



Taxonomic status of the enigmatic *Natrix sexcarinata* Wagler, 1824 (Serpentes: Colubridae: Colubrinae)

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Abstract

Wagler described *Natrix sexcarinata* through a specimen collected on the banks of the Amazon River in Brazil, without citing a specific location. The species was later transferred to different Neotropical genera (*Chironius*, *Herpetodryas*, *Phrynonax*, and *Pseustes*) currently allocated in the Family Colubridae. The taxonomic instability of *Natrix sexcarinata* is probably due to its brief original description in combination with its supposedly inaccurate illustration. Despite the holotype being lost during World War II, some authors have pointed out that its description is somewhat similar to the widespread concept of *Pseustes poecilonotus*. More recently, a molecular study proposed the synonymy of the genera *Pseustes* with *Spilotes*, resurrecting the *Phrynonax* genus to allocate *Ph. poecilonotus* and *Ph. polylepis*. However, the taxonomic positioning of *Natrix sexcarinata* remains unsatisfactory with respect to the cis-Andean taxa placed in *Phrynonax* or even *Spilotes* throughout the Amazon. Considering the taxonomic and nomenclatural problems mentioned above, we investigated how many *Phrynonax* species occur along the Amazon Basin and what would be their applicable name. We examined the external morphology (meristic, morphometric, and color pattern data) of 118 *Phrynonax* specimens and prepared the hemipenes of seven specimens to understand geographic, sexual, and ontogenetic variability parameters. Our result suggests the synonymy of *Ph. polylepis* and *N. sexcarinata* under the combination *Phrynonax sexcarinatus*. Based on available evidence, we reinforce that *Phrynonax sexcarinatus* is the only congener that occurs along the Amazon Basin. We have also designated a *Natrix sexcarinata* neotype to stabilize its complex nomenclature.

Key words: Amazon, geographic variation, hemipenial morphology, linear morphometry, nomenclature, polychromatism, *Phrynonax*, *Pseustes*, *Spilotes*

Introduction

Colubridae Opell, 1811 (sensu Zaher *et al.* 2009) comprises about 100 genera and 800 species distributed worldwide except for the poles and most of the Australian region (Uetz *et al.* 2022). Colubridae are currently clustered into two subfamilies, Ahaetullinae and Colubrinae (Zaher *et al.* 2019). In the last two decades colubrid taxonomy has undergone many systematic advances following a long period of relative stability, most boosted by new phylogenetic hypotheses grounded in molecular data (Nagy *et al.* 2004; Siler *et al.* 2013; Lei *et al.* 2014; Montingelli *et al.* 2019; Torres-Carvajal *et al.* 2019, 2021; Burbrink *et al.* 2020). On the other hand, at the same time, several studies based on new samples analyzed through novel approaches for the study of distinct phenotype systems have also contributed to the accurate delimitation of old taxa or the recognition of new species to the science (Kok 2010; Montingelli & Zaher 2011; Costa *et al.* 2013; Fernandes & Hamdan 2014; Hamdan & Fernandes 2015; Albuquerque & Fernandes 2022; Albuquerque *et al.* 2022). In this regard, we highlight the enigmatic case of *Natrix sexcarinata* Wagler, 1824 among the many New World colubrids that remain unsatisfactorily verified concerning their taxonomic status.

Therefore, the aim of this study is to investigate the taxonomy of cis-Andean *Phrynonax* Cope, 1862 populations in order to establish how many species occur along the Amazon Basin. We also evaluated whether the name *Natrix sexcarinata* Wagler, 1824 would be applicable or not to any population currently attributed to the delimited taxa. Finally, we inferred species boundaries for recognized species updating their intraspecific variability, diagnoses and distributions.

Historical resumé

Wagler (1824) described *Natrix sexcarinata* (Fig. 1) based on a specimen from the banks of the Amazon River in Brazil and *Natrix cinnamomea* (Fig. 2) based on a specimen from the Amazon Forest, both lacking any details concerning type locality. Wied (1824) described *Coluber poecilostoma* based on a series of specimens from Southeastern Brazil (Rio de Janeiro, Cabo Frio, Maricá and Saquarema). Wagler (1830) transferred *Natrix sexcarinata* to the genus *Herpetodryas* Schlegel, 1837 and proposed its synonymy to *Natrix cinnamomea* Wagler, 1824. Schlegel (1837) proposed the synonymy of *Natrix sexcarinata* to *Herpetodryas carinatus* (Linnaeus, 1758) and described *Dipsas dieperinkii* based on a specimen from Paramaribo, Suriname. Fitzinger (1843) erects the genera *Thamnobius* for *Coluber poecilostoma* Wied, 1824 and *Pseustes* for *Dipsas dieperinkii* Schlegel, 1837. Gunther (1858) described *Spilotes poecilonotus* based on two specimens, one from Honduras and other from Mexico, and listed *Natrix sexcarinata* and *Natrix cinnamomea* as junior synonyms of *Herpetodryas carinatus* (Linnaeus, 1758). Cope (1860) described *Tropidodipsas lunulata* based on a specimen from Honduras. Cope (1862) described the *Phrynonax* genus to accommodate *Tropidodipsas lunulata*. Peters (1867) described *Ahaetulla polylepis* through a specimen from Suriname, with no specific location. Peters (1869) described *Spilotes fasciatus* based of a specimen from Maroni, Suriname. Günther (1872) suggested that *Spilotes fasciatus* may comprise an affinity for *Spilotes poecilonotus* Günther, 1858 (without proposing a synonym). Cope (1875) described *Spilotes chrysobronchus* based on a specimen from “the coast region” of Costa Rica. Bocourt (1888) described *Spilotes argus* based on a specimen from Mexico and proposed the synonymy of *Spilotes fasciatus* Peters, 1869 to *Spilotes lunulatus* (Cope, 1860).

Boulenger (1891) considered *Natrix sexcarinata* Wagler, 1824 a valid species of *Herpetodryas*. Cope (1893) described *Synchalinus corallioides*, a new genus and species through a specimen from Buenos Aires, Costa Rica. Günther (1894) suggested that *Phrynonax lunulatus* may represent the junior synonym of *Spilotes poecilonotus* Günther, 1858 and *Spilotes chrysobronchus* would be identical to *Spilotes fasciatus* Peters, 1869, although he did not propose any formal taxonomic act in either case. Boulenger (1894) considered *Herpetodryas sexcarinatus* as a valid species, listing specimens from Rio de Janeiro, São Paulo (Brazil), Asunción (Paraguay), and Venezuela, and *Natrix cinnamomea* was cited as a possible synonym for *Herpetodryas sexcarinatus* (Wagler, 1824). This author proposed the synonymy between *Phrynonax poecilonotus* and *Spilotes argus*, part of *Spilotes poecilonotus* from Günther (1858, 1894) and *Phrynonax lunulatus* (Cope, 1860), part of *Spilotes lunulatus* from Bocourt (1888) and *Phrynonax fasciatus*, and between *Coluber poecilostoma* and *Phrynonax sulphureus* (Wagler, 1824) (Boulenger 1894). Boulenger (1894) also proposed the synonymy between *Phrynonax fasciatus* (Peters, 1869) and *Ahaetulla polylepis* Peters, 1867, but maintains the name *Phrynonax fasciatus* as valid, although *Ahaetulla polylepis* represents the older name. Finally, this author described *Phrynonax guentheri* based on the *Spilotes argus* specimen described by Günther (1894) from Atoyac, Vera Cruz, Mexico and described *Phrynonax eutropis* based on part of the *Spilotes fasciatus* specimen described by Günther (1872) from Trinidad (Boulenger 1894).

Peracca (1896) synonymized *Phrynonax lunulatus* (Cope, 1860), *Phrynonax guentheri* Boulenger, 1894 and *Phrynonax fasciatus* (Peters, 1869) to *Phrynonax poecilonotus* (Günther, 1858). Stejneger (1901) described *Phrynonax lyoni* based on a specimen from Macuto, Venezuela. Werner (1913) described *Phrynonax atriceps* without indicating any type locality. Barbour & Amaral (1924) described *Phrynonax shropshirei* based on two specimens from the vicinity of Gatún, in the Panama Canal Zone. Amaral (1929) recognized two species in the *Phrynonax* genus, *Ph. poecilonotus* (Günther, 1858) and *Ph. sulphureus* (Wagler, 1824), both containing several subspecies. *Phrynonax sulphureus* is considered a cis-Andean species categorized into two subspecies (*Ph. s. sulphureus* and *Ph. s. poecilostoma*). *Phrynonax poecilonotus* is considered a trans-Andean species comprising five subspecies (*Ph. p. poecilonotus*, *Ph. p. poecilonotus argus*, *Ph. p. polylepis*, *Ph. p. chrysobronchus*, and *Ph. p. shropshirei*). Amaral (1929) considered *Tropidodipsas lunulata* Cope, 1860 a junior synonymy of *Ph. p. poecilonotus*; *Phrynonax guentheri* Boulenger, 1894 a junior synonymy of *Ph. p. argus*; and *Spilotes fasciatus* Peters, 1869, *Phrynonax eutropis* Boulenger, 1894, *Phrynonax lyoni* Stejneger, 1901, and *Phrynonax atriceps* Werner, 1913 as junior synonymies of *Ph. p. polylepis*. Amaral (1929) also highlighted that *Thamnobius* Fitzinger, 1843 was already preoccupied with the insect genus *Thamnobius* Schoenherr, 1836 and Brongersma (1937) rediscovered the *Dipsas dieperinkii* type and confirmed its synonymy to *Pseustes sulphureus*.

When redescribing *Chironius quadricarinatus* (Boie, 1827), Bailey (1955) dedicated a paragraph to the name *Natrix sexcarinata*. This author pointed out an uncertainty on whether *Natrix sexcarinata* represents a *Chironius* species or another colubrid genus. Hoge (1962) suggested that no specimen following Wagler's (1824) original

description represents *Natrix sexcarinata* (sensu stricto) and, therefore, describes the second *Pseustes sexcarinatus* specimen on the basis of a specimen collected at km 86 of the Belém-Brasília Highway, Pará, Brazil. Peters & Orejas-Miranda (1970) considered four species within the *Pseustes* genus, namely *Ps. poecilonotus*, *Ps. sexcarinatus*, *Ps. shropshirei* and *P. s. sulphureus*, with four subspecies recognized as *Ps. poecilonotus* (*Ps. p. poecilonotus*, *Ps. p. argus*, *Ps. p. chrysobronchus*, and *Ps. p. polylepis*). Peters & Orejas-Miranda (1970) considered the following junior synonyms for *Ps. p. poecilonotus* (Günther, 1858): *Tropidodipsas lunulata* Cope, 1860; *Ps. p. argus* (Bocourt, 1888) as a senior synonym of *Phrynonax guentheri* Boulenger, 1894; *Ps. p. chrysobronchus* (Cope, 1875) as a senior synonym of *Synchalinus corallioides* Cope, 1893; and *Ps. p. polylepis* (Peters, 1867) as a senior synonym of *Spilotes fasciatus* Peters, 1869, *Phrynonax eutropis* Boulenger, 1894, *Phrynonax lyoni* Stejneger, 1901 and *Phrynonax atriceps* Werner, 1913. Dixon *et al.* (1993) pointed out that *Natrix sexcarinata* and *Natrix cinnamomea* do not represent *Chironius* species. Giraudo & Scrocchi (2002) commented that the species identified in Argentina as *Pseustes sexcarinatus* were actually *Chironius quadricarinatus* representatives (Boie, 1827). Wallach *et al.* (2014) listed *Pseustes sexcarinatus* as a valid species and highlighted this is as a probable senior synonymy for *Ps. poecilonotus* Günther, 1858.

Jadin *et al.* (2013) performed a molecular phylogeny for the *Pseustes* and *Spilotes* genera, recovering six lineages, where *Pseustes sulphureus* represents the sister group of *Spilotes pullatus* (Linnaeus, 1758) in a highly supported clade. As the type species of *Pseustes* is *Dipsas dieperinkii*, a junior synonym for *Pseustes sulphureus*, one of the implications based on the topology recovered by Jadin *et al.* (2013) is that the *Pseustes* Fitzinger, 1843 and *Spilotes* Wagler, 1830 genera would be monotypic and sister taxa. The authors, therefore, proposed a formal synonymy between *Pseustes* and *Spilotes*. Jadin *et al.* (2013) revalidated the *Phrynonax* Cope, 1862 to accommodate species from the other clade. Jadin *et al.* (2013) recovered three distinct lineages within the *Phrynonax* clade, where the analytical terminals were identified based on the geographic proximity of the type locality of both *Phrynonax poecilonotus* and *Phrynonax polylepis*. Thus, the trans-Andean clade was identified as *Phrynonax poecilonotus* and the cis-Andean clade, as *Phrynonax polylepis*, comprising the third lineage cited as *Phrynonax* sp. Finally, Jadin *et al.* (2013) do not comment on *Phrynonax shropshirei*. Natera-Mumaw *et al.* (2015) revalidated *Phrynonax lyoni* Stejneger, 1901, differentiating this species from *Ph. shropshirei* based on coloration, naso-ocular distance, loreal contact with the supralabials, number of keeled scales, shape of the apical pits and shape of the last infralabial. Natera-Mumaw *et al.* (2015) also note that the *Tropidodipsas lunulata* holotype displays several similarities with the *Phrynonax shropshirei* holotype. Finally, some authors have not accepted the resurrection of *Phrynonax lyoni* (e.g., Uetz *et al.* 2022). See Table 1 a summary of the current taxonomic status of proposed names.

TABLE 1. Summary of changes from the original taxon proposition to currently most accepted taxonomy without considering the results of the present study.

Taxon	Current Taxonomy
<i>Natrix sexcarinata</i> Wagler, 1824	Senior synonym of <i>Phrynonax polylepis</i> (Peters, 1867)
<i>Natrix cinnamomea</i> Wagler, 1824	Junior synonym of <i>Chironius quadricarinatus</i> Boie, 1827
<i>Coluber poecilostoma</i> Wied, 1824	<i>Spilotes sulphureus poecilostoma</i> (Wagler, 1824)
<i>Dipsas dieperinkii</i> Schlegel, 1837	Junior synonym of <i>Spilotes sulphureus</i> (Wagler, 1824)
<i>Spilotes poecilonotus</i> Günther, 1858	<i>Phrynonax poecilonotus poecilonotus</i> (Günther, 1858)
<i>Tropidodipsas lunulata</i> Cope, 1860	Junior synonym of <i>Phrynonax poecilonotus</i> (Günther, 1858)
<i>Ahaetulla polylepis</i> Peters, 1867	<i>Phrynonax polylepis</i> (Peters, 1867)
<i>Spilotes fasciatus</i> Peters, 1869	Junior synonym of <i>Phrynonax polylepis</i> (Peters, 1869)
<i>Spilotes chrysobronchus</i> Cope, 1875	<i>Phrynonax poecilonotus chrysobronchus</i> (Cope, 1875)
<i>Spilotes argus</i> Bocourt, 1888	<i>Phrynonax poecilonotus argus</i> (Bocourt, 1888)
<i>Synchalinus corallioides</i> Cope, 1893	Junior synonym of <i>Phrynonax p. poecilonotus</i> (Günther, 1858)
<i>Phrynonax guentheri</i> Boulenger, 1894	Junior synonym of <i>Phrynonax p. poecilonotus</i> (Günther, 1858)
<i>Phrynonax eutropis</i> Boulenger, 1894	Junior synonym of <i>Phrynonax polylepis</i> (Günther, 1858)
<i>Phrynonax lyoni</i> Stejneger, 1901	Junior synonym of <i>Phrynonax polylepis</i> (Günther, 1858)
<i>Phrynonax atriceps</i> Werner, 1913	Junior synonym of <i>Phrynonax polylepis</i> (Günther, 1858)
<i>Phrynonax shropshirei</i> Barbour & Amaral, 1924	<i>Phrynonax shropshirei</i> Barbour & Amaral, 1924

Material and methods

Material. We examined 118 specimens currently assigned to *Phrynonax polylepis* along the Amazon Basin. Specimens are listed in Appendix I. The collection acronym follows Sabaj (2020).

Techniques. Specimens were sexed through a midventral incision on the base of the tail to verify the presence or absence of the hemipenis, except for specimens with everted organs. Measurements were taken with a dial caliper to the nearest 0.1 mm, except for Total Length (TL), Snout-Vent Length (SVL) and Caudal Length (CL), which were obtained through a cotton thread stretched above a flexible ruler to the nearest 1.0 mm. It should be noted that the thread was constantly immersed in ethanol to reduce the effect of the size variation due to drying. The following variables were also determined with the dial caliper: Head Length (HL), from the quadrate-mandibular angle of articulation to the anterior end of the rostral scale; Head Width (HW), in its widest portion; Loreal Height (LH) and Loreal Length (LL), from respective opposite border sides. We evaluated the conditions of some scalation characters, as follows: number of internasal and prefrontal scales; frontal-preocular contact (on both sides); number of supralabials (on both sides); supralabial-eye contact (on both sides); number of infralabials (on both sides); number of infralabials contacting the first pair of chin shields (on both sides); symphyseal scale condition (first pair of infralabials separating or not the symphyseal scale from the chin shields); number of preoculars (on both sides); number of postoculars (on both sides); temporal formula (on both sides); condition of the nasal scales (divided or not; on both sides); cloacal shield condition (single or divided); number of ventral scales; number of subcaudal scales; condition of subcaudal scales (single or divided) and number of dorsal scale rows (anterior/midbody/posterior). We also verified the macro-ornamentation conditions of the dorsal scales with respect to keels (presence or absence), number of rows with keels on the anterior, midbody and posterior regions, and presence and number of apical pits. Maxillae were examined *in situ* under a stereomicroscope through a narrow latero-medial incision mostly performed with the spine of a scalpel blade to avoid specimen injuries, between the supralabials and the maxillary arch. Teeth and empty sockets were counted after removing the tissues covering the maxillary bone.

Qualitative coloration characters were coded based on specimens preserved in collections (70% ethanol). Three main color-based morphotypes were observed, as follows: Pattern A: dorsum of the head beige with scattered brown spots or blotches; ventral surface of the head and supralabials cream; supralabials and infralabials displaying beige vertical bars on the scale edges; dorsum of the body and tail beige with transverse brown blotches; ventral surface of the body cream-white anteriorly, gradually darkening from the second third of body to the cloacal region until reaching a beige ground color; belly speckled with brown spots or blotches concentrated on the posterior region; ventral surface of the tail beige speckled with brown spots and blotches. Pattern B: dorsum of the head brown; supralabials and ventral surface of the head cream-yellow; dorsum of the body and tail uniformly brown; ventral surface of the body yellow anteriorly, gradually darkening from the second third of body until becoming uniformly brown posteriorly; ventral surface of the tail almost uniformly brown. Pattern C: represents variable levels of combinations between Patterns A and B. Digital photos in life housed at the iNaturalist Website <<https://www.inaturalist.org/home>> were used to complemented the color in life patterns (Fig. 3).

The applied hemipenes eversion method was modified from Pesantes (1994), replacing the potassium hydroxide solution with distilled water (Passos et al. 2016). The organs remained for 15 min in an alcohol Alizarin red solution to stain ornamented calcareous structures prior to inflation with petroleum jelly, according to an adaptation from the original procedure employed by Uzzell (1973) and modified by Harvey & Embert (2008). The terminology for hemipenial descriptions follows Dowling & Savage (1960) and Zaher (1999). Two hemipenes were used for descriptions (MNRJ 18023 and MNRJ 19527) and another five organs for comparison purposes to *Spilotes pullatus* (MNRJ 23611, MNRJ 25479) and *Spilotes sulphureus* (MNRJ 23885, MNRJ 25005, MNRJ 26494).

Geographic Data. Locality coordinates were obtained by consulting original data in museum catalogues or digital databases. Whenever possible, the provenance of records obtained from the literature or in museum databases without specific field coordinates were refined using the Google Earth Pro v7.1.2 <<https://www.google.com/earth>> or Google Maps <<https://www.google.com.br/maps>> software. When georeferenced data (latitude and longitude) was available, but the state or municipality was not specified in the collection data, information was obtained by using Google Maps <<https://www.google.com.br/maps>>. The maps were produced using QGIS 3.26 <<https://qgis.org>>.

Operational Analytical Units. Six operational analytical units (termed called subpopulations hereafter) were determined according to the Amazon Basin interfluves (Fig. 4) as follows: north of the Amazon River and east of

the Negro River (A), south of the Amazon River and east of the Tocantins-Araguaia River (B), south of the Amazon River and west of the Tapajós River (C), and south of the Amazon River and between the Tocantins-Araguaia and Tapajós Rivers (D). Thus, we hypothetically considered hydrography as a possible natural barrier to the dispersion of individuals among Amazonian subpopulations (*sensu* Wallace 1852), as recently reported for anurans (Godinho & Silva 2018), snakes (Henderson *et al.* 2009; Dal Vechio *et al.* 2021), birds (Oliveira *et al.* 2017; Ribas *et al.* 2011), and mammals (Boubli *et al.* 2015).

Statistical Tests. All statistical tests were performed in the R environment (R Core Development Team 2020). Some individuals were eventually withdrawn from the analyses due to the accumulation of missing data above 30% of the variable. In some cases, the use of “dplyr” package for data transformation was required. Different packages were used to perform specific analyses, as follows: “car” for the Levene test; “psych” to determine the adequate sample size for each analysis separately, after removing individuals or variables; “rstatix” to determine outliers and run the Dunn’s test; “gmodels” for the Pearson’s Chi-square test; “RVAideMemoire” for the Shapiro-Wilk test per group; “DescTools” for the Tukey HSD test; and “MASS” for the Discriminant Function Analysis. The packages “ggplot2” and “ggthemes” packages were employed to construct all graphs the graphs, except for the pie charts, which were created using Google Sheets, in which the “patchwork” was employed to modify graph styles. A 0.05 alpha was employed. The R script and the raw data are available at <<https://doi.org/10.6084/m9.figshare.21708023.v1>>.



FIGURE 1. Illustration employed in the description of *Natrix sexcarinata* Wagler, 1824 based on a specimen from the banks of the Amazon River in Brazil, modified from the original.



FIGURE 2. Illustration employed in the description of *Natrix cinnamomea* Wagler, 1824 based on a specimen from the Amazon Forest without detailed location, modified from the original.

Quantitative Analyses. Data normality was assessed by the Shapiro-Wilk test data and the homogeneity of variances was verified by the Levene test. The Student t test was applied to detect secondary sexual dimorphism concerning the evaluated variables. When no homogeneity of variances was detected and/or normality was not reasonable to assume, the Mann-Whitney test with a continuity correction was performed to detect secondary sexual

dimorphism. The SVL was used as a proxy to test the effect of ontogenetic allometry and we excluded specimens with juvenile coloration (see below) from the exploratory multivariate analyses. An Analysis of Variance (ANOVA) was used to investigate ontogenetic differences when the data were parametric and comprised more than two groups and the Student t test was applied when the data were parametric and comprised two groups. A Kruskal-Wallis test was used when the data were not parametric and comprised over two groups, while a Mann-Whitney test, with a continuity correction, was used when the data were non-parametric and comprised two groups. An Analysis of Variance (ANOVA) was used to investigate differences among groups (= subpopulations), excluding outliers. When the ANOVA detected differences between subpopulations, the Tukey test was then applied to determine which subpopulations differed for a given variable. The Kruskal-Wallis test was applied when the data were non-parametric or if no homogeneity of variances was verified. When the Kruskal-Wallis test detected differences between subpopulations, the Dunn test was employed to determine which subpopulations differed. In the case of variables displaying secondary sexual dimorphism, analyses were performed separately for males and females. A Principal Component Analysis (PCA) and a Discriminant Function Analysis (DFA) were performed based on the correlation matrix due to differences in the variance scale between different variables (e.g., meristic and morphometric data). The PCAs and DFAs were performed separately for males and females due to secondary sexual dimorphism.

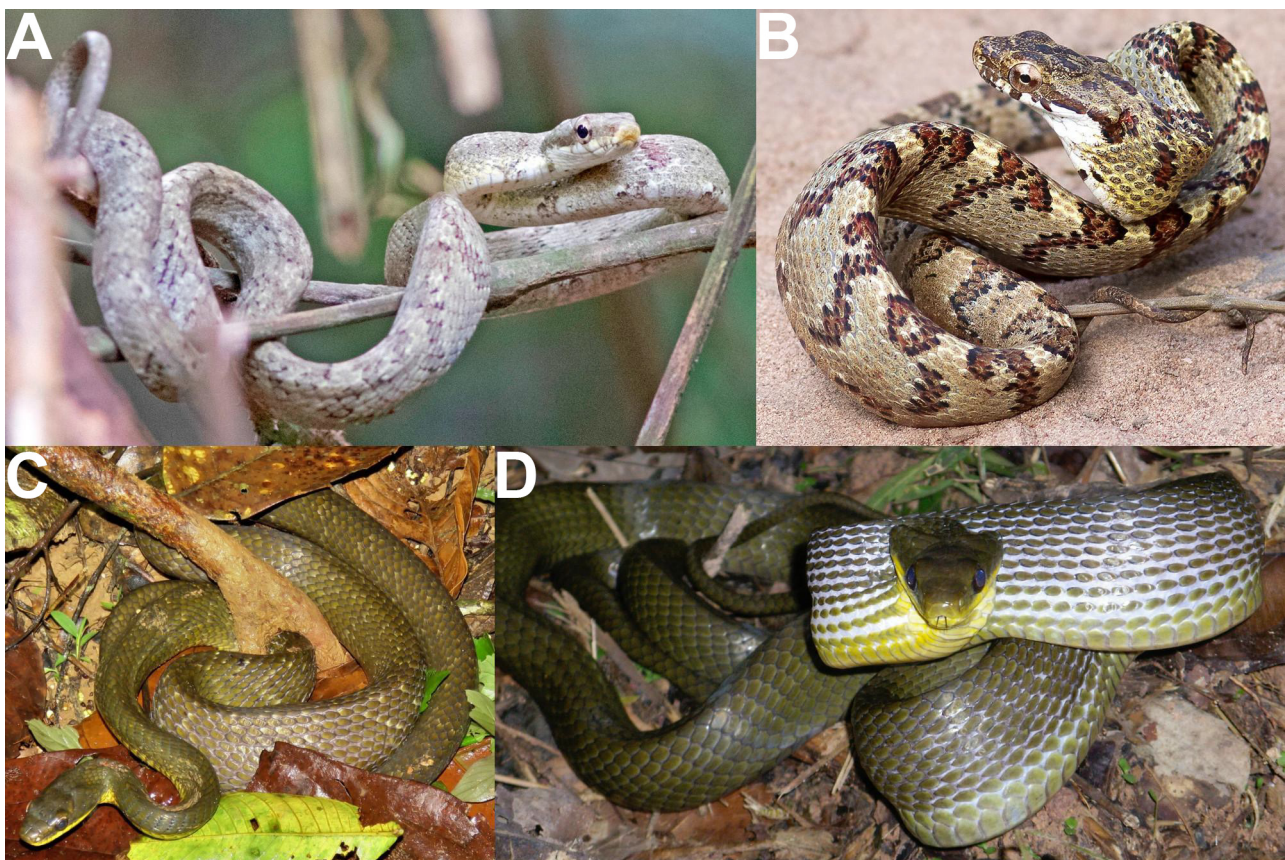


FIGURE 3. General view of *Phrynonax polylepis* in life from Parauapebas, in the state of Pará (A); Sinop, in the state of Mato Grosso (B); from Bujari, in the state of Acre (C); and Belterra, in the state of Pará (D), all in Brazil. Color Pattern A is depicted in Figures A–B, while Color Pattern B is depicted in figures C–D. Modified images from original photographs by Fábio Giordano (A), Antonino Gonçalves Medina (B), Martin Acosta (C), and Miguel A. Casado (D). All photos are available at <<https://www.inaturalist.org/home>>.

Qualitative Analyses. A Pearson’s chi-square test was used to evaluate secondary sexual dimorphism in frequency, while Pearson’s chi-square test with Yates’ continuity correction was applied to evaluate secondary sexual dimorphism when only two categories were considered. The Fisher’s Exact test was employed for the detection of secondary sexual dimorphism when characteristics were present in less than five individuals in at least one of the groups, while Fisher’s Exact test or Fisher’s Exact test with simulated p-value (2000 pseudoreplicates) was used if more than two characteristics were present. In addition, Pearson’s Chi-square test was used to detect whether the frequency of certain characteristics would be associated with one of the four investigated subpopulations.

The Fisher's Exact Test (p -value simulated per 2000 pseudoreplicates) was used when characteristics in less than five individuals were present to detect differences between subpopulations. Separate analyses were conducted for variables displaying secondary dimorphism. As the number of keels may vary in the same individual depending on the series of dorsal scale rows, this character was treated as a categorical variable.

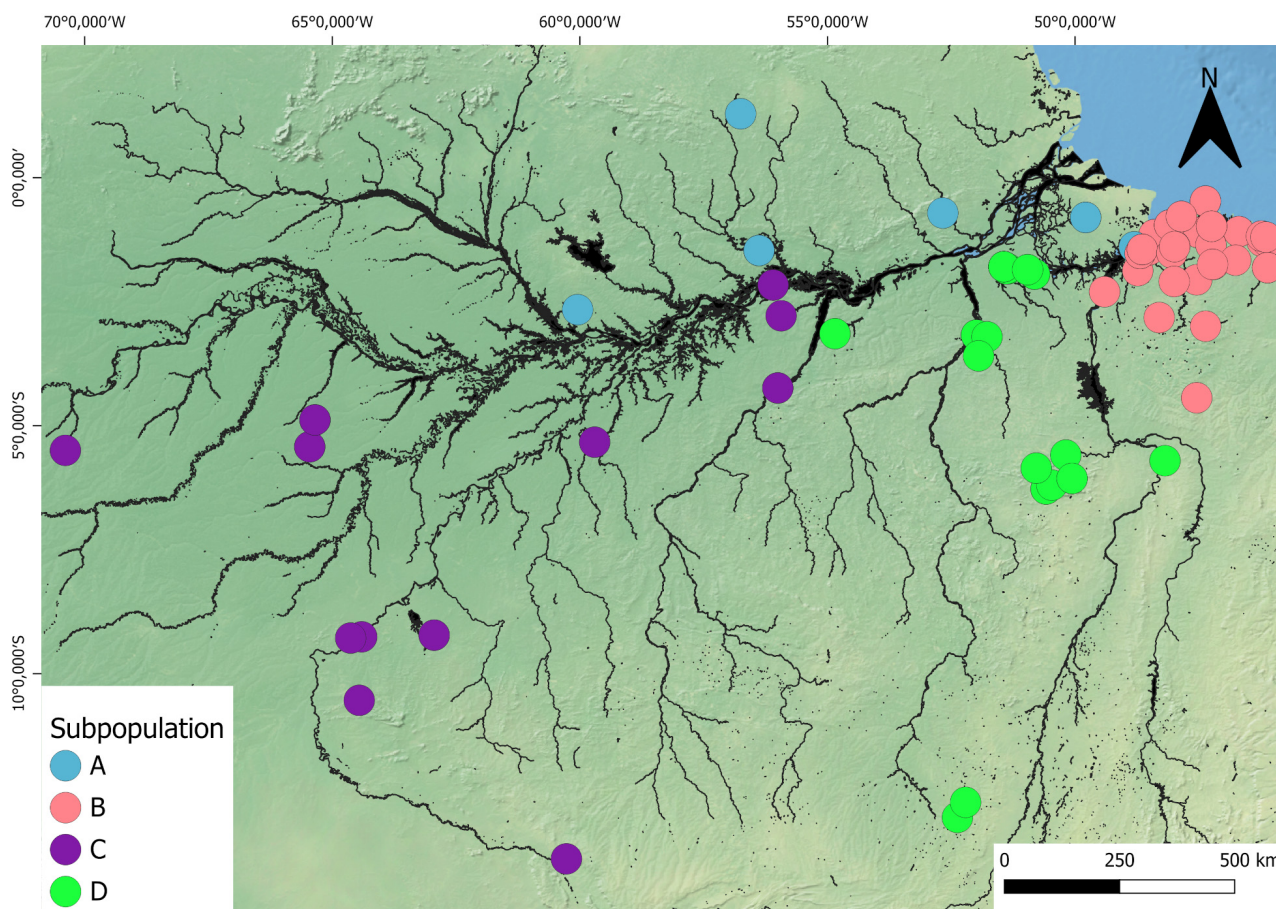


FIGURE 4. *Phrynonax polylepis* distribution based on examined samples. Different colors represent subpopulations labeled as distinct Operational Taxonomic Units, following possible natural dispersion barriers across the main interfluves along the Amazon Basin (see Material and Methods for additional explanations).

Results

A total of 118 *Phrynonax* specimens from the Amazon Basin were analyzed, and 100 individuals (46 females and 54 males) were sexed.

Quantitative Analyses. Sexual dimorphism was detected for ventrals ($p < 0.05$, $W = 2049$, $n = 96$) and SVL ($p < 0.002$, $W = 1711$, $n = 100$). Evidence of ontogenetic variations were noted for the nasal scales on both the right ($p < 0.0002$, $W = 1185$, $n = 80$) and left sides ($p < 0.0006$, $W = 1136$, $n = 80$), the presence/absence of keels on dorsal scales ($p < 0.0002$, $W = 144$, $n = 114$) and the color pattern in both females ($p < 0.03$, $H = 7.8019$, $n = 38$) and males ($p < 0.05$, $F = 33.54$, $n = 42$). In contrast, differences related to the SVL and number of keels on the midbody ($p < 0.005$, $H = 31.329$, $n = 50$) were evidenced only in males. Differences in the number of postoculars on the right side ($p < 0.04$, $W = 122.5$, $n = 115$) were noted. The post-hoc comparisons concerning color patterns indicated significant differences between color patterns A and B, for females, with a significant difference between all coloring patterns for males (Fig. 5A). Therefore, we associate Pattern A with immature individuals, Pattern B with adults and Pattern C with subadults, which may comprise mature or immature individuals (Fig. 3). From this point on, we apply the juvenile and adult classification following this color criterion. In addition, the post-hoc comparison for the number of keels in the middle of the body indicated a difference in relation to the SVL between specimens without dorsal scale keels in relation to specimens with seven rows of keeled dorsal scales.

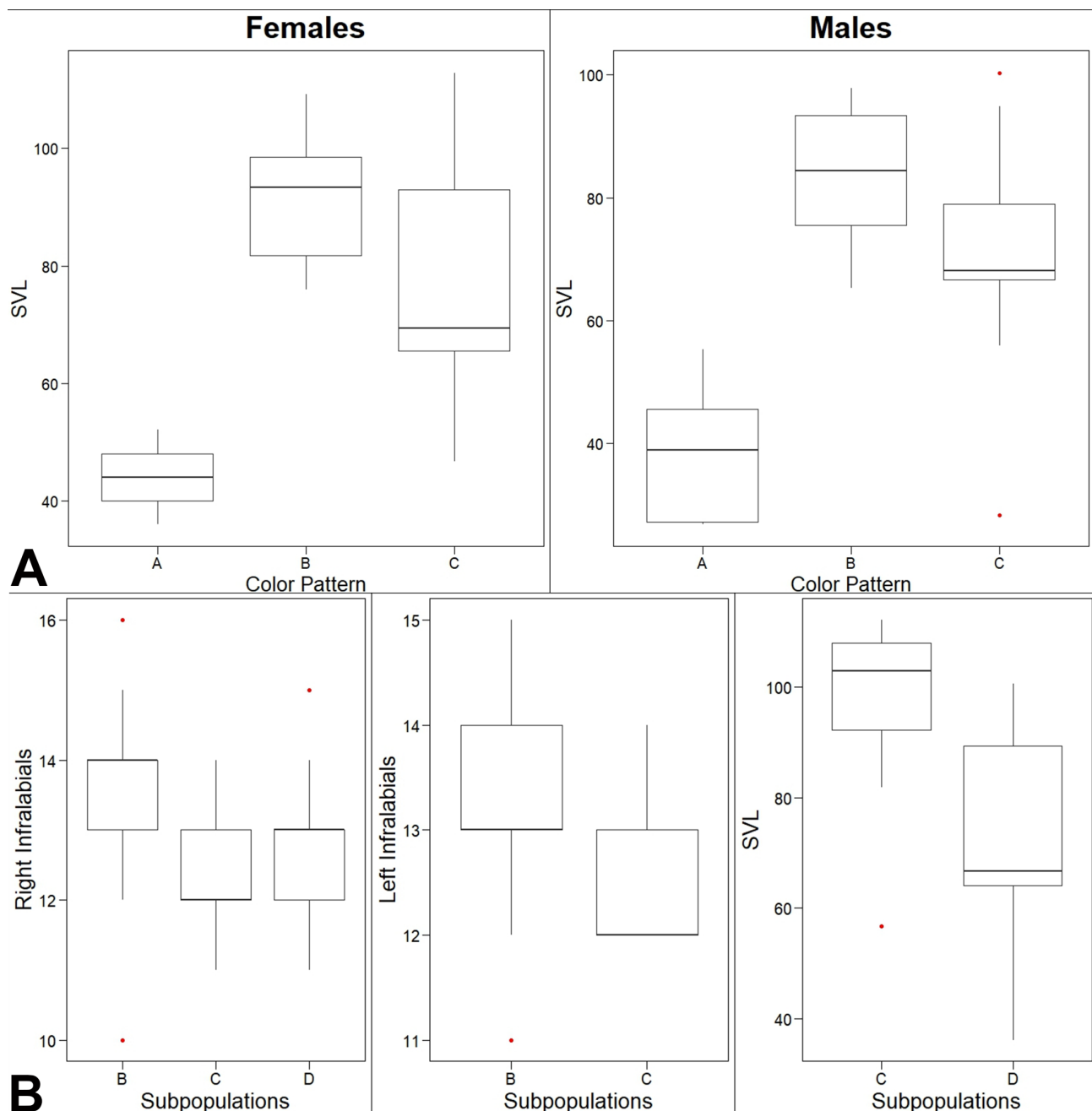


FIGURE 5. Association between snout-vent length and color pattern changes in females (left) and males (right) (A) and differences in the number of right infralabials (left), left infralabials (center) and snout-vent lengths (right) (B) in *Phrynonax polylepis* from the Amazon.

Significant differences among subpopulations were observed for the number of infralabials on the right ($p < 0.05$, $H = 24.347$, $n = 116$) and left ($p < 0.01$, $H = 11.387$, $n = 118$) sides, and the SVL in females ($p < 0.04$, $H = 8.4501$, $n = 46$). The post-hoc comparison of the right infralabials indicated a difference between population B in relation to subpopulation C and D, while the post-hoc comparison for the left infralabials demonstrated a difference between subpopulation B only in relation to subpopulation C. According to the post-hoc comparison, the difference in the SVL of females is observed for between subpopulations C and D (Fig. 5B). Although the exploratory PCA were unable to discriminate the groups labeled *a posteriori*, an exploratory DFA demonstrated some differences mainly concerning subpopulation A, even though a very restricted sample from the Guiana Plateau for both males and females was available (Fig. 6). Regarding females, discrimination was observed mainly along the axis between subpopulations A, B+D and C, strongly correlated with LL. For males, discrimination was observed mainly along the axis between subpopulations B and C+D and was strongly correlated with left LH and right LL.

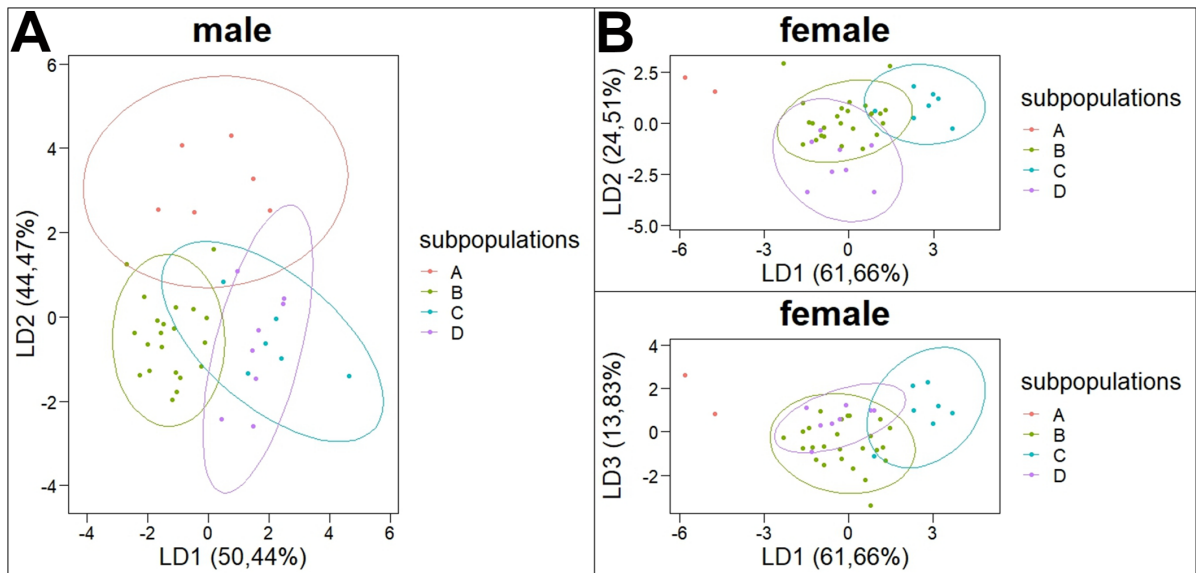


FIGURE 6. Plot of the Discriminant Function Analysis scores for *Phrynonax polylepis* males (A) and females (B) with 95% confidence ellipses.

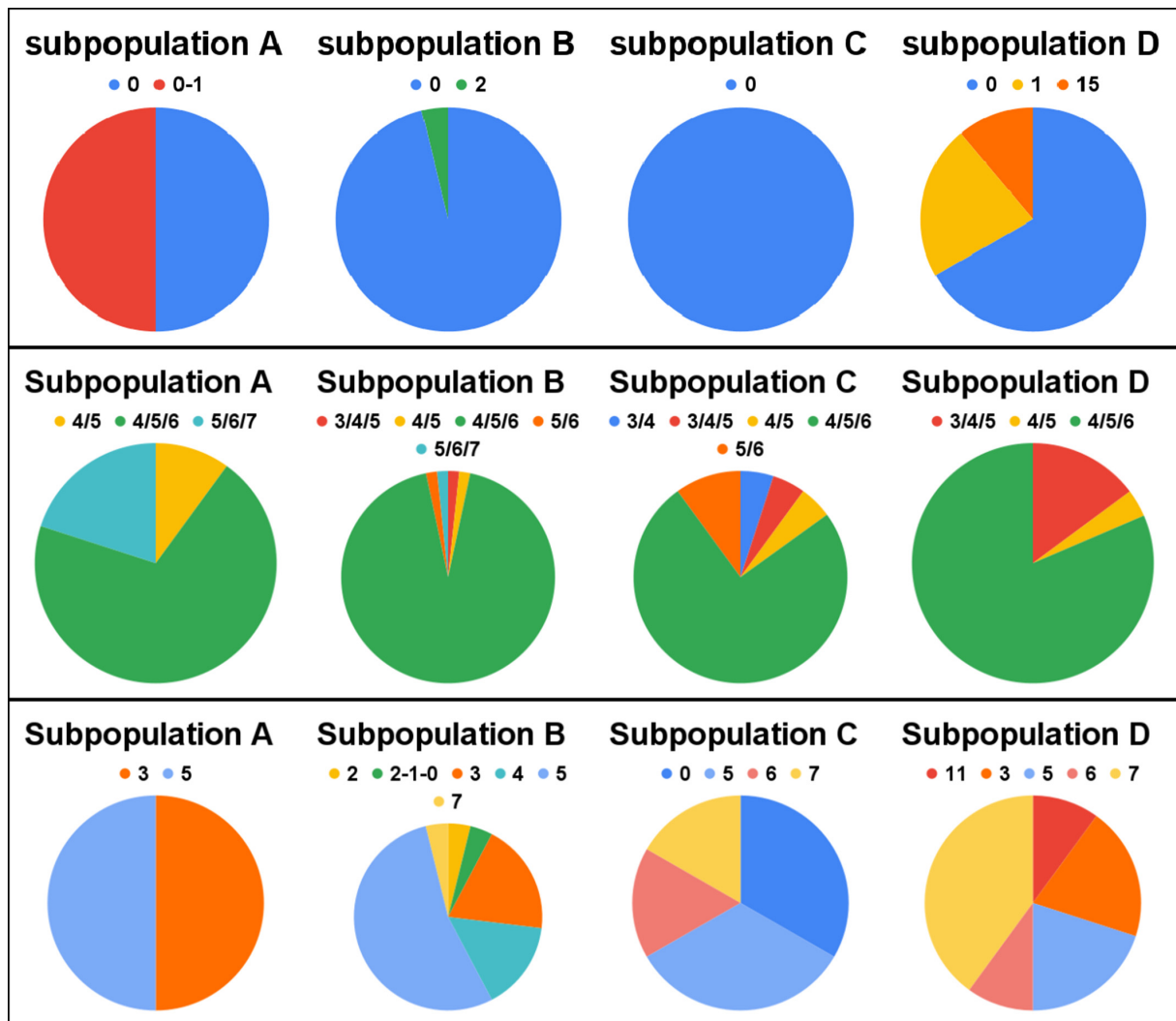


FIGURE 7. Cumulative frequency for the number of anterior keeled dorsal scale rows (top; only for females), number of right supralabials contacting the orbit (center), and number of posterior keeled dorsal scale rows (bottom; only for females) for *Phrynonax polylepis* subpopulations.

Qualitative Analysis. Sexual dimorphism was detected for the number of keeled dorsal scale rows on the anterior ($p < 0.005$, $n = 93$), midbody ($p < 0.005$, $n = 94$), and posterior ($p < 0.005$, $n = 95$) regions, in addition to color pattern frequency ($p < 0.03$, $n = 82$). Significant differences were observed among subpopulations for the number of anterior ($p < 0.02$, $n = 43$) and posterior ($p < 0.03$, $n = 44$) keels only for females, and for the number of supralabial scales contacting the orbit on the right side ($p < 0.01$, $n = 117$) (Fig. 7). However, the visual section of the graphs indicates that, despite a difference in frequencies, this distinction takes place between the less dominant patterns. Regarding the number of keels in females, the absence of keels was the modal pattern on the anterior region in all investigated subpopulations, except for subpopulation A, which contained very few female individuals. With respect to the frequency of the supralabials contacting the orbit, the modal pattern in all subpopulations was the fourth, fifth and sixth contacting the orbit.

Taxonomic decision

The results reported herein support the recognition of only one evolutionary unit, as there is no exclusive feature allowing for the unambiguous discrimination or diagnosis of any of the evaluated subpopulations based on the character systems analyzed in the present study. For example, all observed differences are related to sex (i.e., meristic and morphometrics), age classes (i.e., ontogenetic coloration changes) or incomplete segregation among subpopulations (see above). Therefore, we investigated which of the available names would be applicable to the unique species recognized herein.

In this regard the oldest applicable name would be *Natrix sexcarinata* Wagler, 1824. However, the holotype housed at the Zoologische Staatssammlung München (ZSM 1744/0) is considered lost (Franzen & Glaw 2007; Dr. Frank Glaw, pers. comm. in 14 September 2022). Thus, we can only refer to its original description and illustration to decide on the applicability of this name. To facilitate comparisons, the characters described by Wagler (1824) were compared to the characters in the present study (in parentheses). The specimen used in the original description of *Natrix sexcarinata* had one anterior temporal scale (1–3), six rows of keeled scales on the dorsum (0–17), 13 teeth [possibly maxillary] (11–19, but see below), a single cloacal shield (single or divided), 202 ventral scales (186–215) and 125 subcaudal scales (95–142). When considering the holotype illustration (Fig. 1), six supralabial scales (6–10), nine infralabial scales (10–16), one preocular scale (1–2) and two postocular scales (2–3) are observed. In the case of dorsal scale rows, the illustration unfortunately does not present a complete view of the back, but it is possible to count more than 14 rows at some points. Thus, the number of scales at midbody would probably be of over 15 rows, diverging from all *Chironius* species (see Torres-Carvajal *et al.* 2019). Only 58 ventral scales can be identified in the illustration, not all the ventrals are visible in the figure and this number is not informative for taxonomic purposes. In addition, some discrepancies with respect to the original description/illustrations are probably due to different measurement and/or anatomical structure preparation methods. Regarding the hemipenis, the French text indicates that “*L’individu décrit, qui est un mâle, a une verge extrêmement grosse, dont l’extrémité est ronde, simple et armée de toute part de gros aiguillons pointus, et qui ressemble au fruit du maronnier*” (free translation: “The described individual, who is a male, has an extremely large penis, the extremity of which is round, simple and armed on all sides with large pointed spikes, and which resembles the fruit of the chestnut tree”). On the other hand, the hemipenis illustration in Wagler (1824) was probably created from a semi-everted organ, and the spines appear as if they were at the most distal region, compatible with *Phrynonax* hemipenes (Amaral 1929: Figure 6). With respect to teeth, the low indicated number is probably due to the non-counting of toothless alveoli, given that Wagler (1824) mentions that the teeth are well spaced. As suggested by Hoge (1962), it is reasonable to assume illustration errors, considering discrepancies between some of Wagler’s (1824) descriptions and the types of other species that are not currently lost (e.g., *Natrix scurrula* and *Natrix sulphurea*). With respect to coloration characters, Wagler (1824) describes “*caput supra nigro-fuscum, immaculatum; labia, mentum et gula flavida; totum corpus et cauda subtus nigricanti-fusca, immaculata; truncus anticus infra flavicanti-fuscus, posticus et cauda nigricanti-fusca; in utroque latere scutorum abdominalium lineola longitudinalis dilutior, obsoleta et inde vix conspicua, interdum subimpressa*” (free translation: “above head black-brown, immaculate; yellowish lips, chin, and throat; the entire body and tail below is blackish-brown, immaculate; foretrunk belly yellowish-brown, back and tail dark brown; a more diluted longitudinal line, worn and therefore barely visible, sometimes underprinted is present on both sides of the abdominal scales”). As pointed out by Hoge (1962), a slight difference between the Latin and French descriptions in terms of the tail coloration is noted.

In sum, considering the available data from Wagler (1824), we believe that these features are largely congruent with the character distribution observed in the examined *Phrynonax* specimens, despite the small discrepancies mentioned above. On the other hand, some morphological similarities are noted between the Amazonian *Phrynonax* and *Natrix sulphurea* (= *Spilotes sulphureus*) populations. To complicating matters more, the type locality of *Spilotes sulphureus* is relatively vague (“Rio Jápura from its mouth [Brazil, 03°08’S, 64°66’W] to Araracuara [Colombia, 00°24’S, 72°17’W]”; see Vanzolini 1981, Franzen & Glaw 2007) and both species occur largely in sympatry along the Amazon (Nogueira *et al.* 2019). Therefore, in addition to associating the name *Natrix sexcarinata* with the cis-Andean populations of South America currently allocated in *Phrynonax*, we designate a neotype for *Ph. sexcarinatus* to stabilize the nomenclature of the species with regard to *Spilotes sulphureus*. We reject *Spilotes sulphureus* as synonymous of *Natrix sexcarinata*, beyond its phylogenetic position recovered by Jadin *et al.* (2013), as the medial portion of the hemipenis is less similar to Wagler’s 1824 plate than that of *Phrynonax polylepis*, while the absence of a subocular scale and the presence of two postocular scales depicted in the Wagler plate and the six keel rows in the lost type also point to *Phrynonax polylepis*, as *Spilotes sulphureus* presents all dorsal scales keels except for the paraventrals. The neotype selection was based on samples closer to the Amazon River, as the type locality is the bank of the Amazon River in the Latin description by Wagler (1824), while it is defined as swampy surroundings of forests near the Amazon River in the French text (see below).

***Phrynonax sexcarinatus* (Wagler, 1824) Revalidated**

Ahaetulla polylepis Peters, 1867. (Type locality: Suriname; holotype ZMB 5899).

Spilotes fasciatus Peters, 1869. (Type locality: Maroni River, Suriname; holotype ZMB 6455).

Phrynonax atriceps Werner, 1913. (Type locality: unknown; holotype formerly housed at ZMH but lost, according to Hallermann 1998).

Neotype. Adult female, MNRJ 20302, collected by Emiliane Pereira Gonçalves and team between November 13 and December 08, 2006, Porto Trombetas (01°28’01.3”S, 56°22’46.0”W; ca. 40 m above sea level; asl hereafter), municipality of Oriximiná, state of Pará, Brazil. By present designation (see remarks). No tissue sample from this specimen was preserved (Fig. 8).

Diagnosis and Definition. *Phrynonax sexcarinatus* can be distinguished from all congeners by a unique combination of the following characters: dorsal scale rows usually keeled in adult specimens, except for the first series, usually smooth; dorsal scale rows usually 21/23/15; postoculars usually two; temporal formula usually 2+2; supralabials usually eight, fourth to sixth contacting the orbit; infralabials usually 13, the first eight contacting the first pair of chinshields; maxillary teeth 11–19; ventral scales 196–211 in females, 186–215 in males; subcaudal scales 95–142 in females, 110–139 in males; color in preservative (70% ethanol), adults presenting the dorsum of the head brown, supralabials and gular region cream, ventral surface of the body cream anteriorly, darkening to brown posteriorly, ventral surface of the tail brown, dorsum of the body and tail uniform brown; color in preservative (70% ethanol), juveniles with the dorsum of the head beige with scattered brown spots or blotches, supralabials and infralabials cream with brown vertical bars on the posterior edges, a cream gular region, dorsum of the body and tail beige with transverse dark blotches, ventral surface of the body creamish-white anteriorly, darkening posteriorly to beige, belly with scattered dark brown spots or blotches concentrated on the posterior of the body, ventral surface of the tail beige speckled with dark brown spots; maximum SVL 1128 mm in females, 1200 mm in males; relative tail length 32.7–46.7% SVL in females, 34.2–45.7% SVL in males.

Comparison. *Phrynonax sexcarinatus* differs from all congeners (in parenthesis) due to a uniform brown dorsal color pattern in adults (vs. brown dorsum with dark brown paravertebral bands and dorsal scales with scattered yellow spots or blotches on the vertebral region in *Ph. poecilonotus*, dorsum orange or reddish with yellow stripes in *Ph. shropshirei*, and dorsum reticulated with yellow and black in *Ph. lyoni* [= *Ph. polylepis* sensu Uetz *et al.* 2022]). *Phrynonax sexcarinatus* differs from *Spilotes* species (sensu Jadin *et al.* 2013; in parenthesis) by presenting a maximum SVL of approximately 1200 mm (vs. maximum SVL of over 2500 mm), hemipenis unilobed, unicapitate with evident capitular constriction, and two insertion points of the hemipenis retractor muscle on the hemipenial apice (vs. a noncapitate hemipenis and a single insertion point for the hemipenis retractor muscle); differs from *Spilotes pullatus* by usually having 23 dorsal scale rows on the midbody (vs. 16–18 dorsal scale rows at midbody), usually 14–16 maxillary teeth (vs. usually 20 maxillary teeth), adults with a uniform brown coloration (vs. adults

never uniform brown), hemipenis with the apical portion of the capitulum rounded, spines similar in size and spaced with the exception of the most basal, which are smaller, and calyces on the asulcate side similar to the sulcate side (vs. hemipenis with the apical capitulum portion of triangular with lateral and apical bulbs, spines increasing in size from the base to distal region of hemipenial body, and very deep calyces on the asulcate side); differs from *Spilotes sulphureus* by the absence of the subocular scale, usually two postocular, temporals usually 2+2, usually seven rows of keeled dorsal scale rows (vs. subocular usually present, usually three postoculars, temporals usually 1+2, only the paraventral rows without keels), hemipenis with apical portion of the capitulum rounded, hemipenial body covered with spines on both sides of the organ and hemipenial spines approximately half the size of the spine in *S. sulphureus* (vs. hemipenis with the apical portion of the capitulum triangular with lateral bulbs, hemipenial body with spines restricted to the lateral side on the sulcate side of the organ and hemipenial spines approximately twice the size of the spine in *P. sexcarinatus*).

Neotype Description. Adult female; SVL 1128 mm, CL 446 mm, HL 44.7/45.3 mm (left/right, hereafter), HW 24.6 mm; rostror–orbital distance 13.9/14.5 mm, naso–orbital distance 8.4/9.0 mm, interocular distance 16.6 mm, internasal distance 9.5 mm; rostral 7.6 mm width, 4.4 mm high; internasals, divided, 5.8/ 5.7 mm long, 3.3/3.3 mm wide; prefrontals, divide, 7.5/7.5 mm wide, 5.9/6.4 mm length; frontal 8.7 mm wide, 10.0 mm long; supraocular 6.3/6.3 mm wide, 11.1/11.1 mm long; parietal 9.5/9.8 mm wide, 11.6/11.8 mm long; LL 3.6/4.6 mm, LH 2.2/2.2 mm; preocular 1.5/2.9 mm long, 6.0/5.5 mm high; symphyisial 3.1 mm long, 5.6 mm wide; anterior chinshields 10.3/10.5 mm long, 4.9/5.2 mm wide; eye diameter 7.3/7.2 mm; preocular 1/1; postocular 2/3; temporal formula 2+2/3+2; supralabials nine, fourth to sixth contacting the orbit; infralabials 14, eight first infralabials contacting the first pair of chin shields; first pair of infralabials in contact behind the symphyisial; anterior dorsal scales 22, with almost no keeled scale rows; dorsal scales on the midbody 23, with seven keeled scale rows; posterior dorsal scales 15, with five keeled scale rows; two apical pits separated from each other by the midline (= keel); ventral scales 201; cloacal shield whole; subcaudal scales divided in 123/124 series; terminal spine present; maxillary teeth on the right side 16.

Dorsum of the head uniformly brown; gular region and supralabials cream; supralabials and infralabials with some inconspicuous brown vertical bars on the posterior edges of the posterior supralabials; dorsum of the body and tail uniformly brown; ventral surface of the body cream-yellow anteriorly, gradually darkening to beige or a light brown ground color posteriorly; belly anteriorly presenting some brown spots or blotches concentrated on the lateral region of the ventral scales; ventral surface of the tail completely brown (Fig. 8).

Morphological Variation. Prefrontals divided ($n = 117$) or whole ($n = 1$); frontal in contact ($n = 124$ sides) or not contacting ($n = 104$ sides) the preocular scale; single nasal ($n = 91$ sides), divided ($n = 71$ sides), with the division visible at the top ($n = 41$ sides) or at the bottom ($n = 15$ sides); preocular one ($n = 227$ sides) or two ($n = 7$ sides); postoculars two ($n = 220$ sides) or three ($n = 12$ sides); temporal formula 1+1 ($n = 6$ sides), 1+2 ($n = 14$ sides), 2+1 ($n = 6$ sides), 2+2 ($n = 145$ sides), 2+3 ($n = 17$ sides), 3+2 ($n = 11$ sides), 3+3 ($n = 4$ sides) with some specimens displaying a unusual pattern ($n = 31$ sides); supralabials 6 ($n = 2$ sides), 7 ($n = 14$ sides), 8 ($n = 150$ sides), 9 ($n = 67$ sides) or 10 ($n = 3$ sides); 3–4th supralabials contacting the orbit ($n = 2$ sides), 3–5th ($n = 12$ sides), 4–5th ($n = 9$ sides), 4–6th ($n = 200$ sides), 4–7th ($n = 1$ side), 5–6th ($n = 3$ sides) or 5–7th ($n = 7$ sides); infralabials 10 ($n = 1$ side), 11 ($n = 6$ sides), 12 ($n = 54$ sides), 13 ($n = 98$ sides), 14 ($n = 61$ sides), 15 ($n = 13$ sides) or 16 ($n = 1$ side); infralabial pairs contacting the anterior chin shields 5th ($n = 5$ sides), 6th ($n = 11$ sides), 7th ($n = 86$ sides), 8th ($n = 122$ sides) or 9th ($n = 10$ sides); anterior dorsal scale rows 20 ($n = 1$), 21 ($n = 85$), 22 ($n = 18$), 23 ($n = 24$) or 24 ($n = 1$); midbody dorsal scale rows 15 ($n = 4$), 16 ($n = 5$), 17 ($n = 15$), 18 ($n = 39$), 19 ($n = 9$), 20 ($n = 24$), 21 ($n = 26$), 22 ($n = 25$), 23 ($n = 53$), 24 ($n = 4$) or 25 ($n = 3$); posterior dorsal scale rows 13 ($n = 15$), 14 ($n = 24$), 15 ($n = 95$), 16 ($n = 1$) or 18 ($n = 1$); absent anterior dorsal scale rows with keels in females ($n = 39$), 1 ($n = 3$), 2 ($n = 1$) or 15 ($n = 1$); absent anterior dorsal scale rows with keels in males ($n = 29$), 1 ($n = 15$), 2 ($n = 1$), 3 ($n = 6$) or 5 ($n = 1$); absent midbody dorsal scale rows with keels in females ($n = 1$), 1 ($n = 3$), 2 ($n = 1$), 3 ($n = 7$), 4 ($n = 6$), 5 ($n = 20$), 6 ($n = 3$), 7 ($n = 4$) or 17 ($n = 1$); absent midbody dorsal scale rows with keels in males ($n = 4$), 2 ($n = 1$), 4 ($n = 5$), 5 ($n = 12$), 6 ($n = 9$), 7 ($n = 12$), 9 ($n = 1$), 10 ($n = 3$), 11 ($n = 2$), 13 ($n = 1$), 14 ($n = 1$), 15 ($n = 1$) or 17 ($n = 1$); absent posterior dorsal scale rows with keels in females ($n = 3$), 1 ($n = 1$), 2 ($n = 2$), 3 ($n = 8$), 4 ($n = 4$), 5 ($n = 19$), 6 ($n = 2$), 7 ($n = 6$) or 11 ($n = 1$); absent posterior dorsal scale rows with keels in males ($n = 3$), 3 ($n = 1$), 4 ($n = 5$), 5 ($n = 10$), 6 ($n = 9$), 7 ($n = 12$), 8 ($n = 5$), 10 ($n = 3$), 11 ($n = 2$) or 12 ($n = 1$); subcaudals divided ($n = 69$) or mostly divided and some while ($n = 38$); maxillary teeth 11 ($n = 1$), 13 ($n = 4$), 14 ($n = 9$), 15 ($n = 10$), 16 ($n = 10$), 17 ($n = 15$), 18 ($n = 8$) or 19 ($n = 4$); apical pits absent ($n = 12$), 1 ($n = 10$), 2 ($n = 101$) or 3 ($n = 1$), usually with one on each side of the

midline keel ($n = 86$); without keels ($n = 10$) or with keels ($n = 105$); ventrals 196–211 in females (mean = 201.0, SD = 3.0, $n = 45$), 186–215 in males (mean = 195.2, SD = 5.0, $n = 51$); subcaudals 95–142 in females (mean = 125.4, SD = 7.8, $n = 46$), 110–139 in males (mean = 125.2, SD = 6.7, $n = 47$); loreal scale present ($n = 111$) or absent ($n = 4$); LH 0.9–3.0 mm (mean = 2.1, SD = 0.4, $n = 88$) in females; LH 0.7–2.0 mm (mean = 1.9, SD = 0.5, $n = 100$) in males, 1.4–4.6 (mean = 3.0, SD = 0.6, $n = 88$) in females; LL 0.9–4.0 (mean = 2.6, SD = 0.7, $n = 100$) in males; SVL 361.0–1128.0 mm (mean = 837.8, SD = 18.1, $n = 46$) in females, 239.0–1200.0 mm (mean = 70.4, SD = 21.8, $n = 54$) in males; CL (% SVL) 32.7–46.7% (mean = 38.5, SD = 2.7, $n = 46$) in females, 34.2–45.7% (mean = 39.2, SD = 2.7; $n = 53$) in males. Color Pattern A ($n = 2$; SVL mean: 44.1), B ($n = 27$; SVL mean: 91.4) or Color Pattern C ($n = 8$; SVL mean: 83.8) in females; Color Pattern A ($n = 5$; SVL mean: 38.8), Color Pattern B ($n = 18$; SVL mean: 83.1) or Color Pattern C ($n = 21$; SVL mean: 72.2) in males. All values include juveniles and adults.

Color in life. Juveniles displaying a brown dorsum with reddish transverse blotches; blotches may be more or less conspicuous and surrounded by some black pigmentation; dorsum of the head brown covered with reddish spots or blotches; supralabials and infralabial may display the same color as the dorsal stains in the body or be brown. Adults uniform greenish brown; supralabials and the anterior belly region yellowish (Fig. 3).

Hemipenial Morphology. The fully everted and maximally expanded hemipenes renders unilobed, unicapitate, and unicalyculate organs; capitulum slightly bulbous and rounded in the distal region; distal region of the capitulum with two insertion points of the musculus retractor hemipenis magnus; evident capitular constriction; capitulum with papillate calyces; calyces restricted to the sides and proximal region of the capitulum; central region of the capitulum naked; asulcate side with the naked capitular region smaller than in the sulcate side; centrolinear sulcus spermaticus; smooth intrasulcar region; subelliptic hemipenial body, narrower than the capitular region of the organ; distal region of the hemipenial body covered by spines on both sides of the organ; similarly sized and spaced spines, except the most basal, which are smaller; proximal region of the hemipenial body naked (Fig. 9).

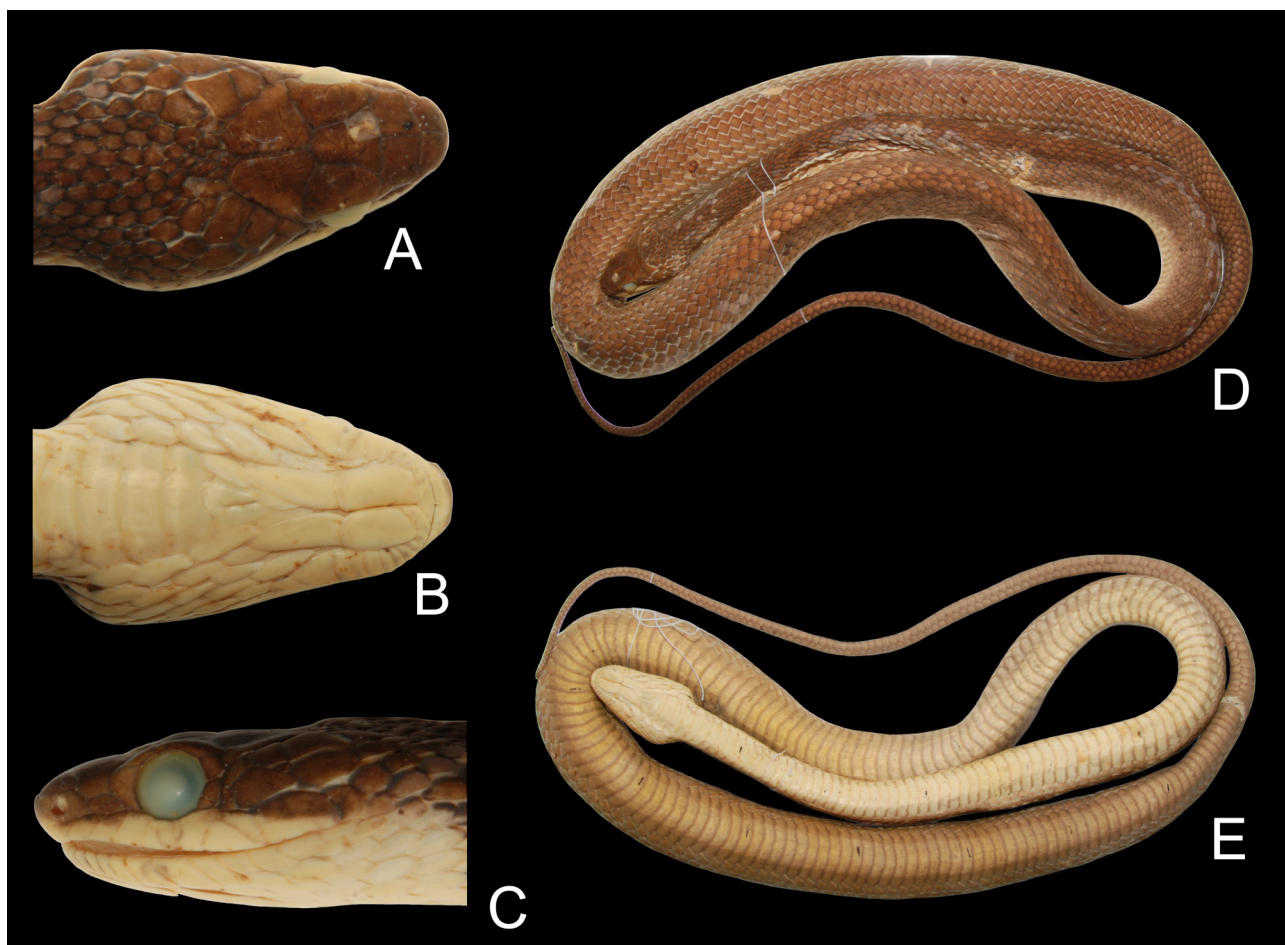


FIGURE 8. Dorsal (A), ventral (B) and lateral (C) views of the head and dorsal (D) and ventral (E) views of the body of the *Phrynonax sexcarinatus* (MNRJ 20302) neotype from Porto Trombetas, Oriximiná municipality, in the state of Pará, Brazil. Specimens measured 1128 mm snout-vent length and 446 mm tail length.



FIGURE 9. Aulcate (A) and asulcate (B) sides of the hemipenis of the *Phrynonax sexcarinatus* (MNRJ 18023) specimen from the Carajás National Forest, Parauapebas municipality, in the state of Pará, Brazil. Scale = 1 cm.

Distribution. From the island of Trinidad Island on the Caribbean Coast (ca., 10° N) to La Guardia, in Bolivia (ca., 18° S), in the east of the Andes from Gualaquiza in Ecuador (ca., 78°W) to Junco do Maranhão, in Brazil (ca., 46°W). *Phrynonax sexcarinatus*' distribution follows the Tropical and Subtropical Moist Broadleaf Forests domains (Olson *et al.* 2001), ranging from 1–1538 m elevations (see Nogueira *et al.* 2019: plate 143 [as *P. polylepis*]).

Remarks. The ICZN (1999: 84-85) lists seven qualifying conditions for a neotype designation detailed in Article 75. Criterion (i) is fulfilled because both the taxonomic status and the type locality are unclear, as detailed above. Criterion (ii) is fulfilled concerning the diagnosis and comparisons. Criterion (iii) is fulfilled by comparing the data from this study with the characters described by Wagler (1824) in detail. Criterion (iv) is fulfilled insofar as Franzen & Glaw (2007) declare that the holotype was lost during World War II and we confirmed this information (see above). Criterion (v) is also fulfilled by comparing data from this study to the characters described by Wagler (1824), considering it is the only source of information on *Natrix sexcarinata*. Criterion (vi) is fulfilled, and we reinforce that we chose a neotype close to the Amazon River, in agreement with the original description. Criterion (vii) is fulfilled, because the neotype is deposited at the MNRJ.

Discussion

The name *Natrix sexcarinata* Wagler, 1824 has been considered over time a junior synonym for some species that are currently allocated within the genus *Chironius* (Schlegel 1837, Duméril Bibron & Duméril 1854, Boulenger 1891, 1894). Bailey (1955) seems to have been the first reference since Schlegel (1837), who synonymized *Herpetodryas sexcarinata* with *Herpetodryas carinatus*, to consider that *Natrix sexcarinata* from Wagler (1824) may not be a *Chironius* representative. *Natrix sexcarinata* was only associated with *Pseustes* by Hoge (1962), who suggests that the original *Natrix sexcarinata* illustrations display several putative inaccuracies. Another problem concerning the *Natrix sexcarinata* description comprises minor differences between the Latin and French translation. Wagler (1824) describes *Natrix cinnamomea* on an earlier page than *Natrix sexcarinata*. Subsequently, Wagler (1830) proposed the synonymy of both species, apparently considering *Natrix sexcarinata* as a senior synonym. By ICZN (1999) rules, Wagler (1830) himself applies the effect of the first review on the priority of *N. sexcarinata* with respect to *N. cinnamomea*. On the other hand, Hoogmoed & Gruber (1983) considered *Natrix cinnamomea* as *nomen dubium*, disagreeing with Werner (1897) who revalidated this name by supposedly finding its holotype. However, Hoogmoed & Gruber (1983) argued that the specimen found by Werner (1897) was not the holotype described by Wagler (1824). Furthermore, Werner (1897) does not mention whether the specimen he found had an epidermis or not, as Wagler (1830) states in relation to the *N. cinnamomea* holotype “*Natrix cinnamomea* Wagl.l.c. icon et descr. e specimine sine epidermide” (free translation: “*Natrix cinnamomea* Wagl.l.c. icon and descr. from a specimen without epidermis”).

Nevertheless, it is noteworthy that some *Phrynonax* characteristics present high-level polymorphism, such as the number of keeled dorsal scales. Amaral (1929) pointed out that dorsal scales may be strongly or weakly keeled, depending on specimen conservation state. We complement Amaral’s statement by noting that, depending on the way the keeled scales are counted, with or without the aid of a stereomicroscope, different conclusions can be reached regarding their number. In fact, when examined under higher magnification, some specimens that do not appear to have keeled scales in fact display the evident presence of a keel. In addition, depending on the size of the keel, its presence can be felt through touch, even if it is not very visible. Thus, the number of keeled series and even the presence or absence of these structures represents characters with limited taxonomic value among *Phrynonax* members.

Peters & Orejas-Miranda (1970) include the locality of Misiones, Argentina in the *Pseustes sexcarinatus*’s distribution. However, as pointed out by Giraud & Scrocchi (2002), this record was probably the result of a misidentification with some *Chironius* species. Additionally, another probable source of confusion may be caused by the description of *Synchalinus corallioides* Cope, 1893, from Buenos Aires, Costa Rica, which may have been confused with the capital of Argentina. Furthermore, based on the taxonomic decisions expressed by Jadin *et al.* (2013) separating the cis-Andean and trans-Andean lineages, *Synchalinus corallioides* Cope, 1893 was removed from the synonymy of *Ph. sexcarinatus*.

Jadin *et al.* (2013) consider *Natrix sexcarinata* as a synonym of *Chironius quadricarinatus* (Boie, 1827) based on Dixon *et al.* (1993) and Giraud & Scrocchi (2002). However, none of these studies considers *N. sexcarinata* a synonym for *C. quadricarinatus*. Although *Phrynonax lyoni* has been resurrected by Natera-Mumaw *et al.* (2015), most authors do not recognize this taxon as valid (see Uetz *et al.* 2022) which could, consequently, could either be added or not to the synonymy of *Ph. sexcarinatus* in the future. *Phrynonax* members exhibit significant geographic variations and Jadin *et al.* (2013) demonstrated at least three main lineages, two of them trans-Andean.

We cannot discard the possibility that future studies, including further geographic representation, may demonstrate the existence of cryptic lineages within *Phrynonax sexcarinatus*. In fact, a certain level of segregation was noted for the Guiana Shield subpopulations with respect to southern subpopulations (Fig. 6), and studies with denser sampling efforts in that area may be required to better delimit boundaries with respect to populations on both sides of Amazon River. Therefore, future prospects comprise the inclusion of samples from the Guiana Shield, mainly from the Venezuelan coast, to test the limits between *Ph. sexcarinatus*, *Ph. lyoni* [as defined by Natera-Mumaw *et al.* (2015), and *Ph. eutropis* (a species described from Trinidad with priority over *Ph. lyoni*)]. However, considering the polychromatism of *Ph. sexcarinatus*, we propose a neotype to stabilize the nomenclature in the case of future cryptic diversity identifications.

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APPENDIX I

Examined specimens

States (uppercase separated by semicolons), municipalities (underlines separated by commas) and localities (plain text separated by commas) are listed in alphabetical order. Geographical coordinates are noted in brackets [latitude/longitude]. Asterisk notations following acronyms represent individuals with everted hemipenes prepared.

***Phrynonax sexcarinatus* (n = 118).** **AMAZONAS:** Benjamin Constant: Jaurary River: (MNRJ 648 [-5.49820175/-70.3902567]), Borba: (MNRJ 3011 [-5.3321309/-59.6995527499999995]), Coari: Porto Urucu (MPEG 20687 [-4.8842799999999999/-65.3491463], MPEG 23877 [-4.8842799999999999/-65.3491463], MPEG 23892–93 [-5.4247222000/-65.455556000], MPEG 21148 [-4.8842799999999999/-65.3491463], MPEG 22262 [-4.8842799999999999/-65.3491463]), Manaus: Km 55 of Br-174 Highway: (MPEG 18991 [-2.6606456/-60.0435303]); **MARANHÃO:** Junco do Maranhão: Nova Vida: Br-316 Highway 25 Km from Gurupi River: (MPEG 11086 [-1.8138889000/-46.1075000000], MPEG 14741 [-1.8138889000/-46.1075000000], MPEG 14745 [-1.8138889000/-46.1075000000]); **MATO GROSSO:** Comodoro: (MNRJ 24135 [-13.734497999314/-60.270304436811]), Querência: (MPEG 21983 [-12.8986111000/-52.3725000000], MPEG 21994 [-12.5943484999999999/-52.2077547999999999]); **PARÁ:** Almeirim: Monte Dourado: (MPEG 21468 [-0.7119444000/-52.6669444000]), Barcarena: (MPEG 16409 [-1.4457442/-48.6382261999999999], MPEG 16429 [-1.4457442/-48.6382261999999999], MPEG 20678 [-1.4457442/-48.6382261999999999]), Vila dos Cabanos: (MPEG 23454 [-1.5268842/-48.683155150000005], MPEG 23443 [-1.5268842/-48.683155150000005]), Belém: Ilha do Mosqueiro (MPEG 566 [-1.1500000000/-48.4000000000], MPEG 730 [-1.1500000000/-48.4000000000], MPEG 1430 [-1.14146/-4839208225], MPEG 2596 [-1.4558333000/-48.5044444000], MPEG 3271 [-1.4558333000/-48.5044444000], MPEG 3275 [-1.4558333000/-48.5044444000], MPEG 5464 [-1.4558333000/-48.5044444000]), Marambaia: (MPEG 1489 [-1.4023724/-48.4522394499999999]), Benevides: Jardim Neopolis: (MPEG 18616 [-1.3632295/-48.2498169999999999], MPEG 18615 [-1.3632295/-48.2498169999999999]), Santa Bárbara (MPEG 1101 [-1.2983333000/-48.2658333000], MPEG 2646 [-1.2983333000/-48.2658333000]), Pratinha: Genipaua Road (MPEG 10920 [-1.2269444000/-48.2736111000], MPEG 10922 [-1.2269444000/-48.2736111000]), Bragança: Bom Jesus: (MPEG 3584 [-1.0863889000/-46.6894444000], MPEG 3602 [-1.0863889000/-46.6894444000]), Bujaru: Km 25: (MPEG 15449 [-1.5181478999999999/-48.03943715]), Canaã dos Carajás: Carajás National Forest: (MPEG 26908 [-6.064644444444444/-50.05666666666667]), Capitão Poço: (MPEG 8156 [-1.7469444000/-47.2022222000], MPEG 3540 [-1.7469444000/-47.2022222000]), São Pedro: (MPEG 10658 [-1.7480556000/-47.217778000]), Castanhal: Boa vista: Apeú: (MPEG 709 [-1.3013889000/-47.9847222000], MPEG 4752 [-1.3788889000/-47.9863889000], MPEG 5733 [-1.3788889000/-47.9863889000], MPEG 5741 [-1.3788889000/-47.9863889000], MPEG 6926 [-1.3788889000/-47.9863889000], MPEG 6934 [-1.3788889000/-47.9863889000]), Macapazinho (MPEG 10910 [-1.3894444000/-47.9847222000]), Curuça: Marauá: (MPEG 4887 [-0.7802778000/-47.8488889000], MPEG 7109 [-0.7802778000/-47.8488889000]), Dom Eliseu: Pa-222 Highway: Sítio Bela Vista: (MPEG 13399 [-4.4380556000/-47.5391667000]), Igarapé-Açú: Km 23 of Maracanã Road: (MPEG 1910 [-1.1044444000/-47.5119444000], MPEG 3427 [-1.1044444000/-47.5119444000]), Itaituba: Amazônia National Park: (MPEG 25090 [-4.23993/-56.0006000000000006], MPEG 25092 [-4.23993/-56.0006000000000006]), Juruti: Beneficiamento: (MPEG 23269 [-2.16345277777778/-56.095286111111], MPEG 23298 [-2.16345277777778/-56.095286111111], MPEG 24031 [-2.16345277777778/-56.095286111111]), Mãe do Rio: Igarapé Pirajauara: Acará Road: (MPEG 9408 [-2.0583072000000002/-47.5389836]), Marabá: Tapirapá-Aquiri National Forest: (MPEG 24280 [-5.8561117/-50.7808181999999999]), Salobo Project: (MPEG 26663 [-5.5927124/-50.1832516]), Melgaço Caxiuana National Forest: Pedreira Village: (MPEG 20308 [-1.8537805555556/-50.954780555556]), Ferreira Pena Ecological Station: (MPEG 20206 [-1.793825/-51.434733333333]),

MPEG 20238 [-1.793825/-51.434733333333], MPEG 20865 [-1.793825/-51.434733333333], MPEG 20868 [-1.793825/-51.434733333333], MPEG 20886–87 [-1.793825/-51.434733333333], MPEG 20929 [-1.793825/-51.434733333333], MPEG 22074 [-1.8377778000/-51.3516667000], MPEG 22145 [-1.8363889000/-51.3822222000]), Moju: Luso Village: Ubá River: Km 36 Mojú–Acará Road: (MPEG 13336 [-1.8750685908871758/ -48.730217585583176]), Oriximiná: Grão-Pará Ecological Station: (MPEG 23747 [1.28958/-56.75052]), Porto Trombetas: (MPEG 24005 [-1.4670345/-56.379436], MPEG 21251 [-1.4670345/-56.379436], MNRJ 20302 [-1.4670345/-56.379436], neotype of *Phrynonax sexcarinatus*), Saracazinho River: (MPEG 16401 [-1.4670345/-56.379436]), Ourém: Puraquequara: (MPEG 7043 [-1.3555556000/-47.2522222000]), Palestina do Pará: Jarbas Passarinho Port: Araguaia River: Transamazônica Highway: (MPEG 12952 [-5.7066667000/-48.1794444000]), Paragominas: (MPEG 25752 [-2.9940028499999998/-47.3586307]), Parauapebas: Carajás Mountain Range: (MNRJ 19527* [-6.276943899999999/-50.581666999999996], MPEG 19656 [-6.276943899999999/-50.581666999999996]), Carajás National Forest: (MPEG 26696 [-6.064644444444444/-50.0566666666667], MNRJ 18023* [-6.1987065999999995/-50.4657223]), Peixe-Boi: (MPEG 677 [-0.4730556000/-47.3619444000]), MPEG 1385 [-0.4730556000/-47.3619444000]), Porteu: Caxiuanã-PPBio: (MPEG 23153–54 [-1.9436689499999995/-50.8150767], MPEG 23208 [-1.9436689499999995/-50.8150767]), Santa Bárbara do Pará: Gunma Ecological Park: (MPEG 21326 [-1.3938889000/-48.8011111000], MPEG 23597 [-2.3000000000/-49.4000000000]), Santarém: Agropecuária Treviso Ltda: (MPEG 19044 [-3.1455556000/-54.8458333000]), surroundings of Igarapé Curupira: 35 Km from the road to Santarém: (MPEG 415 [-2.7841667000/-55.9333333000]), Santarém Novo: (MPEG 3480 [-0.9794444000/-47.2386111000], MPEG 5924 [-0.9794444000/-47.2386111000]), Santo Antônio do Tauá: (MPEG 1130 [-0.8013889000/-49.7819444000], MPEG 1532 [-0.8013889000/-49.7819444000], MPEG 5703 [-1.1802778000/-48.1291667000]), Senador José Porfírio: Volta Grande Project: (MPEG 24984 [-3.5926194782251/-51.946239519758]), Tomé-Açú: Km 12 of PA-15 Highway at Concordia Road: (MPEG 11722 [-2.0930556000/-47.9941667000]), Vila Nova: Tomé-Açú-Paragominas Road: (MPEG 12780 [-2.8202778000/-48.2963889000]), Vigia: Santa Rosa: Vigia Road: (MPEG 9338–39 [-0.9555556000/-48.0861111000], MPEG 11877 [-0.9555556000/-48.0861111000]), Viseu: Bela Vista: (MPEG 2256 [-1.2819444000/-46.2183333000], MPEG 5235 [-1.2819444000/-46.1116667000]), Km 220 of BR-316 Highway: (MPEG 10846 [-1.6642305555556/-46.753591666667]), sem localidade específica (MPEG 2350 [-1.1775000000/-46.2308333000], MPEG 12566 [-1.1979801/-46.1407388]), Vitória do Xingu: Belo Monte Hydroelectric Power Plant: (MPEG 26417 [-3.2087353788141/-51.775140167943], MNRJ 24365–66 [-3.1727912999999996/-51.9892722]); **RONDÔNIA**: Itapuã do Oeste: Jamari National Forest: (MPEG 25873–74 [-9.22355445/-62.94190924999999]), Nova Mamoré: Guajará-Mirim State Park: (MPEG 19501 [-10.537937500000002/-64.4549375]), Porto Velho: Jirau Hydroelectric Power Plant: Jacu-Paraná River: (MPEG 24204 [-9.2572942050702/-64.404801504919], MPEG 24205 [-9.2825867113123/-64.628331751866]).