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Systematics of the rare Amazonian genus *Eutrachelophis* (Serpentes: Dipsadidae), with an emended diagnosis for *Eutrachelophis papilio*

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ABSTRACT

Integrative analyses of multiple data sources and increased coverage in genetic and taxa sampling have been increasingly clarified the phylogenetic relationships of caenophidian snakes. However, some knowledge gaps remain, especially at higher-levels and among genera, and unclear relationships of some taxa with scant available information. One of these taxa is the recently described Amazonian genus *Eutrachelophis* (Dipsadidae), whose members are rarely recorded and lack associated molecular information. By analyzing recently collected specimens from Amazonian expeditions, we found a series of *Eutrachelophis papilio* and obtained molecular information (two mitochondrial genes and one nuclear gene) for two specimens. This allowed the first assessment of the molecular phylogenetic relationships of the genus *Eutrachelophis*. Molecular phylogenetic trees of the caenophidian diversification were inferred considering the information of 10 genes (five mitochondrial and five nuclear), under both Bayesian and Maximum Likelihood optimality criteria. Resulting trees corroborate the distinctiveness and taxonomic validity of *Eutrachelophis*, and its family and subfamily level allocation. A highly supported clade composed of *Eutrachelophis* and another enigmatic Amazonian genus, *Arcanumophis*, was recovered nested in the subfamily Xenodontinae. The *Eutrachelophis* + *Arcanumophis* clade is recovered as sister to a clade containing the remaining genera of tribe Xenodontini. These results do not corroborate that the phenotypic apomorphies of *Eutrachelophis* are secondarily developed within Xenodontini diversification, therefore refuting the recent allocation of this genus in this tribe. In the light of these results, we reassessed the morphological similarities of *Eutrachelophis*, *Baliodryas* and *Arcanumophis* and their distinctiveness among xenodontines. Based on combined phenotypic and molecular evidence, we propose the revalidation of tribe Eutrachelophiini to better reflect the high evolutionary distinctiveness of these snakes. We also obtained novel data on the morphometrics, meristics, color variations, natural history and geographical distributions from the analyzed museum specimens of *Eutrachelophis papilio*. We found a considerable variation in the range of analyzed morphological characters, including in some considered as diagnostic, justifying the designation of an emended diagnosis for the species. Despite these advances, some gaps remain with respect to these snakes, such as the taxonomic validity of *Eutrachelophis* species, molecular phylogenetic relationships of *Baliodryas*, and the internal and hemipenial morphology of *Arcanumophis*. Further investigation on these issues and reassessment of museum specimens should increase the knowledge associated with these rare snakes.

1. Introduction

Even with the continuous increase in the knowledge of evolutionary relationships of snakes, conflicting hypotheses remain in their taxonomy and systematics (Myers 2011; Zaher et al., 2019). One of the most emblematic cases occurs in the higher-level

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taxonomy of the megadiverse clade of New World snakes Caenophidia Hoffstetter, 1939 (Zaher et al., 2019). Some authors (e.g. Myers 2011) argue for a practical taxonomy, in retaining a single family Colubridae Oppel, 1811, encompassing the subfamilies Colubrinae Oppel, 1811, Dipsadinae Bonaparte, 1838 and Xenodontinae Bonaparte, 1845. Conversely, other authors argue for a taxonomy more reflected by the phylogenetic distinctiveness of these clades, recognizing both Colubridae and Dipsadidae Bonaparte, 1838 as distinct families, and maintaining Xenodontinae as a subfamily of Dipsadidae given the lack of morphological synapomorphies (e.g. Zaher et al., 2009; 2019; Vidal et al., 2010). Such conflicts are largely influenced by the pervasive occurrence of knowledge gaps, as the low support for some clades in molecular-based phylogenetic hypotheses, incomplete lineage sorting, and scarcity of available information for some taxa (Curcio et al., 2009; Zaher et al., 2009; Nogueira et al., 2019).

Despite the increasing knowledge advances resulting from the incorporation of molecular data in systematics, unstable phylogenetic positions are recovered in different taxonomic scales of the caenophidian snake radiation (Grazziotin et al., 2012; Zaher et al., 2019). For example, interrelationships among major dipsadid clades and the phylogenetic positioning of some of its genera (e.g. *Cercophis* Fitzinger, 1843; *Xenopholis* Peters, 1869; *Farancia* Gray, 1842; *Heterodon* Latreille, 1801) are still poorly understood (Zaher et al., 2019). Molecular-based phylogenetic positioning of some taxa were also considered unexpected under the light of morphological evidence [e.g. *Liophis amarali* (Wettstein, 1930), *Waglerophis* Romano & Hoge, 1972], leading to constant changes in classic systematics and taxonomy (see Zaher et al., 2009). In general, these issues result from marked divergences during molecular and morphological diversification of snakes (Miralles et al., 2018), and can only be overcome by the employment of robust analyses with higher sampling of individuals and genes, and a more effective integration of evolutionary evidences (Zaher et al., 2019; Melo-Sampaio et al., 2021). In addition, some higher-level snake taxa remain poorly documented or without any associated molecular information to support their phylogenetic position and distinctiveness (Pyron et al., 2011). However, the increased fieldwork in some regions with historical difficult access, and reassessments of material deposited in zoological collections has helped to fill these gaps with novel data on underrepresented taxa (e.g. Hoogmoed et al., 2019).

1.1. History of the enigmatic genus Eutrachelophis Myers & McDowell (2014)

One underrepresented snake taxon with many associated knowledge gaps is the Neotropical dipsadid genus *Eutrachelophis* Myers & McDowell, 2014. This genus was recently created to accommodate two morphologically distinct Amazonian species [the so-called 'beautiful-necked snakes', *Eutrachelophis bassleri* Myers & McDowell, 2014 and *Eutrachelophis steinbachi* (Boulenger, 1905)]. The morphological distinctiveness of these species compared to other dipsadids led Myers & McDowell (2014) to consider this genus as the sole representative of a new tribe (Eutrachelophiini Myers & McDowell 2014). Through analyses of historically collected material, Zaher & Prudente (2020) recently described a new species of this genus (*Eutrachelophis papilio* Zaher & Prudente 2020) and provided morphological remarks to support the genus taxonomy. Under such new evidence, especially hemipenial characters, Zaher & Prudente (2020) erected a new genus (*Baliodryas* Zaher & Prudente 2020) to accommodate the distinct *Eu. steinbachi*, and synonymized Eutrachelophiini with Xenodontini. Based on newly collected specimens, Echevarría & Venegas (2015) provided additional details on the color in life of *Eu. bassleri*, and Citeli et al. (2020) provided additional details on the color in life, morphology, geographic range and conservation status of *Eu. papilio*.

Since the early 20th century, these enigmatic snakes remained known by a few specimens, in some cases from widely distant localities (Zaher & Prudente 2020). Currently, *Eu. bassleri* is known by 13 specimens from the lowland forests of western Amazonia, in Ecuador and Peru (Myers & McDowell 2014; Echevarría & Venegas 2015; Zaher & Prudente 2020), *Eu. papilio* by six specimens from the lowland forests of central Amazonia (all from Brazil, at Juruá–Purus and Purus–Madeira interfluves; Zaher & Prudente 2020; Citeli et al., 2020), and *Baliodryas steinbachi* by 14 specimens from Andean foothills of Bolivia, and a single locality in Brazil (Zaher & Prudente 2020). Data on the genetic variation of these species are unknown, and their phylogenetic relationships were unclear and only hypothesized through morphological comparisons (Myers & McDowell 2014; Zaher & Prudente 2020). Therefore, even with continuous knowledge advances on these taxa, the amount of information supporting wider interpretations and hypotheses is still very limited.

Based on newly generated molecular data for historically collected material of *Eu. papilio*, here we infer the phylogenetic relationships of genus *Eutrachelophis* and consequently test the phenotypic-based previous hypothesis. Based on combined evidence of molecular phylogenetic relationships and phenotypic comparisons of *Eutrachelophis* and closely related genera, we reassessed the taxonomic validity of the tribe Eutrachelophiini. New material of *Eu. papilio* also considerably increased the number of its known specimens, and we reassessed its geographic distribution, external morphology variation and natural history. We detected relevant morphological divergences that do not fit the original species description, justifying an updated emended diagnosis.

2. Material and methods

We directly examined a series of nine specimens of *Eu. papilio*, collected between 2003 and 2010 and housed in the Collection of Amphibians and Reptiles (INPA-H) of the Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Amazonas, Brasil. To access molecular information, we obtained available tissue samples for two of these specimens, deposited in the Collection of Genetic Resources from the same institute (INPA-HT). We also examined photographs of four specimens from closely-related genera housed in the American Museum of Natural History (AMNH) and British Museum of Natural History (BMNH). A complete list of examined specimens is presented in supplemental material, Appendix I, with detailed information for *Eu. papilio* specimens.

2.1. Molecular data acquisition and phylogenetic inferences

We investigated the phylogenetic relationships of *Eu. papilio* (representing the genus *Eutrachelophis*) within the diversification of caenophidian snakes based on the genetic variation. Genomic DNA from tissue samples were extracted following the protocols of the Wizard® Genomic DNA Purification Kit (Promega, Madison, WI, USA). Through Polymerase Chain Reactions (PCR), we generated novel data for fragments of two genes of the mitochondrial DNA (mtDNA): the RNA *16S subunit ribosomal RNA* (*16S*) and the protein-coding gene (CDS) *NADH dehydrogenase subunit 4* (*ND4*), and one CDS of the nuclear DNA (nuDNA): *recombination activating gene 2* (*RAG2*). Amplification of *16S* was only successful for one of the new samples. The *16S* and *ND4* were amplified using the primers 16Sar/16Sbr and ND4L/ND4H, respectively (Arévalo et al., 1994; Palumbi et al., 1991), following the methods of Moraes et al. (2020). The

RAG2 was amplified using the primers EM1-F/EM1-R, following the methods of Gamble et al. (2008). PCR products were purified with PEG (polyethyleneglycol) 8000 and sequenced using the Big Dye Terminator sequencing kit (Applied Biosystems, Waltham, MA, USA) in an automated sequencer ABI 3130 XL (Applied Biosystems, Waltham, MA, USA) at the Laboratório Temático de Biologia Molecular (LTBM) from INPA. Newly generated sequences were deposited in the GenBank online repository (Clark et al., 2016), and their accession numbers can be found in supplemental material (Appendix II).

Newly generated sequences were combined with a comprehensive molecular dataset focused on the caenophidian snakes diversification, compiled by downloading additional sequences from the GenBank (see Appendix II). In addition to the aforementioned molecular markers, we extend our dataset by including information of seven additional genes, being three of the mtDNA: the RNA *12S subunit ribosomal RNA* (*12S*), and the CDS *NADH dehydrogenase subunit 2* (*ND2*) and *cytochrome b* (*CYTB*), and other four CDS genes of the nuDNA: *brain-derived neurotrophic factor* (*BDNF*), *oocyte maturation factor* (*CMOS*), *neurotrophin-3* (*NT3*) and *recombination activating gene 1* (*RAG1*). The gene with the highest taxa coverage was the *16S* (96%) while the one with the lowest coverage was the *RAG1* (21%) Taxa coverage for the remaining genes varied between 27.5% and 89%. We refrained from downloading other available molecular markers, as they were not minimally representative considering our dataset, and would have increased the volume of missing data.

Due to the greater morphological affinity of *Eutrachelophis* with members of the tribe Xenodontini Bonaparte, 1845 (Dipsadidae, Xenodontinae) (Zaher & Prudente 2020), our molecular sampling was focused on those taxa. Representative species for 87% of the currently known diversity of dipsadid genera (86/99) were included (molecular information is unavailable for the remaining 13 genera). Within Xenodontinae, representatives of 14 known tribes were included (i.e. only lacking the recently erected tribe Incaspidini Arredondo et al., 2020), besides representatives of some genera currently considered as *incertae sedis*. We acknowledge that generic changes have been recently proposed for the tribe Philodryadini Cope, 1886 (Arredondo et al., 2020; Melo-Sampaio et al., 2021). Given the nomenclatural incongruences between these studies, we opt to keep the sampled species of Philodryadini as part of a single genus, *Philodryas* Wagler, 1830, while waiting for further resolution. However, it is noteworthy that our analyses included representatives for most of the genera erected in those recent studies (Arredondo et al., 2020; Melo-Sampaio et al., 2021), except for *Incaspis* Donoso-Barros, 1974.

Furthermore, we included in the analyses samples for 43 species representing the three genera currently considered as part of Xenodontini besides *Eutrachelophis* (*Lygophis* Fitzinger, 1843, *Xenodon* Boie, 1826 and *Erythrolamprus* Wagler, 1830. The genus *Baliodryas* remains without associated molecular data. To support the results of diversification patterns, representative taxa for other 15 caenophidian snake families were included (Xenodermidae Gray, 1849; Pareidae Oppel, 1811; Viperidae Oppel, 1811; Homalopsidae Bonaparte, 1845; Elapidae Boie, 1826; Pseudoxyrhopiidae Günther, 1881; Atractaspidae Günther, 1858; Psammophiidae Dowling, 1967; Lamprophiidae Fitzinger, 1843; Natricidae Bonaparte, 1838; Calamariidae Bonaparte, 1838; Sibynophiidae Dunn, 1928; Pseudoxenodontidae McDowell, 1987; and Colubridae Oppel 1811). One sample representing the family Boidae Gray, 1825 [*Boa constrictor* (Linnaeus, 1758)] was included as outgroup.

Each gene was independently aligned using the MAFFT online server with default parameters, except for the use of E–INS–i strategy for RNAs and G–INS–i strategy for CDS (Katoh & Standley 2013). The 10 genes (five from mtDNA + five from nuDNA) were concatenated, reaching a final dataset with 6144 nucleotide sites and 236 snake species representing 129 genera and 17 families. Using this alignment, phylogenetic trees were inferred under both Bayesian inference (BI) and maximum likelihood (ML) as the optimality criteria. The BI analysis was performed at MrBayes v.3.2.6 (Ronquist et al., 2012). The dataset was initially divided into 25 partitions: one for the RNAs and one for each codon position of the CDS, and we determined the models of nucleotide evolution and best-fit partition schemes using PartitionFinder v2.1.1 (Lanfear et al., 2017), under the Bayesian Information Criterion (BIC). Best scheme indicated 12 partitions, and seven different best-fitting nucleotide substitution models (Table 1). The analysis was conducted under two independent runs of 10^7 generations, starting with random trees and four Markov chains (one cold). Convergence of parameters were assessed (i.e., standard deviation of split frequencies <0.01 and estimated sample size >200) using Tracer v.1.7 (Rambaut et al., 2018). A burn-in of 25% of samples and trees were discarded and we then extracted the maximum clade credibility tree. The ML analysis was performed at RaxML v.8.2.10 (Stamatakis 2014). The GTR+Γ model was applied and we ran 1000 pseudoreplications to estimate non-parametric bootstrapping values. Both BI and ML analyses were conducted at the CIPRES Science Gateway online (Miller et al., 2010). Additionally, MEGA v.7 (Kumar et al., 2016) was used to compute the uncorrected pairwise genetic distances between the taxa considering the most representative gene in our sampling (*16S*), with gaps removed using a pairwise deletion option.

2.2. Phenotypic, natural history and distribution data acquisition and analyses

Nineteen morphometric measurements were taken from eight adult *Eu. papilio* specimens. The snout-vent length, ventrally measured from center of rostral to the posterior margin of cloacal scale (SVL); and the tail length, from posterior margin of cloacal scale to terminal scale (TL) were taken with a flexible ruler to the nearest 1.0 mm. Remaining measurements were taken in the cephalic region with a digital caliper to the nearest 0.01 mm: head length, from center of rostral to the corner of mouth (HL); head width, at level of angle of jaw (HW); ocular diameter, from the anterior to the posterior margin (OD); rostral length and width (RL; RW); frontal length and width (FL, FW); parietal length and width (PL; PW); prefrontal length and width (PFL; PFW); internasal length and width (InL; InW); loreal length and height (LL; LH); and anterior and posterior chinshields length (ACL; PCL). We also obtained 14 meristic data from the nine specimens, by counting the number of: dorsal scales at the anterior, middle, and posterior region of the body (DO); gular scale rows (GU); preventral scales (PV);

Table 1
Best-fit partition schemes and models of nucleotide substitution considered for the Bayesian inference of phylogenetic relationships.

Subsets	Models	Partitions: gene(codon)
1	GTR+Γ+I	*12S, 16S*
2	GTR+Γ+I	*ND2*(1)
3	GTR+Γ+I	*ND2*(2), *CYTB*(2), *ND4*(3)
4	GTR+Γ	*ND2*(3), *ND4*(1)
5	GTR+Γ+I	*CYTB*(1), *ND4*(2)
6	GTR+Γ	*CYTB*(3)
7	K80+Γ+I	*RAG1*(3), *BDNF*(1), *BDNF*(2)
8	K80+Γ+I	*BDNF*(3)
9	HKY+Γ	*CMOS*(1), *RAG2*(3)
10	HKY+Γ+I	*CMOS*(3), *RAG2*(2), *CMOS*(2), *RAG1*(2), *RAG2*(1)
11	SYM+Γ+I	*NT3*(3), *NT3*(1)
12	K80+Γ	*RAG1*(1), *NT3*(2)

ventral scales (VE); subcaudal scales (SC); supralabial scales (SL); supralabial scales in contact with the loreal scale (SLL); supralabial scales in contact with the orbit (SLO); infralabial scales (IL); infralabial scales touching anterior and posterior chinshields (ILA; ILP); preocular scales (PrO); postocular scales (PsO); and temporal scales (TE). Color patterns in life were assessed through photographs and field notes directly associated with four of the nine new specimens. Morphological terminologies followed Savage (1960) and Zaher & Prudente (2020), and ventral scale counts followed Dowling (1951). Scales were counted and measured on the right side of the head. Sex was inferred based on hemipenis eversion (when available), subcaudal probing (Marais 1984), and body proportions. We compared the observed morphological variation of the new specimens with available data for *Eu. papilio* in the literature ($n = 6$; Zaher & Prudente 2020; Citeli et al., 2020) to investigate whether the measurement ranges varied. In a similar way, we compared phenotypic data for the genus *Eutrachelophis,* summarized from our observations and literature data (Myers & McDowell 2014; Smaga et al., 2019; Zaher & Prudente 2020; Citeli et al., 2020), with the variation on diagnostic characteristics of related genera. To minimize the effect of ontogenetic bias in summarized measurements, data concerning immature specimens (INPA-H 41140 and other two records from the literature) were not considered in the morphometric variation and comparisons of *Eu. papilio*. The specimen INPA-H 41140 was considered as immature due to its considerably smaller size when compared to the other eight specimens. Combining all the known data for the morphological variation of *Eu. papilio* (Zaher & Prudente 2020; Citeli et al., 2020, our study), we tested for the occurrence of sexual dimorphism, using a 2-group Mann–Whitney U test (Zar 1999) in the R environment (R Core Team 2020). Differences were investigated in six variables mainly used as predictors for snake body proportions: four morphometric (SVL, TL, HL and HW) and two meristic (VE and SC). We employed a non-parametric test, since our small sample size violated assumptions of univariate normality and homoscedasticity, evaluated with Kolgomorov-Smirnov and Levene's tests, respectively (Zar 1999). Four specimens were excluded from these statistical analyses, as their tails are incomplete (supplemental material; Supp. Tables 1 and 2).

We inferred geographic distributions of species by compiling data associated with the newly analyzed specimens (see Appendix I) and literature data (Myers 1986; Myers & McDowell 2014; Echevarría & Venegas 2015; Smaga et al., 2019; Zaher & Prudente 2020; Citeli et al., 2020). We plotted these data on a map using the software QGIS v.3.18 (QGIS Development Team 2021). Novel natural history data for *Eu. papilio* were based on our field observations in the upper Madeira River basin, Brazil.

3. Results

3.1. Phylogenetic relationships and genetic distances

The molecular-based phylogenetic trees of caenophidian diversification resulting of BI and ML analyses mostly agreed in topology and nodal support of major clades. We choose to depict and discuss the BI tree phylogenetic relationships, also presenting the support results corresponding to the ML tree (Figs. 1, S1, S2; Appendix C). We recovered the monophyly with high support for all included families represented by more than one genus (Figs. S1 and S2). Nodal support generally increased at the base of the phylogenies, and at the generic levels (Figs. 1, S1, S2). Conversely, nodal support decreased considering relationships among genera, subfamilies and some endoglyptodont and colubroidean families (Figs. S1 and S2). Within Dipsadidae, we recovered uncertain positions for the genera *Heterodon* and *Farancia*, and relatively well supported early divergence between the Asiatic genus *Thermophis* Malnate, 1953 and a clade containing New World genera of dipsadid diversification (Figs. S1 and S2). Monophyly of dipsadid subfamilies (Dipsadinae, Xenodontinae and Carphophiinae Zaher et al. 2009) and their interrelationships overall exhibit low nodal supports, and Dipsadinae are evidenced as paraphyletic with the external positioning of the genus *Rhadinaea* Cope, 1863 (Figs. S1 and S2).

Within Xenodontinae, the best-represented taxon in our sampling, monophyly of most of the genera represented by more than one species were corroborated with high support values (Fig. 1). Only *Oxyrhopus* Wagler, 1830 was recovered as paraphyletic due to the external positioning of *Oxyrhopus fitzingeri* (Tschudi, 1845) (Fig. 1). Positioning of the *incertae sedis* genera *Uromacer* Duméril, Bibron & Duméril, 1854, *Crisantophis* Villa, 1971, *Manolepis* Cope, 1885 and *Xenopholis* were corroborated as uncertain due to lower nodal supports (Fig. 1). The phylogenies also recovered with high support the monophyly of some major clades corresponding to 12 xenodontine tribes, except in the case of a lower supported clade attributed to Alsophiini Fitzinger, 1843 (Fig. 1). Some relationships among genera of the tribes Alsophiini, Pseudoboini Bailey, 1967, Tachymenini Bailey, 1967, and Hydropsini Dowling, 1975 overall received lower nodal supports and should be treated as uncertain. In contrast, relationships among genera are overall highly supported within the tribes Echinanterini Zaher et al., 2009, Elapomorphini Jan, 1862, and Xenodontini *sensu stricto* (i.e. considering only the genera *Lygophis*, *Erythrolamprus* and *Xenodon*) (Fig. 1). Other six xenodontine tribes are currently monogeneric and do not apply to these comparisons [Caaeteboiini Zaher et al., 2009; Conophiini Zaher et al., 2009; Hydrodynastini Zaher et al., 2009; Psomophiini Zaher et al., 2009; Saphenophiini Zaher et al., 2009; Tropidodryadini Zaher et al., 2009; and Philodryadini (but see section 2.1)]. All of the among–tribes relationships were low or only moderately supported (Fig. 1).

The genus *Eutrachelophis*, sampled here for the first time and represented by *Eu. papilio*, was recovered nested with a high support within the dipsadids and xenodontines (Fig. 1). This result confirms the previous phenotypic allocation of this genus in those taxa (Myers & Mcdowell 2014; Zaher & Prudente 2020). Tree topologies also corroborated the phenotypic hypothesis of a closer affinity of *Eutrachelophis* with members of the tribe Xenodontini *sensu stricto* (Myers & Mcdowell 2014; Zaher & Prudente 2020), as they were recovered grouped in a well-supported clade (Fig. 1). The genus *Arcanumophis* Smaga, Ttito, & Catenazzi, 2019, recently erected to allocate a poorly known snake species from Peruvian Amazonia (Smaga et al., 2019), was also recovered as part of this clade and closely related to *Eutrachelophis* (Fig. 1). Despite the greater affinity of *Eutrachelophis* and *Arcanumophis* with Xenodontini *sensu stricto*, both tree topologies do not recover these genera nested within this clade. In fact, the branch lengths between the clade containing *Eutrachelophis* + *Arcanumophis* and the clade representing Xenodontini *sensu stricto* are considerable (Fig. 1).

Based on the unveiled molecular-based phylogenetic position of *Eutrachelophis*, we focused our comparisons of the *16S* genetic p-distances within xenodontines. Mirroring the phylogenetic results, genetic distances between *Eu. papilio* and *Arcanumophis problematicus* (Myers, 1986) were among the lowest values (8.4%), but distances also reached low values when comparing *Eu. papilio* to some members of Alsophiini [*Hypsirhynchus parvifrons* (Cope, 1862); 7.5%; *Arrython vittatum* (Gundlach in Peters, 1861); 8.3%] and Elapomorphini [*Phalotris reticulatus* (Peters, 1860); 8.3%; *Phalotris lemniscatus* (Duméril et al., 1854); 8.8%]. Genetic distances between *Eu. papilio* and the remaining xenodontines varied from 9.2%–14.7%, and within Xenodontini *sensu stricto* varied from 9.7%–14.4%. To test for the consequences of including *Eutrachelophis* and *Arcanumophis* within Xenodontini based on molecular

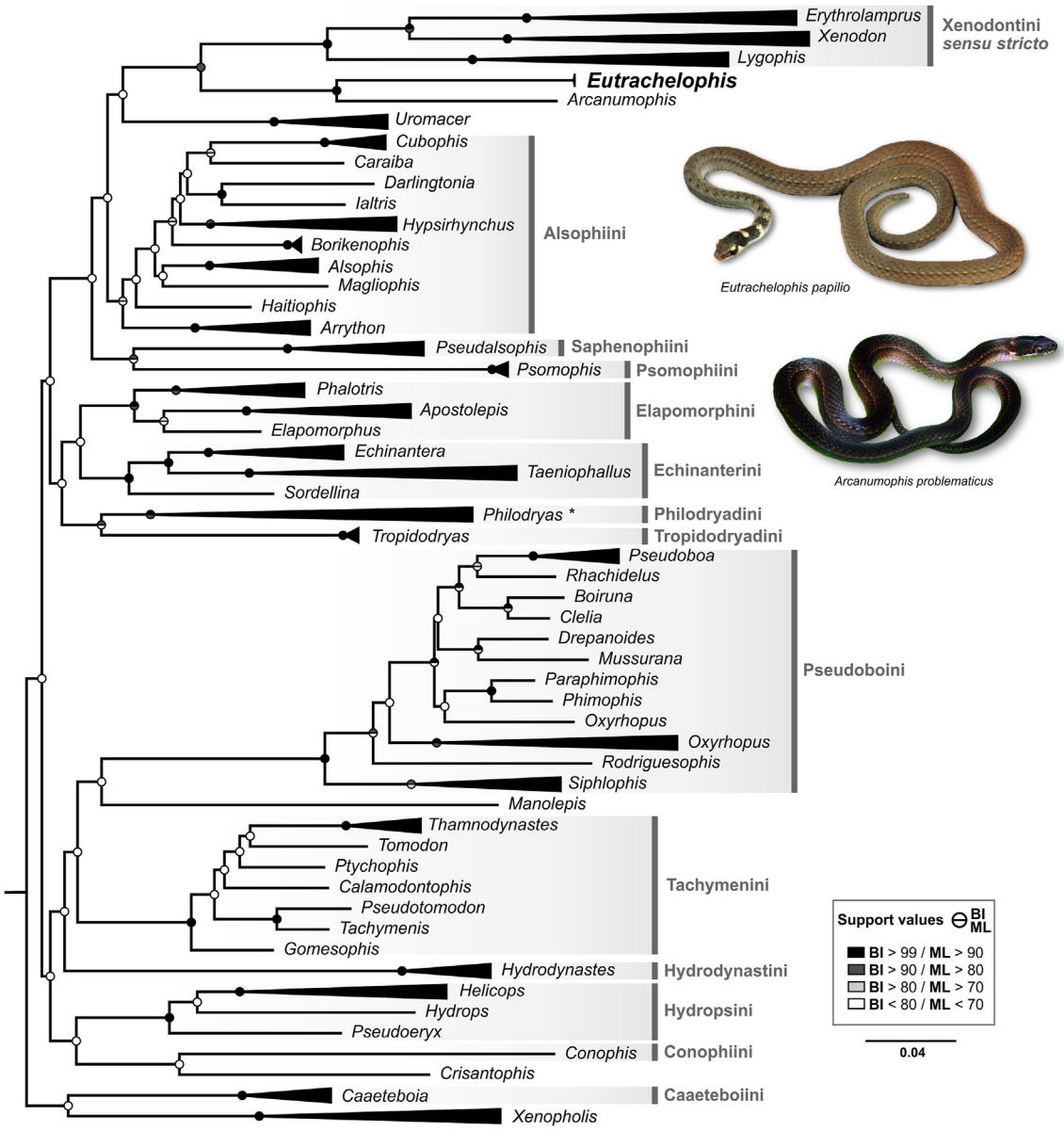

Fig. 1. Phylogenetic tree of subfamily Xenodontinae (Dipsadidae), inferred from a concatenated dataset of 10 genes (five of mtDNA and five of nuDNA) using Bayesian inference (BI). Nodal supports corresponding to a tree inferred by Maximum Likelihood (ML) are included. Support values are shown in divided circles (upper portion indicate posterior probabilities of BI and lower portion indicate bootstraps of ML). Branch scale is indicated as the number of substitutions per site. Phylogenetic position of the genus *Eutrachelophis* is highlighted as closely related to the genus *Arcanumophis* and genera of tribe Xenodontini *sensu stricto*. External groups representing a wide sampling of the caenophidian snake diversification were omitted to improve visualization, but they are evidenced in the supplemental material (Supp. Figs. 1, 2). (*) See recent changes proposed by Arredondo et al. (2020) and Melo-Sampaio et al. (2021). Inset photographs by Laurie Vitt (*Eu. papilio*) and Alessandro Catenazzi (*A. problematicus*).

evidence, we compared the mean genetic distances among genera of the most diverse xenodontine tribes, considering single species as representatives for the genera. We taxonomically divided the dataset including *Eutrachelophis* + *Arcanumophis* as part of Xenodontini or as a distinct clade. Even with one of the lowest numbers of known genera, the mean genetic distance within Xenodontini *sensu stricto* was considerably higher (8.5%) when compared to other tribes (5.3%–7.2%) (Fig. 2). Such distance increased to 10.0% with the incorporation of the *Eutrachelophis* + *Arcanumophis* clade to Xenodontini (Fig. 2). These results corroborate the evidence that Xenodontini as currently defined group considerably distinct evolutionary lineages when compared to the diversification of other tribes, and such evolutionary diversity is even more accentuated with the incorporation of the *Eutrachelophis* + *Arcanumophis* clade to this tribe.

3.2. Phenotypic comparisons of Eutrachelophis, Arcanumophis, and closely related genera

Through the combination of novel observations and data available in the literature, we compared the phenotypic variation of *Eutrachelophis*, *Arcanumophis* and genera of Xenodontini *sensu stricto*, all evidenced as closely related according to our molecular-based phylogenetic results (Fig. 1; section 3.1). In the original description of *Eutrachelophis*, Myers & McDowell (2014) listed a series of putative phenotypic synapomorphies for this genus that also supported the erection of the tribe Eutrachelophiini. Zaher & Prudente (2020) reanalyzed those synapomorphies and argued that they did not constitute uniquely derived features of *Eutrachelophis* and the newly erected genus *Baliodryas*, instead likely constituted secondary losses within the Xenodontini diversification.

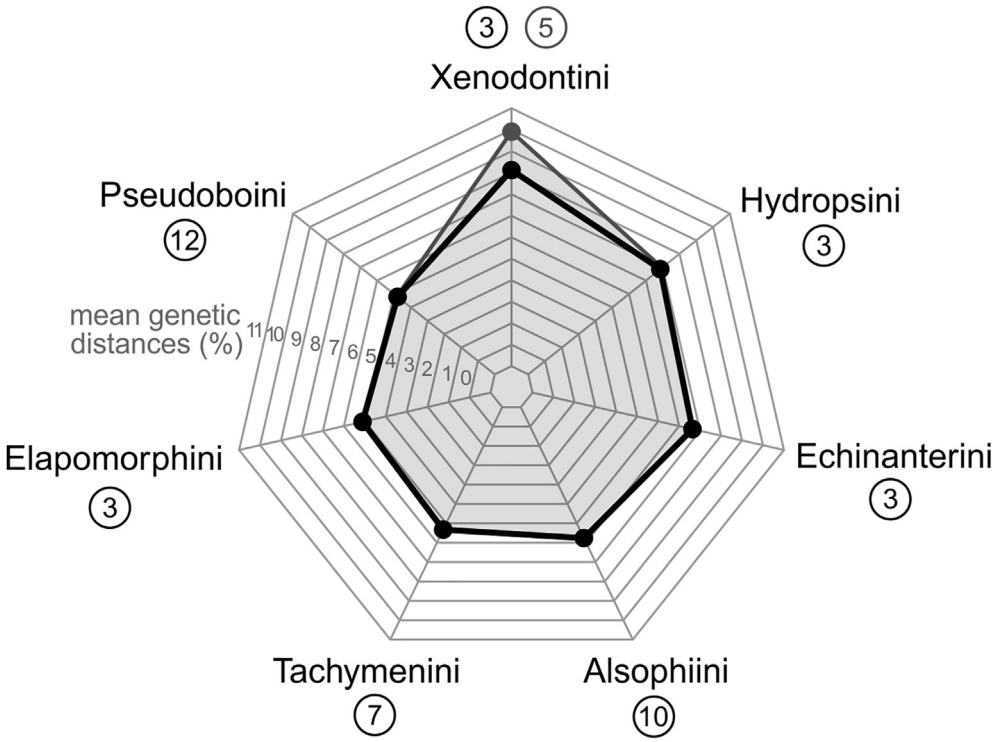

Fig. 2. Comparison of mean uncorrected pairwise genetic distances among genera of the most diverse xenodontine tribes (black polygon), highlighting the high evolutionary distinctiveness contained within Xenodontini when compared with the other tribes. Distinctiveness is increased when considering genera *Eutrachelophis* and *Arcanumophis* as part of this tribe (in dark grey). Genetic distances are based on a fragment of the *16S* rRNA of the mitochondrial DNA. Numbers close to tribe names correspond to the number of genera included in the analysis.

This assumption supports their arguments for the reallocation of *Eutrachelophis* and *Baliodryas* within Xenodontini and the consequent synonymization of Eutrachelophiini with this tribe. However, our molecular-based phylogenetic inference (Fig. 1, section 3.1) clearly conflicts with this hypothesis, as the clade *Eutrac helophis* + *Arcanumophis* was not recovered nested within the Xenodontini *sensu stricto*. Therefore, we reassessed the knowledge on the aforementioned synapomorphies in the light of our new evidence.

The posterior projection of Harderian gland, between the *profundus* and *superficialis* muscles, certainly constitute a non-exclusive character for *Eutrachelophis*, as it is shared by *Lygophis lineatus* (Linnaeus, 1758) and *Erythrolamprus aesculapii* (Linnaeus, 1758; Zaher and Prudente, 2020). This is also the case for the pituitary vein foramen condition (either between sphenoid and parietal, or enclosed within sphenoid), which are, to some extent, shared by the genera *Lygophis* and *Erythrolamprus* (Zaher & Prudente 2020). However, a combination of some morphological characters distinguish *Eutrachelophis* and *Baliodryas* from other genera of Xenodontini *sensu stricto*. Short and slender temporal bones are present in *Eutrachelophis* and *Baliodryas*, but absent in other xenodontines, except for *Erythrolamprus pyburni* (Markezich & Dixon 1979) and *Erythrolamprus atraventer* (Dixon & Thomas 1985), indicating secondary development in those species. The partial overlap of the mandibular trigeminal foramen and the anterior border of the *fenestra ovalis* is evidenced as a relevant character and considered a synapomorphy for *Eutrachelophis* when compared to *Baliodryas* and other genera of Xenodontini *sensu stricto* (Zaher & Prudente 2020). Considering hemipenial characters, Zaher & Prudente (2020) argued that *Eutrachelophis* have secondarily developed unilobed organs with highly modified apical disks, presumably derived from an ancestral bilobed condition within Xenodontini *sensu stricto*. However, considering that the hemipenial condition present in *Eutrachelophis* is so unique among xenodontines, it is difficult to certainly define it as derived from an "apical disk", and therefore any definition of polarity in this morphological distinctiveness is largely biased. In fact, this hemipenial condition is so unique that Myers & McDowell (2014) considered that these nude areas on the unilobed organ should be instead described as "apical nude domes".

Both *Eutrachelophis* and *Arcanumophis* share a suite of morphological similarities; notably the rostral crease. All of our examined specimens of *Eutrachelophis* share this single diagnostic character currently supporting the genus *Arcanumophis* (Smaga et al., 2019). Other morphological characters shared by *Eutrachelophis* and *Arcanumophis* include (Myers 1986; Myers & McDowell 2014): dorsal vertebrae hypapophyses reduced to lower hemal keels; presence of paired elongated white nuchal markings (previously suggested as a diagnostic character for *Eutrachelophis*; Myers & McDowell 2014); a dorsolateral line of lighter dots, black bordered ventrally; and supralabials finely bordered by contrasting colors (black in *Eutrachelophis* and cream in *Arcanumophis*) (Smaga et al., 2019). The morphological condition of fully expanded hemipenis of *A. problematicus* remains unknown. However, by analyzing the uneverted organ of this species, Myers (1986) noticed a wide nude area in its proximal region, which he hypothesized as resulting in a "flattened apical disk" after eversion. Smaga et al. (2019) incorrectly associated this condition as an unambiguous "apical disk", and based on this, suggested the allocation of *Arcanumophis* in Xenodontini. In fact, based on this evidence and our phylogenetics analyses, we can assume that the hemipenis of *Arcanumophis* is very similar to that of *Eutrachelophis*, although slightly bilobed. This association is supported by the fact that the condition of the uneverted organ of *Eu. bassleri* is similarly

described as having a proximal "nude area of folded tissue" (Myers & McDowell 2014). Moreover, Xenodontini is also supported by a behavioral synapomorphy: the neck-flattening behavior in case of harassment (Myers 1986; Zaher 2009; Zaher & Prudente 2020). To the best of our knowledge, such behavior has not been reported to date in any opportunity of recording *Eutrachelophis*, *Arcanumophis* and *Baliodryas*, including for some of the specimens analyzed by us. Therefore, in the light of our combined molecular, phenotypic and behavioral evidences of affinities between the genera *Eutrachelophis* and *Arcanumophis,* and its differences to the remaining xenodontines (Fig. 3), we propose the revalidation of Eutrachelophiini to better represent the evolutionary distinctiveness of this clade (section 3.4).

3.3. Updates on the variation of Eutrachelophis papilio external morphology

The increase of morphological data known to *Eu. papilio* (from six to 14 specimens) resulted in higher variational ranges for most of the measured morphological characters (Supp. Tables 1 and 2). This change was more evident considering the morphometric variation, as for 17 of the 19 measurements the incorporation of newly obtained data resulted in new limits for their ranges. Due to the fact that two of the new specimens had larger body sizes (SVL, TL) in relation to the currently known variation (Supp. Table 1), most of the morphometric measurements from the cephalic region had their upper limits equally increased (HW, OD, RL, RH, PFL, PFW, LL, ACL) (Supp. Table 1). Some morphometric measurements obtained from the new specimens modified both the lower and upper limits of their currently known variation (INL, PL, PW, PCL), while others represented new lower limits (HL, LH) (Supp. Table 1). Only the newly obtained measurements for INW and FW were entirely contained in the currently known variation for the species (Supp. Table 1). Variations in meristic characters were more conserved among newly analyzed specimens and currently known variation, with eight of the measurements being completely uniform (DO, G, PV, SL, SLO, PrO, PsO, TE) (Supp. Table 2). Conversely, six meristic measurements were found to be more variable than indicated by the current knowledge (Supp. Table 2). The supralabials contacting loreal were found to vary from only one to two scales, and the known lower limits for the variation in VE, SC, and IL decreased based on the new evidence (Supp. Table 2). The decrease in the IL also increased the variation in ILA and ILP, which varied both in number and disposition (Supp. Table 2). We did not detect sexual dimorphism for the analyzed morphometric characters: SVL ($U_{16.5} = 1.279$, $P = 0.1983$), TL ($U_{11} = 0.6464$, $P = 0.5$), HL ($U_{15} = 1.1$, $P = 0.266$), HW ($U_5 = 1.386$, $P = 0.1714$); and meristic characters: VE ($U_{13} = 1.371$, $P = 0.1622$), SC ($U_9 = 0.1251$, $P = 0.8413$). However, these results should be considered as exploratory because they are based on a small sample size ($n = 8$), and knowledge advance and increase in sample sizes may evidence discordant results.

Color variation of preserved specimens mostly fitted to that described by Zaher & Prudente (2020). However, we observed a new condition for ventral coloration, immaculate pale yellow in most specimens (INPA-H 13984, 27389, 27390, 32246, 32291, 32365, 41090, 42751) or immaculate white as described in species' diagnosis (condition only observed in the immature specimen INPA-H 41140, which was conserved in formaldehyde) (Figs. 4, 5). We also observed variation regarding the dorsal extension of the white ocelli at the level of ventrals 4–5. In some specimens, these white ocelli were separated by three darker colored scales rows, as in the species' diagnosis (INPA-H 27390, 32365, 41090, 42751). However, this distance between white ocelli decreased to two scale rows in other specimens (INPA-H 27389, 32291) and to just one scale row barely evident in the remaining ones (INPA-H 13984, 32246, 41140). In the latter condition, ocelli are almost fused in a line crossing the dorsum. New information for color in life for some of these specimens also mostly fitted to that described by Citeli et al. (2020), whereas with some relevant variations (Fig. 6). This includes the bright yellow ventral color in some specimens (INPA-H 23890, 32291); and dorsal coloration of the first body third, which varied from shades of grayish-brown (MPEG 2386) to greenish-gray

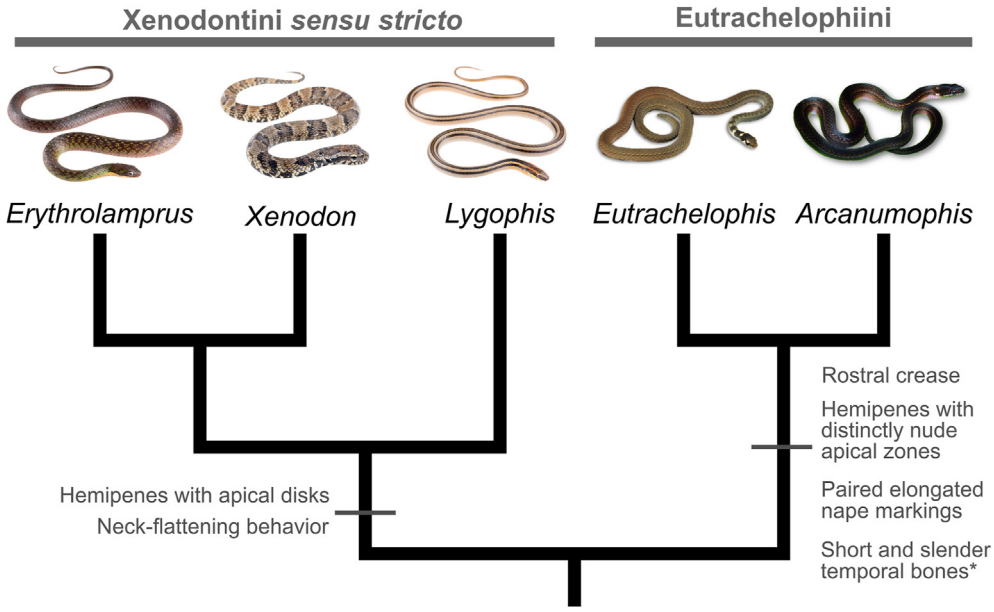

Fig. 3. Generalized cladogram representing the molecular-based phylogenetic relationships of *Eutrachelophis* and *Arcanumophis* and other genera of tribe Xenodontini *sensu stricto* (see section 3.1). Phenotypic and behavioral characteristics shared by the subclades are evidenced, supporting their segregation in different taxa that better represents their evolutionary distinctiveness. Therefore, *Eutrachelophis* and *Arcanumophis* are considered as representatives of tribe Eutrachelophiini. (*) Provisionally attributed as shared by *Arcanumophis*, awaiting confirmation. Inset photographs by Alejandro Arteaga (*Erythrolamprus*, *Xenodon*, *Lygophis*), Laurie Vitt (*Eutrachelophis*) and Alessandro Catenazzi (*Arcanumophis*).

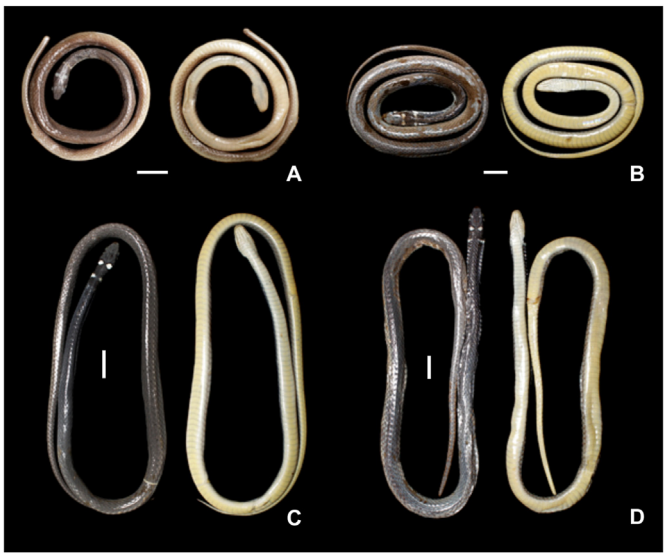

Fig. 4. Dorsal and ventral views of some preserved specimens of *Eutrachelophis papilio* Zaher & Prudente, 2020, showing variation in external morphology and color. (A) INPA-H 41140; (B) INPA-H 41090; (C) INPA-H 42751; (D) INPA-H 32365. Scale bar = 10 mm. (For interpretation of the references to colour/colour in this figure legend, the reader is referred to the Web version of this article.)

(INPA-H 32365) (Fig. 6). However, the most striking color variation derived from our new evidence occurs in the ocellar nape markings (Figs. 4–6). These markings are white in preservative and light orange in life, and most of the specimens have a single black-rimmed ocellus fused on the dorsum (butterfly-shaped; INPA-H 13984, 27389, 27390, 32246, 32291, 41090), fitting in the species' diagnosis. We observed variation in the color of these ocellus, ranging from uniformly colored (INPA-H 13984), or with darker scales in the medial portion (INPA-H 27389, 27390, 32246, 32291, 41090). This is also reflected in a variation in their shapes, as the medial angle that gives the characteristic of a butterfly shape varies and, in some cases, makes the ocellus almost rectangular (INPA-H 13984). In three other specimens (INPA-H 32365, 41140, 42751), the darker coloration in the medial portion of these ocellar markings reaches equal intensity to the background color (in one scale row), so that the markings cannot be classified as single and butterfly-shaped, becoming better classified as paired rounded ocelli (Figs. 4–6). Given the slightly variable body size of specimens possessing both phenotypes, we do not initially considered this variation as generated by ontogenetic changes. However, due to the low number of museum specimens known for *Eu. papilio* and *Eu. bassleri*, as well as limited evidence for their color variation in life, ontogenetic changes may be obscured and cannot be discarded as the drivers of the observed variation. The phenotype with paired rounded ocelli also could initially be attributed to *Eu. bassleri*, but we considered it as part of the *Eu. papilio* variation due to high ventral counts, a taxonomically more robust character than the highly variable ocellar nape markings (Myers & McDowell 2014), and geographic co-occurrence of both phenotypes in central Amazonia (Fig. 7). Moreover, both of these phenotypes of *Eu. papilio* (i.e. with butterfly-shaped ocellus or paired rounded ocelli) are represented in our phylogenetic analysis, separated by low genetic distances.

Considering this morphological variation, six meristic characters were explicitly considered for the diagnosis of the *Eu. papilio* (VE, SC, SLL, IL, ILA, ILP), as well as one coloration character (shape of ocellar nape markings). Our results clearly show that the phenotypic variation found through analyses of additional specimens does not fit in the proposed diagnosis of the species, based on less specimens (Zaher & Prudente 2020). To account for this new information, we provide below an emended diagnosis for *Eu. papilio*, in order to more adequately illustrate its morphological variation. We also provide new information on the species' geographic distribution and natural history associated with the new material.

3.4. Systematic account

Family Dipsadidae Bonaparte, 1838.
Subfamily Xenodontinae Bonaparte, 1845.
Tribe Eutrachelophiini Myers & McDowell, 2014, **status revalidated**.

3.4.1. Type genus
Eutrachelophis Myers & McDowell, 2014, by original designation.

3.4.2. Type species
Eutrachelophis bassleri Myers & McDowell, 2014.

3.4.3. Generic content
Arcanumophis Smaga, Ttito, & Catenazzi, 2019 **stat. nov.**; *Baliodryas* Zaher & Prudente, 2020; *Eutrachelophis* Myers & McDowell, 2014.

3.4.4. Species content
Arcanumophis problematicus (Myers, 1986) **stat. nov.**; *Baliodryas steinbachi* (Myers and McDowell, 2014); *Eutrachelophis bassleri* Myers and McDowell, 2014; *Eutrachelophis papilio* Zaher & Prudente, 2020.

3.4.5. Diagnosis
Members of Eutrachelophiini can be diagnosed from other xenodontine genera based on the following combination of characters: (2) short and slender temporal bones; (3) hemipenis bi or unilobed, distally with distinctly nude zones, and lacking calyces, grooves, or apical disks; (4) rostral scale with prominent crease; (5) paired elongated ocellar nape markings; (6) absence of horizontal neck-flattening behavior.

3.5. Eutrachelophis papilio Zaher & Prudente, 2020

3.5.1. Holotype
Adult male (MPEG 25471), from Fazenda Scheffer, Ituxi River (08° 20' S, 65° 43' W, 75 m asl), Lábrea, Amazonas, Brazil.

3.5.2. Diagnosis
This species presents: (1) 15/15/15 dorsal scales, with apical pits on anterior region of body; (2) rostral acuminate, with a distinct crease; (3) preocular present, single; (4) postoculars present, 1 + 1; (5) loreal present; (6) temporals 1 + 2; (7) supralabials eight, 2nd or 2nd–3rd in contact with loreal, 3rd–5th contacting the orbit; (8) infralabials 8–10, 1st–4th or 1st–5th in contact with anterior chinshields, 4th–5th or 5th–6th in contact with posterior chinshields; (9) ventrals 136–145 (136–145 in males, 139–145 in females); (10) subcaudals 56–76 (64–76 in males, 56–72 in females); (11) head and neck dark brown, first body third greyish-brown to greenish-grey, second body third light brown, last third light gray, two inconspicuous dorsolateral white stripes margined with black, supralabials white followed by a white neck blotch, dorsally black-rimmed; (12) ventral pattern varying from uniformly white to yellowish; (13) black-rimmed ocellar nape markings white in preservative and light orange in life, either butterfly-shaped ocellus fused on the dorsum or paired rounded ocelli; (14) maxillary teeth

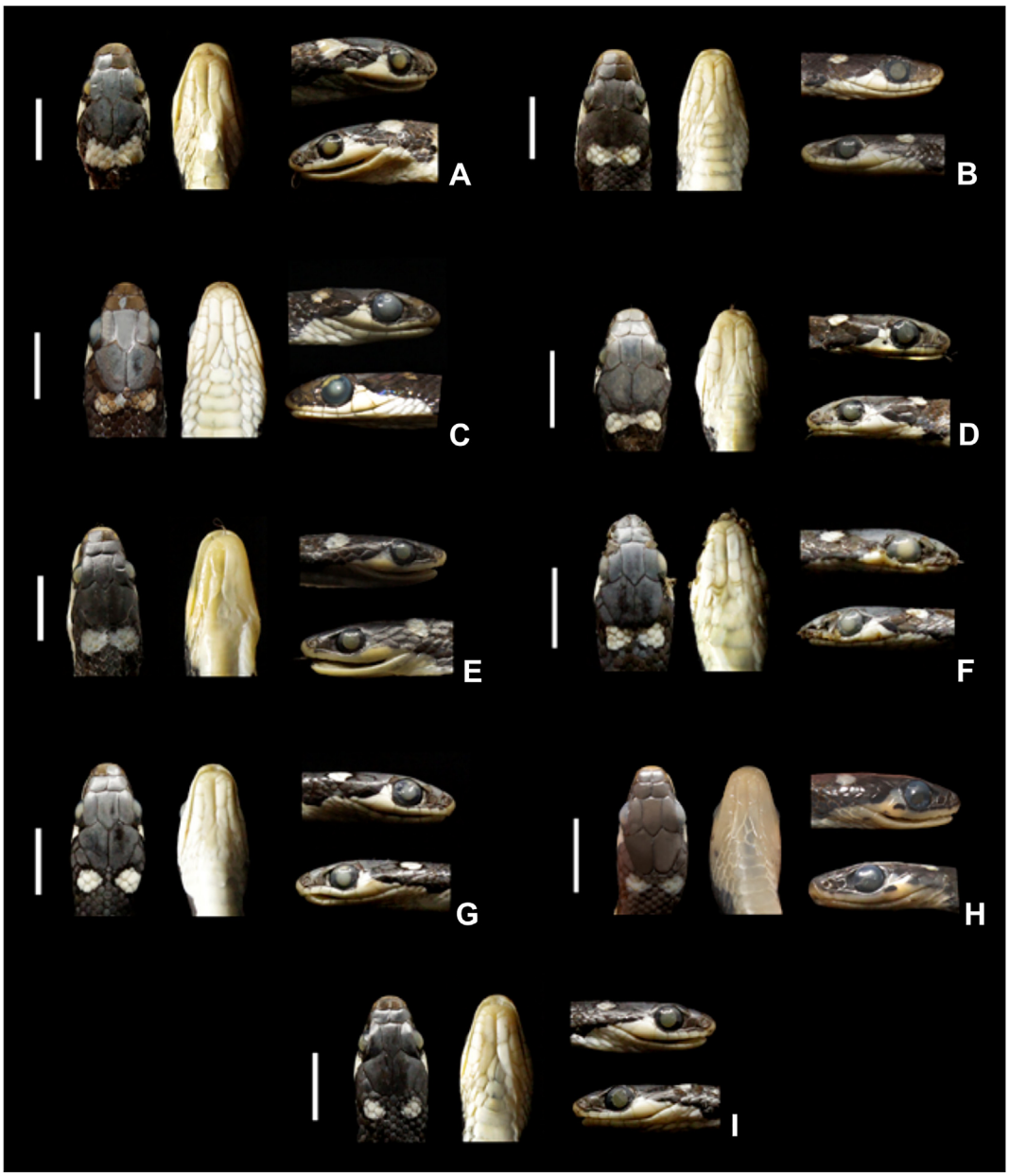

Fig. 5. Dorsal, ventral and lateral views of the head and nape of preserved specimens of *Eutrachelophis papilio* Zaher & Prudente, 2020, showing variation in external morphology and color (note the variation in ocelar nape markings). (A) INPA-H 13984; (B) INPA-H 32246; (C) INPA-H 41090; (D) INPA-H 27390; (E) INPA-H 32291; (F) INPA-H 27389; (G) INPA-H 42751; (H) INPA-H 41140; (I) INPA-H 32365. Scale bar = 10 mm. (For interpretation of the references to colour/colour in this figure legend, the reader is referred to the Web version of this article.)

22–25, curved, equal in size; (15) SVL 235–337 mm, TL 92–124 mm.

3.5.3. Variation

Largest male SVL 266 mm, TL 110 mm. Largest female SVL 337 mm, TL 124 mm. Snout–vent length in males 251–266 mm (mean 260 ± standard deviation 7; $n = 5$), in females 235–337 (279 ± 34; $n = 7$). Tail length in males 99–110 mm (105 ± 6; $n = 3$), in females 92–124 (106 ± 12; $n = 6$). Head length in males 9.17–11.17 (9.86 ± 0.82; $n = 5$), in females 9.91–12.30 (10.64 ± 1.02; $n = 6$). Head width in males 3.93–6.29 (5.53 ± 1.01; $n = 5$), in females 4.49–6.54 (5.80 ± 0.89; $n = 5$). Ventral scales in males 136–145 (141 ± 3; $n = 7$), in females 139–145 (141 ± 2; $n = 6$). Subcaudal scales in males 64–76 (69 ± 5; $n = 5$), in females 56–72 (67 ± 6; $n = 5$). For detailed values and additional characters, see Supp. Tables 1 and 2.

3.5.4. Comparisons

According to its original description (Zaher & Prudente 2020), *Eu. papilio* was considered to be diagnosed from its sole congener, *Eu. bassleri*, by three main characters: (1) shape of ocellar nape markings; (2) ventral scale counts; and (3) hemipenial morphology. Considering the characters 1 and 2, *Eu. papilio* presents butterfly-shaped ocellus and more ventrals (139–145), while *Eu. bassleri* has a pair of rounded ocelli and less ventrals (128–139). Our new data on the variation of the *Eu. papilio* evidenced that the butterfly-shaped ocellus may not be fused on the dorsum, forming a pair of rounded ocelli, and that lower limits of ventral scales range in this

Fig. 6. Variation of color in life of the closely related genera *Eutrachelophis* and *Arcanumophis*. (A–D) *Eutrachelophis papilio* Zaher & Prudente, 2020: (A) MPEG 2386, holotype, (B) INPA-H 32365, (C, D) INPA-H 32291. (E, F) *Arcanumophis problematicus* (Myers 1986). Photographs by Laurie Vitt (A), Rafael de Fraga (B), Pedro Ivo Simões (C, D) and Alessandro Catenazzi (E, F). (For interpretation of the references to colour/colour in this figure legend, the reader is referred to the Web version of this article.)

species may reach 136 scales. Therefore, both of these diagnostic characters overlap between *Eu. papilio* and *Eu. bassleri* and cannot unambiguously distinguish them. The new evidence also showed the variation of infralabial scales in *Eu. papilio*, and how many/which of them touch the chinshields, overlap with the known variation of *Eu. bassleri*, considered in its diagnosis (Zaher & Prudente 2020). In addition, the presence of greenish dorsal color in the first body third in life also overlapped between these species (Echevarría & Venegas 2015). Furthermore, it is also noteworthy that various characters from skull osteology and viscerae failed to be useful in distinguishing these two species (see Myers & McDowell 2014; Zaher & Prudente 2020). Therefore, after our new evidence, differences between *Eu. papilio* and *Eu. bassleri* are only supported by hemipenial characters: the format (long and tapering distally in *Eu. papilio*, short and rounded distally in *Eu. bassleri*) and the development of intrasulcular spines (vestigial in *Eu. papilio,* well-developed in *Eu. bassleri*). Moreover, when the ocellar markings are paired and round, they seem more prominent in size in *Eu. papilio*, and orange in life (vs. reduced in size and white in *Eu. bassleri*; Echevarría and Venegas, 2015). However, such characters are quite subject to variation and may be weak to morphologically support these two taxonomic entities as full species. Although the morphological similarities between these entities seems now greater than their known differences, we prefer not to synonymize them based on our limited evidence in other taxonomically informative characters (see section 4).

3.5.5. Geographic distribution

Most of the new specimens of *Eu. papilio* were collected within its currently known distribution range: southwestern Amazonia, at the Juruá-Purus and Purus-Madeira interfluves (Fig. 7; Zaher & Prudente 2020; Citeli et al., 2020). However, new geographic records filled relevant knowledge gaps in the species distribution and provided the first evidence of its occurrence in the Madeira-Tapajós interfluve, confirming that the large Madeira River does not represent a geographical barrier to its occurrence.

3.5.6. Natural history

Specimens from the upper Madeira River were found in both primary *terra firme* (non-seasonally flooded) and *várzea* (seasonally flooded) forests. They were found active above or curled under the leaf litter during the day (between 9 h and 14 h). These findings suggest that the species is primarily cryptozoic and diurnal, which is supported by the results of Citeli et al. (2020). Populations in

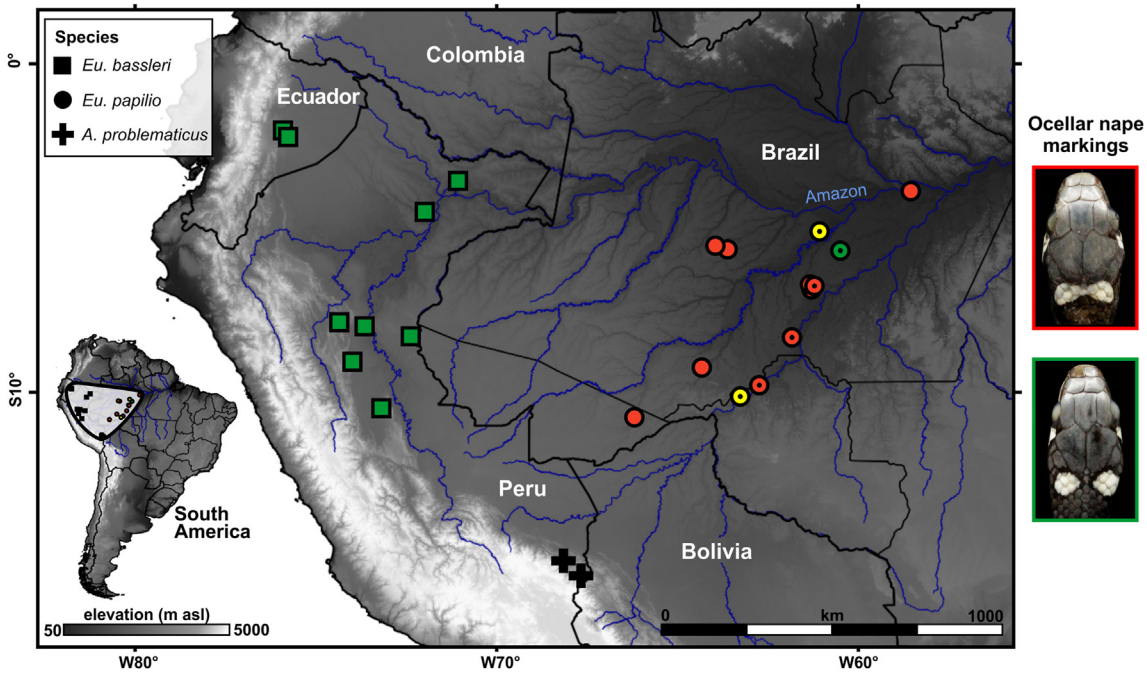

Fig. 7. Geographic distribution of the closely-related genera *Eutrachelophis* (represented by *Eu. bassleri* and *Eu. papilio*) and *Arcanumophis* (monotypic, *A. problematicus*) in southwestern Amazonia, upon an elevation background. Distributions based on data of newly analyzed specimens (dotted symbols) and literature records (see section 2.2). Distinct dot colors correspond to the variation in ocellar nape markings within *Eutrachelophis* specimens: (green) paired round ocelli; (red) butterfly-shaped ocellus; (yellow) co-occurrence of both ocellar nape conditions. (For interpretation of the references to colour/colour in this figure legend, the reader is referred to the Web version of this article.)

várzea forests should be particularly monitored, aiming to investigate whether the species migrates away as the river level rises, or becomes temporarily scansorial, although such field observations may be challenging. While one of us (RF) was sweeping the leaf-litter to detect cryptozoic species, he found a curled individual of *Eu. papilio* showing its yellow belly. We interpreted this behavior as emitted in a defensive context, although we were not able to distinguish whether the snake was performing a thanatosis strategy, or showing this bright color as an aposematic signal.

4. Discussion

Phylogenetic relationships of the rarely recorded Amazonian genera *Eutrachelophis* and *Arcanumophis* have remained controversial by the lack of integrative consideration of multiple evolutionary data sources. The scarcity of available material and incomplete knowledge of intraspecific variations has largely contributed to this instability. Our study provides new insights in phylogenetic relationships of these genera and fills some associated knowledge gaps. Varying on evolutionary and taxonomic scales, we expanded the knowledge associated with these snakes at supra-generic, generic, interspecific, and intraspecific levels.

Considering our molecular-based phylogenetic inference of caenophidian diversification, similar results in both well-supported and low-supported levels have been reported over the years in phylogenetic studies using similar molecular and taxa sampling (Zaher et al., 2009; 2019; Grazziotin et al., 2012). Differences in positioning and delimitation of major clades considering our results and those previously reported are restricted to the lower supported levels of the phylogenetic trees and are natural considering the associated uncertainties (Zaher et al., 2019). For instance, the paraphyly of Dipsadinae reported here is biased by the lower volume of molecular data available for the terminals of the genus *Rhadinaea* included in our analysis.

In fact, adaptive radiations, as in the case of snake diversification, are known to generate low resolutions in the innermost branches of molecular-based phylogenetic trees (Degnan & Rosenberg 2006). This is a result of the rapid diversification generating high probabilities of non-corresponding gene trees (Degnan & Rosenberg 2006). This is also exemplified by the historically conflicting hypothesis on the phylogenetic relationships of major clades of the neoavian diversification, another classic case of adaptive and 'explosive' radiation (Suh 2016). Interestingly, the increased volume of molecular information in recent phylogenomic analyses of these birds did not increase the phylogenetic resolution at the deeper nodes (Reddy et al., 2017). This case clearly shows that solely the increase in molecular coverage may not be enough to resolve the phylogenetic relationships among some major snake clades. Instead, the best approach may be to assume a hard polytomy and primarily seek for congruence in distinct analyses using different methods and evolutionary data sources, as well as distinct research groups (Suh 2016).

Our molecular-based phylogenetic inference clearly supports that *Eutrachelophis* and *Arcanumophis* are closely related. Combining this result with their phenotypic affinities, we here considered *Arcanumophis* as part of Eutrachelophiini, even with the absence of detailed evidence for all the characters supporting the tribe (mostly osteological, visceral and hemipenial morphology). *Arcanumophis problematicus* seems to be an extremely rare species whose occurrence records are spaced for many years (Myers 1986; Smaga et al., 2019), justifying its inclusion in this tribe considering the available phenotypic and molecular evidence. The unique phenotypic condition of this genus compared to the other xenodontines had already been postulated since its original description (Myers 1986) and its allocation in Eutrachelophiini satisfactorily matches its evolutionary distinctiveness. Similar situation occurs with respect to the genus *Baliodryas*. Even without the support of molecular information, we tentatively considered this genus as part of Eutrachelophiini based on its historical allocation in this taxon,

and its remarkable phenotypic similarities with *Eutrachelophis* [which led Myers & McDowell (2014) consider them congeneric]. However, it is noteworthy that this monotypic genus also has many phenotypic apomorphies when compared to *Eutrachelophis* and *Arcanumophis*, especially regarding hemipenial morphology (Myers & McDowell 2014; Zaher & Prudente 2020). Therefore, based on our results and literature data, it is impossible to determine whether its phenotypic disparity should be interpreted as a secondary change within Eutrachelophiini or an ancestral condition in such diversification. This should be properly assessed with the further increase of available data for this species.

Our reports on phenotypic overlapping considering the current diagnoses of *Eu. papilio* and *Eu. bassleri* certainly obscure the validity of these taxa as full species. Considering the ocellar nape markings on snakes, Myers & McDowell (2014) discussed the possibility that they are not directly subjected to selective pressures, due to marked intraspecific variability. In addition, they also explicitly show that intraspecific variation in tail size can generate distinct hemipenial morphologies (Myers & McDowell 2014). This effect may be one of the reasons causing the single morphological variation that currently diagnoses *Eu. papilio* and *Eu. bassleri*. Biogeographically, distribution ranges of both species are not limited by large rivers and are mostly constrained to a single area of endemism recognized for vertebrates (Silva et al., 2005), corroborating the idea that *Eu. bassleri* and *Eu. papilio* may instead correspond to different phenotypes at extremes of an intraspecific clinal variation. In fact, morphological variations usually masquerade the species boundaries between xenodontines closely related to *Eutrachelophis*, which are currently recognized as species complexes (e.g., Torres-Carvajal and Hinojosa, 2020). Such statements clearly support a hypothesis that *Eu. papilio* may be a junior synonym for *Eu. bassleri*. However, it is noteworthy that some qualitative divergences are still evident in skull osteology of type specimens of these species, especially in the shape of vomerian, nasal and ectopterygoid processes (H. Zaher, pers. comm.; see Myers & McDowell 2014; Zaher & Prudente 2020). Therefore, a lack of additional evidence for *Eu. bassleri* specimens prevent us from making taxonomic decisions in this case. Only the gathering of novel molecular and phenotypic data can help to reveal new diagnostic characters segregating this taxon from *Eu. papilio*, or ultimately provide evidence for their synonymization. Such novel data are especially necessary from topotypic populations of *Eu. bassleri*, and from populations connecting these two species across the undersampled western Brazilian Amazonia (Fig. 7).

Our study also demonstrates the singular value of biological collections, and the reassessments of its deposited material as a tool to increase our knowledge on spatial and temporal patterns of biological diversity (Meineke et al., 2018; Monfils et al., 2020). All the new specimens and tissue samples of *Eutrachelophis* used as the basis for this study were historically deposited in the INPA collections as belonging to the genus *Taeniophallus* Cope, 1895. Based on this case, we can predict that such misidentification is also occurring more widely in herpetological collections, and strongly suggest the reassessment of specimens labelled as from genus *Taeniophallus* in collections housing Amazonian material. Our study also highlights the importance of fieldwork in poorly sampled or neglected areas for advancing knowledge about snake diversity. This correlation is evidenced by some recent relevant findings across Amazonia, such as rediscoveries of species and description of new taxa (Melo-Sampaio et al., 2021; Smaga et al., 2019). Under these approaches, additional specimens of Eutrachelophiini genera and related taxa can be revealed, helping to fill the knowledge gaps that remain associated with these enigmatic snakes.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jcz.2021.10.003.

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