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Source: Copeia, 2013(4):634-640. 2013.

Published By: The American Society of Ichthyologists and Herpetologists

DOI: <http://dx.doi.org/10.1643/CH-12-102>

URL: <http://www.bioone.org/doi/full/10.1643/CH-12-102>

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A Second Species of *Trachycephalus* Tschudi (Anura: Hylidae) with a Single Vocal Sac from the Brazilian Amazon

Ivan Nunes¹, Pablo Suárez², Marcelo Gordo³, and José P. Pombal, Jr.¹

A new species of *Trachycephalus* from the Brazilian Amazon Rain Forest, morphologically similar to *T. hadroceps* (Duellman and Hoogmoed), is described. This new species is characterized by having the skin not co-ossified with the skull; skin on dorsum bearing many low and medium round tubercles; a vocal sac not externally visible; well-developed paratoid gland; snout rounded in profile; third finger disc almost the same size of the eye; absence of tarsal fold; iris pinkish-beige with a horizontal dark gray bar; dorsal color pattern in life light brownish-orange with scattered brown dots. *Trachycephalus hadroceps* is restricted to the left margin (north) of the Amazon River, in the Guiana Shield, and possibly in the adjacent Brazilian Amazon Rain Forest, and the new species occurs on the right margin (south) of the Amazon River. It is a canopy treefrog, which probably uses treeholes filled with water as breeding sites.

FAIVOVICH et al. (2005) studied the systematics of the family Hylidae based on molecular data and found the genus *Trachycephalus* Tschudi paraphyletic with respect to *Phrynohyas* Fitzinger, thus placing *Phrynohyas* in synonymy with *Trachycephalus*, a decision that was followed by subsequent authors (e.g., Kwet and Solé, 2008; Lavilla et al., 2010; Wiens et al., 2010). As recognized by Faivovich et al. (2005), *Trachycephalus* was diagnosed by 37 transformations of nuclear and ribosomal DNA, and a possible morphological synapomorphy is the presence of a paired vocal sac that protrudes at a posterior angle to the jaw when inflated (see Trueb and Duellman, 1971; Tyler, 1971; Faivovich et al., 2005). The hylid frog genus *Trachycephalus* is distributed from Mexico to northern Argentina and eastern Brazil, and currently includes 12 species (Frost, 2013): *Trachycephalus atlas* Bokermann, 1966; *T. coriaceus* (Peters, 1867); *T. dibernardoi* Kwet and Solé, 2008; *T. hadroceps* (Duellman and Hoogmoed, 1992); *T. imitatrix* (Miranda-Ribeiro, 1926); *T. jordani* (Stejneger and Test, 1891); *T. lepidus* (Pombal, Haddad and Cruz, 2003); *T. mambaiensis* Cintra, Silva, Silva, Garcia, and Zaher, 2009; *T. mesophaeus* (Hensel, 1867); *T. nigromaculatus* Tschudi, 1838; *T. resinificatrix* (Goeldi, 1907); and *T. typhonius* (Linnaeus, 1758).

Hyla hadroceps was described by Duellman and Hoogmoed (1992) based on a single male (KU 60720) collected in an “area north of Acarai Mountains, west of New River (ca. 02°N, 58°W), Rupununi District, Guyana”. Lescure and Marty (2000), despite the single vocal sac, transferred *Hyla hadroceps* to the genus *Phrynohyas* based on overall similarities; this was corroborated in a phylogenetic analysis using the mitochondrial ribosomal gene 12S by Guillaume et al. (2001), and posteriorly confirmed as part of *Trachycephalus sensu* Faivovich et al. (2005) in the most comprehensive phylogenetic analysis of Hylidae at that time. According to Ávila-Pires et al. (2010), *T. hadroceps* occurs in the Guiana region, north of the Amazon River.

The taxonomic study of *T. hadroceps* revealed a related population south of Amazon River. We describe this new species herein.

MATERIALS AND METHODS

Institutional abbreviations are in Sabaj Pérez (2010), except NHMW (Naturhistorisches Museum, Zoologische Abteilung, Wien, Austria) and QCAZ (Museo de Zoología, Pontificia Universidad Católica Del Ecuador, Quito, Ecuador). Additional specimens examined are presented in Material Examined section. We used 14 morphometric characters described in Duellman (2001), as modified by Napoli (2005): SVL (snout–vent length), HL (head length), HW (head width), ED (eye diameter), TD (tympanum diameter), UEW (upper eyelid width), IOD (interorbital distance), IND (internarial distance), END (eye–nostril distance), NSD (nostril to tip of snout distance), TL (tibia length), FL (foot length including tarsus), 3FD (third finger disk diameter), and 4TD (fourth toe disk diameter). The remaining measurements were TED (tympanum to eye distance: straight line distance between the anterior border of the tympanum and posterior corner of the eye), HAL (hand length: straight line distance between the wrist and the tip of the third finger), FAL (forearm length: straight line distance between the elbow and the wrist), and THL (thigh length; following Heyer et al., 1990). All measurements were taken with Vernier calipers (precision 0.05 mm) through an ocular micrometer in a Zeiss stereomicroscope. All measurements are in millimeters. Standards for dorsal outline and profile of the snout follow Heyer et al. (1990). Webbing formulae follow Savage and Heyer (1967) as modified by Myers and Duellman (1982).

The specimens used were diagnosed as adult males due to well-developed nuptial pads on inner margin of finger I and vocal slits.

Trachycephalus helioi, new species

Figures 1, 2, 3A

Holotype.—MPEG 32558, adult male, Brazil, Pará State, Juruti Municipality, Acampamento Mutum, 02°36'46.09"S, 56°11'38.53"W, approximately 80 m a.s.l., Marcelo Gordo, 15 January 2011.

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© 2013 by the American Society of Ichthyologists and Herpetologists DOI: 10.1643/CH-12-102

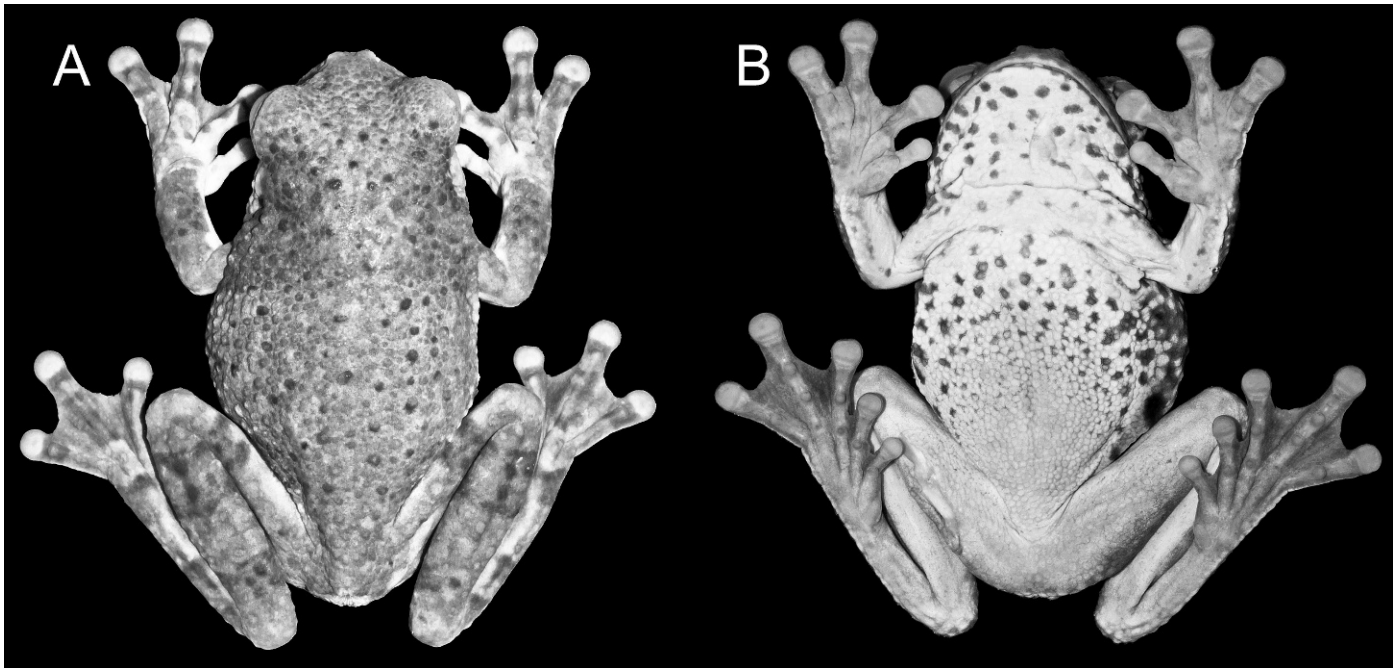


Fig. 1. Dorsal (A) and ventral (B) views of the holotype of *Trachycephalus helioi*, new species, MPEG 32558, SVL 57.6 mm.

Paratypes.—MNRJ 81611 (ex. MPEG 20506), MPEG 20507, adult males, Brazil, Pará State, Juruti Municipality, Barroso Farm, 02°27'53"S, 56°00'23"W, approximately 110 m a.s.l., Pablo Suárez, 8 March 2006.

Generic assignment.—To date, there is no identifiable morphological synapomorphy supporting the genus *Trachycephalus* (see Faivoich et al., 2005). We assign the new species to this genus based on overall similarity to the other species of *Trachycephalus*, mainly *T. hadroceps* (a species without lateralized vocal sac), which was diagnosed by molecular data (Faivoich et al., 2005).

Diagnosis.—A species of the genus *Trachycephalus* Tschudi, morphologically similar to *T. hadroceps*, diagnosed by the following combination of characters: male SVL 53.7–62.7 mm, head skin not co-ossified with the skull; skin on dorsum bearing many low and medium rounded tubercles; vocal sac not externally visible; well-developed paratoid glands; snout rounded in profile; third finger disc almost the same size of the eye; tibia longer than thigh; absence of tarsal fold; iris pinkish-beige with an horizontal dark gray bar; dorsal color pattern in life light brownish-orange with scattered brown dots.

Comparisons with other species.—*Trachycephalus helioi* is promptly distinguished from *T. atlas*, *T. jordani*, *T. mam-baiensis*, and *T. nigromaculatus* by the skin of the head not co-ossified with underlying dermal bones (co-ossified in these species). The fact that the vocal sac is not visible externally distinguishes *Trachycephalus helioi* from almost all species of the genus *Trachycephalus* (except *T. hadroceps*) that share a paired vocal sac that protrudes at a posterior angle to the jaw when inflated. *Trachycephalus helioi* can be distinguished from *T. hadroceps*, the most morphologically similar species, by the rounded snout in profile (vertical in *T. hadroceps*); well-developed paratoid gland (poorly developed in *T. hadroceps*); skin on the dorsum bearing many low and

small rounded tubercles (low and large in *T. hadroceps*); a larger 3FD/ED ratio (0.91–0.98% in *T. helioi* and 0.55–0.54% in *T. hadroceps*); tarsal fold being absent (present in *T. hadroceps*); iris pinkish-beige with an horizontal black bar (iris whitish-beige with a horizontal black bar and a vertical thin black line below the pupil, with a small black blotch in the upper pupil, in *T. hadroceps*); dorsal color pattern in life light brownish-orange with scattered brown dots (dorsum brown, with irregular darker brown markings and transversal bars in *T. hadroceps*; Duellman and Hoogmoed, 1992).

Description of holotype.—Body robust (Fig. 1); small size for the genus; head wider than longer; snout short, rounded in dorsal and profile views; nostrils dorsolateral, elliptical, protruded; *canthus rostralis* rounded, indistinct; loreal region slightly concave; eyes protuberant; tympanum visible, nearly circular; supratympanic fold developed, associated with the paratoid gland, from the posterior corner of the eye to the shoulder; vocal sac not visible externally (Fig. 1B, 2B); vocal slits laterally on mouth floor; tongue large, rounded, notched posteriorly, barely free; vomerine teeth in two straight series, below to the choanae; choanae oval. Arm slender, forearm moderately robust (Fig. 1A, B); axillary membrane extending about one half length of upper arm; fingers short; nuptial pad with dark-colored minute spines on the inner margin of metacarpal of the finger I; relative finger lengths $I < II < IV < III$; finger webbing formula $I2-2^{1/2}II1-2-III2-2IV$; discs of the finger nearly rounded and large-sized; disc of the finger I noticeably smaller than the others; dermal ridge along outer edge of toe IV, extending to the forearm; inner metacarpal tubercle single, elongated and elliptical; outer metacarpal tubercle divided in two rounded parts (poorly visible in Fig. 2C); subarticular tubercles single, rounded, except in the distal tubercle of the finger IV, which is bifid; supernumerary tubercles small and rounded (Fig. 2C). Pectoral fold present. Legs moderately slender (Fig. 1A, B); toes slender and long, relative lengths

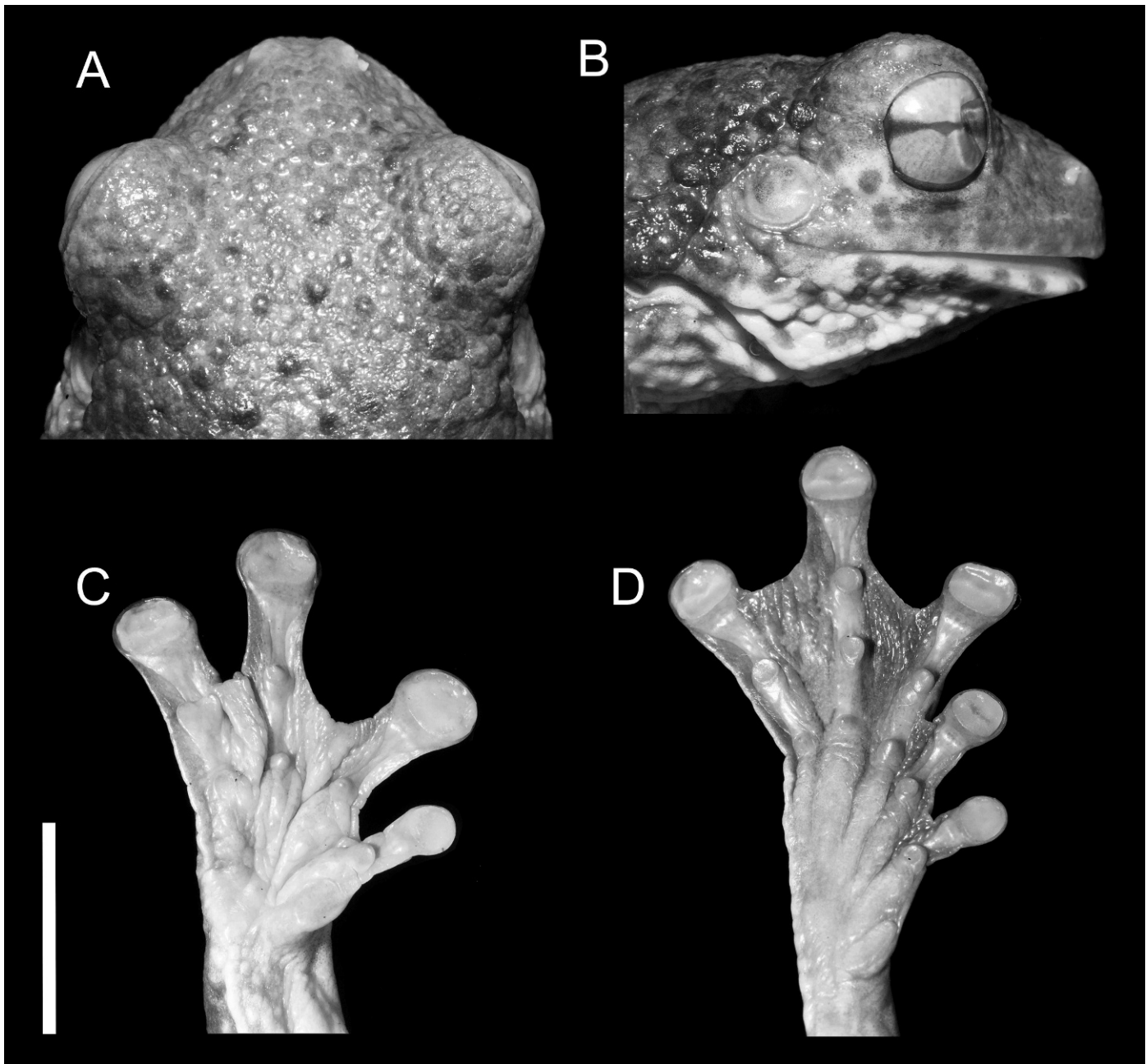


Fig. 2. Dorsal (A) and lateral (B) views of the head, hand (C) and foot (D) of the holotype of *Trachycephalus helioi*, new species, MPEG 32558. General scale = 10 mm.

$I < II < V \leq III < IV$; toe webbing formula $II^{1/2}-2III1-1^{1/2}III1-1^{1/2}IV1-1V$ (webbing folded between toes II and III in the Fig. 2D); toe discs nearly rounded, medium-sized; disc of the toe I much smaller than the others; dermal ridge along outer edge of toe V, extending to the tarsus; foot with inner medium-sized and single metatarsal tubercle, oval; outer metatarsal tubercle single, conic, and rounded (poorly visible in Fig. 2D); subarticular tubercles small, single and rounded; supernumerary tubercles single, small and rounded, present only on distal phalanges (Fig. 2D); tarsal fold, below to the toe I, absent. Cloacal opening directed posterodorsally, at upper level of thighs; some flat, irregular, tubercles scattered around and below cloacal opening. Dorsal skin with low and medium rounded tubercles; gular region, under surfaces of arms, and tibia regions smooth; skin on venter and inferior region of thigh strongly granulated.

Measurements of holotype (mm).—SVL 57.6; HL 19.0; HW 21.6; IND 5.0; NSD 2.8; END 5.4; UEW 7.0; ED 5.9; IOD 6.5; TD 3.9; TED 3.3; FAL 11.7; HAL 18.0; 3FD 3.6; THL 27.9; TL 28.6; FL 40.3; 4TD 3.3.

Color of holotype.—In life, dorsal color pattern, including limbs, light brownish-orange with scattered brown dots. Weak transversal brown bars on the limbs, one in the forearm and two in the thigh and tibia. A weak transversal thick dark bar on the top of the dorsum. Hidden surfaces of thighs and inguinal region beige. Ventral region beige, with few scattered brown dots. Iris pinkish-beige with a horizontal dark gray bar. In preservative, same pattern as described above, but colors faded, and the dark bar on the top of dorsum became more evident.



Fig. 3. (A) Living holotype of *Trachycephalus helioi*, new species, MPEG 32558, Municipality of Juruti, Pará State, and (B) specimen of *T. hadroceps*, Guyana, unvouchered photo by Walter Hödl.

Variation.—The specimens are alike with respect to their morphology. Measurements of two paratype males (females unknown) are as follows (MNRJ 81611–MPEG 20506, respectively): SVL 53.7–62.7; HL 18.9–20.7; HW 20.7–24.0; IND 4.8–5.4; NSD 2.5–3.2; END 4.9–5.7; UEW 7.2–7.4; ED 5.8–6.0; IOD 5.0–6.6; TD 3.8–4.3; TED 3.0–3.7; FAL 12.0–12.7; HAL 16.7–18.5; 3FD 3.4–4.2; THL 26.8–28.5; TL 27.6–29.8; FL 36.4–40.7; 4TD 3.0–3.8. The specimens vary in the intensity of the dark bars on dorsal region, including limbs, and paratype MNRJ 81611 has some irregular dark brown blotches on the dorsum.

Vocalization.—Not recorded.

Tadpole.—Unknown.

Habitat and natural history.—*Trachycephalus helioi* inhabits the canopy of the tropical rain forest of terra-firme (areas that are never flooded by rivers). Males call from trees, 5–25 m high, from evening until dawn. No amplexant pairs, clutches, or tadpoles have been observed. Considering the vocalization site and its similarity with *T. hadroceps* (see Lescure and Marty, 2000), we speculate that the new species might reproduce in water accumulated in tree cavities high in the trees. In the region of the type-locality the species is quite abundant and can be heard vocalizing during the rainy season. Its vocalization resembles the continuous barking of a dog. The collected specimens presented abundant glandular secretion when handled.

Distribution.—It is known only from few localities in the Municipality of Juruti, State of Pará, Brazil (Fig. 4).

Etymology.—The specific epithet is a patronym for a friend and colleague herpetologist Helio Ricardo da Silva, in recognition to his contributions to the study of amphibians.

Remarks.—The hypothesis of Amazon Basin rivers as geographic barriers to anuran species distributions has received mixed support by empirical information. Sometimes the species boundaries are coincident with allopatric distributions related to large rivers (Simões et al., 2008), sometimes not (Gascon et al., 1998). This theme has been discussed in the recent scientific literature to try to explain which process affects anurans' species distributions and diversification patterns (Simões et al., 2008; Kaefer et al., 2012). The presence of cryptic species only detectable by acoustic or genetic traits, for example, is pointed to as one of the reasons which contribute to this contradictory empirical

evidence (Simões et al., 2008; Kaefer et al., 2012). Despite the absence of larval and acoustic information, *Trachycephalus helioi* is perfectly distinguishable from *T. hadroceps* by its external morphology and color pattern. So they are similar, but not cryptic, and the Amazon River acting as a geographic barrier is a reasonable explanation. In addition, *Trachycephalus hadroceps* is nested within the most derived clade of the genus *Trachycephalus* as a sister taxon of '*T. typhonius* + *T. resinifictrix*' (Faivovich et al., 2005). Given this, the lack the external vocal sac seems to be a reversal condition through a re-establishment of an ancestral character state due to the loss of an evolutionary novelty (the putative *Trachycephalus* synapomorphy of presence of a paired vocal sac that protrudes at a posterior angle to the jaw when inflated; Faivovich et al., 2005). Thus, another species lacking a visible vocal sac here described should be the sister taxon of *T. hadroceps*, which demands further phylogenetic analysis.

MATERIAL EXAMINED

Additional specimens.—*Trachycephalus atlas*: Brazil, Bahia, Maracás: MZUSP 74304 (ex. WCAB 33669), holotype, 74169–74170, 74305; AMNH 76223–76225; MNRJ 4028, 14208–14209; USNM 164102–164103, paratopotypes.

Trachycephalus coriaceus: Brazil, Amazonas, Manaus: INPA 1609–1617. Ecuador, "Western Ecuador": BMNH 1947.2.13.75, holotype of *Hyla quadrangulum* Boulenger. Guyana, "East Berbice": USNM 566122. Surinam: ZMB 8507, 76887–76888 syntypes (by photo and notes).

Trachycephalus dibernardoi: Brazil, Paraná, Marumbi: MNRJ 55150–55151; Santa Catarina, São Bento do Sul: MNRJ 44419; Rio Grande do Sul, São Francisco de Paula: MCP 2422, holotype, 3693, 6063, 7213, paratopotypes; Machadinho: MCP 6584, paratype.

Trachycephalus hadroceps: Guyana, Rupununi District: KU 60720, holotype. French Guyana, Nature Reserve at Araya River: MNHN 1999.8601–1999.8603, 2000.5170.

Trachycephalus imitatrix: Brazil, Rio de Janeiro, Teresópolis: MNRJ 154, lectotype, 5129, paralectotype, 5130–5149, 51033–51034, 75336; MZUSP 108956, 108974–108975, topotypes; Itatiaia: MNRJ 55148.

Trachycephalus jordani: Ecuador, Guayas, Cerro Masvale: QCAZ 23460, 23471, 37339, 37341; Santiago de Guayaquil: USNM 12274, holotype, QCAZ 23414, 39328–39329, topotypes.

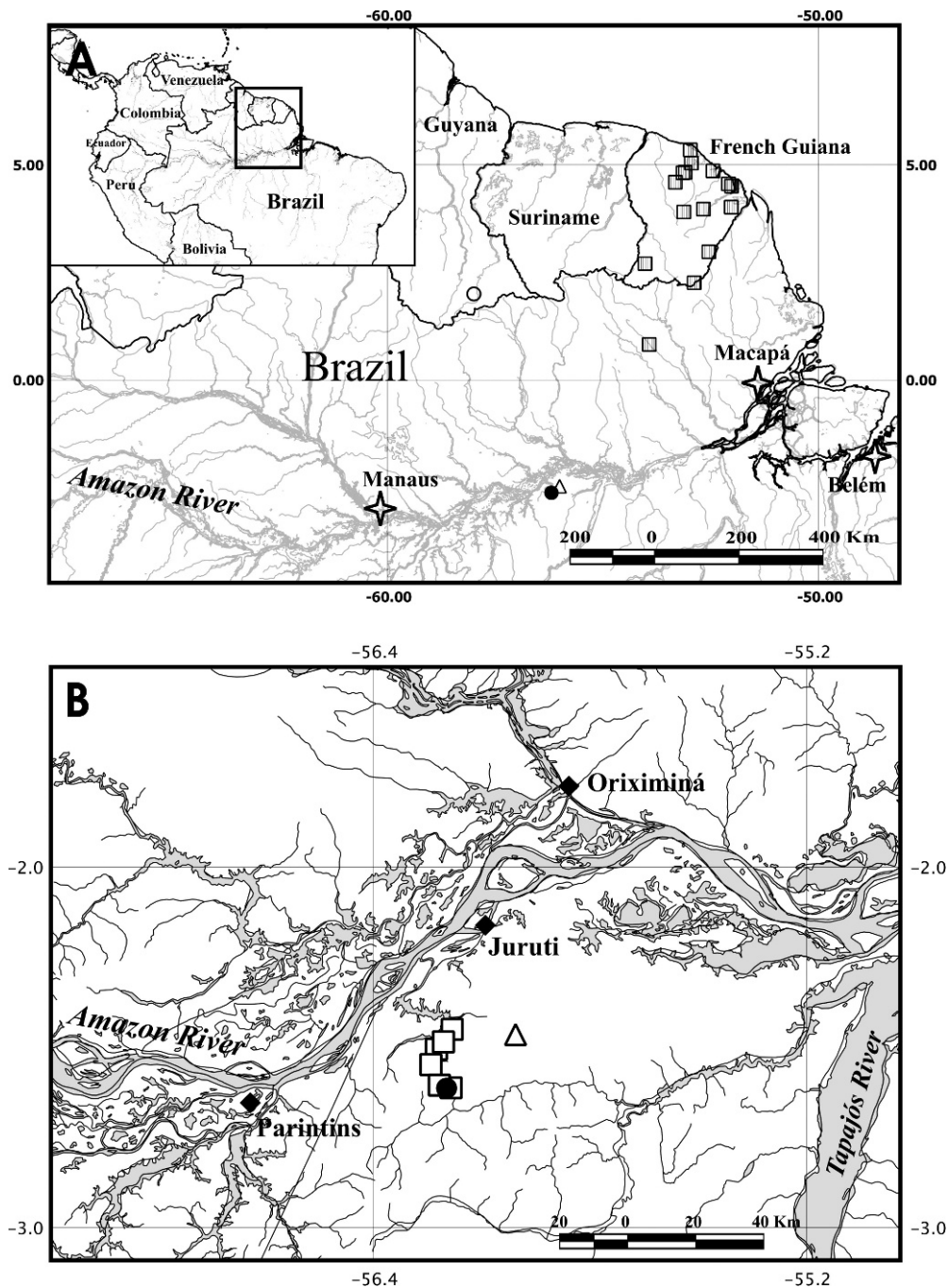


Fig. 4. (A) Map with known geographic distribution of *Trachycephalus helioi*, new species, and *T. hadroceps* in the Amazonian Rain Forest and Guyana Shield. Captions for *Trachycephalus hadroceps*: holotype = open circle, literature records = dashed squares; captions for *T. helioi*, new species: holotype = closed circle, paratypes = triangles. (B) Detailed map of the geographic distribution of *T. helioi*, new species. Captions: holotype = closed circle, paratypes = triangles, open squares = sound recordings.

Trachycephalus lepidus: Brazil, São Paulo, Capão Bonito: MNRJ 17464, holotype; São Miguel Arcanjo: MZUSP 136548–136551.

Trachycephalus mambaiensis: Brazil, Goiás, Mambai: MZUSP 135715, holotype, 135714, 135716–135717, paratopotypes.

Trachycephalus mesophaeus: Brazil, Rio Grande do Sul, Porto Alegre: ZMB 6810 Holotype (by photo and notes); Santa Catarina, Humboldt: AMNH 15519–15526; Joinville: MNRJ 1602, 2102, 2116, 10646, 13331–13335; Santa Luzia: MNRJ 3102, 3510, 44418.

Trachycephalus nigromaculatus: Brazil, Rio de Janeiro, Rio de Janeiro: AMNH 17412, 78244, MNRJ 241, 245, 1843, 2111, 2536, 3092, 3742, 74838. South America: MNHN 4608–4609, syntypes (by photo and notes).

Trachycephalus resinifictrix: Brazil, Amazonas, Manaus: MNRJ 74126, MZUSP 57345, 60119–60122, 69929–69931, 84541; Pará, Oriximiná: MNRJ 47916, 48579, “Mission of San Antonio do Prata, at the River Maracanã”: BMNH 1947.2.23.24, holotype.

Trachycephalus typhonius: Argentina, Misiones, Eldorado: MACN 2854, 2901, 3000, 3513–3519, 3929, 4144–4145,

4172, 4309, 5685, 27898–27900. Brazil, “Amazon River”: BMNH 1936.3.12.119, lectotype of *Hyla lichenosa*; Pará, Santarém: NHMW 19013, holotype of *Hyla wettsteini* (by photo and notes), NHMW 16503, holotype of *Hyla zernyi* (by photo and notes); Rondônia, “banks of Branco River, a sub-tributary of Madeira River”: MNRJ 4054, holotype of *Hyla adenoderma*. Bolivia, Santa Cruz: AMNH 34070–34071, 39552, 39557, 144500–144501, NRM 2049, holotype of *Hyla palpebrogranulata* (by photo and notes), USNM 280993, 281772–281777, 346463. Ecuador, Montalvo: MNRJ 55221, Pastaza: NRM 1958, holotype of *Hyla macrotis* (by photo and notes), USNM 165981–165986. Guatemala, Escuintla: AMNH 74377–74390, 101053–101110. Guyana, East Berbice: USNM 566123; East Demerara: USNM 162939–162941; Georgetown: MCZ 2618; Northwest District: USNM 164179; no further locality data: UMMZ 55834, 80495. México, Chiapas, Acacoyagua: USNM 115013, holotype of *Acrodytes modesta*, USNM 115010–115012, 115015–115025, paratypes of *Acrodytes modesta*; Guerrero, La Venta: FMNH 100046, holotype of *Acrodytes inflata*; Nayarit, “4.8 miles east of San Blas”: UIMNH 67060, holotype of *Phrynohyas corasterias*; Sinaloa, Presidio: BMNH 83.2.7.1, holotype of *Phrynohyas latifasciata*; Veracruz, no specific locality data: USNM 38264–38265, 38303, 114980–115008; no further locality data: BMNH 59.9.20.2, 81.10.31.20, syntypes of *Hyla nigropunctata*. Paraguay, Assunción: USNM 5837, holotype of *Scytotis hebes*, 341195–341199, MNRJ 151, 2880, topotypes of *Scytotis hebes*. Peru, Pevás, Apiaçu: MNRJ 2531; Madre de Dios, Puerto Maldonado: USNM 247254–247258, 247615–247617; Pucallpa: ZFMK 29993, holotype of *Argenteohyla altamazonica*. Surinam, Paramaribo: UUZM 134, holotype (by photo and notes), MCZ 7662, topotype; no further locality data: USNM 13820–13821, 14618. Venezuela, Zulía, Pueblo Nuevo: UMMZ 55570, holotype of *Phrynohyas ingens*, 55567–55569, paratypes of *Phrynohyas ingens*.

ACKNOWLEDGMENTS

This study is part of the Ph.D. thesis of the senior author. We are grateful to D. Frost (AMNH), M. Wilkinson and G. Bittencourt (BMNH), A. Resetar and H. Voris (FMNH), R. Vogt (INPA), R. Brown (KU), J. Faivovich (MACN), G. Pontes (MCP), J. Losos and J. Rosado (MCZ), A. Ohler (MNHN), A. Prudente (MPEG), H. Zaher (MZUSP), L. Coloma and S. Ron (QCAZ), C. Phillips (UIMNH), R. Nussbaum (UMMZ), and W. Ronald Heyer (USNM) for loans or allowing us to examine specimens under their care; B. Clarke and C. McCarthy (BMNH), A. Ohler (MNHN), G. Heinz (NHMW), S. Kullander and B. Kajrup (NRM), H. Mejlön (UZZM), D. Rödder (ZFMK), and M.-O. Rödel and F. Tillack (ZMB) for the photos and notes on the specimens under their care; W. Hödl (University of Vienna, Austria) for the photo of the living specimen of *Trachycephalus hadroceps*; M. Mesquita for the assistance with the Figure 1; J. Faivovich (MACN) for the careful review of the manuscript; C. Gascon for the English review (National Fish and Wildlife Foundation, USA), and W. Jennings (Humboldt State University, USA; Museu Nacional, Brazil) for English comments; IN and JPPJ acknowledge Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ); IN acknowledges Smithsonian Institution (Washington, D.C., USA) for fellowship and support; MG acknowledges MPEG and ALCOA for field support, S. Neckel-Oliveira for

his coordination of the project at the Juruti site, and L. Frazão for help in the field; PS thanks CNPq, Museu Paraense Emílio Goeldi (MPEG), and Universidade Federal do Pará (UFPA) for financial support, and F. Pimenta, A. Lima, and A. Bahia Gomes for field and/or laboratory support.

LITERATURE CITED

- Ávila-Pires, T. C. S., M. S. Hoogmoed, and W. A. Rocha. 2010. Notes on the vertebrates of northern Pará, Brazil: a forgotten part of the Guianan Region, I. Herpetofauna. Boletim do Museu Paraense Emílio Goeldi, Ciências Naturais 5:13–112.
- Duellman, W. E. 2001. The Hylid Frogs of Middle America. Second edition. Society for the Study of Amphibians and Reptiles, Ithaca, New York.
- Duellman, W. E., and M. S. Hoogmoed. 1992. Some hylid frogs from the Guiana Highlands, Northeastern South America: new species, distributional records and generic reallocation. Occasional Papers of the Museum of Natural History, The University of Kansas 147:1–21.
- Faivovich, J., C. F. B. Haddad, P. C. A. Garcia, D. R. Frost, J. A. Campbell, and W. C. Wheeler. 2005. Systematic review of the frog family Hylidae, with special reference to Hylinae: phylogenetic analysis and taxonomic revision. Bulletin of the American Museum of Natural History 294:1–240.
- Frost, D. R. 2013. Amphibian Species of the World: an Online Reference. V5.6 (9 January 2013). Available at: <http://research.amnh.org/herpetology/amphibia/index.html>, American Museum of Natural History, New York. Accessed on 6 March 2013.
- Gascon, C., S. C. Loughheed, and J. P. Bogart. 1998. Patterns of genetic population differentiation in four species of Amazonian frogs: a test of the riverine barrier hypothesis. Biotropica 30:104–119.
- Guillaume, C. P., P. Gaucher, and F. M. Catzeflis. 2001. Does *Hyla hadroceps* belong to the genus *Phrynohyas* (Hylidae: Batrachia)? First approach using the mitochondrial gene 12S, rRNA. 11th ordinary general meeting of Societas Europaea Herpetologica (SEH), Zalec, Slovenia, 13–17 VII 2001. Summary in Biota 2(suppl.):68–69.
- Heyer, W. R., A. S. Rand, C. A. G. Cruz, O. L. Peixoto, and C. E. Nelson. 1990. Frogs of Boracéia. Arquivos de Zoologia 31:231–410.
- Kaefer, I. L., B. M. Tsuji-Nishikido, and A. P. Lima. 2012. Beyond the river: underlying determinants of population acoustic signal variability in Amazonian direct-developing *Allobates* (Anura: Dendrobatoidea). Acta Ethologica 15: 187–194.
- Kwet, A., and M. Solé. 2008. A new species of *Trachycephalus* (Anura: Hylidae) from the Atlantic Rain Forest in southern Brazil. Zootaxa 1947:53–67.
- Lavilla, E. O., J. A. Langone, J. M. Padial, and R. O. de Sá. 2010. The identity of the crackling, luminescent frog of Suriname (*Rana typhonia* Linnaeus, 1758) (Amphibia, Anura). Zootaxa 2671:17–30.
- Lescure, J., and C. Marty. 2000. Atlas des Amphibiens de Guyane. Publications Scientifiques du Muséum national d'Histoire naturelle, Paris.
- Myers, C. W., and W. E. Duellman. 1982. A new species of *Hyla* from Cerro Colorado, and other tree-frog records and geographical notes from Western Panama. American Museum Novitates 2752:1–32.

- Napoli, M. F.** 2005. A new species allied to *Hyla circumdata* (Anura: Hylidae) from Serra da Mantiqueira, Southeastern Brazil. *Herpetologica* 61:63–69.
- Sabaj Pérez, M. H. (ed.).** 2010. Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an online reference. Version 2.0 (8 November 2010). Available at: <http://www.asih.org/>, American Society of Ichthyologists and Herpetologists, Washington, D.C. Accessed on 15 November 2010.
- Savage, J. M., and W. R. Heyer.** 1967. Variation and distribution in tree frogs genus *Phyllomedusa* in Costa Rica, Central America. *Beiträge zur neotropischen Fauna* 5:111–131.
- Simões, P. I., A. P. Lima, and W. E. Magnusson.** 2008. Acoustic and morphological differentiation in the frog *Allobates femoralis*: relationships with the upper Madeira River and other potential geological barriers. *Biotropica* 40:607–614.
- Trueb, L., and W. E. Duellman.** 1971. A synopsis of Neotropical hylid frogs, genus *Osteocephalus*. Occasional Papers of the Museum of Natural History, The University of Kansas 1:1–47.
- Tyler, M. J.** 1971. The phylogenetic significance of vocal sac structure in hylid frogs. Occasional Papers of the Museum of Natural History, The University of Kansas 19:319–360.
- Wiens, J. J., C. A. Kuczynski, X. Hua, and D. S. Moen.** 2010. An expanded phylogeny of treefrogs (Hylidae) based on nuclear and mitochondrial sequence data. *Molecular Phylogenetics and Evolution* 55:871–882.