Zootaxa 5219 (4): 388–396
https://www.mapress.com/zt/

Correspondence

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)
https://doi.org/10.11646/zootaxa.5219.4.6
http://zoobank.org/urn:lsid:zoobank.org:pub:0A28ED7F-EA9C-4093-B2BB-F6AC318D8085

The tadpole of *Hylodes perere* Silva & Benmaman 2008 (Anura: Hylodidae)

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The Neotropical frog family Hylodidae comprises 46 species endemic to the Atlantic Forest whose local distribution is predominantly associated with undisturbed montane and submontane habitats in Brazil and Argentina (Frost 2021). *Hylodes* Fitzinger, the most diverse hylodid genus, contains 26 species informally known as "torrent-frogs" due to obligatory association with fast-flowing streams and creeks in which the adults breed and the tadpoles develop (e.g., Malagoli *et al.* 2017). Despite standing out among anurans by exhibiting diurnal habit and sophisticated visual signaling displays that include foot-flagging and either synchronized or independent movements of vocal sacs (de Sá *et al.* 2016), the total number of species recognized in *Hylodes* remains fairly underestimated. Specifically, 65% of the known diversity in the genus (17 spp.) was described in the last fifty years (Frost 2021) and molecular evidence suggests that at least eight cryptic lineages await formal taxonomic treatment (Montesinos 2017).

Adding to the difficulty of identifying *Hylodes* species posed by the broadly conserved phenotypes of adults, the lack of adequate sampling of specimens makes the identification of putative diagnostic traits cumbersome. Recent research suggests that the incorporation of new sources of phenotypic evidence—such as the larval morphology—into the systematics of *Hylodes* (and Hylodidae as a whole) should help clarify species boundaries (Montesinos 2017). Although some authors have argued that *Hylodes* tadpoles are taxonomically uninformative due to exhibiting a supposedly conservative body plan (e.g., Sazima & Bokermann 1982; Malagoli *et al.* 2020), significant variation in larval morphology has been increasingly identified across species (e.g., Wassersug & Heyer 1988; Pombal *et al.* 2002).

Despite the fact that 21 out of 26 *Hylodes* species have their tadpoles described, the lack of material of certain larval stages and/or inadequate or incomplete descriptions hinder a successful identification of some tadpoles. The body size, shape, and color patterns of *Hylodes* larvae have been overemphasized in some studies to the detriment of internal anatomical structures. Thirteen of the 21 descriptions of *Hylodes* tadpoles published to date included descriptions of the internal oral anatomy (Weber & Caramaschi 2013; Nogueira-Costa *et al.* 2019). Herein, we describe the external body and buccopharyngeal morphology of the tadpole of *H. perere* Silva and Benmaman, representing the 22nd formally described *Hylodes* tadpole, and compare it to all known larval forms in the genus. Additionally, we comment on the phylogenetic significance of some larval characters to the systematics of Hylodidae.

We analyzed 63 tadpoles of *Hylodes perere* from the Municipality of Santa Bárbara do Monte Verde, State of Minas Gerais, Brazil, housed in the Coleção Herpetológica da Universidade Federal Rural do Rio de Janeiro, Seropédica, RU (63 tadpoles between Stages 25–29; Appendix 1). For comparison, we analyzed 476 tadpoles representing 18 *Hylodes* species, housed in the following institutions: Coleção de Anfíbios Célio Fernando Baptista Haddad (CFBH, UNESP, Rio Claro), Coleção de Anfíbios da UNESP de São José do Rio Preto (DZSJRP, São José do Rio Preto), Coleção Herpetológica da Universidade Federal de Minas Gerais (UFMG, Belo Horizonte), Coleção Herpetológica da Universidade Federal

 Accepted by F. Candioti: 27 Oct. 2022; published: 12 Dec. 2022

Rural do Rio de Janeiro (RU, Seropédica), Coleção Herpetológica do Museu Nacional do Rio de Janeiro (MNRJ, Rio de Janeiro), and Coleção Herpetológica do Museu de Zoologia da Universidade de São Paulo (MZUSP, São Paulo) (Appendix 1). Only *H. caete, H. regius* and *H. pipilans* were compared using information exclusively obtained from the literature (Nogueira-Costa *et al.* 2019; de Sá *et al.* 2020; Malagoli *et al*. 2020).

Specimens were staged (Gosner 1960) and 17 measurements were taken with a caliper to the nearest 0.1 mm: total length (TL), body length (BL), body width at the level of spiracle (BW), head width at the level of eyes (HW), body height (BH), internarial distance (IND), interorbital distance (IOD), eye diameter (ED), eye–naris distance (END), naris–snout distance (NSD), snout–spiracle distance (SSD), tail height (TAH), upper tail fin height (UTF), lower tail fin height (LTF), tail muscle height at base of tail (TMH), tail muscle width at base of tail (TMW), and oral disc width (ODW). Measurements followed Kok & Kalamandeen (2008), and terminology followed Altig & McDiarmid (1999) and Kok & Kalamandeen (2008). Descriptions of the lateral line system followed Schlosser (2002).

For the study of the buccopharyngeal anatomy, two tadpoles (Gosner Stages 34–35; RU 2463) were dissected according to Wassersug (1976) and, after inspection under stereomicroscope, one individual was submitted to the protocol of Alcade & Blotto (2006) for scanning electron microscopy (SEM). The terminology adopted for description of buccopharyngeal structures is detailed in Wassersug (1976).

Tadpole description (Fig. 1A–F and Table 1). Body oval in dorsal, ventral, and lateral views, wider posteriorly, wider than tall (BH/BW = 0.87 ± 0.09). Snout rounded. Eyes rounded, dorsal, diameter equals to roughly 21% of head width (ED/HW = 0.21 ± 0.01), approximately 63% of interorbital distance (ED/IOD = 0.63 ± 0.08), and approximately the same width as eye–nostril distance (ED/END = 1.05 ± 0.11); iris black. Nostrils rounded, dorsolateral, closer to eyes than to snout (END/NSD = 0.65 ± 0.08), dorsal region swollen, rim pigmented forming a black ring, complete or not. Interorbital distance shorter than internasal distance (IOD/IND = 0.82 ± 0.08). Medio-ventral depression anterior to the convoluted intestine present (Fig. 1B: ch. 1). Spiracle sinistral, positioned in the middle third and bottom half of the body (SSD/BL = 0.59 ± 0.02), oriented posterodorsally, translucent or with opening white. Four pairs of lateral lines (post-infra-orbital and post-supra-orbital lines present) forming the anterior lateral line system. Three pairs of lateral lines (oral divided from the beginning in an anterior sinuous line parallel to the infraorbital line and a longitudinal line descending ventrally) forming the posterior lateral line system. Fusion of medial and dorsal lateral lines varies between caudal myomeres 11 and 12 or 12 and 13. Stitches rounded, arranged in continuous lines. Two pairs of white spots on the ventral and ventrolateral surfaces of the body; one pair of spots anteroventrally, near the medio-ventral depression. Vent tube short, dextral, opening extending beyond the inferior portion of the external wall, attached to the ventral margin of fin. Tail taller than body (TAH/BH = 1.15 ± 0.20). Body approximately one third and tail approximately two thirds of the total length (BL/TL = 0.36 ± 0.02). Caudal musculature robust, tapering gradually to become pointed, approximately more than half of tail height (TMH/TAH = 0.56 ± 0.05). Dorsal fin originating exactly at the posterior limit of the body, approximately 55% taller than ventral fin (UTF/LTF = 1.55 ± 0.28). Tail muscle width approximately 43% of body width (TMW/BW = 0.43 ± 0.08). Oral disc directed ventrally, diameter about 50% of head width at eye level (ODW/HW = 0.50 ± 0.05), emarginate laterally, bordered by one row of papillae along the anterior lip, interrupted in great extension, and one row of alternate papillae along the posterior lip, short row of submarginal papillae ascending and descending laterally at the corner of the anterior and posterior lip (Fig. 1E: ch. 2), respectively. Labial tooth row formula 2(2)/3(1); A1 = A2, P1 = P2 > P3; A2 gap small. Jaw sheaths strongly developed, fully keratinized, serrated (Fig. 1E: ch. 3); anterior jaw sheath arched in inverted "V", smooth lateral processes, posterior jaw sheath V-shaped. Pre-oral region with dark brown blotches. In preservative, dorsum and flanks brown, dark blotches randomly distributed, in lower numbers on the flanks. A pair of dark brown blotches between nostrils and pre-orbital lateral line. Ventral surface cream, translucent, nacreous, immaculate. Tail muscle light brown, dark brown blotches randomly distributed all over, dark brown stripe extending dorsally until the first third of the tail, sometimes interrupted, reaching up to two thirds of the tail. Fins cream, translucent, with dark brown blotches, ventral fin with fewer and smaller blotches.

Buccopharyngeal anatomy (Fig. 1G, H). Buccal floor triangular, larger at the caudal end. Two pairs of infralabial papillae; first pair (from medial to lateral) tall, conical, and covered with pustulations; second pair hand-like, with four branches, covered with pustulations. Lingual bud elliptical; single pair of lingual papillae long, finger-like. Buccal floor arena elliptical, lateral region with 22–25 short, conical papillae; papilla at the same level as the buccal pocket branched; prepocket papillae present, 6–7, short, conical. Buccal floor arena covered with rounded and conical pustulations (>300); pustulation denser on posterior half; few (10–11) conical papillae scattered over the posterior arena. Buccal pockets deep, oblique, slit-shaped. Ventral velum present; spicular support conspicuous; marginal projections present, parallel to filter plates; three projections on medial area long, triangular; medial notch present, well-marked. Secretory pits evident and

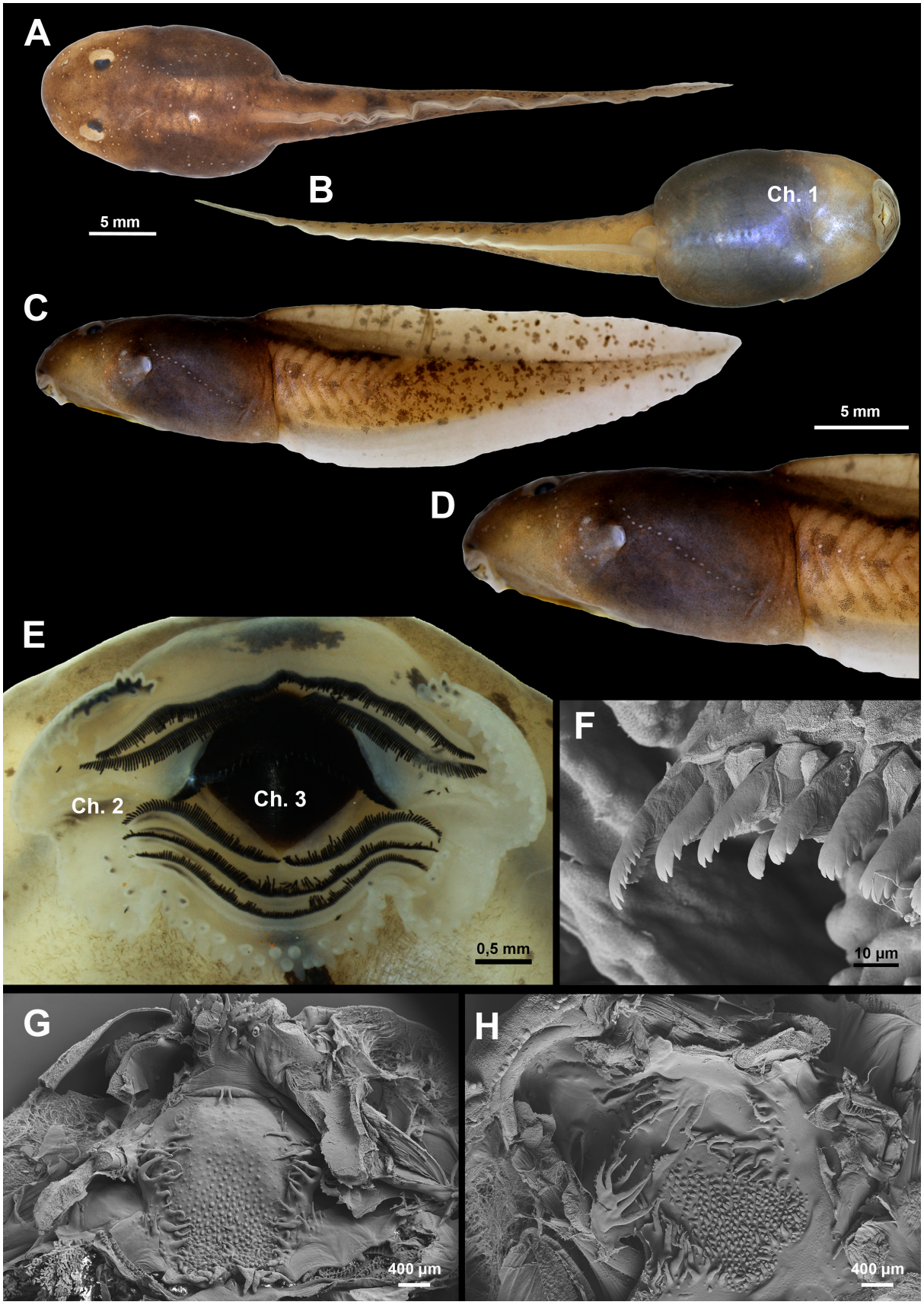

FIGURE 1. Tadpole of *Hylodes perere*. (A) dorsal view, (B) ventral view, (C) lateral view, (D) head detail showing the lateral line system, (E) oral disc, (F) labial tooth detail, (G) buccal floor, (H) buccal roof. Putative synapomorphies are represented by ch. 1 (medio-ventral body depression), ch. 2 (submarginal papillae in dorsolateral and ventrolateral areas of the oral disc), and ch. 3 (strongly keratinized jaw sheaths).

TABLE 1. Mean ± standard deviation (mm) of 17 measurements of tadpoles of *Hylodes*.

Species	TL	BL	BW	HW	BH	IND	IOD	ED	END	NSD	SSD	TAL	UTF	LTF	TMH	TMW	ODW
H. amnicola	51.99	19.45	12.45	10.85	10.26	3.80	4.24	2.13	1.78	3.27	11.23	11.92	4.30	3.19	6.53	4.65	4.41
n = 2	± 0.62	± 0.59	± 1.15	± 0.37	± 0.25	± 0.03	± 0.38	± 0.03	± 0.15	± 0.22	± 0.62	± 2.57	± 0.48	± 0.59	± 0.21	± 0.32	± 0.04
H. asper	40.87	13.46	7.94	7.10	6.10	3.20	2.33	1.73	1.57	2.38	8.62	7.58	2.04	1.60	4.44	3.85	3.35
n = 17	± 9.45	± 2.84	± 1.99	± 1.74	± 1.49	± 0.91	± 0.83	± 0.35	± 0.44	± 0.66	± 1.88	± 2.22	± 0.57	± 0.33	± 1.77	± 1.62	± 0.87
H. babax	31.47	10.69	6.50	5.14	4.89	2.25	2.25	1.09	1.04	1.79	6.48	6.66	2.13	1.78	3.16	2.51	2.61
n = 12	± 8.99	± 2.84	± 1.77	± 1.54	± 1.16	± 0.58	± 0.62	± 0.32	± 0.31	± 0.43	± 1.64	± 2.04	± 0.69	± 0.47	± 1.38	± 0.93	± 0.64
H. charadranaetes	45.25	15.20	9.30	7.83	6.17	3.36	3.05	1.64	1.45	2.60	9.14	9.08	2.73	2.24	4.98	4.26	3.79
n = 8	± 9.58	± 3.24	± 1.77	± 1.58	± 1.41	± 0.61	± 0.58	± 0.29	± 0.28	± 0.54	± 1.87	± 2.22	± 0.64	± 0.48	± 1.32	± 1.22	± 0.77
H. dactylocinus	46.98	15.21	8.57	7.92	6.43	3.30	3.76	1.83	1.46	2.66	9.61	8.94	2.82	2.33	4.96	4.12	4.67
n = 11	± 5.80	± 1.92	± 1.52	± 1.19	± 0.98	± 0.44	± 0.66	± 0.24	± 0.19	± 0.37	± 1.21	± 1.58	± 0.57	± 0.42	± 0.96	± 0.85	± 0.79
H. fredi	47.63	15.20	7.89	6.86	6.41	2.78	2.37	1.41	1.46	2.07	8.42	6.55	1.59	1.15	4.64	4.20	3.56
n = 5	± 14.80	± 4.47	± 2.86	± 2.74	± 2.17	± 0.70	± 0.53	± 0.37	± 0.50	± 0.64	± 2.72	± 2.40	± 0.86	± 0.69	± 1.75	± 1.72	± 0.97
H. heyeri	45.29	16.38	10.22	8.54	7.55	3.37	3.50	1.75	1.74	2.27	9.95	9.76	3.12	2.50	5.37	4.50	4.26
n = 15	± 7.18	± 2.54	± 2.28	± 1.56	± 1.70	± 0.42	± 0.84	± 0.27	± 0.38	± 0.36	± 1.72	± 2.43	± 0.72	± 0.48	± 1.44	± 1.10	± 0.71
H. japi	47.60	16.76	9.11	8.11	7.08	3.57	3.24	1.59	1.63	2.65	9.42	9.21	2.99	2.00	4.80	4.53	4.13
n = 3	± 4.91	± 1.23	± 0.45	± 0.32	± 0.43	± 0.05	± 0.17	± 0.13	± 0.27	± 0.05	± 0.58	± 1.76	± 0.12	± 0.18	± 0.48	± 0.72	± 0.33
H. lateristrigatus	49.22	15.92	9.73	8.08	6.21	3.46	3.58	1.63	1.66	2.90	9.49	9.74	2.73	2.36	5.20	4.43	3.72
n = 12	± 8.06	± 2.61	± 1.71	± 1.42	± 1.06	± 0.57	± 0.86	± 0.33	± 0.32	± 0.45	± 1.66	± 1.83	± 0.50	± 0.33	± 1.12	± 1.02	± 0.64
H. magalhaesi	43.45	16.02	10.16	8.23	7.96	3.13	2.62	1.69	1.76	2.11	9.00	8.72	3.00	2.13	4.98	3.73	4.30
n = 4	± 15.61	± 5.27	± 3.24	± 2.67	± 2.66	± 1.05	± 0.97	± 0.62	± 0.55	± 0.77	± 2.78	± 2.56	± 0.74	± 0.44	± 2.34	± 1.56	± 1.50
H. meridionalis	63.13	23.48	13.40	11.43	9.80	4.30	5.97	2.50	2.85	3.62	12.99	11.65	3.46	2.72	7.18	6.73	6.49
n = 8	± 7.04	± 2.50	± 1.95	± 1.62	± 1.41	± 0.47	± 0.93	± 0.41	± 0.59	± 0.44	± 1.28	± 1.66	± 0.43	0.47	± 0.90	± 1.17	± 0.80
H. nasus	56.35	19.17	10.12	9.41	7.13	3.99	3.22	2.03	1.96	3.56	11.60	9.48	2.68	2.20	5.68	5.47	4.75
n = 19	± 5.52	± 2.51	± 1.76	± 1.39	± 1.76	± 0.50	± 0.48	± 0.23	± 0.30	± 0.53	± 1.59	± 1.31	± 0.39	± 0.25	± 1.09	± 0.98	± 0.66
H. ornatus	22.97	8.06	4.61	4.14	3.43	1.65	1.55	0.89	0.95	1.51	4.83	4.15	1.17	0.97	2.56	2.54	2.07
n = 5	± 28.91	± 9.62	± 4.77	± 4.57	± 3.21	± 2.02	± 1.47	± 0.99	± 0.89	± 1.78	± 5.87	± 4.61	± 1.31	± 1.07	± 2.71	± 2.53	± 2.32
H. otavioi	42.62	13.42	7.57	6.89	5.81	3.04	2.57	1.49	1.40	2.19	7.81	8.67	2.73	2.15	4.47	3.52	3.06
n = 3	± 3.97	± 1.00	± 0.59	± 0.28	± 0.56	± 0.30	± 0.18	± 0.17	± 0.08	± 0.24	± 0.47	± 0.88	± 0.28	± 0.37	± 0.46	± 0.26	± 0.26

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TABLE 1. (Continued)

Species	TL	BL	BW	HW	BH	IND	IOD	ED	END	NSD	SSD	TAL	UTF	LTF	TMH	TMW	ODW
H. perere	**46.97**	**17.00**	**10.55**	**8.47**	**9.11**	**3.46**	**2.86**	**1.80**	**1.73**	**2.68**	**9.97**	**10.57**	**3.44**	**2.28**	**5.86**	**4.65**	**4.30**
n = 24	**± 8.02**	**± 2.47**	**± 1.57**	**± 1.35**	**± 1.23**	**± 0.47**	**± 0.52**	**± 0.33**	**± 0.31**	**± 0.48**	**± 1.45**	**± 2.55**	**± 0.79**	**± 0.65**	**± 1.44**	**± 1.37**	**± 0.92**
H. perplicatus	36.77	14.47	9.01	7.24	6.56	2.70	1.93	1.74	1.50	2.29	8.37	7.29	2.67	1.85	3.37	2.97	3.44
n = 4	± 5.58	± 2.56	± 2.05	± 1.34	± 1.49	± 0.17	± 0.15	± 0.42	± 0.18	± 0.45	± 1.49	± 1.07	± 0.56	± 0.27	± 0.64	± 0.59	± 0.42
H. phyllodes	39.73	13.36	7.16	6.48	4.86	2.92	2.20	1.37	1.45	2.45	7.94	6.55	1.88	1.55	3.61	3.23	3.11
n = 12	± 5.43	± 1.73	± 0.90	± 0.91	± 0.56	± 0.43	± 0.53	± 0.25	± 0.23	± 0.35	± 1.12	± 0.82	± 0.26	± 0.33	± 0.58	± 0.60	± 0.45
H. sazimai	47.92	16.35	10.10	8.30	7.26	3.25	2.63	2.02	1.62	2.42	9.30	9.83	3.16	2.30	5.95	5.01	3.93
n = 3	± 7.85	± 2.31	± 1.60	± 1.09	± 1.41	± 0.41	± 0.62	± 0.32	± 0.29	± 0.30	± 1.15	± 2.52	± 0.72	± 0.35	± 1.63	± 1.39	± 0.89
H. uai	48.87	16.12	10.30	7.92	7.31	3.36	3.06	1.79	1.60	2.59	9.44	10.69	3.41	2.57	5.89	5.01	3.97
n = 17	± 10.35	± 3.15	± 1.97	± 1.45	± 1.62	± 0.66	± 0.57	± 0.32	± 0.31	± 0.47	± 1.69	± 2.08	± 0.62	± 0.38	± 1.46	± 1.39	± 0.66

abundant on the velar surface; secretory ridges present. Glottis fully exposed. Branchial basket triangular, wider than long, about 1/4 of buccal length and 1/2 of buccal width. Three filter cavities, shallow, partially covered by ventral velum.

Buccal roof elliptical with prenarial arena oval. Prenarial papilla absent. Internal nares elliptical, transversely oriented regarding the longitudinal axis; posterior valve free, with low, conical projection. Postnarial arena diamond-shaped, with six conical, pustulated, postnarial papilla. Lateral ridge papillae hand-like, with five conical branches. Median ridge short, triangular, with irregular, pustulated apex. Buccal roof arena triangular, bordered with 14–16 papillae on each side; buccal arena covered with rounded and triangular pustulations (>200); few, conical papillae scattered posteriorly. Lateral roof papillae present, 6–7. Glandular zone well-defined; secretory pits large, evident. Dorsal velum arch-shaped, medially interrupted.

Comparison with other species. The tadpole of *Hylodes perere* differs from *H. asper*, *H. caete*, *H. fredi*, *H. nasus*, *H. phyllodes*, *H. pipilans*, and *H. sazimai* by presenting an oval body in dorsal view (oboval in *H. asper*; elliptical in *H. caete, H. fredi,* and *H. pipilans*; and slightly oval or elliptical in *H. nasus*, *H. phyllodes*, and *H. sazimai*). It further differs from *H. amnicola*, *H. perplicatus, H. fredi*, *H. pipilans, H. meridionalis*, and *H. regius* by the dorsal fin originating exactly at the posterior limit of the body (originating before the final portion of the body in *H. amnicola* and *H. perplicatus,* and after the final portion of the body in *H. fredi, H. pipilans, H. meridionalis,* and *H. regius*). *Hylodes perere* differs from *H. dactylocinus* by presenting rounded snout (slightly truncate), and from *H. amnicola*, *H. charadranaetes*, *H. fredi*, and *H. phyllodes* by presenting a complete black ring on the nostril (absent). *Hylodes perere* differs from *H. asper* and *H. magalhaesi* by lacking ornamentation on the nostril (leaf-shaped in *H. asper* and crenate in *H. magalhaesi*), and from *H. babax, H. charadranaetes, H. dactylocinus, H. fredi, H. heyeri, H. lateristrigatus, H. magalhaesi, H. meridionalis, H. nasus, H. otavioi, H. phyllodes, H. sazimai,* and *H. uai* by presenting rounded stitches forming the lateral lines (dashed).

Morphometrically, *H. perere* differs from all congeneric species, except *H. fredi*, by presenting a dorsal fin twice as higher as the ventral fin (UTF/LTF = 1.55 ± 0.28 in *H. perere*; UTF/LTF = 1.52 ± 0.49 in *H. fredi*; <1.50 in all other species). It differs from *H. fredi* by presenting fins higher than body (TAH/BH = 1.15 ± 0.20 in *H. perere*; TAH/BH = 1.02 ± 0.08 in *H. fredi*). *Hylodes perere* differs from *H. amnicola*, *H. dactylocinus*, *H. heyeri*, *H. lateristrigatus*, *H. meridionalis,* and *H. regius* by exhibiting interorbital distance narrower than internasal distance (IOD/IND = 0.82 ± 0.08 in *H. perere*; IOD/IND = 1.12 ± 0.09 in *H. amnicola*; IOD/IND = 1.14 ± 0.11 in *H. dactylocinus*; IOD/IND = 1.03 ± 0.13 in *H. heyeri* and *H. lateristrigatus*, IOD/IND = 1.39 ± 0.14 in *H. meridionalis*; IOD/IND = 1.42 in *H. regius*).

The buccopharyngeal morphology of *H. perere* differs from *H. dactylocinus* in exhibiting a medial notch (absent). *Hylodes perere* differs from *H. heyeri*, *H. magalhaesi*, *H. ornatus*, and *H. sazimai* by having a triangular median ridge (half-circle in *H. heyeri*, circular in *H. magalhesi*, irregular in *H. ornatus*, and trapezoidal in *H. sazimai*). *Hylodes perere* is also distinguished by having a higher number (22–25) of papillae on the buccal floor arena than *H. dactylocinus* (18–20), *H. heyeri* (20), *H. lateristrigatus* (14–18), *H. magalhaesi* (15–20), and *H. sazimai* (16–18), and lower number of papillae than *H. asper* (28), *H. charadranaetes* (27–30), and *H. pipilans* (28–30). *Hylodes perere* is finally differentiated by showing a higher number (14–16) of papillae on the buccal roof arena than *H. heyeri* (11–12), *H. pipilans* (8–10) and *H. uai* (11–12), and lower number of papillae than *H. asper* (18–21) and *H. phyllodes* (17–19).

Remarks. *Hylodes* species are restricted to mountain streams of the Atlantic Forest, rarely occur in sympatry, and are easily distinguished from non-hylodid anurans by exhibiting a medio-ventral depression anterior to the convoluted intestine (Haddad & Pombal 1995; Fig. 1B: ch. 1). This chracter state is also present *in Crossodactylus* and *Megaelosia* (Montesinos 2017), but *Hylodes* tadpoles can be differentiated by lacking medial emarginations on the lower lip (the presence of such emarginations is likely a synapomorphy of *Crossodactylus*; P.H.D. pers.obs.) and by its size (considered giant in *Megaelosia* species; e.g. Sichieri *et al.* 2020).

The larvae of 21 out of the 26 recognized *Hylodes* species have already been formally described morphologically, a proportion without correspondence in most anuran groups. However, several species comparisons (especially those supported by meager morphological descriptions) were based in great part or exclusively on information from the literature. Consequently, misleading or inaccurate comparisons and diagnoses containing errors and inconsistencies continue to be propagated. The primary examination of larval specimens and broad taxonomic scope of our comparisons allowed us to identify presumably informative characters that deserve further investigation in a cladistic framework. Hylodidae is part of a larger clade called Neoaustrarana and it is sister to Alsodidae (*Limnomedusa* + (*Alsodes* + *Eupsophus*)); direct comparison with tadpoles from that clade suggested putative synapomorphies for hylodids. The majority of hylodids present submarginal papillae in dorsolateral and ventrolateral areas of the oral disc. The distribution of these papillae in Alsodidae (present in some *Alsodes* but absent in *Eupsophus* and *Limnomedusa*; Barrasso *et al.* 2016; Vera Candioti *et al.* 2011; PHD pers. obs.) renders this character a putative synapomorphy for Hylodidae (Fig. 1E: ch. 2). All hylodid larvae

have strongly keratinized jaw sheaths (Fig. 1E: ch. 3), as do the tadpoles of *Limnomedusa* (PHD pers. obs.) which could render the optimization of this character ambiguous. Nevertheless, the upper jaw sheath of all hylodids has an inverted V shape, not observed in other closely related taxa, representing another putative synapomorphy for the family. We suggest these characters be added to the list of putative larval synapomorphies of Hylodidae, in addition to the medio-ventral body depression anterior to the convoluted intestine (Haddad & Pombal 1995; Pombal *et al*. 2002; Fig. 1B: ch. 1) and the presence of the m. *rectus abdominis* anterior (Dias *et al*. 2021). Further studies incorporating larval characters into phylogenetic analyses of Hylodidae are likely to uncover new synapomorphies for the family.

We thank Célio F.B. Haddad, Carlos F.D. Rocha, Denise Rossa-Feres, Felipe Toledo, Hussan D. Zaher, José P. Pombal Jr., and Paulo C.A. Garcia for granting access to specimens housed in the herpetological collections under their care. We are in debt to two reviewers for critically reviewing the manuscript; however, any mistakes are our responsibility. RM thanks the Brazilian Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (PNPD/CAPES 88882.316078/2019-01). PHD thanks the Marie Sklodowska-Curie Actions (MSCA-IF-2020, MEGAN; 101030742).

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Appendix 1. Examined material.

Hylodes perere: Serra Negra, Municipality of Santa Bárbara do Monte Verde, State of Minas Gerais, Brazil (21°57’49.2” S, 43°48’15” W, 1117 m): six tadpoles stage 25, one tadpole stage 26, one tadpole stage 27: RU 2187; two tadpoles stage 25, two tadpoles stage 26, two tadpoles stage 27, three tadpoles stage 28, one tadpole stage 29: RU 2455; twenty one tadpoles stage 25, two tadpoles stage 26, five tadpoles stage 27, one tadpole stage 28: RU 2463; seven tadpoles stage 25, one tadpole stage 27: RU 7077; eight tadpoles stage 25: RU 7180.

Hylodes amnicola: Parque Estadual do Ibitipoca, Municipality of Lima Duarte, State of Minas Gerais, Brazil (21°42’44” S, 43°53’48” W): MNRJ 24862, MNRJ 24999.

Hylodes asper: Mazomba, Municipality of Itaguaí, State of Rio de Janeiro, Brazil (22°52’27.1” S, 43°54’53.8” W): RU 7271; Barreira, above of Soberbo river, Municipality of Guapimirim, State of Rio de Janeiro, Brazil: MNRJ 35037–40, MNRJ 35042; Garrafão river, Municipality of Teresópolis, State of Rio de Janeiro, Brazil: MNRJ 44560; Sítio Dona Ana, Barreira, Municipality of Guapimirim, State of Rio de Janeiro, Brazil: MNRJ 44561.

Hylodes babax: FLOE Uaimií, Municipality of Ouro Preto, State of Minas Gerais, Brazil: UFV 222.

Hylodes charadranaetes: Theodoro de Oliveira, Municipality of Nova Friburgo, State of Rio de Janeiro, Brazil: MNRJ 67517.

Hylodes dactylocinus: Estação Ecológica da Juréia–Itatins, State of São Paulo, Brazil: MZUSP 129280–81; Estação Ecológica da Juréia–Itatins, Praia do Guaraú, Municipality of Peruíbe, State of São Paulo, Brazil: MZUSP 129282–83.

Hylodes fredi: Ilha Grande, Municipality of Angra dos Reis, State of Rio de Janeiro, Brazil: RU 7464.

Hylodes heyeri: Serro e Gemido, Municipality of São José dos Pinhais, State of Paraná, Brazil (25º41' S, 49º03' W): DZSJRP 902.1; Ilha do Cardoso, Municipality of Cananéia, State of São Paulo, Brazil: CFBH 9057.

Hylodes japi: Região da Ermida, Serra do Japi, Municipality of Jundiaí, State of São Paulo, Brazil (23° 13´40" S, 46° 57´59" W): CFBH 33864.

Hylodes lateristrigatus: São Lourenço, Municipality of Santa Teresa, State of Espírito Santo, Brazil (19˚55’28,7” S; 40˚37’25.6” W): MNRJ 35056.

Hylodes magalhaesi: Monte Verde, Municipality of Camanducaia, State of Minas Gerais, Brazil: CFBH 8287–88; Municipality of Campos do Jordão, State of São Paulo, Brazil: CFBH 10128, CFBH 25076, MNRJ 35051.

Hylodes meridionalis: Municipality of Treviso, State of Santa Catarina, Brazil: CFBH 11078; Municipality of São Francisco de Paula, State of Rio Grande do Sul, Brazil: CFBH 12134; Serra do Rio do Rastro, Municipality of Lauro Müller, State of Santa Catarina, Brazil: CFBH 12135; Municipality of Praia Grande, State of Santa Catarina, Brazil: CFBH 21148.

Hylodes nasus: Serra do Barata, Realengo, Municipality of Rio de Janeiro, State of Rio de Janeiro, Brazil: MNRJ 2027; Floresta da Tijuca, Municipality of Rio de Janeiro, State of Rio de Janeiro, Brazil: MNRJ 29206–07, MNRJ 30276–77, MNRJ 35054, MNRJ 74735; Cachoeira do Horto Botânico, Floresta da Tijuca, Municipality of Rio de Janeiro, State of Rio de Janeiro, Brazil: MNRJ 38362, MNRJ 43719, MNRJ 53443; Parque Nacional da Tijuca (Bom Retiro), Municipality of Rio de Janeiro, State of Rio de Janeiro, Brazil: MNRJ 74438; Estrada D. Castorina Flor, Tijuca, Municipality of Rio de Janeiro, State of Rio de Janeiro, Brazil: MNRJ 74722–34.

Hylodes ornatus: Riacho antes do brejo da Lapa, Municipality of Itamontes, State of Minas Gerais, Brazil: MNRJ 35053.

Hylodes otavioi: Serra do Cipó Km 126, State of Minas Gerais, Brazil: CFBH 9065.

Hylodes perplicatus: Municipality of São Bento do Sul, State of Santa Catarina, Brazil: CFBH 12137; Estrada Rio–Natal, Corupá, near the Vermelho River, Municipality of São Bento do Sul, State of Santa Catarina, Brazil: MNRJ 30338.

Hylodes phyllodes: Municipality of São Luís do Paraitinga, State of São Paulo, Brazil: CFBH 12161; Riacho na beira da Estrada que liga Lídice a Angra dos Reis, Lídice, Municipality of Rio Claro, State of Rio de Janeiro, Brazil: MNRJ 35034; Estrada para a cachoeira da Dona Carmem, Lídice, Municipality of Rio Claro, State of Rio de Janeiro, Brazil: MNRJ 35035; Picinguaba, Municipality of Ubatuba, State of São Paulo, Brazil: MNRJ 35036; Trilha a direita da praia Cassandoquinha, Municipality of Ubatuba, State of São Paulo, Brazil: MNRJ 40169.

Hylodes sazimai: Observatório de Capricórnio, Joaquim Egídio, Municipality of Campinas, State of São Paulo, Brazil: CFBH 9043, CFBH 25077, MNRJ 35080.

Hylodes uai: Municipality of Itabirito, State of Minas Gerais, Brazil: UFMG 1026a, 1026b, UFMG 1023c.