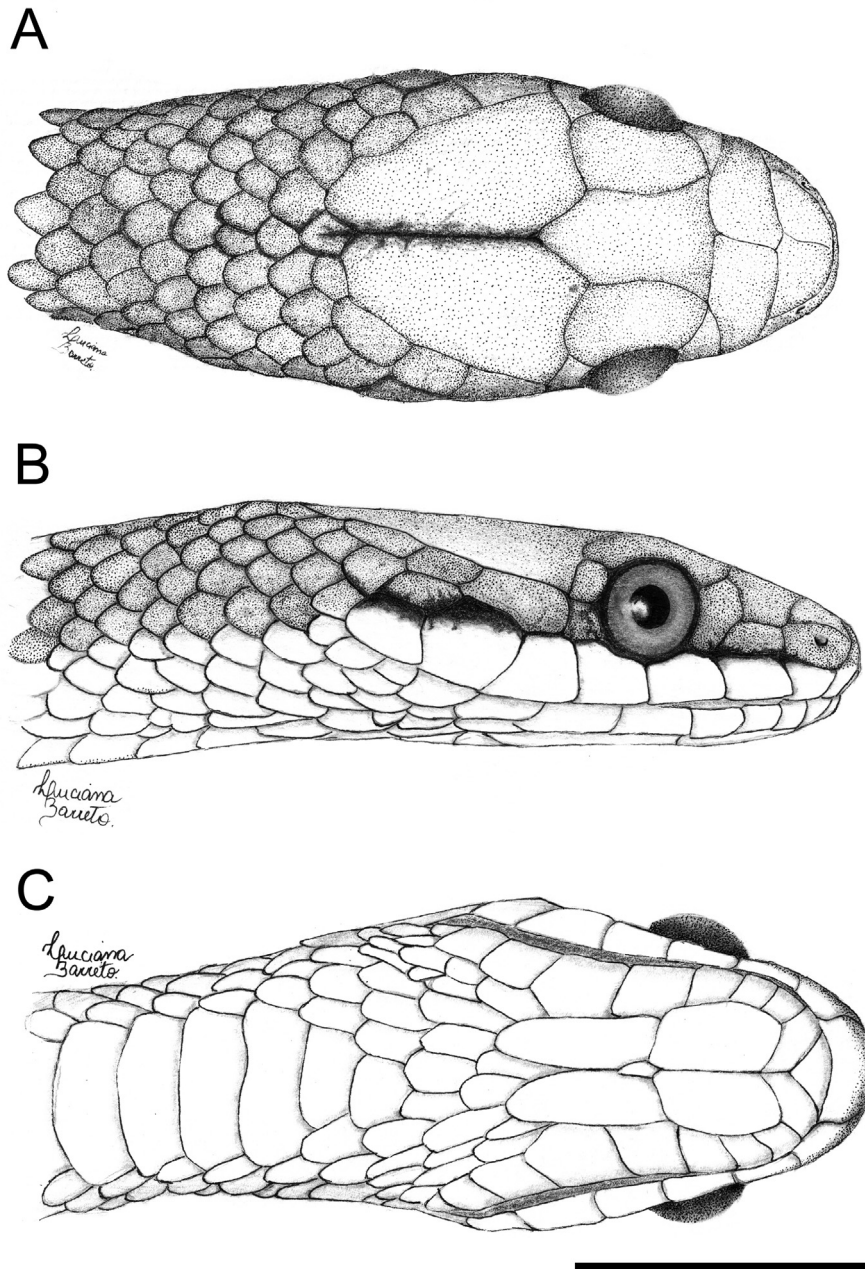
Fig. 8. Dorsal (A), lateral (B) and ventral views (C) of the holotype of *Chlorosoma dunupyana* sp. nov. (UFAC-RB 345) from Parque Zoobotânico, Rio Branco, Acre, Brazil.

6.2. Novel relationships within Philodryadini

Zaher et al. (2009) suggested that improving the phylogenetic coverage of the genus *Philodryas* might implicate in changes of their proposed classification, being some of the generic names they synonymized (*Xenoxybelis*, with our emphasis added), being applicable to the recovered monophyletic subunits. By including new samples of an unknown lineage of snakes, our results recovered ancient phylogenetic relationships and provide new insights on the evolution of this clade. The relationships of *Chlorosoma laticeps* with *Ch. viridissimum* and *Ch. dunupyana* reinforces the hypothesis of a past connection during Pleistocene between two Neotropical rainforest ecoregions (Carnaval & Moritz 2008; Prates et al. 2016). Among squamate reptiles, recent results also

corroborated the affinities of Southwestern Amazonian taxa with South Atlantic Forest species (Rodrigues et al. 2014; Prates et al. 2017) and for viperid snakes were recovered multiple connections (Dal Vechio et al. 2018). Historically, *Chlorosoma viridissimum* has been the most difficult taxon to recover in a robust phylogenetic relationship within Philodryadini. Previous authors apparently had an insufficient amount of data to elucidate its position due to the absence of closely-related Amazonian and Atlantic forest species.

The taxonomy and nomenclatural history of the genus *Philodryas* is complex (see Zaher et al. 2008). Recently, Zaher et al. (2014) described *Philodryas amaru* and proposed an arrangement with 18 species. Cacciali et al. (2016), after studying *P. mattogrossensis* populations, resurrected *Philodryas erlandi* Lönnberg, 1902 to
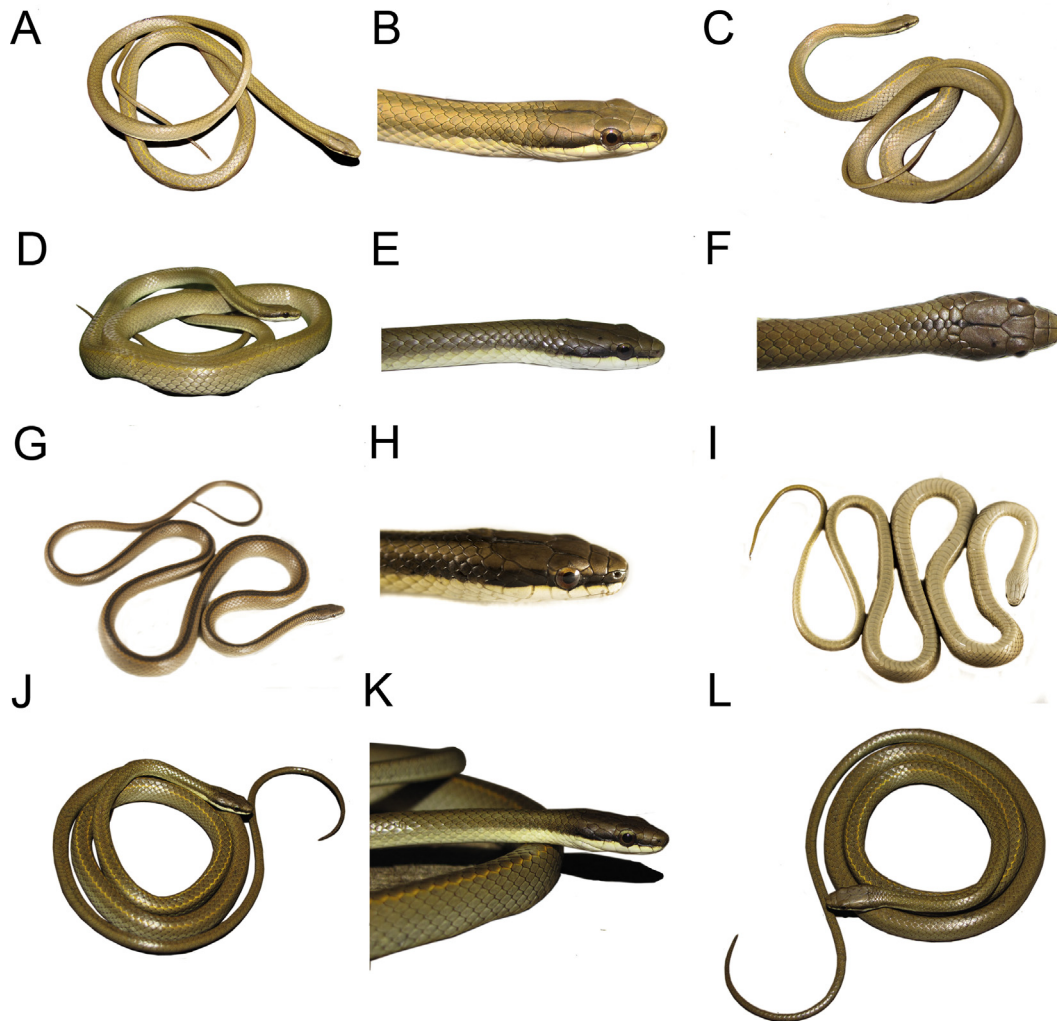
Fig. 9. General view of *Chlorosoma dunupyana* in life: (A—C) Adult female paratype (UFAC-RB 346) from type locality. (D—F) Adult female paratype (UFAC-RB 357) from Chácara de Jesus, Rio Branco. (G—I) Adult male paratype (CORBIDI 19094). (J—L) Adult male paratype (UFAC-RB 421) from type locality.

accommodate Chacoan populations. Considering the complex nomenclature, the distinct morphology and habitus of some species clusters and inconclusive phylogenetic affinities of some congeners, we anticipate more partitions for the genus *Philodryas* soon, as more Andean taxa will be positioned within the phylogeny of this group. West of Andes' *Philodryas* (WAP hereafter) deserve special attention because hemipenial morphology is distinct from remaining *Philodryas*. Our WAP sample, although restricted to *Philodryas simonsii* Boulenger, 1900 and *Philodryas tachymenoides* (Schmidt & Walker, 1943) shows a hemipenes with small spines in the body and two enlarged in the base and absence of calyces in asulcated face in the former distinct from East of Andes' *Philodryas* (Fig. 12). Besides, WAP share at least one putative synapomorphy (ungrooved postdiastemal tooth). This combined set of characters may represent a monophyletic group distinct from East of Andes' *Philodryas* as noted by Zaher et al. (2014).

6.3. Are phenotypic characters still important for improving snake systematics?

The most comprehensive publication with respect to a single phenotypic character system for the New World snakes was the monographic work of Zaher (1999) about hemipenial

morphology in xenodontines. This author highlighted some important putative synapormophies for this subfamily: two distinct ornamented regions (body and lobes) and enlarged lateral spines. Zaher (1999) explicitly recognized some similarities of hemipenial morphology among groups that were later recognized as tribes. Although this seminal work has greatly improved the knowledge about the genus *Philodryas* (containing at the time nine species), the absence of west Andean species prevented more insights into the systematics of the group, as was pointed out by Zaher et al. (2014). The hemipenial morphology of *Chlorosoma dunupyana* is unique amongst Dipsadidae snakes with the combination of unilobed and ellipsoid organ (proximal and distal portion narrower), calyces restricted to capitular portion on sides of hemipenes, presence of few large spines adjacent of capitulum, and lacking lateral row of enlarged spines on the hemipenial body.

Among cis-Andean species, *Philodryas cordata* Donnelly & Myers, 1991 possesses a particular set of characters not shared by any other congener, as the hemipenes have a small, circular depression (naked pocket) on one side of the organ, lacking the noticeably enlarged spines (lateral spines did not increase distally) and being a heart-shaped structure with no indication of capitation (Donnelly & Myers 1991). However, such a goal is beyond this
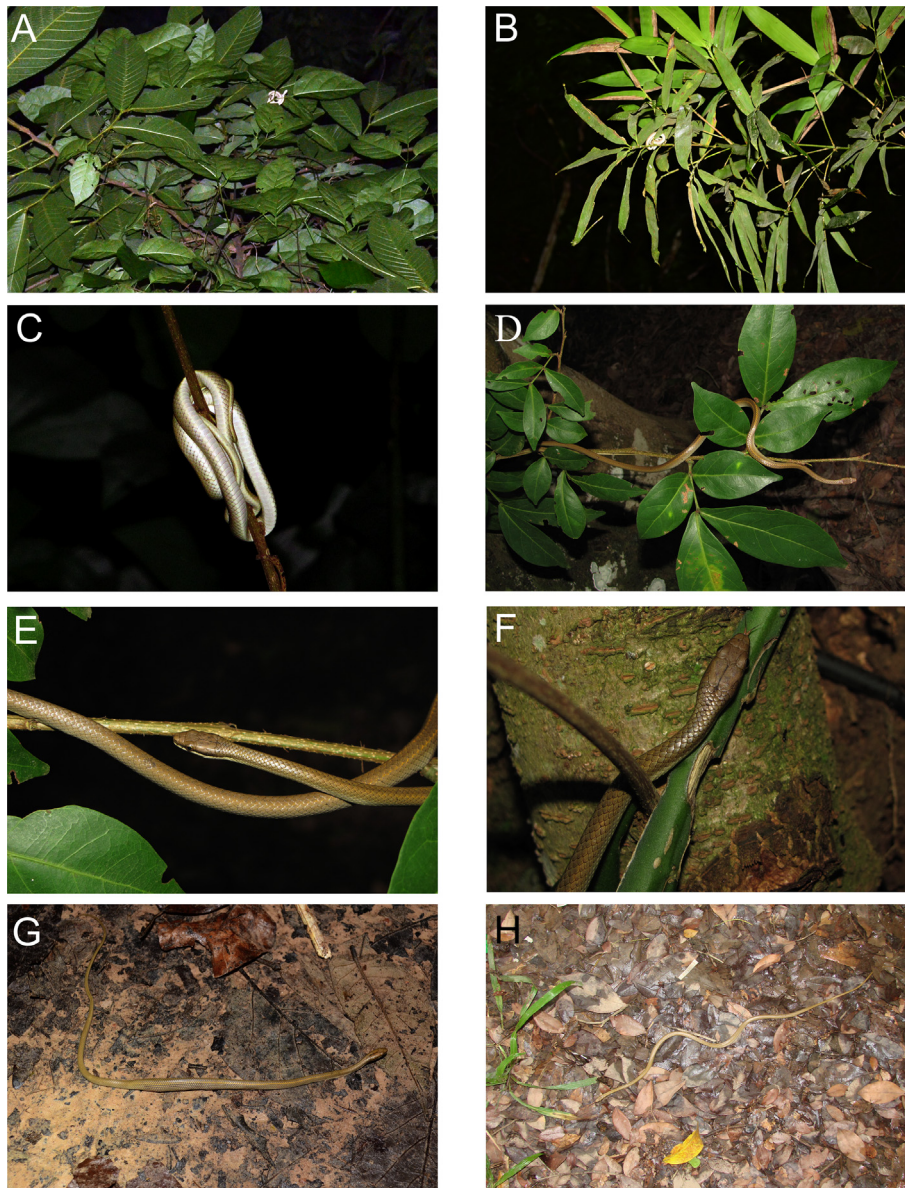
Fig. 10. *Chlorosoma dunupyana* sp. nov. natural history. (A) Subadult male (UFAC-RB 554) sleeping on vegetation. (B) Subadult female (MNRJ 25242) sleeping on thorny bamboo (*Guadua weberbaueri*). (C) Adult female (UFAC-RB 357) sleeping on twig. (D–F) Adult male (UFAC-RB 421) moving on vegetation. (G) Subadult female (MNRJ 25242) active on the ground with stomach content. (H) Adult female (UFAC-RB 346) active on the ground.

study's scope and thus we prefer to maintain it in the genus *Philodryas*, which avoids an unsupported change as well as keeping the reliability of hemipenial morphology characters within the tribes Philodryadini and Tropidodryadini (Figs. 2 and 12).

The number of vertebrae is directly related to body-size in snakes (Pleomerism; Lindsey 1975), but adaptations relating to fast movements depend of cohesion between musculature and bones. Lillywhite (2014) reviewed the adaptive features for arboreality seen in snakes, emphasizing the role of vertebral zygapophyses in the act of climbing, providing a paradoxal "hard but soft bridge" to facilitate a snake's extension in the absence of substrate during gaps when it climbs. Morphological attributes related to arboreality are well developed in *Chlorosoma* and *Xenoxybelis*. Although no study has stressed the highly derived morphological specializations for arboreality in *Xenoxybelis*, here we have pointed out useful characters for their diagnosis. Pizzatto et al. (2007) states that

arboreal snakes have evolved a series of changes to vertical strata occupation such as circumference decreasing, slender and flattened body shape, and longer tails.

The slender body form of *Chlorosoma dunupyana* and *Xenoxybelis* as compared to *Philodryas* helps illuminates their habitat niche segregation. Arboreal snakes are generally slender with low relative mass and a laterally compressed body form compared with strictly ground-dwelling relatives (Lillywhite 2014). *Chlorosoma* although more robust than *Xenoxybelis*, also has a slender body compared to *Pseudablabes* and *Philodryas* (Martins & Oliveira, 1999). However, these snakes often move on the ground during foraging, nesting, dispersing, and other behaviours (Cunha & Nascimento 1978; Starace 1998), differing from typical ground dwelling species such as most species of *Philodryas*. Therefore, habitat preference and niche parameters have scarcely been discussed for *Philodryas* (sensu Zaher et al., 2014) literature. Recently,
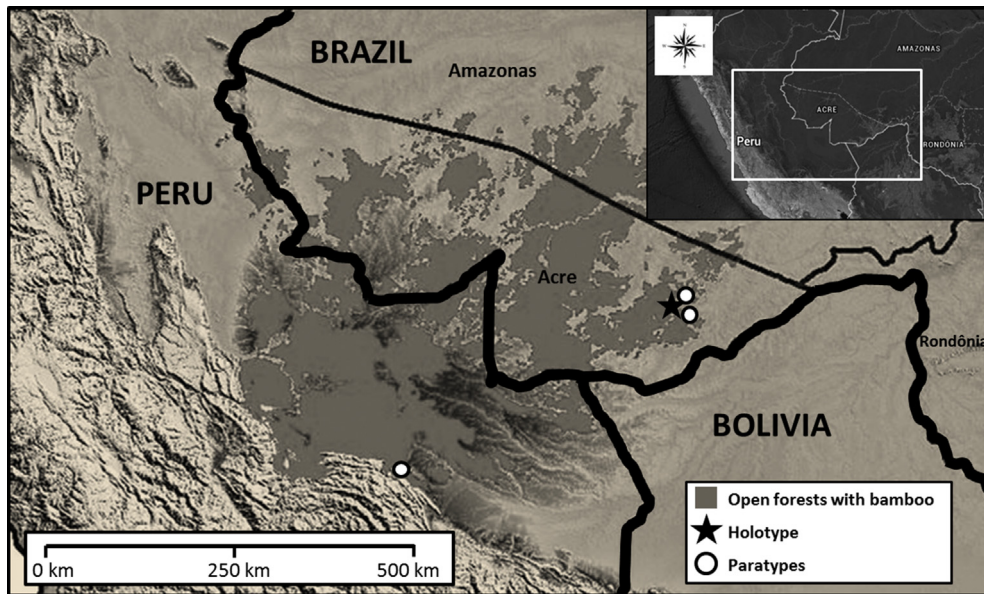
Fig. 11. Distribution of *Chlorosoma dunupyana*. Shaded areas are open-forest with bamboo.
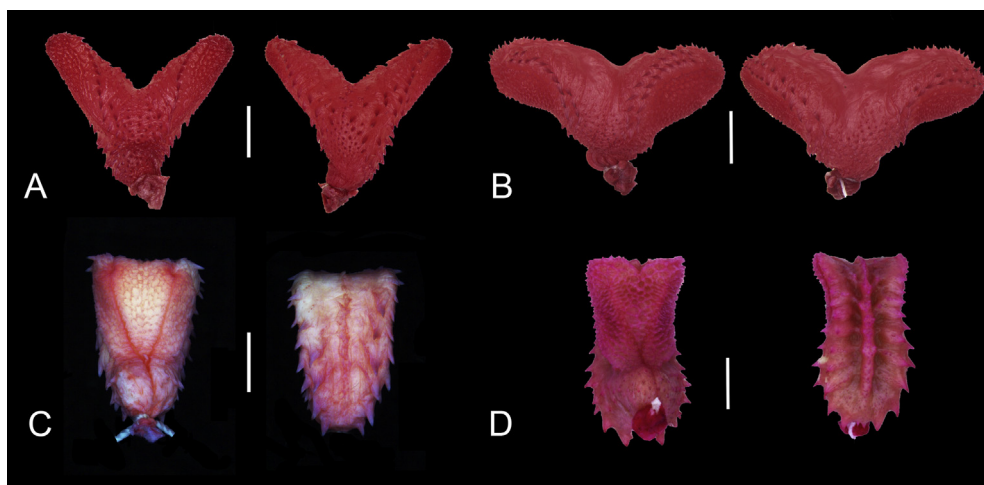

Fig. 12. Hemipenial morphology of Tropidodryadini and *Xenoxybelis* showing the asulcated and sulcated views. (A) MNRJ 13263 *Tropidodryas serra* from Cananéia, São Paulo, Brazil. (B) MNRJ 7406 *Tropidodryas striaticeps* from Lima Duarte, Minas Gerais, Brazil. (C) MNRJ 3876 *Xenoxybelis argenteus* from Presidente Figueiredo, Amazonas, Brazil. (D) MNRJ 26161 *Xenoxybelis boulengeri* from Boca do Acre, Amazonas, Brazil.

Cacciali et al. (2016) discovered the existence of habitat preferences among putative sister species *P. erlandi* Lönnberg, 1902 and *P. mattogrossensis*.

6.4. The principle of 'cumulative congruence' as a criterion to promote changes in taxonomic complex groups or ghost lineages

Many recently published competing phylogenetic hypotheses based on molecular evidence have broadly and positively impacted the field of comparative biology. However, in the face of this competition, many suggested taxonomic changes can be considered premature (see Myers & McDowell 2014), since the hypotheses generated have been a matter of recent dispute (Hedges 2013; Kaiser et al. 2013; Vences et al. 2013; Figueroa et al. 2016 and references therein). In general, we agree with most of the points stressed by Vences et al. (2013), but the idea here is to expand just

one of the main topics (i.e., Phenotypic Diagnosability) emphasized by those authors. We believe that the accumulation of evidence and congruence from distinct and apparently independent systems of characters—as suggested by the "consensus protocol" of Padial et al. (2010)—is currently the best solution for the choice in promoting new taxonomic changes in taxonomically complex groups. The proposition of new names brings instability to the higher-classification schemes—being accepted or not—with re-definitions, synonymy, or changing of hierarchical rankings of taxa (e.g., subfamily vs. family for the same taxon composition). On the other hand, the decision to change (or not) will always be an idiosyncratic task that is subject to some degree of "data reliability" (Pinna et al. 2018). Therefore, for that reason, new re-classifications must be anchored by the maximum available evidence and simultaneously depend on progress resulting from well-resolved alpha taxonomy (Montingelli et al. 2019).

Declaration of competing interest

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jcz.2020.10.008.

Specimens Examined

Pseudablabes agassizii (n = 2): BRAZIL: **Minas Gerais**: Pirapora (MNRJ 3728); Sete Lagoas (MNRJ 21530).

Pseudablabes arnaldoi (n = 1): BRAZIL: **Rio Grande do Sul**: Arvorezinha (MCP 14396).

Pseudablabes patagoniensis (n = 2): BRAZIL: **Rio de Janeiro**: Quissamã (MNRJ 26275); São Paulo: Botucatu (MNRJ 19336).

Chlorosoma laticeps (n = 1): BRAZIL: **Espírito Santo**: Linhares (MNRJ 23683).

Chlorosoma viridissimum (n = 4): BRAZIL: **Acre**: Rio Branco (MNRJ 26648, UFAC-RB 359); **Rondônia**: Parecis (MNRJ 24096); **Pará**: Parauapebas (MNRJ 18030).

Philodryas aestiva (n = 2): BRAZIL: **Minas Gerais**: Serra do Caraça (MNRJ 20483). São Paulo: Botucatu (MNRJ 23005).

Philodryas nattereri (n = 3): BRAZIL: **Bahia**: Caitité (MNRJ 8711), Curaçá (MNRJ 7990); **Ceará**: Quixeramobim (MNRJ 16926).

Philodryas olfersii (n = 5): BRAZIL: **Amazonas**: Humaitá (MNRJ 21042); **Goiás**: Uiraçu (MNRJ 8443); **Mato Grosso do Sul**: Corumbá (MNRJ 20985); **Rio de Janeiro**: São João da Barra (MNRJ 17417—17418).

Philodryas psammophidea (n = 1): BRAZIL: **Mato Grosso**: km 1221 of west road (MNRJ 765).

Philodryas simonsii (n = 3): ECUADOR: **Loja**: Jimbura (QCAZ 13878). PERU: **Arequipa**: Caylloma, Lluta (CORBIDI 11237—38).

Philodryas tachymenoides (n = 1): PERU: **Lima**: Huarochiri, San Andres (CORBIDI 13323).

Xenoxybelis argenteus (n = 14) BRAZIL: **Acre**: Senador Guiomard (UFAC-RB 319, 530, 640); **Amapá**: Serra do Navio (MNRJ 3723); **Amazonas**: Benjamin Constant (MNRJ 1546), Manaus (MNRJ 3875), Presidente Figueiredo (MNRJ 3876); **Mato Grosso**: unknown

locality (MNRJ 209, 336); **Pará**: Belém (MNRJ 8712), Oriximiná (MNRJ 16782—16784, 17939).

Xenoxybelis boulengeri (n = 5): BRAZIL: **Acre**: Feijó (UFAC-RB 328); **Amazonas**: Benjamin Constant (MNRJ 649), Boca do Acre (MNRJ 26161), Humaitá (MNRJ 19783); **Rondônia**: Vista Alegre do Abunã, Porto Velho (UFAC-RB 639).

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