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On the type series of *Hylodes petropolitanus* Wandolleck, 1907 (Anura, Cycloramphidae), with taxonomic considerations of *Eupsophus fuliginosus* Fitzinger, 1861

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ABSTRACT

Thoropa comprises seven recognized species, including *T. bryomantis*, *T. lutzi*, *T. megatympanum*, *T. miliaris*, *T. petropolitana*, *T. saxatilis*, and *T. taophora*. It was believed that the syntypes of *T. petropolitana* were destroyed during the Dresden bombings in World War II; however, there are two extant syntypes of *T. petropolitana* in the amphibian collection of the American Museum of Natural History where they were transferred from the Staatlichen Museum für Tierkunde Dresden in 1923. Herein we designate a lectotype for *T. petropolitana* and provide a taxonomic history of the species, a synonymy, a redescription, a summary of its geographic distribution, and comments about its conservation. We also review the taxonomic status of *Eupsophus fuliginosus* Fitzinger, 1861, and discuss its implication for the taxonomic status of *T. petropolitana*.

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INTRODUCTION

The frog genus *Thoropa* Cope, 1865, comprises seven valid species, six of which are endemic to the Atlantic Forest—including *T. bryomantis* Assis et al., 2021; *T. lutzi* Cochran, 1938; *T. miliaris* (Spix, 1824); *T. petropolitana* (Wandolleck, 1907); *T. saxatilis* Cocroft and Heyer, 1988; and *T. taophora* (Miranda-Ribeiro, 1923)—and one, *T. megatympanum* Caramaschi and Sazima, 1984, endemic to the *campo rupestre* in the Espinhaço mountain chain. The species are separated into two phenetic groups: the *T. miliaris* group, composed of the "large" species *T. megatympanum*, *T. miliaris*, *T. saxatilis*, and *T. taophora*, and the *T. petropolitana* group, composed of the "small" species *T. bryomantis*, *T. lutzi*, and *T. petropolitana* (Assis et al., 2021; Nunes-de-Almeida et al., 2016; Sabbag et al., 2022a; Sabbag et al., 2018).

Thoropa lutzi and *T. petropolitana* have not been observed in nature for decades, despite numerous searches at known localities of occurrence (Sabbag et al., 2018). *Thoropa petropolitana* was known to occur mainly in the Serra dos Órgãos mountain range, in Rio de Janeiro state (Carvalho-e-Silva et al., 2020; ICMBio, 2018a), although there are also records in Espírito Santo and São Paulo states (Assis et al., 2021; Feio, 2002; Rossa-Feres et al., 2011). For that reason, both species are assigned to threat categories in international, Brazilian, and regional red lists (Haddad, 2008; Morais et al., 2012; Pimenta et al., 2005). Specifically, *T. petropolitana* is listed as "critically endangered" and "possibly extinct" in the International Union for Conservation of Nature – IUCN Red List (IUCN and Instituto Boitatá, 2023), "critically endangered" and "possibly extinct" in the official Brazilian Red List (DOU, 2022a), "critically threatened" in Espírito Santo state (DOE-ES, 2022), "endangered" in Rio de Janeiro state (Bergallo et al., 2000a), and "data deficient" in São Paulo state (Bressan et al., 2009).

For decades, the type specimens of *Hylodes petropolitanus* were believed to have been destroyed during the Dresden bombings in World War II (Obst, 1977). However, during a systematic revision of the genus, we discovered extant syntypes of *Thoropa petropolitana* in the amphibian collection of the American Museum of Natural History. We then summarize the taxonomic history of *T. petropolitana*, designate a lectotype, redescribe the species on the basis of the type material and additional specimens from multiple amphibian collections, and clarify its identity relative to other species of *Thoropa*. We also provide information about the natural history and geographic distribution of *T. petropolitana* and investigate the taxonomic status of *Eupsophus fuliginosus* Fitzinger, 1861, currently a junior synonym of *T. miliaris* (Cochran, 1955; Frost, 2025) but possibly related to *T. petropolitana* (Cocroft and Heyer, 1988).

MATERIALS AND METHODS

We examined specimens of *Thoropa* from the following zoological collections (by acronym, following Sabaj, 2020; see appendix): AAG-UFU, AL-MN, AMNH, CAS, CAS-SUA, CFBH, CM, DZSJRP, EI-UFRRJ, FMNH, IRSNB, MBML, MCNAM, MCP, MCZ, MNHN, MNRJ, MVZ, MZUESC, MZUFV, MZUSP, NMW, TNHC, UFMG, UFRRJ, UMMZ, USNM, ZMUC, ZUEC, and ZUFRJ. *Thoropa petropolitana* syntypes at AMNH and specimens from IRSNB, MNHN, NMW, and ZMUC were analyzed through photographs and data provided by collec-

tion managers. Examined specimens of *Thoropa petropolitana* and the other *Thoropa* species are listed in supplementary appendix SA1 available online (https://doi.org/10.5531/sd.sp.72). To compile specimen records, we kept the names of localities as registered but corrected spelling and abbreviated Brazilian state names.

We examined specimens using a stereomicroscope with the aid of Lugol's solution (Bock and Shear, 1972) or methylene blue when necessary. For adults, we analyzed 15 meristic characters using methods previously described (Duellman, 2001) and summarized by Watters et al. (2016), with the addition of two more measurements (arm diameter and forearm diameter, following Sabbag et al., 2022a), as follows: snout-vent length (SVL), head length, head width, tympanum diameter, eye diameter, interorbital distance, internarial distance, eye-nostril distance, eye-snout distance, forearm diameter, arm diameter, hand length, femur length, tibia length, and foot length. For tadpoles, we analyzed the following 12 measurements, as defined by McDiarmid and Altig (1999): total length, body length, tail length, body width, body height, maximum tail height, nostril-snout distance, eye-snout distance, eye-nostril distance, interorbital distance, oral disc width, and eye diameter. Additionally, we also measured the SVL of adult specimens of the other species of *Thoropa* for body size comparisons, not considering juvenile males (males without PEPs, see below). We took measurements to 0.1 mm using Mitutoyo® digital callipers, with the exception of the tadpole specimen of AMNH, measured with ImageJ (Schneider et al., 2012) from scope pictures.

We numbered fingers from II to V (sensu Fabrezi and Alberch, 1996). Some skull features follow the terminology of Trueb (1993), while terminology for snout shape follows Duellman (1970). The term "meniscus" is used following Colaço et al. (2020). The term "discoidal fold" follows Taboada et al. (2013). Vocal sac and slit terminologies follow Elias-Costa et al. (2017). Nuptial pad terminology follows Luna et al. (2018). For most male *Thoropa petropolitana*, we counted the papillary epidermal projections (PEPs sensu Luna et al., 2018) on both hands. We identified males through the presence of PEPs and (depending on the species) vocal slits and vocal sacs, and we identified females through the presence of oocytes. When a specimen did not possess PEPs and it was not possible to observe oocytes by dissection or through translucent skin, we scored it as a "probable female." We considered a male to be adult when it had any PEP (following Sabbag et al., 2022a, concept of adult male for some *Thoropa* species) and a female to be adult when it possessed expanded and convoluted oviducts, or enlarged oocytes.

Given that *Thoropa petropolitana* was described in 1907 and many additional specimens have been collected in the intervening century, we provide an updated diagnosis and redescription. We performed a thorough analysis of all publications that studied or cited *T. petropolitana* and its synonyms since Wandolleck (1907) first described the species as *Hylodes petropolitanus*. With these publications, we built a chresonymy with the valid synonyms of *T. petropolitana* including all scientific publications. We did not include a chresonymy of *Cystignathus fuliginosus* and *Eupsophus fuliginosus* due the nomenclatural problems associated with these taxa (see Results section below). To redescribe *T. petropolitana*, we compiled information on tadpole morphology, coloration in life, natural history, and the advertisement call from literature. Additionally, we constructed a distribution map of the specimens with ArcGIS v.10.1 (ESRI). As all

the specimens of *T. petropolitana* were collected without GPS equipment, we obtained geographical coordinates through Google Earth™ v.7.3.4 when precise locality details were available or used the centroid coordinates in ArcGIS v.10.1 (ESRI) when only the Brazilian municipality was available (supplementary appendix SA1). We did not map localities given only as Brazil or a Brazilian state. Since the last collection dates to 1982, we also undertook two field trips to search for new specimens of *T. petropolitana* in Parque Nacional da Serra dos Órgãos, Rio de Janeiro state.

RESULTS

Taxonomic history of *Hylodes petropolitanus* Wandolleck, 1907: Wandolleck (1907) described *Hylodes petropolitanus* on the basis of adults, tadpoles, and egg clutches (as evidenced by his text and figs. 9A–F; fig. 1), all collected in the municipality of Petrópolis ("Urwäldern von Petropolis," Rio de Janeiro, Brazil in the original text) by Friedrich Ohaus in 1906 (no specimen numbers reported). The species was referred to *Hylodes* Fitzinger, 1826, on the basis of the presence of T-shaped terminal phalanges, a typical characteristic of what was then considered *Hylodes*.

Shortly thereafter, Boulenger (1909) transferred *Hylodes petropolitanus* to the genus *Elosia* Tschudi, 1838, forming the combination of *Elosia petropolitanus*, but subsequent authors continued using the original combination (e.g. Baumann, 1912; Nieden, 1923). Without comment, Noble (1917) used the new combination *Eleutherodactylus petropolitanus*.

Miranda-Ribeiro (1923) studied the hylodids in the Museu Paulista and considered *Rana miliaris* Spix, 1824 (type species of *Thoropa* Cope, 1865) and *Hyla abbreviata* Spix, 1824, to pertain to the genus *Ololigon* (incorrect spelling of *Ololygon* Fitzinger, 1843) under the combinations *Ololigon* [sic] *miliaris* and *Ololigon* [sic] *abbreviatus*. In the same study, Miranda-Ribeiro (1923) concluded (albeit without having examined the specimens) that Wandolleck (1907) had described *Hylodes petropolitanus* on the basis of juvenile specimens and recognized three varieties (i.e., subspecies according to the International Code of Zoological Nomenclature, ICZN, 1999, Art. 45.6.4) of *O. abbreviatus*: *Ololigon abbreviatus taophora*, *Ololigon abbreviatus petropolitana*, and *Ololigon abbreviatus abbreviata*. Subsequently, Miranda-Ribeiro (1926) synonymized *Ololigon abbreviatus* (and its varieties) with *O. miliaris*.

Noble (1925) studied *Hylodes petropolitanus* in respect to osteology, life history, and relationships with other genera. Next, Müller (1927) considered *Hylodes petropolitanus* to be a valid species and transferred it to *Eleutherodactylus* Duméril and Bibron, 1841. In the same year, Noble (1927) transferred *Hylodes petropolitanus* to *Borborocoetes* Bell, 1843, under the new combination of *Borborocoetes petropolitanus*, since the osteology of *H. petropolitanus* is nearly identical to *Borborocoetes miliaris* (= *Thoropa miliaris*; Noble, 1925).

Parker (1932) succinctly discussed the genera *Eupsophus* Fitzinger, 1843; *Borborocoetes* Bell, 1843; *Ololygon* Fitzinger, 1861; *Thoropa* Cope, 1865; and *Borborocoetea* Strand, 1928, and considered *Eupsophus* to have precedence over the other four generic names. Nevertheless, Cochran (1938) described a new species of *Thoropa* (*T. lutzi* Cochran, 1938, holotype USNM

FIG. 1. Part of plate 1 from Wandolleck (1907), showing figures 9 and 9a–9f of what is currently known as *Thoropa petropolitana*: (9) dorsal view of a male's hand; (9a) dorsal view of male body; (9b) internal view of mouth; (9c) spawn; (9d) male head in lateral view; (9e) tadpole in lateral view; (9f) tadpole in dorsal view.

97622) from Recreio dos Bandeirantes, in the southeast of the municipality of Rio de Janeiro (Federal District at that time), and Lutz (1947), in her analysis of the development of non-aquatic frogs, stated that *Hylodes petropolitanus* belongs to *Thoropa*, forming the new combination *Thoropa petropolitana*.

In contrast, Cochran (1955) determined that both *Borborocoetes* and *Thoropa* are synonyms of *Eupsophus* Fitzinger, 1843, recognizing *Rana miliaris*, *Hylodes petropolitanus*, and *Thoropa lutzi* as valid species under the following combinations: *Eupsophus miliaris*, *E. petropolitanus*, and *E.*

lutzi. Cochran (1955) also considered *Ololigon abbreviatus taophora* Miranda-Ribeiro and *Eupsophus fuliginosus* Fitzinger, 1861, to be synonyms of *Rana miliaris* (sensu Spix).

Gallardo (1965) recognized the osteological similarity of the pectoral girdles of *Thoropa* and *Eupsophus* but concluded that differences in the atlas and sternum allow *Thoropa* to be recognized as a valid genus with three species in Brazil. Bokermann (1965) agreed with Gallardo's (1965) resurrection of *Thoropa* and summarized the available information on adults, tadpoles, and advertisement calls to support the recognition of *T. miliaris*, *T. petropolitana*, and *T. lutzi*. He also concluded that *T. petropolitana* and *T. lutzi* are more closely related to each other than to *T. miliaris*.

Caramaschi and Sazima (1984) described *Thoropa megatympanum* and Cocroft and Heyer (1988) described *T. saxatilis*. After that, the taxonomy of *Thoropa* species remained stable until Feio et al. (2006) revised the taxonomy of *T. miliaris*, designating a neotype for *T. miliaris* and resurrecting *T. taophora* (Miranda-Ribeiro, 1923). More recently, the populations of *Thoropa* from the northern region of the Serra da Mantiqueira in Southeast Brazil (previously identified as *T. lutzi*) were described as *T. bryomantis* by Assis et al. (2021), bringing the total number of recognized species to seven.

Rediscovery of *Hylodes petropolitanus* Wandolleck, 1907, syntypes and lectotype designation: As noted above, Noble (1925) briefly discussed the life history, osteology (on basis of the dissection of an adult), and relationships of *Thoropa petropolitana* (as *Hylodes petropolitanus*). In his account, he (Noble, 1925: 14) acknowledged the donation of specimens from Wandolleck's (1907) description to AMNH:

> Thanks to the kindness of the Director of the Dresden Museum, there is now in the collections of the American Museum one of the adults, one of the larvae, and two of the eggs which Wandolleck described.

No other information about the syntypes of *Thoropa petropolitana* was presented until the publication of the "Frogs of Southeastern Brazil" by Cochran (1955), who traveled to Europe in 1938 to study herpetological collections in museums. In the section on *T. petropolitana* (as *Eupsophus petropolitanus*), she reported that she examined three syntypes of this species under voucher number KZAEM D 2037 (currently MTKD D 2037), two with spines on their hands (males of 20 and 22 mm SVL, respectively) and one without spines (presumably a female, 21 mm SVL; Cochran, 1955: 300). In the list of specimens examined, she clarified that KZAEM D 2037 included three adults and "many tadpoles."

During World War II, the herpetological collections of the Staatlichen Museum für Tierkunde Dresden were transferred to cellars of the Residenzschloss, the castle in the city of Dresden (Fritz, 2002; U. Fritz, personal commun.); however, during the bombings on 13–14 February, 1945, the castle was destroyed, along with most of the herpetological collections, reducing the number of specimens from 6704 to 98 (Fritz, 2002; Obst, 1977; Reichert, 1954, 1956). Obst (1977) reported that the collection catalog was preserved, and he listed the extant and destroyed types of the Staatlichen Museums für Tierkunde, Dresden. The syntypes of *Hylodes petropolitanus* Wandol-

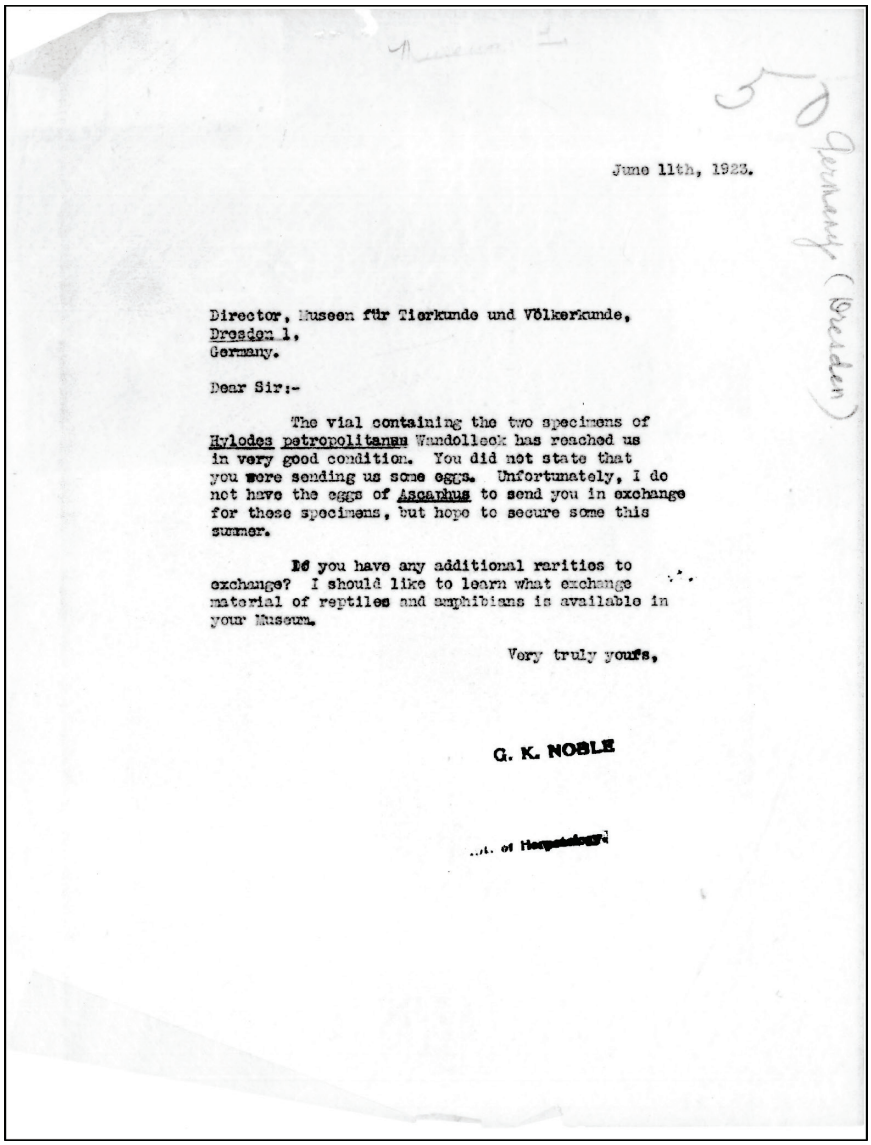
leck, 1907, under record number MTKD D 2037—four adults, five tadpoles, and two egg clutches—were listed as destroyed (Obst, 1977). Through corresponding with Markus Auer (Museum für Tierkunde, Dresden; on 15 February 2023), we confirmed that the original catalog of the collection includes the following information about MTKD D 2037: "4 + 5 Kaulquappen mit 2 Eierhaufen Spir. Type" (in English: 4 + 5 tadpoles with 2 egg masses spirit. Type), and nothing else. The sum of adult specimens examined by Noble (1925) and Cochran (1955) correspond to the number of adult specimens informed in the museum's catalog.

The G.K. Noble archive at the AMNH includes the correspondence exchanged between G.K. Noble and a representative of the Director of the Dresden Museum (no personal name is given in the correspondence) between May 7 and June 11, 1923, confirming that one male, one tadpole, and two eggs were donated to Noble/AMNH (fig. 2). Noble (1925) did not report specimen numbers, but AMNH A32976 (adult male) and AMNH A193770 (a single tadpole) were cataloged as having been collected by "Wandalleck" and identified by Werner C.A. Bokermann in 1968 as "*Thoropa lutzi*." The adult (AMNH A32976) is a male with nuptial pads and a small incision on the chest that allows the pectoral girdle to be examined, consistent with Noble's (1925) account. The eggs mentioned in the correspondence were not found.

Considering Bokermann's identification of the specimens as *Thoropa lutzi*, we compared the adult and tadpole to topotypes of *T. petropolitana* and the holotype and topotypes of *T. lutzi* (see examined material in supplementary appendix SA1), confirming that they agree with the topotypes of *T. petropolitana* and not with *T. lutzi*. Consequently, we conclude that the adult male and one tadpole deposited under voucher number AMNH A32976 are syntypes of *Hylodes petropolitanus* Wandolleck, 1907. Given that the syntypes include different semaphoronts, in accordance with amended article 74.7.3 of the Code (ICZN, 2003), we designate the adult male AMNH A32976 as lectotype of *Hylodes petropolitanus* Wandolleck, 1907, in order to clarify the application of the name, with the tadpole AMNH A193770 becoming a paralectotype.

Taxonomic history of *Eupsophus fuliginosus* Fitzinger (1861): Although currently in the synonymy of *Thoropa miliaris*, Cocroft and Heyer (1988) considered the holotype of *Eupsophus fuliginosus* to be probably *T. petropolitana*. To clarify the identity of this specimen, we detail the history of the name *Eupsophus fuliginosus*.

After studying the material collected by the Austrian Novara Expedition that circumnavigated the globe between April 1857 and July 1859, Fitzinger (1861: 387) concluded that some of the amphibian specimens represented previously unknown species, including "*Eupsophus fuliginosus* von Brasilien"; however, Fitzinger (1861) did not present a diagnosis, illustration, citation, or specimen number for *E. fuliginosus*. As such, according to article 12 of the Code (ICZN, 1999), *Eupsophus fuliginosus* Fitzinger, 1861, is a nomen nudum, as noted previously by Parker (1932). Seven years later, Steindachner (1867: 25) provided a validating description of the species, which he explicitly attributed to Fitzinger as "*Cystignathus* (*Eups.*) *fuliginosus* Fitzinger." However, Article 50.1.1 explicitly indicates that the authorship of a nomenclatural act must also satisfy the criteria of availability. Since Fitzinger (1861) does not satisfy the criteria of availability, the authorship of this name cannot be attributed to him and must instead be attributed to Steindachner (1867).



June 11th, 1923.

Director, Museen für Tierkunde und Völkerkunde,
Dresden 1,
Germany.

Dear Sir:-

The vial containing the two specimens of Hylodes petropolitanus Wandolleck has reached us in very good condition. You did not state that you were sending us some eggs. Unfortunately, I do not have the eggs of Ascarhus to send you in exchange for these specimens, but hope to secure some this summer.

Do you have any additional rarities to exchange? I should like to learn what exchange material of reptiles and amphibians is available in your Museum.

Very truly yours,

G. K. NOBLE

Asst. of Herpetology

FIG. 2. One of the letters exchanged between G.K. Noble and an unnamed representant of the Director of the Dresden Museum, confirming that one male, one tadpole, and two eggs arrived at the AMNH.

The Novara expedition visited 18 locations around the world and was in Rio de Janeiro state from 5–31 August 1857 (Gans, 1955). In Rio de Janeiro, the expedition visited some places in the city and surroundings, including the Serra da Estrella (currently Serra da Estrela, in the municipality of Magé; Bokermann, 1966a) and Petrópolis. Fitzinger (1861) reported only that the specimens of his *E. fuliginosus* were collected in "Brasilien," and it was Steindachner (1867) who narrowed the type locality to "Umgebung von Rio de Janeiro" (surroundings of Rio de Janeiro). Parker (1932) reported that the specimen examined by Fitz-

inger (1861: 342) was "an example of *Borborocoetes grayi* Bell" (currently a junior synonym of *Eupsophus roseus*) and considered *E. fuliginous* to be a nomen nudum.

Cochran (1955) included *Eupsophus fuliginosus* in the synonymy of *E. miliaris* (currently *Thoropa miliaris*) and listed the citation of Parker (1932). She also examined the type specimen of *E. fuliginosus* (Cochran, 1955: 297), currently identified as NHMW 15847 (see Häulp and Tiedemann, 1978), and considered it to resemble a juvenile specimen of *E. miliaris*. Nevertheless, Cocroft and Heyer (1988) considered Fitzinger's *E. fuliginosus* to be *T. petropolitana*. This conclusion is supported by the (1) collection locality; (2) adult size; (3) dorsal color pattern; (4) relative lengths of fingers I and II (here numbered fingers II and III); and (5) expansion of the tip of the fingers (Cocroft and Heyer, 1988). The specimen lacks PEPs, but Cocroft and Heyer (1988) were informed by the Wien Museum of Natural History that it was a male. They opted to consider Fitzinger's *E. fuliginous* to be a nomen dubium until a more rigorous examination of holotype could be carried out.

We compared digital images of the holotype of *Cystignathus fuliginosus* (kindly provided by Georg Gassner and Silke Schweiger, NHMW) to the lectotype of *Hylodes petropolitanus*. Our observations corroborate those of Cocroft and Heyer (1988) regarding the dorsal color pattern (forming an X) of *Thoropa petropolitana*; relative lengths of fingers II and III; and expansion of the finger tips. Although Cocroft and Heyer (1988) reported that the holotype is a male, thereby contradicting Steindachner's (1867: 25) report that it is a juvenile female ("Ein kleines Weibchen"), the lack of PEPs (present in adult males), the NHMW curators concurred with Steindachner that it is a female, and its SVL (ca. 23 mm; see Cochran, 1955) and conspicuous discoidal ventral fold lead us to conclude that it is an adult female. Based on our comparison of the holotype of *C. fuliginosus* and the lectotype *H. petropolitanus*, we conclude that there are no diagnostic characteristics to recognize them as different species.

In summary, *Eupsophus fuliginosus* Fitzinger, 1861, is a nomen nudum, as correctly proposed by Parker (1932) and indirectly by Cochran (1955 "1954"), and *Hylodes petropolitanus* Wandolleck, 1907, is a junior synonym of *Cystignathus fuliginosus* Steindachner, 1867. To our knowledge, the combination *Cystignathus fuliginosus* Steindachner, 1867 (not *Eupsophus fuliginosus* Fitzinger, 1861), was never employed after 1899. In contrast, *Hylodes petropolitanus* Wandolleck, 1907—or the combinations *Eupsophus petropolitanus* (Wandolleck, 1907), *Thoropa petropolitanus* (Wandolleck, 1907) or *Thoropa petropolitana* (Wandolleck, 1907)—have been used in more than 25 publications by more than 10 authors between 1974 and 2023 including Heyer (1975); Obst (1977); Lynch (1978); Heyer and Crombie (1979); Flier et al. (1980); Maxson and Heyer (1982); Wassersug and Heyer (1983); Erspamer et al. (1986); Roseghini et al. (1986); Cocroft and Heyer (1988); Wassersug and Heyer (1988); Altig and Johnston (1989); Nishikawa and Wassersug (1989); Duellman and Trueb (1994); IUCN (1996); Glaw et al. (1998); Bergallo et al. (1999); Duellman (1999); Heyer (1999); McDiarmid and Altig (1999); Bergallo et al. (2000b); Caramaschi et al. (2000); Van Sluys et al. (2000); Carvalho-e-Silva and Peixoto (2004); Giaretta and Facure (2004); Paglia et al. (2004); Rocha et al. (2004); Young et al. (2004); Eterovick et al. (2005); Haddad and Prado (2005); Pimenta et al. (2005); Silvano and Segalla (2005); Úbeda and Nuñez (2006); Cruz and Feio (2007); Gasparini et al. (2007); Gherardi and Cabral (2007); Passamani

and Mendes (2007); Wells (2007); DOE-SP (2008); Feio (2008); ICMBio (2008a); Rossa-Feres et al. (2008); Stuart et al. (2008); Altig et al. (2009); Araújo et al. (2009); Garcia et al. (2009); Paglia and Fonseca (2009); Rocha et al. (2009); Silva (2009); Tanizaki-Fonseca et al. (2009); Van Sluys et al. (2009); DOE-SP (2010); Almeida et al. (2011); Nascimento and Campos (2011); Rossa-Feres et al. (2011); Morais et al. (2012); Trindade-Filho et al. (2012); Acton (2013); Lopes et al. (2013); DOU (2014); Segalla et al. (2014); DOU (2015); Valencia-Aguilar et al. (2015); Campos et al. (2016); Gan et al. (2016); Garey and Provete (2016); Nunes-de-Almeida et al. (2016); Pereyra et al. (2016); Schulte and Rödder (2016); Segalla et al. (2016); Rossa-Feres et al. (2017); Dorigo et al. (2018); Haddad et al. (2018); ICMBio (2018a); Luna et al. (2018); Sabbag et al. (2018); Ferreira et al. (2019a, 2019b); Fraga et al. (2019); Jorgewich-Cohen et al. (2019); Moura et al. (2019); RAN (2019); Segalla et al. (2019); Vasconcelos et al. (2019); Verdade et al. (2019); Carvalho-e-Silva et al. (2020); Cholak et al. (2020); Colaço et al. (2020); Guerra et al. (2020); Assis et al. (2021); Dias et al. (2021); Galetti et al. (2021); Lisboa et al. (2021); Segalla et al. (2021); Straube et al. (2021); Colaço and da Silva (2022); DOU (2022b); DOU (2022a); DOE-ES (2022); Lavilla et al. (2022); Sabbag et al. (2022b); Sabbag et al. (2022a); IUCN and Instituto Boitatá (2023); Toledo et al. (2023); Colaço et al. (2024); Sabbag et al. (2024).

Consequently, although *Cystignathus fuliginosus* Fitzinger in Steindachner, 1867 predates *Hylodes petropolitanus* Wandolleck, 1907, article 23.9.1 of the Code (ICZN, 1999) stipulates that prevailing usage of a name should be maintained when "the senior synonym has not been used as a valid name after 1899 [art. 23.9.1.1], and the junior synonym or homonym has been used, in at least 25 works, published by at least 10 authors in the immediately preceding 50 years and encompassing a span of no less than 10 years [art. 23.9.1.2]." Both conditions are met in this case. As such, we consider *Hylodes petropolitanus* Wandolleck, 1907, to be a nomen protectum and *Cystignathus fuliginosus* Steindachner, 1867, a nomen oblitum.

Amphibia Linnaeus, 1758

Anura Hogg, 1839

Cycloramphidae Frost et al., 2006

Thoropa petropolitana (Wandolleck, 1907)

Eupsophus fuliginosus Fitzinger, 1861 (species description: 387, 414): nomen nudum.

Cystignathus fuliginosus Steindachner, 1867 (species description: 25): nomen oblitum.

Hylodes petropolitanus Wandolleck, 1907 (species description: 7 [text and fig. D], 8 [text and figs. E–F], 9; pl. captions [figs. 9A–F]; pl. 1 [figs. 9A–9F]); Werner (1908: 94); Ohaus (1909: 35); Baumann (1912: 114 [table], 143 [table], 145, 150, 161 [table], 170 [fig. captions: pl. 5, map III]); Nieden (1923: XXX [systematic index], 408 [species key], 461 [text and figs. 327–328], 462, 567 [alphabetic index]); Miranda-Ribeiro (1923: 830, 831, 840, 842, 843); Noble (1925: 14); Miranda-Ribeiro (1926: 53, 58–60, 202 [references]); Müller (1927: 275); Noble (1927: 84); Lutz (1928: 640); Lutz (1929: 8, 20); Guenther (1931: 392 [index]); Noble (1931: 75, 558 [index]); Noble (1954: 75, 558 [index]); Cochran (1955: 300 [specimens examined]; 417 [index])); Bokermann

(1966b: 67, 94, 176 [species index]); Obst (1977: 173, 174); Benchimol and Sá (2007: 243, 252 [facsímile reprint], 262); Lavilla et al. (2022: 215).

Elosia petropolitanus: Boulenger (1909: 34); Lavilla et al. (2022: 215).

Eleutherodactylus petropolitanus: Noble (1917: 812); 275–276); Cochran (1955: 298, 414, 420); Lavilla et al. (2022: 215).

Ololigon abbreviatus: Miranda-Ribeiro (1923: 840 pt., 841 pt., 843 pt.).

Ololigon abbreviatus petropolitana: Miranda-Ribeiro (1923: 844; pl. [first specimen, by inference from text, p. 844]); Cochran (1955: 297, 298, 420 [index]); Lavilla et al. (2022: 215).

Ololigon abbreviatus petropolitaus [sic]: Miranda-Ribeiro (1923: fig. D) incorrect spelling.

Ololigon miliaris petropolitana: Miranda-Ribeiro (1926: 61); Cochran (1955: 298, 420 [index]).

Borborocoetes petropolitanus: Noble (1927: 61 [fig. 6], 68); Lavilla et al. (2022: 215).

Eupsophus petropolitanus: Cochran (1955: X, 291 [species key], 297–300, 383 [graphic], 414 [index]; pl. 26 [figs. A–D]); Lynch (1972: 2–3); Liner (2009: 14); Lavilla et al. (2022: 215).

Hylodes petropolitanas: Cochran (1955: 298 [taxonomic list]) incorrect spelling.

Thoropa petropolitanus: Cei (1968: 203); Lynch (1971: 129, 130); Lynch (1972: 2 [by inference]); Müller (1972: 96); Erspamer et al. (1986: 129 [table 2]); Liner (2009: 21).

Thoropa petropolitana: Lutz (1947: 246); Lutz (1948: 30 [table 1], 32); Lutz (1954: 157, 161, 169, 179 [species key], 207 [pl. IX, figs. 8, 10], 229); Cochran (1955: 298, 422 [index]); Gallardo (1965: 81, pt.); Bokermann (1965: 526, 237 [fig. 7], 528 [text and figs. 12–13], 529, 530 [text and fig. 14], 531 [text and figs. 19–20], 532 [text and fig. 23], 533 [text, adult species key, tadpole species key], 534, 535, 536; figs. 3, 4); Bokermann (1966b: 67, 64, 176 [species index]); Cei et al. (1967: 330 [table 1]); Bücherl and Buckley (1971: 505 [table II], 684 [index]); Lynch (1971: 26 [fig. 3A], 228 [appendix]); Lynch (1972: 10); Heyer (1975: 18 [fig. 4H], 38, 48 [appendix supplementary data]); Lynch (1978: 28, 50, 52, 54 [specimens examined]); Heyer and Crombie (1979: 17–20); Flier et al. (1980: 504 [text, and table 1]); Maxson and Heyer (1982: 12 [table 3], 13, 14); Wassersug and Heyer (1983: 761 [resúmen], 763, 764 [figs. 1A–C], 765, 766 [text and table 1], 768); Cocroft and Heyer (1988: 209, 210, 213 [adult species key], 214 [tadpole species key], 215 [fig. 3, pt], 216 [text and fig. 6], 218, 219); Heyer et al. (1988: 233); Wassersug and Heyer (1988: 2, 61 [table 1A], 63 [table 1B], 65 [table 1C], 67 [table 1D], 69, 73, 74, 79); Altig and Johnston (1989: 97 [fig. 7G]); Nishikawa and Wassersug (1989: 17 [table 1], 18 [fig. 2A, by inference; fig. 2B pt, by inference, fig. 2C pt, by inference], 19 [fig. 3A–E pt, by inference], 20 [fig. 4]); Heyer et al. (1990: 322); Duellman and Trueb (1994: 41, 46 [table 2.11], 161 [fig. 6.17A], 666 [index]); IUCN (1996: 67); Glaw et al. (1998: 256); Bergallo et al. (1999: 23); Duellman (1999: 324 [appendix 5:1], 630 [index]); Heyer (1999: 24 [text and fig. 5], 25); McDiarmid and Altig (1999: 27, 32 [fig. 3.3E], 107, 113, 299 [fig. 12.1G]); Van Sluys et al. (2000: 148); Bergallo et al. (2000b: 149); Caramaschi et al. (2000: 75, 76, 78 [table 1]); Izecksohn and Carvalho-e-Silva (2001: 88, 146 [index]); Carvalho-e-Silva and Peixoto (2004: e. T21817A9322082 [IUCN Red List Website]); Giaretta and Facure (2004: 8); Paglia et al. (2004: table 2); Rocha et al. (2004: 8); Young et al. (2004: 68 [appendix 3]); Eterovick et al. (2005: 168, 173, 179 [appendix]); Haddad and Prado (2005: 215); Pimenta et al. (2005: supporting online material table S3); Silvano and Segalla (2005: 654, 655 [table 1]); Úbeda and Nuñez (2006: 441, 444 [references]); Cruz and Feio (2007: 123); Gasparini et al. (2007: 76–77, 80 [table 6.1], 82 [acknowledgments], 86 [picture]); Gherardi and Cabral (2007: 111 [table 7.2]); Passamani and Mendes (2007: 132 [annex 1]); Wells (2007: 355 [table 8.1], 359, 519 [table 11.1], 1144 [index]); DOE-SP (2008: 9); Feio (2008: 317–318); ICMBio (2008b: 500 [index], 501 [index]); ICMBio (2008a: 290 [table 2], 291 [table 3], 315–318, 896–897); Rossa-Feres et al. (2008: 86); Stuart et al. (2008: 102);

Altig et al. (2009: 129); Araújo et al. (2009: 200 [table 1], 208); Garcia et al. (2009: 334 [table 3]; 633 [annex 3]); Paglia and Fonseca (2009: 3575 [table 5]); Rocha et al. (2009: 119 [annex 9.1]); Silva (2009: 2 [chart and figure]); Tanizaki-Fonseca et al. (2009: 281); Van Sluys et al. (2009: 176, 181, 182 [references]); DOE-SP (2010: 7); Izecksohn and Carvalho-e-Silva (2010: 90, 148 [index]); Almeida et al. (2011: 544, 548 [table 2], 560 [specimens examined]); Nascimento and Campos (2011: 169, 173, 212); Rossa-Feres et al. (2011: 51 [table 1]); Morais et al. (2012: 2633 [abstract], 2635, 2637 [table 1], 2638); Trindade-Filho et al. (2012: supplementary material table S1); Acton (2013: 95); Lopes et al. (2013: 27); DOU (2014: 124 [annex 1]); Segalla et al. (2014: 40); DOU (2015: 149); Valencia-Aguilar et al. (2015: 2 [table S1, supplemental]); Gan et al. (2016: 46); Garey and Provete (2016: 234–235, 237 [table 2], 240); Nunes-de-Almeida et al. (2016: 1 [abstract], 2, 3 [table 1 and figure 1], 4 [text and table 2], 5, 6 [figure 2C], 7 [text and figure 3], 8 [text and table 3], 9; supporting information); Pereyra et al. (2016: supplementary information); Schulte and Rödder (2016: 256 [appendix]); Segalla et al. (2016: 37); Rossa-Feres et al. (2017: 268 [table 1]); Dorigo et al. (2018: 3 [table 1], 7); Haddad et al. (2018: 55–56, 128 [index]); ICMBio (2018b: 202); Luna et al. (2018: 417 [figure 11A], supplementary information); Sabbag et al. (2018: 141, 143 [figure 1], 144, 147 [figure 3]); Ferreira et al. (2019a: 261–262); Ferreira et al. (2019b: 143 [table 1], 154, 162 [appendix 1]); Fraga et al. (2019: 375 [table 16.3]); Jorgewich-Cohen et al. (2019: 64, 67 [table 1]); Moura et al. (2019: 397, 400); RAN (2019: third page [table]); Segalla et al. (2019: 74); Vasconcelos et al. (2019: 44 [table 2.1]); Verdade et al. (2019: 171, 173 [references]); Carvalho-e-Silva et al. (2020: 3 [table 1], 7, 8 [figure 5], supplementary material); Cholak et al. (2020: 1); Colaço et al. (2020: 20, 25 [appendix B]); Guerra et al. (2020: supplementary material S1); Lopes et al. (2020: 3291 [table 1], 3293, 3293 [figure 1]); Assis et al. (2021: 505–506, 507 [text and table 1], 509, 514, 515 [tables 2 and 3], 516, 517 [table 4], 518 [figures 8 and 9], 519 [figure 10], 522); Dias et al. (2021: 1299 [text and table 1], 1301, 1301 [table 2], 1304, 1305 [figures 4 and 5], 1306 [figure 7], 1307 [figure 8], 1309, 1316, supporting information); Galetti et al. (2021: 308); Lisboa et al. (2021: 279); Segalla et al. (2021: 149 [table 1]); Straube et al. (2021: 4 [table 1]); Colaço and da Silva (2022: 296, 313); DOU (2022b: 94 [annex 2]); DOU (2022a: 71); DOE-ES (2022: 6 [annex I]); Lavilla et al. (2022: 215); Sabbag et al. (2022b: 2); Sabbag et al. (2022a: 1 [abstract], 2, 2 [figure 1], 3–8, supplementary material); IUCN and Instituto Boitatá (2023: cover); Toledo et al. (2023: lines 80 and 81 [table in supplemental material]); Colaço et al. (2024: 70); Sabbag et al. (2024: 321).

Lectotype: Adult male (AMNH A32976) collected in the municipality of Petrópolis, Rio de Janeiro state, Brazil ("Urwäldern von Petropolis"), by Friedrich Ohaus in 1906 (fig. 4).

Topotypic paralectotypes: One extant tadpole (AMNH A193770) collected with the lectotype (fig. 4). Another four adult specimens (three males and one female), five larvae, and two egg clutches (MTKD D 2037), collected in the municipality of Petrópolis, Rio de Janeiro state, Brazil by Friedrich Ohaus in 1906, were all destroyed in the Dresden bombing in World War II, on 13 February 1945 (Obst, 1977).

General physical state of the extant type specimens: Both specimens are well fixed and in very good condition considering they were collected and fixed more than 115 years ago. However, their skin has lost most of its pigmentation and is translucent, with the color pattern barely detectable on the dorsum, lateral head, flank, and dorsal surfaces of the limbs of the lectotype (AMNH A32976). The lectotype (AMNH A32976) bears a tag tied around the groin and a narrow sagittal incision through the ventral skin and muscles from the medial gula to

TABLE 1. Snout-vent length range of species of *Thoropa*, separated by group (*T. petropolitana* group and *T. miliaris* group), for adult females and adult males, with respective ranges of measurements (minimum and maximum) and sample size. Measurements are given in millimeters (mm).

Species	Females	n	Males	n
***Thoropa petropolitana* group**	23.2 ± 0.5 (19.3–26.4)	16	20.2 ± 0.2 (14.2–27.3)	231
Thoropa bryomantis	25.1 ± 1.0 (24.1–26.1)	2	22.2 ± 0.2 (20.6–23.8)	24
Thoropa lutzi	– –	–	25.1 ± 0.3 (22.4–27.3)	22
Thoropa petropolitana	23.0 ± 0.5 (19.3–26.4)	14	19.4 ± 0.1 (14.2–22.9)	185
***Thoropa miliaris* group**	49.2 ± 0.7 (26.0–73.8)	204	49.7 ± 0.5 (22.1–101.7)	823
Thoropa megatympanum	41.8 ± 0.8 (31.8–54.0)	45	40.4 ± 0.5 (22.7–59.5)	228
Thoropa miliaris	49.9 ± 0.8 (26.0–65.6)	104	50.2 ± 0.5 (22.1–98.8)	427
Thoropa saxatilis	41.2 ± 2.3 (28.1–57.6)	20	38.9 ± 1.7 (25.2–56.6)	32
Thoropa taophora	61.1 ± 1.3 (40.8–73.8)	35	66.1 ± 1.3 (23.4–101.7)	136

the posterior abdomen. Its hands contact the throat, the fingers are not splayed or straight, but the nuptial pad is visible, and its PEPs can be counted (see below). The legs and feet of the adult are folded in articulations but not too close to the body. The toes are not splayed or straight. The untagged tadpole (topotypic paralectotype AMNH A193770) is in stage 27 or 28 (tadpole staging sensu Gosner, 1960). The tail is curved, and both the abdominal flap and final part of ventral fin have a small dextral incision.

Lectotype measurements (mm): SVL 18.6; head length 6.7; head width 6.8; tympanum diameter 1.3; eye diameter 2.7; interorbital distance 1.5; internarial distance 1.6; eye to nostril distance 1.8; eye to snout distance 2.8; forearm diameter 1.9; arm diameter 1.7; hand length 5.7; femur length 10.6; tibia length 10.7; foot length 9.7.

Topotypic paralectotype measurements (mm): Total length 19.9; body length 6.3; tail length 13.6; body width 3.7; body height 2.3; maximum tail height 1.6; nostril to snout distance 1.8; eye to snout distance 1.8; interorbital distance 1.5; eye to nostril distance 0.7; oral disc width 1.4; eye diameter 0.8.

Diagnosis: *Thoropa petropolitana* is diagnosed from its congeners by the following combination of characteristics. Adults: (1) small size (SVL males 14.2–22.9 mm, *N*= 191; females 19.3–26.4 mm, *N* = 14); (2) males with paired, elongate, curved vocal slits; and (3) vocal sac paired, subgular; (4) females on average larger than males; (5) spine-shaped PEPs generally

TABLE 2. Measurements of adult male, adult female, and undetermined adult of *Thoropa petropolitana*, with respective ranges of measurements (minimum and maximum) and sample size. Measurements are given in millimeters (mm).

Measurement	Females	n	Males	n	Undetermined	n
Snout-vent length	23.0 ± 0.5 (19.3–26.4)	14	19.4 ± 0.1 (14.2–22.9)	185	18.8 ± 0.4 (9.5–26.7)	102
Head width	8.1 ± 0.1 (7.0–8.8)	14	7.2 ± 0.1 (5.6–8.3)	109	7.1 ± 0.2 (4.3–9.5)	76
Head length	7.9 ± 0.2 (6.7–9.3)	14	7.3 ± 0.1 (5.4–8.3)	109	7.1 ± 0.2 (4.4–9.6)	76
Tympanum diameter	1.6 ± 0.1 (1.1–1.8)	14	1.4 ± 0.0 (1.0–2.3)	109	1.4 ± 0.0 (0.9–2.0)	76
Eye diameter	2.7 ± 0.1 (2.2–3.0)	14	2.3 ± 0.0 (1.7–3.0)	109	2.3 ± 0.1 (1.5–3.4)	76
Interorbital distance	2.0 ± 0.1 (1.6–2.7)	8	1.6 ± 0.0 (1.0–2.0)	56	1.6 ± 0.1 (1.1–2.2)	36
Internarial distance	1.7 ± 0.1 (1.3–2.0)	8	1.5 ± 0.0 (1.1–2.1)	56	1.5 ± 0.1 (1.0–2.3)	36
Eye-nostril distance	1.8 ± 0.1 (1.5–2.1)	8	1.7 ± 0.0 (1.1–2.2)	56	1.6 ± 0.1 (1.0–2.1)	36
Eye-snout distance	3.3 ± 0.1 (3.0–3.7)	8	3.0 ± 0.0 (2.2–3.4)	56	2.9 ± 0.1 (1.7–4.0)	36
Foot length	11.6 ± 0.7 (7.6–14.2)	8	10.5 ± 0.1 (8.5–12.9)	54	10.1 ± 0.4 (6.2–14.3)	36
Hand length	6.8 ± 0.2 (5.8–7.9)	8	5.9 ± 0.1 (4.6–7.5)	54	5.7 ± 0.2 (4.1–7.9)	36
Tibia length	12.9 ± 0.4 (11.7–14.5)	8	10.7 ± 0.1 (8.4–12.6)	56	10.5 ± 0.4 (6.2–13.9)	36
Femur length	12.1 ± 0.3 (11.2–13.9)	8	10.5 ± 0.1 (8.0–11.9)	56	10.2 ± 0.4 (6.1–14.1)	36
Forearm diameter	1.6 ± 0.1 (1.2–2.1)	14	1.7 ± 0.0 (1.1–2.3)	108	1.4 ± 0.0 (0.9–2.3)	76
Arm diameter	2.0 ± 0.1 (1.5–2.5)	14	1.7 ± 0.0 (1.2–2.7)	108	1.7 ± 0.0 (0.8–2.6)	76
Right-hand PEPs	– –	– –	9.7 ± 0.2 (0.0–21.0)	162	– –	– –
Left-hand PEPs	– –	– –	9.6 ± 0.2 (4.0–17.0)	169	– –	– –

TABLE 3. Measurements of tadpoles of *Thoropa petropolitana*, with respective ranges of measurements (minimum and maximum) and sample size. Measurements are given in millimeters (mm).

Measurement	Mean (SD) Range	n
Total length	27.3 ± 1.1 (13.3–37.8)	37
Body length	8.3 ± 0.5 (4.1–24.2)	37
Tail length	19.1 ± 0.9 (9.6–28.9)	37
Body width	4.7 ± 0.2 (2.2–6.4)	37
Body height	2.6 ± 0.1 (1.6–3.4)	37
Maximum tail height	1.7 ± 0.1 (0.9–2.4)	37
Nostril-snout distance	1.3 ± 0.1 (0.6–1.8)	37
Eye-snout distance	2.4 ± 0.1 (1.2–3.2)	37
Eye-nostril distance	1.3 ± 0.1 (0.6–2.0)	37
Interorbital distance	1.2 ± 0.1 (0.4–1.7)	37
Oral disc width	2.3 ± 0.1 (0.9–3.3)	36
Eye diameter	1.2 ± 0.1 (0.7–3.3)	37

restricted to finger II, dorsal to the articulation between the proximal phalanx and metacarpus (metacarpal-phalangeal articulation); (6) supernumerary tubercles on hand absent; (7) fingers II<III; (8) finger V surpassing penultimate articulation of finger IV; (9) advertisement call composed of one note. Tadpoles: (10) abdominal flap large with deeply bilobate posterior margin; (11) ventral fin forming medial groove posteriorly; (12) vent tube attached to ventral fin; (13) spiracle orifice ventral to abdominal flap (contra Dias et al., 2021); (14) dorsal color pattern of tail forming series of pale diamonds.

Comparison within the *Thoropa petropolitana* group: *Thoropa petropolitana* is smaller than the other species of the group, with males SVL 14.2–22.9 mm, and females SVL 19.3–26.4 mm (in *T. bryomantis*, male SVL 20.6–23.8 mm and female SVL 24.1–26.1 mm; in *T. lutzi*, male SVL 22.4–27.3 mm); table 1; supplementary appendix SA1). *Thoropa petropoli-*

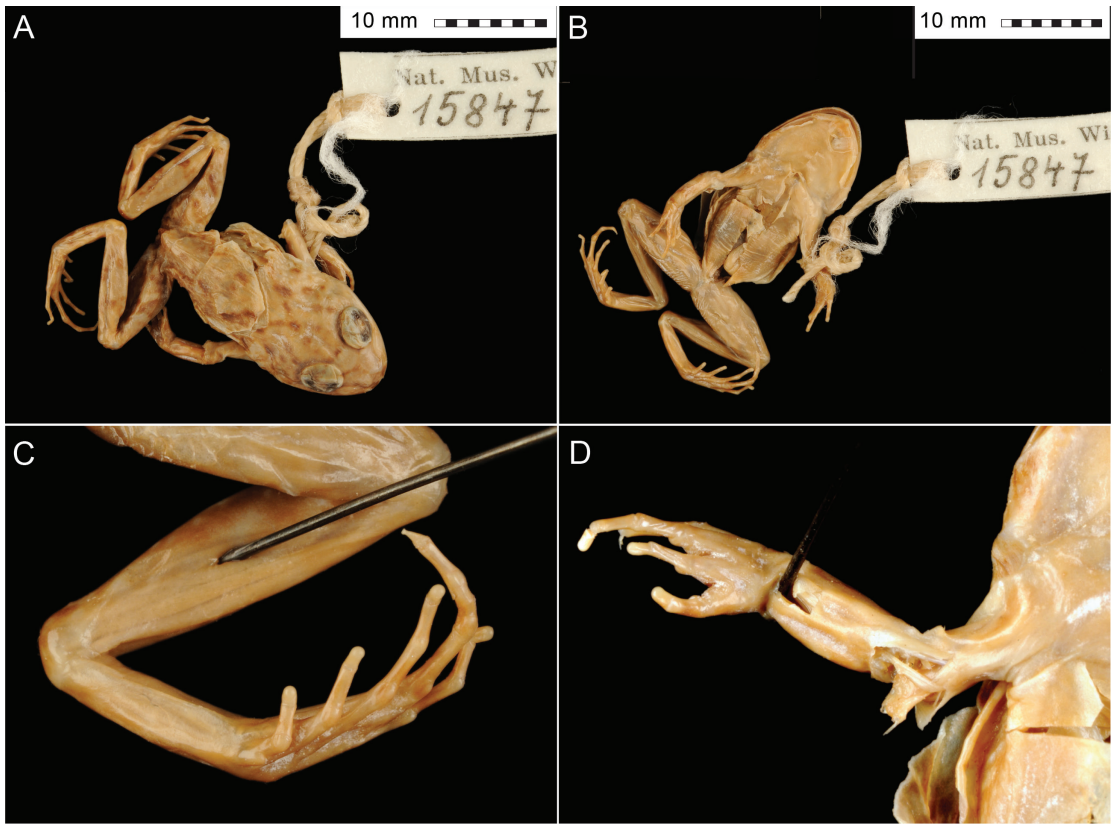


FIG. 3. The holotype of *Eupsophus fuliginosus* (NHMW 15847). Image provided by the Wien Natural History Museum. **A,** dorsal view. **B,** ventral view. **C,** ventral foot detail. **D,** dorsal hand detail.

tana has a paired vocal sac (*T. lutzi* and *T. bryomantis* have single and subgular vocal sac; Assis et al., 2021; this study). *Thoropa petropolitana* has spine-shaped PEPs (*T. lutzi* and *T. bryomantis* have cone-shaped PEPs; Assis et al., 2021; Luna et al., 2018). In *T. petropolitana*, PEPs are generally restricted to the dorsal surface of the metacarpal-phalangeal articulation of finger II (*T. lutzi* and *T. bryomantis* have PEPs on finger II and inner metacarpal tubercle; Assis et al., 2021). In *T. petropolitana*, finger V surpasses the penultimate articulation of finger IV (usually not surpassing in *T. lutzi* and *T. bryomantis*). *Thoropa petropolitana* has fingertips slightly dilated (dilated in *T. lutzi* and *T. bryomantis*; this study; Assis et al., 2021; Cocroft and Heyer, 1988). The advertisement call of *T. petropolitana* is pulsatile (nonpulsatile in *T. lutzi* and *T. bryomantis* Nunes-de-Almeida et al., 2016). In tadpoles of *T. petropolitana*, the medial groove of the ventral fin starts in the posterior part of the tail (starts in the anterior half of the tail in *T. lutzi*; unknown in *T. bryomantis*) and the vent tube is attached to the ventral fin (ventral fin and to the abdominal flap in *T. lutzi*, Dias et al., 2021; unknown in *T. bryomantis*).

Comparison with the *Thoropa miliaris* group: As stated above, *Thoropa petropolitana* is on average smaller than other species of the genus, with males SVL 14.2–22.9 mm, and females SVL 19.3–26.4 mm (in the *T. miliaris* group, male SVL 22.0–101.7 mm, female

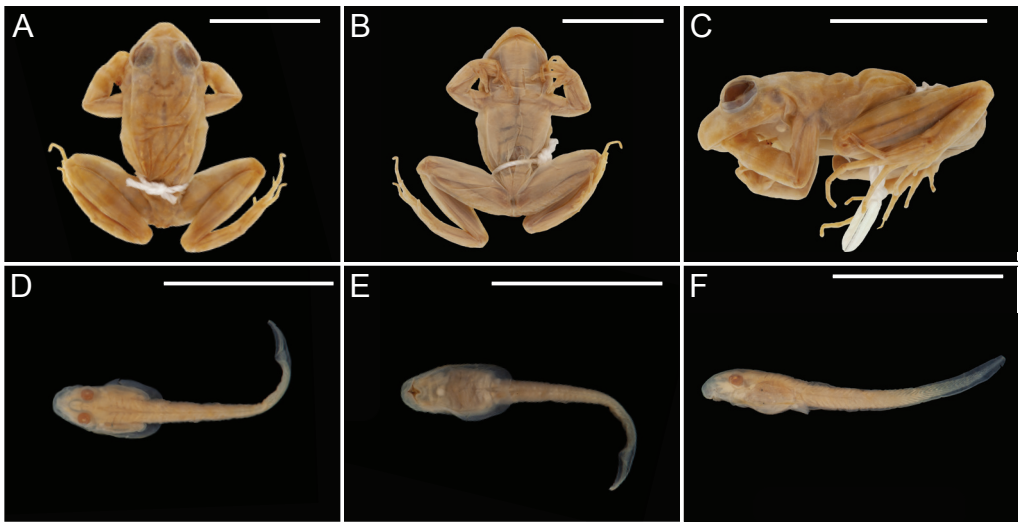


FIG. 4. Syntypes of *Hylodes petropolitanus* at AMNH. Lectotype AMNH A32976: **A**, dorsal view; **B**, ventral view; **C**, lateral view. Paralectotype AMNH A193770: **D**, dorsal view; **E**, ventral view; **F**, lateral view. White bars indicate 1 cm.

SVL 26.0–73.8 mm; table 1; supplementary appendix SA1). Additionally, females are, on average, larger than males in *T. petropolitana* (not in the *T. miliaris* group; table 1). Vocal slits and vocal sac are present in *T. petropolitana* (absent in the *T. miliaris* group; Assis et al., 2021; this study). PEPs are generally restricted to the dorsal metacarpal–phalangeal articulation of finger II in *T. petropolitana* (finger II, inner metacarpal tubercle, and fingers III and IV in the *T. miliaris* group; Sabbag et al., 2022a). Supernumerary tubercles on the hands are absent in *Thoropa petropolitana* (present in the *T. miliaris* group). Fingertips are weakly dilated in *T. petropolitana* (dilated in *T. miliaris* group; this study; Cocroft and Heyer, 1988). The advertisement call of *T. petropolitana* is composed of a single note (more than one note in the *T. miliaris* group; Nunes-de-Almeida et al., 2016). In tadpoles of *T. petropolitana*, the medial groove of the ventral fin arises in the posterior portion of the tail (medial groove extending along entire length of tail in the *T. miliaris* group) and the abdominal flap is continuous and large, both posteriorly and laterally (poorly developed and discontinuous in *T. megatympanum* and *T. miliaris*; this study; Colaço and da Silva, 2022; Dias et al., 2021) and posteriorly bilobate in *T. petropolitana* (posteriorly rounded in *T. taophora* and *T. saxatilis*; Dias et al., 2021; this study). The spiracle opening is ventral to the abdominal flap in *T. petropolitana* (spiracle opening dorsal to the abdominal flap or at midline of lateral body in the *T. miliaris* group). The vent tube is attached to the ventral fin in *T. petropolitana* (free in *T. miliaris*, attached to the ventral fin and abdominal flap in *T. taophora*; Dias et al., 2021). In *T. petropolitana*, finger II is shorter than finger III (finger II longer than finger III in *T. miliaris*, *T. megatympanum*, and *T. taophora*) and finger V surpasses the penultimate articulation of finger IV (finger V not surpassing the penultimate articulation of finger IV in *T. megatympanum* and *T. saxatilis*).

Lectotype description: Body small relative to other *Thoropa* spp.; head as wide as long (head length 4.7% of SVL); snout acuminate in dorsal and lateral views; nares lateral, located close to tip of snout; internarial distance 12.2% of interorbital distance; *canthus rostralis* concave; loreal region slightly concave, sloping slightly outward to lip; posterior margin of eye and anterior margin of tympanic ring separated; pupillary meniscus not visible; palpebral membrane lacking reticulation or other pigmentation; eye diameter 44.8% of interorbital distance; tympanum visible, subcircular; tympanic ring conspicuous; supratympanic fold visible, surrounding tympanum from posterior margin of eye to anterior edge of arm insertion; tongue oval, attached anteriorly and laterally, free posteriorly; dentigerous process of vomer transverse, discontinuous, positioned between choanae; choanae wide, elliptic, widely separated; vocal slits present; vocal sac paired, subgular. Discoidal fold evident in ventral view. Mandibular symphysis fitting into single premaxillary fossa.

Arm slender, diameter of upper arm and forearm similar; fingers long, slender, tips weakly dilated; fingers in the following length order: II<III<V<IV or II<II ≈ V<IV; finger webbing absent; subarticular tubercles single, rounded, weak; supernumerary tubercles absent; inner and outer metacarpal tubercles ovoid; PEPs restricted to dorsal surface of finger II above articulation between proximal phalanx and metacarpus, 12 on right hand, 11 on left, dark brown to black at tips, lighter shades of brown toward base.

Leg long, slender; tibia length 55.9% of SVL; toes long, slender, tips weakly dilated; toes in the following length order: I<II<V<III< IV; toe webbing absent; supernumerary tubercles absent; subarticular tubercles simple and rounded, weak; outer metatarsal tubercle round.

Dorsum weakly asperous sagittally, increasingly asperous laterally; dorsal surface of eyelid asperous; dorsal surfaces of members weakly asperous; flank with scattered, inconspicuous, warty macroglands; ventral surfaces smooth.

Coloration in life: Information on the coloration of the lectotype in life is unavailable, so the description here is based on other specimens and the literature. The coloration of the type series in life was described by Wandolleck (1907), as follows (freely translated from the German): ground color of the dorsal part of the body dark gray-blue in juveniles, lighter on the flanks toward the central region of the dorsal part of the body and marbled with yellow-gray in the older specimens; wide stripe crossing horizontally the head over the eyes, connected to a longitudinal strip extending toward the middle of the dorsum; upper lip with four oblique, light stripes extending from the eyes; tympanum yellow-gray with the same marbled and spotted shading of the flanks of the body; the dorsal surface of the extremities of the members alternates between gray-yellow and blue-gray, except on the phalanges; ventral part of the body yellow-white with scattered irregular brown and might exist in the pectoral girdle, in laterals and more frequently in the thigh. Additionally, Bokermann (1965) also reported that live specimens present poorly defined dark blotches on a green background.

A photograph by Eugênio Izecksohn of a live specimen (fig. 6) published by Silva (2009) and Nunes-de-Almeida et al. (2016), probably corresponding to EI 9474 (collected 21 October, 1977, in Parque Nacional da Serra dos Órgãos, Rio de Janeiro state), shows the dorsum to be light brown-yellow with scattered irregular gray-brown spots; the snout is brown, slightly

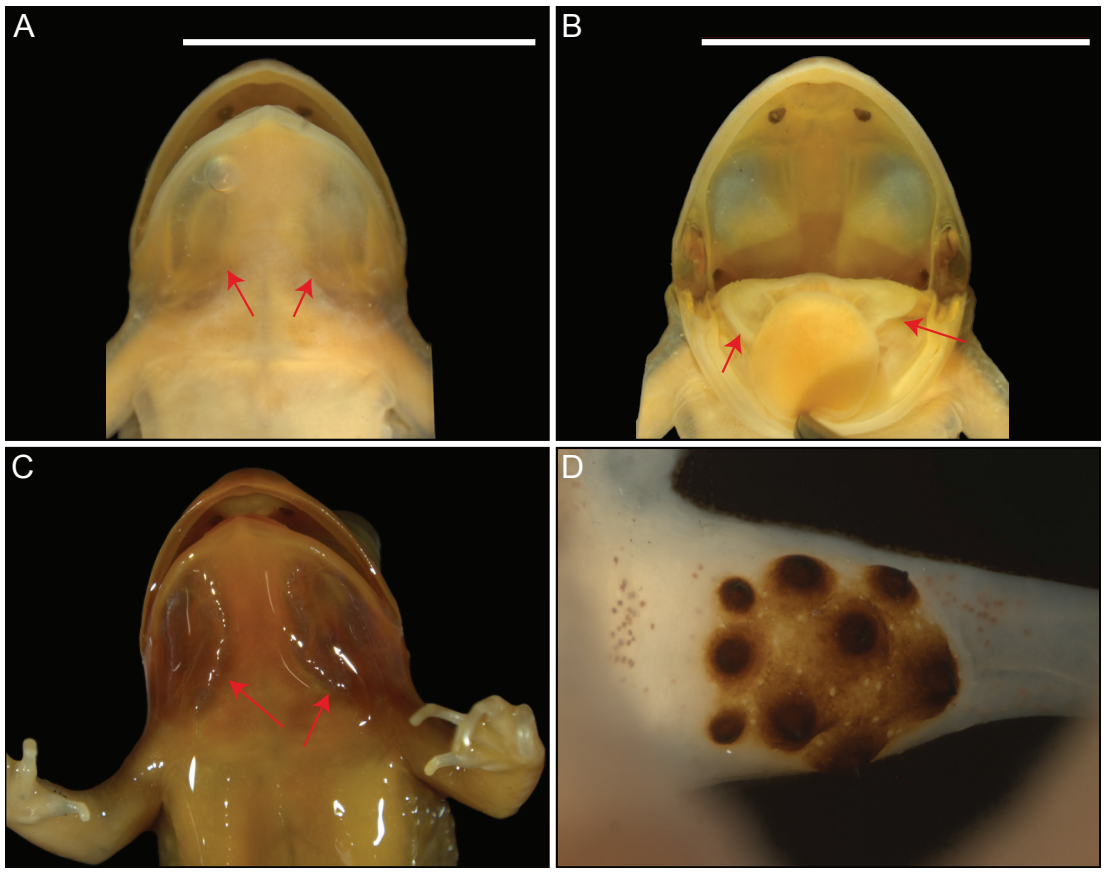


FIG. 5. Morphological details of *Thoropa petropolitana*. Adult male EI 2586: **A**, ventral view of head (red arrows indicate vocal sacs); **B**, view inside buccal cavity (red arrows indicate vocal slits); **C**, ventral view of head stained with Lugol (red arrows indicate vocal sacs). Adult male EI 9476: **D**, dorsal view of metacarpal-phalangeal articulation of finger II showing brown PEPs. Scale bars = 1 cm.

darker than the dorsum; the eyelid is whitish; between the eyelids there is a light transverse stripe delimiting the base of a large dark brown, triangular blotch extending from the middle of the dorsal region where two dark brown blotches bifurcate laterally, leaving between them a whitish region; the supratympanic fold is brown, slightly darker than the dorsum; a large, dark brown blotch occurs on the posterior third of the dorsum; the members possess well-defined, dark brown, transverse stripes.

Coloration in preservative: The background is light yellow with a large, triangular, light-brown blotch between the eyelids that bifurcates to form two oblique stripes extending posteriad to the midlevel of the dorsum; the eyelid is whitish and the supratympanic fold is light brown. The botch on the posterior third of the dorsum is light brown, as are the transverse strips on the members. All the ventral surfaces are whitish. See supplementary appendix SA2, available online (https://doi.org/10.5531/sd.sp.72), for photographs of some fixed specimens.

Variation: SVL varies between 14.2 and 22.9 mm (N = 191) in males and 19.3 and 26.4 mm (N = 14) in females (table 2, supplementary appendix SA1). Adult males possess vocal slits

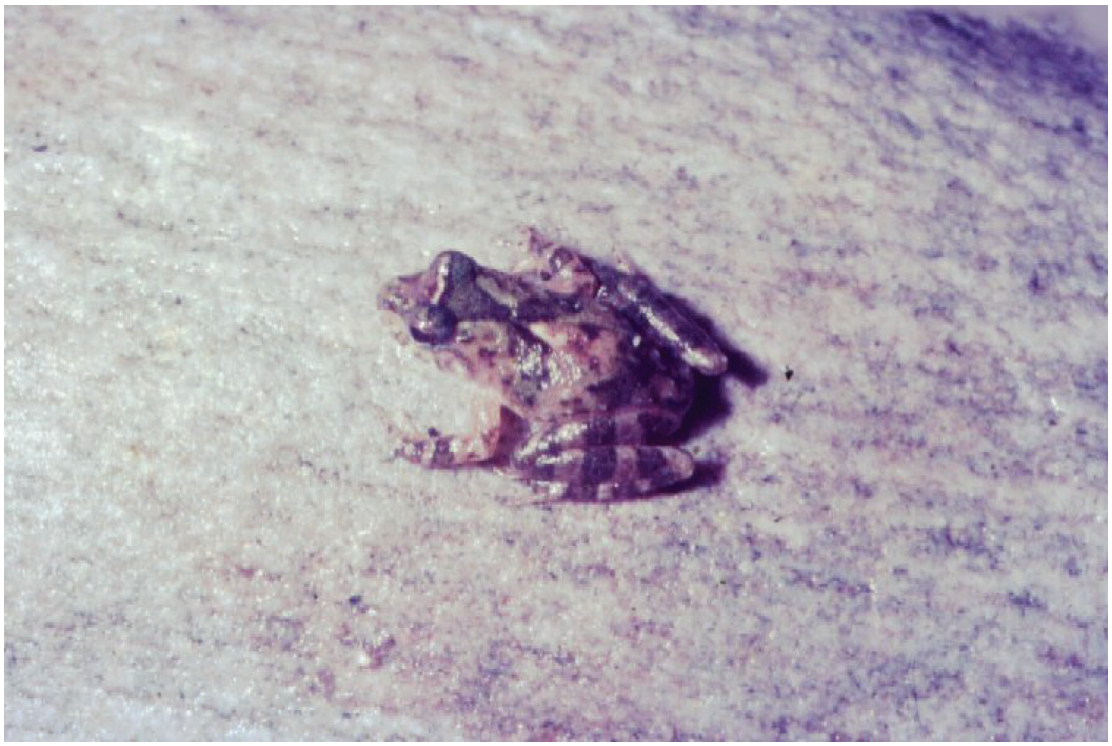


FIG. 6. Only known photograph of *Thoropa petropolitana* in life. Specimen EI 9474, collected in Alto Soberbo, Rodovia Rio–Teresópolis, Magé, Rio de Janeiro state, September 14, 1977, by C.A.G. Cruz, O.L. Peixoto, E. Izecksohn, and S.P. Carvalho-e-Silva. Photograph of Eugênio Izecksohn. Photograph published by Silva (2009) and Nunes-de-Almeida et al. (2016).

and paired subgular vocal sac, probably separated by the *m. geniohyoideus* (figs. 5A–C; Elias-Costa et al., 2021).

The relative lengths of fingers and toes is somewhat variable among specimens. Specifically, finger II can be shorter than or approximately equal to finger V, and toe V can be shorter than or approximately equal to toe III. In most specimens, the subarticular tubercles are inconspicuous. Nevertheless, topical application of Lugol's solution (Bock and Shear, 1972) reveals them to be present beneath all finger and toe articulations. Similarly, in some specimens the metacarpal and the inner metatarsal tubercles are inconspicuous but are revealed to be present by Lugol's solution.

Among adult males, PEPs vary slightly in size, position, shape, and extent of keratinization of the stratum corneum (Sabbag et al., 2022a). Indeed, in seven specimens the PEPs are completely white on one of the hands (e.g., MNRJ 24152 and EI 9483; supplementary appendix SA1). In others, PEPs are brown, with their borders being light brown (fig. 5D). Some males also exhibit PEPs in other regions of the hand beyond the metacarpal-phalangeal articulation. For example, USNM 208609 also possesses one PEP on the terminal phalanx of finger II of the right hand, whereas USNM 208610 has two PEPs on the terminal phalanx of finger II of the right hand, one on the terminal phalanx of finger II of the left hand, and one on each inner metacarpal tubercle

of both hands (supplementary appendix SA1). The number of PEPs is 0–21 on the right hand and 4–17 on the left (this study; Sabbag et al., 2022a). Some specimens can possess higher numbers of PEPs, because unkeratinized (white) PEPs are difficult to individualize and count.

Tadpoles (table 3, supplementary appendix SA1): Dias et al. (2021) and Colaço and da Silva (2022) described the anatomical characteristics of many Cycloramphidae species, including *T. petropolitana*. Our observations agree with their accounts, with the exception that the spiracular orifice is ventral to the abdominal flap and not dorsal, as reported by Dias et al. (2021). We highlight that *T. petropolitana* tadpoles present a well-developed, posteriorly deeply bilobate abdominal flap and a sinistral, tubular, lateral spiracle that is directed posterodorsad, lacks an inner wall, and is open ventrally to the abdominal flap. Also, the medial groove of the ventral fin starts in the posterior part of the tail, and the vent tube is attached to the ventral fin (Dias et al., 2021).

Natural history: The first information about the natural history of *Thoropa petropolitana* was provided in Wandolleck's (1907) description as the transcription of a personal communication from the collector Friedrich Ohaus. According to Ohaus, the species inhabits granitic walls with fast-running water where it feeds on insects; the egg clutches are large and attached to protruding parts of rocks or placed amidst mosses and lichens where they maintain contact with the water; the tadpoles also inhabit rock walls and present a "suctorial disc" on the base of the tail and a "suctorial pad" on the abdomen, which they use to slip over the rocks and move quickly in the flowing water, showing the ability to return to the water; they are camouflaged with the rocks (Wandolleck, 1907).

Bokermann (1965) reported that amplexus was not observed and that the green background of dorsum seems to enable camouflage with algae and slime on the rocks. Bokermann (1965) also reported that—unlike *Thoropa miliaris*—males are not territorial and call with many other males.

Heyer and Crombie (1979) described the sequence of the reproductive behavior, embryo development in the eggs, predation, and territoriality, including some comparisons with *Thoropa miliaris*. They mention axillary amplexus, a small number of eggs (16), male territoriality, and male clutch attendance. Cocroft and Heyer (1988) commented about territoriality of the genus, drawing attention, among other things, for dorsal scratches in *T. miliaris* probably due to male-male combat using PEPs, but they could not find scratches in *T. petropolitana*.

Advertisement call: According to Friedrich Ohaus, *Thoropa petropolitana* calls like a "small parrot" (Wandolleck, 1907). Bokermann (1965) described the advertisement call as a single, short, uniform note with energy concentrated between ca. 1500 and 4500 Hz and a duration of less than 0.1 s, sounding like a click repeated at irregular intervals of 5–10 s or more (Bokermann, 1965). Lutz (1954) also described the call as a click. Recently, Nunes-de-Almeida et al. (2016) redescribed the advertisement call of *T. petropolitana* on the basis of the same recording used by Bokermann (1965). Nunes-de-Almeida et al. (2016) defined the call as "simple" (i.e., composed of a single note) and repeated at irregular intervals (mean intercall interval 14.64–31.54 s); the mean duration is 36 ms; calls have a mean of 132.33 pulses; pulses have a mean duration of 3 ms and are grouped into pseudopulses composed of, on average, 11.17 pulses [sic; pseudopulses?]; the mean dominant frequency is 3.81 kHz; and calls have three frequency bands with no frequency modulation.

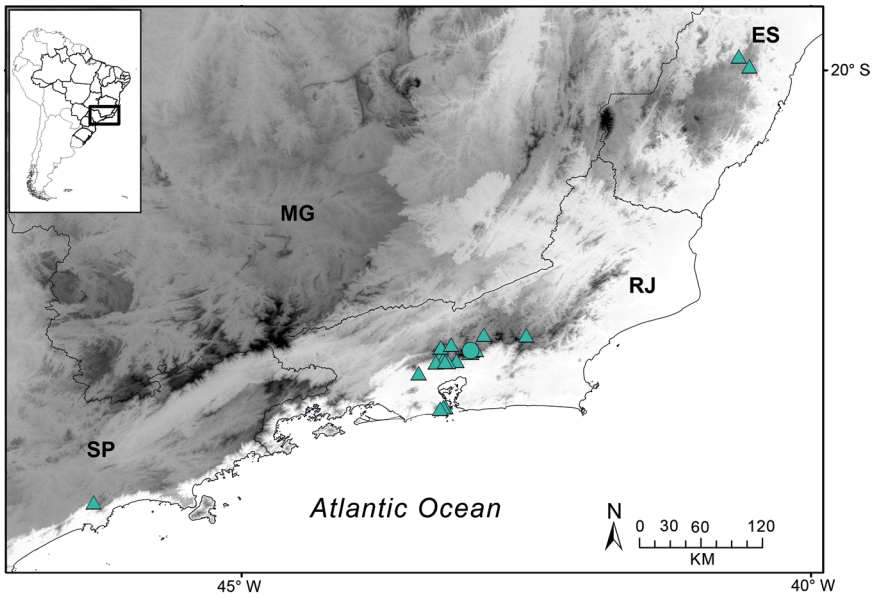


FIG. 7. Distribution map of *Thoropa petropolitana* (Wandolleck, 1907). We obtained geographical coordinates from Google Earth® v.7.3.4 (Google) and centroid coordinates from ArcGIS v.10.1 (ESRI, 2012). The type locality is represented by a circle. The locality of the specimens purportedly from "Rio Juruá" (municipality of Eurinepé, Amazon state) is not included. Elevation is represented in shades of gray varying increasing in 50 m increments from sea level (white). SP, MG, RJ, ES indicate Brazilian states, respectively: São Paulo, Minas Gerais, Rio de Janeiro, and Espírito Santo.

Geographic distribution: Confirmed records of *Thoropa petropolitana* are restricted to the montane region of southern Rio de Janeiro state and three disjunct populations: a population in Tijuca in Rio de Janeiro municipality, a northern population in Espírito Santo and a southern population in São Paulo (fig. 7; for comments see Discussion).

DISCUSSION

Thoropa petropolitana males and females differ in SVL and the presence of vocal sacs, vocal slits, and PEPs in males. Females are, on average, larger than males (Bokermann, 1965; Cocroft and Heyer, 1988; Feio, 2002), presenting a mean SVL of 23.0 mm, while males present a mean SVL of 19.4 mm (table 2).

Cocroft and Heyer (1988) proposed an identification key with some characteristics of *Thoropa petropolitana*, most of them in agreement with our study. For the adults, they noted the presence of "finger disks not or only slightly expanded" (confirmed by us); "posterior surface of thigh uniform brown with light flecks or light and dark brown mottle, dorsum mottled with light and dark brown" (confirmed); tympanum 60%–70% the size of the eyes (similar to our results: table 2); tympanic ring and supratympanic fold low and indistinct (not confirmed: they are distinct, albeit less conspicuous than in *T. miliaris*); finger III longer than finger II (as our observations, and also pointed by Heyer, 1999); and males with a single PEPs cluster in finger

II (confirmed). Additionally, although some authors have reported basal toe webbing (Cochran, 1955; Cocroft and Heyer, 1988), close inspection reveals that the apparent webbing is just folded skin at the base of toes.

Although *Thoropa petropolitana* closely resembles other species of the *T. petropolitana* group, it resembles the *T. miliaris* group in PEP size, shape, pattern, and presence of PEPs above the metacarpal-phalangeal articulation (Sabbag et al., 2022a). Assuming that the *T. petropolitana* group is monophyletic, it is unknown if this resemblance owes to plesiomorphy or homoplasy.

The accumulation of information on the reproductive behavior of the *Thoropa petropolitana* group has been somewhat convoluted. Both *Thoropa lutzi* and *T. petropolitana* were initially considered to have nonterritorial males (Bokermann, 1965), but it was later shown that male *T. petropolitana* are solitary and defend their territories (Heyer and Crombie, 1979); information on reproductive behavior is still lacking for *T. bryomantis*. Similarly, although Cochran (1955) mentioned the occurrence of paired vocal sacs, Nunes-de-Almeida et al. (2016) claimed that *T. petropolitana* lacks vocal sacs. Assis et al. (2021) clarified that *T. bryomantis* and *T. lutzi* possess vocal slits and a single subgular vocal sac, and we also observed vocal slits and a paired subgular vocal sac in *T. petropolitana*, contra Nunes-de-Almeida et al. (2016).

As noted above, confirmed records of *Thoropa petropolitana* are from the mountainous region of southern Rio de Janeiro state, the municipality of Rio de Janeiro, and the states of Espírito Santo and São Paulo. The records from the municipality of Rio de Janeiro are all from what is today Parque Nacional da Tijuca. Feio (2002) reported MZUSP 86581 and MZUSP 88241–88252, but none of these specimens could be located. Among the specimens cited by Feio (2002) in the Museu Nacional (AL-MN 413–414, 555–559, and 872), only AL-MN 556–559 and 872 (two adult males and three probable adult females) were located, all of which correspond morphologically to *T. petropolitana*.

The Espírito Santo records are based on 14 specimens of *Thoropa petropolitana* collected in Santa Teresa, five of which are housed in the California Academy of Sciences (CAS-SUA 11731–11735) and the other nine in Museu de Zoologia da Universidade de São Paulo (MZUSP 27718, 27723, 27725–27729, 27732–27733). The CAS specimens were recorded as having been collected at the Estação Biológica do Museu Nacional (currently Estação Biológica de Santa Lúcia) by Augusto Ruschi on 24–27 December 1942. Among these five specimens, we examined three (a juvenile and two probable adult females), all of which correspond morphologically to *T. petropolitana*. Similarly, the nine MZUSP specimens—collected at "Santa Teresa, ES" (no additional information available) during a MZUSP expedition on 1–4 April 1969—also correspond morphologically to *T. petropolitana*. Although these localities in Espírito Santo lie more than 350 km northeast of the localities in Rio de Janeiro, the fact that the specimens were collected more than 20 years apart by different researchers and deposited in different collections leads us to conclude that they are not labeling errors. Subsequent expeditions in Santa Teresa have failed to detect this species (Ferreira et al., 2019b).

Similarly, the São Paulo locality also appears to be legitimate. The three specimens (AL-MN 3578, MNRJ 14607–14608, all females or juvenile males) correspond morphologically to *T.*

petropolitana and were collected by Alphonse Hoge and Bertha Lutz on 17 December, 1959, in "São Paulo," which was restricted by Bokermann (1966a) to either Alto da Serra de Cubatão (Paranapiacaba, Santo André municipality, São Paulo state), more than 300 km southwest of the main distribution of *T. petropolitana* in Rio de Janeiro. We are unaware of any additional records of *T. petropolitana* in this region, which is striking given the intense collecting in the area over the past five decades or more (e.g., Cocroft and Heyer, 1988). However, we are also unaware of any independent evidence suggesting this record to be erroneous and instead suggest these specimens might represent a population that declined and disappeared, as has been documented for many other amphibian populations in this region (Heyer et al., 1988; Toledo et al., 2023; Verdade et al., 2009, 2012).

In addition to the above localities that appear to be correct, several others merit special consideration. First, MZUSP 1489 (adult female with oocytes), MZUSP 1490 (juvenile female), and MZUSP 1491 (adult male) were cataloged as having been collected in Amazonia by Ernest Garbe in December 1901 during and expedition to the Rio Juruá. These specimens were analyzed by Bokermann (1965) and we agree with him that they are *T. petropolitana*; however, the disjunct locality in Amazonas state appears to be incorrect. Ernest Garbe was hired as a naturalist by the Museu Paulista, São Paulo, Brazil (currently MZUSP) on 2 January 1902 through a power of attorney since he was already on an expedition on the Juruá River, Amazonas state, Brazil (Pinto, 1945), far away from São Paulo. According to a personal communication from Walter Garbe (Ernest Garbe's son) to Olivério Pinto (Pinto, 1945), in November 1900 he and his father traveled to Petrópolis municipality (Rio de Janeiro state) to prepare for their expedition to the Juruá River, leaving Petrópolis directly to the Juruá River and regressing to São Paulo. While in Petrópolis, Ernest Garbe and his son collected some specimens of hummingbirds, as documented in the records of MZUSP Ornithology Collection (Pinto, 1945), and it seems that the record of *T. petropolitana* from the Rio Juruá is due to a labeling error (as indicated by Bokermann, 1965) and the specimens were actually collected in Petrópolis, Rio de Janeiro state, in November 1900.

For decades, *Thoropa petropolitana* was abundant in the Serra dos Órgãos, as evidenced by extensive series in museums. For example, MZUSP possesses lots of 50 specimens (collected in 1963), 137 specimens (also 1963), 49 specimens (1964), 77 specimens (also 1964) and a collection in collaboration with the USNM (in 1977) comprising 62 specimens divided between the two museums. As far as we know, *T. petropolitana* was last observed in nature in March 1982 when it was collected by Adriano Lúcio Peracchi and Eugênio Izecksohn in Parque Nacional da Serra dos Órgãos, Magé, Rio de Janeiro, and deposited in the Brazilian National Museum (Museu Nacional, MNRJ 61403–61404). Toledo et al. (2023) published that the last collection was in 1984 (MNRJ 26006), but we identified this specimen as *T. miliaris*. By the end of 1980s, *T. petropolitana* populations had already disappeared (Heyer et al., 1988), and neither specimens nor environmental DNA have been detected since (Lopes et al., 2020). Since 1982, many herpetologists have searched for this species in appropriate habitats (wet rocky outcrops and waterfalls; for details, see Toledo et al., 2023). We also searched for *T. petropolitana* in Parque Nacional da Serra dos Órgãos and the region of Petrópolis and Teresópolis (both in Rio de Janeiro state) between 2015 and 2019 but failed in all attempts. Currently, *T. petropolitana* is

classified as "critically endangered" and "possibly extinct" (DOU, 2022a; IUCN and Instituto Boitatá, 2023).

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APPENDIX

Collections Visited and Analyzed for This Study

Institutional abbreviations mostly follow Sabaj (2020).

AAG-UFU	Coleção do Prof. Dr. Ariovaldo A. Giaretta, UFU, Uberlândia, MG, Brazil;
AMNH	Department of Herpetology, American Museum of Natural History, New York, NY;
CAS	Herpetology Collection, California Academy of Sciences, San Francisco, CA;
CFBH	Coleção de Anfíbios Célio F.B. Haddad, UNESP, Rio Claro, SP, Brazil;
CM	Section of Herpetology, Carnegie Museum of Natural History, Pittsburgh, PA;
DZSJRP	Coleção Científica de Anfíbios do Departamento de Zoologia e Botânica, UNESP, São José do Rio Preto, SP, Brazil;
EI	Coleção de Anfíbios Eugenio Izecksohn da UFRRJ, Seropédica, RJ, Brazil;
FMNH	Amphibian and Reptile Collection, Field Museum of Natural History, Chicago, IL;
IRSNB	Collection de Vertébrés, Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgique;
KUMNH	Zoologisk Museum, Københavns Universitet, Københavns, Danmark.
MBML	Coleção Zoológica do Museu de Biologia Professor Mello Leitão, Santa Teresa, ES, Brazil;
MCNAM	Coleção de Anfíbios do Museu de Ciências Naturais da PUC-MG, Belo Horizonte, MG, Brazil;
MCP	Coleção de Herpetologia do Museu de Ciências e Tecnologia da PUC-RS, Porto Alegre, RS, Brazil;
MCZ	Herpetology Collection, Museum of Comparative Zoology, Harvard University, Cambridge, MA;
MNHN	Muséum National d'Histoire Naturelle, Sorbonne Universités, Paris, France;
MNRJ	Coleção Herpetológica do Museu Nacional, Rio de Janeiro, RJ, Brazil;
MTR	Coleção do Miguel Trefault Rodrigues, USP, São Paulo, SP, Brazil;
MVZ	Museum of Vertebrate Zoology, University of California, Berkeley, CA;
MZUESC	Coleção de Anfíbios do Museu de Zoologia da UESC, Ilhéus, BA, Brazil;
MZUFV	Coleção de Anfíbios do Museu de Zoologia João Moojen da UFV, Viçosa, MG, Brazil;
MZUSP	Coleção Herpetológica do Museu de Zoologia da USP, São Paulo, SP, Brazil;
NMW	Herpetologische Sammlung, Naturhistorisches Museum Wien, Wien, Österreich;
TNHC	Texas Natural History Collections, University of Texas, Austin, TX;
UFMG	Coleção de Anfíbios do Laboratório de Herpetologia da UFMG, Belo Horizonte, MG, Brazil;
UFRRJ-RU	Coleção de Anfíbios da UFRRJ, Seropédica, RJ, Brazil;
UMMZ	Herpetology Collection, Museum of Zoology, University of Michigan, Ann Arbor, MI;
USNM	Division of Amphibians and Reptiles, National Museum of Natural History, Washington, DC;
ZUEC	Coleção de Anfíbios do Museu de Zoologia "Adão José Cardoso" da UNICAMP, Campinas, SP, Brazil;
ZUFRJ	Coleção Herpetológica do Departamento de Zoologia da UFRJ, Rio de Janeiro, RJ, Brazil.

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