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Review of the Rare Genus *Phrynomedusa* Miranda-Ribeiro, 1923 (Anura: Phyllomedusidae) With Description of a New Species

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Abstract: We present the first taxonomic review of the genus *Phrynomedusa* since its description with diagnoses of the genus and species. We present a broad literature review of the genus and provide updates and remarks about the type series, tadpoles, calls, geographic distribution, and natural history of the species of *Phrynomedusa*. Additionally we describe a new species from município de São Luiz do Paraitinga, state of São Paulo, Brazil. *Phrynomedusa dryade* was initially identified as *Phrynomedusa marginata*; however, an integrated analysis of morphological and molecular characters enabled its recognition as a separate new species. For the first time, the advertisement call for one species of *Phrynomedusa* is described in detail. We describe the tadpole and present some field notes about the activity and biology of this new species.

Key words: Atlantic Forest; *Phrynomedusa dryade* sp. nov.; Tadpole; Taxonomy; Vocalization

Miranda-Ribeiro (1923) described *Phrynomedusa* to accommodate a new species of the family Phyllomedusidae Günther, 1858 *Phrynomedusa fimbriata*, whose characteristics did not allow it to be placed in any other phyllomedusine genus known at the time. Subsequent to Miranda-Ribeiro (1923), some authors did not recognize *Phrynomedusa* as valid and placed *P. fimbriata* as incertae sedis (B. Lutz 1950) or allocated it to the synonymy of *Phyllomedusa* (Cochran 1955; Funkhouser 1957; Duellman 1968). Cochran (1955) included *Phrynomedusa fimbriata* in the synonymy of *Phyllomedusa appendiculata* A. Lutz, 1925—not following the priority principle of the International Code of Zoological Nomenclature (Art. 23.1; International Commission on Zoological Nomenclature 1999). Besides the exception made by Cochran (1955), subsequent authors consider *P. appendiculata* a synonymy of *P. fimbriata* (Funkhouser 1957; Duellman 1968; Izecksohn and Cruz 1976; Cruz 1982). Cruz (1985) recognized *P. appendiculata* as a distinct species of *P. fimbriata*. Thereafter, Cruz (1990) resurrected *Phrynomedusa* to include *P. fimbriata*, *P. appendiculata*, and *Phrynomedusa marginata* and described two new species (Cruz 1991). At present, the genus contains five species distributed throughout southeastern and southern Brazil (Frost 2016): *P. fimbriata* Miranda-Ribeiro, 1923, *P. appendiculata* (A. Lutz, 1925), *P. marginata* (Izecksohn and Cruz, 1976), *Phrynomedusa bokermanni* Cruz, 1991, and *Phrynomedusa vanzolinii* Cruz, 1991.

With the exception of *Phrynomedusa appendiculata* and *P. marginata*, all other species of *Phrynomedusa* are known only from their type series. The absence of records for these species over the years has resulted in *P. fimbriata* being recognized as the first anuran to be considered extinct in Brazil (Cruz and Pimenta 2004). Moreover, very little information about the natural history of these Treefrogs is known, being restricted to the articles by A. Lutz and B. Lutz (1939) for *P. vanzolinii* (as *P. appendiculata*) and Weygoldt (1984, 1991) for captive specimens of *P. marginata*.

Recently, new specimens associated with *P. marginata* were discovered at Núcleo Santa Vírgínia, Parque Estadual da Serra do Mar, município de São Luiz do Paraitinga, state of São Paulo, Brazil. These newly discovered specimens are very similar to *P. marginata*; however, combinations of morphological and genetic characters distinguish the new specimens from all species of *Phrynomedusa* including *P. marginata*. Herein we provide a taxomic revision of the genus *Phrynomedusa*, describing for the first time the advertisement call, recorded in its natural habitat, of a species of *Phrynomedusa* which had previously been known only from captive specimens (Weygoldt 1991). We also describe the tadpoles of the new species and compare them with tadpoles of *P. marginata* and *P. vanzolinii* (the only species that have known tadpoles). Lastly, we provide some remarks on the conservation of these Monkey Frogs.

Material and Methods

Specimens Examined

To perform a diagnosis of *Phrynomedusa* and compare it with others family members we examined representatives of each genus of Phyllomedusidae. The examined specimens are listed in the Appendix and the institutional abbreviations follow Sabaj Pérez (2014).

Morphological Characters Analyzed

We collected nine mensural characters using the methods previously described by Duellman (2001), with the definitions of Watters et al. (2016). These measurements (in mm) of adults were obtained with the aid of a Mitutoyo™ digital caliper (precision 0.01) under a Zeiss™ Stemi SV-11 stereomicroscope and include snout–vent length (SVL, direct line distance from tip of snout to posterior margin of vent), head length (straight line from posterior of jaws to the tip of snout), head width (straight line at the widest point; angle at the jaws), internarial distance (shortest distance between the inner margins of nostrils), interorbital distance

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(shortest distance between the anterior corners of orbits), eye diameter (greatest horizontal distance from anterior to posterior corner of eye), eye–nostril distance (straight line from anterior corner of eye to posterior margin of nostril), tympanum diameter (greatest horizontal width of tympanum), tibia length (straight line from the knee to calcar), and foot length (straight line from the base of inner metatarsal tubercle to tip of Toe IV). Our format for webbing formulae is that of Savage and Heyer (1967), with modifications by Savage and Heyer (1997). Like most anuran systematists, we number the fingers from I to IV, even though Fabrezi and Alberch (1996) showed that the first digit was lost in frogs relative to other lissamphibians. The sex of specimens was determined by the observation of secondary sexual characteristics of males (nuptial pads, vocal slits, and expansion of vocal sacs). Illustrations were made with a drawing tube attached to a Zeiss™ Stemi SV-11 stereomicroscope. Descriptions of color and patterns are based on photographs taken in the field and field notes from Luís Olímpio Menta Giasson for the new species or on photographs and original descriptions for the others.

To verify the occurrence of Pterorhodin pigment (Taylor and Bagnara 1969; Bagnara et al. 1973), we made a quick-chemical test for the presence of this red pigment. In the course of the studies of anuran pigments, were verified that the melanins are insoluble in 0.1 N NaOH and that pterorhodin is highly soluble in this base (Bagnara et al. 1973; Bagnara and Ferris 1975). When placed in 0.1 N NaOH, pieces of fresh or preserved phyllomeduside skins will immediately release a cloud of the red pigment that changes to a yellow pigment within 30 min. Thus, to verify the presence of pterorhodin, we put a small piece of skin in a solution of NaOH and observed the reaction.

The description of tadpole external morphology is based on a tadpole in Stage 36 of Gosner (1960). Tadpoles were collected from a pond where the holotype was collected in the Núcleo Santa Virgínia and Núcleo Curucutu at Parque Estadual da Serra do Mar, municípios de São Luiz do Paraitinga and Itanhaém (respectively), state of São Paulo, Brazil, and fixed and preserved in 5% formalin (CFBH 29573–29574, 36926, 38056). The identity of tadpoles was confirmed by comparison of 16s mitochondrial DNA of adults and tadpoles. Measurements and terminology followed the proposal of Altig and McDiarmid (1999a) for total length (direct line distance from tip of snout to posterior tip of tail), body length (direct line distance from tip of snout to body terminus), tail length (direct line distance from body terminus to absolute tail tip), maximum tail height (greatest vertical distance from dorsal to ventral fin margins), internarial distance (shortest distance between the inner margins of nostrils), interorbital distance (shortest distance between the anterior corners of orbits), tail muscle width (greatest transversal distance of tail musculature measure at anterior margin of tail), and tail muscle height (vertical distance from the junction of the body wall with the ventral margin of the tail muscle to dorsal margin of tail musculature), Lavilla and Scrocchi (1986) for body width (greatest transversal distance of body), body height (greatest vertical distance of body measured from dorsal to ventral margins of body), eye–snout distance (straight line from anterior corner of eye to tip of snout), eye–nostril distance (straight line from anterior corner of eye to posterior margin of nostril), nostril–snout distance (straight line from anterior corner of nostril to tip of snout), eye diameter (greatest distance from anterior to posterior corner of eye), and oral disc width (greatest transversal distance from oral disc margins). All measurements were taken with an ocular micrometer fitted to a Zeiss™ Stemi SV-11 stereomicroscope. Terminology for the lateral line system follows Lannoo (1987). Morphological characteristics of known tadpoles of *Phrynomedusa* were obtained from A. Lutz and B. Lutz (1939), Izeckshon and Cruz (1976), Cruz (1982, 1990), and Heyer et al. (1990).

Acoustic Parameters

Vocalizations of four males were recorded at Núcleo Santa Virgínia, Parque Estadual da Serra do Mar, município de São Luiz do Paraitinga, state of São Paulo, Brazil (18 October 2004, air temperature 17°C at 2200 h; 18 November 2004, air temperature 17.5°C at 2230 h; 1 October 2005, air temperature 16°C, water temperature 18°C, at 2215 h and 16°C at 2225 h). Voucher specimens (CFBH 7613, 7684, 7722, 16026) and recordings of vocalizations of Luis Menta Giasson (VLMG 66–67, 71) are deposited in the CFBH collection. Recordings of advertisement calls were made with a Marantz PMD222 professional recorder with a Sennheiser System K6 directional microphone.

Recordings were digitized at a resolution of 16 bit and a 44100-Hz sampling rate. Spectrograms, waveforms, and all measurements were made using Raven Pro (v1.3, Cornell Lab of Ornithology, Ithaca, NY), configured with a Fast Fourier Transformation window of 256 samples; the Hann algorithm. Time grid parameters selected were Overlap 94.9% and Hop Size 13 samples. The frequency grid parameters selected were Discrete Fourier Transformation size = 256 samples and Grid Spacing = 172 Hz. In order to measure the upper and lower limits of the frequency band on the spectrogram, the options Brightness and Contrast were adjusted to 55% and 95%, respectively. The parameters measured were note duration (s), interval between sequential notes (s), number of pulses, pulse duration (s), pulse rate (pulses/s), interval between pulse amplitude peaks (s), lower limit of the frequency band (Hz), upper limit of the frequency band (Hz), and dominant frequency (Hz). The definition of the acoustic parameter "note" follows McLister et al. (1995) in which a note is the total amount of sound energy generated during a single airflow cycle (for a discussion about advantages of this approach see Robillard et al. 2006 and Orrico et al. 2009). Field observations of the movement of the vocal sac during vocalization made adopting this definition easy. The definition of pulse and its measures follow Littlejohn (2001), with the exceptions that herein "pulse period" refers to the interval between the upper limits of amplitude from the pulse, and pulse duration was measured from the first visible wave to the last visible wave of the pulse in the baseline. The same procedures were adopted for measuring other temporal acoustic parameters. The definition of dominant frequency follows Heyer et al. (1990).

Remarks on the Genus *Phrynomedusa*

In his revision of the Phyllomedusinae from the Atlantic Forest, Cruz (1990) presented an extensive definition of *Phrynomedusa* and made some taxonomic considerations in relation to other genera of the family. Subsequently,

Table 1.—Selected measurements (in mm) from adult male and female *Phrynomedusa dryade* from Núcleo Santa Virgínia, Parque Estadual da Serra do Mar, município de São Luiz do Paraitinga, São Paulo, Brazil (with accession numbers from the Celio F.B. Haddad Collection [CFBH]).

	Male					Female
Measurements	CFBH 16026	CFBH 7613	CFBH 7684	CFBH 7716	CFBH 7722	CFBH 16025
Snout–vent length	30.9	28.4	29.5	31.4	31.7	36.1
Head length	10.9	9.7	11.2	11.7	11.4	13.7
Head width	10.4	10.4	10.6	10.9	10.9	13.2
Internarial distance	3.1	2.8	2.9	2.9	3.2	3.1
Interorbital distance	3.3	4.2	3.8	4.1	3.9	5.5
Eye diameter	3.2	3.2	3.4	3.1	3.1	3.5
Eye–nostril distance	2.8	2.7	2.3	2.9	2.9	2.9
Tympanum diameter	1.6	1.2	1.4	1.4	1.4	1.5
Tibia length	14.7	13.7	13.8	15.5	14.5	17.5
Foot length	11.6	12.1	11.1	13.2	12.7	14.9

Caramaschi and Cruz (2002) characterized the family Hylidae and its subfamilies and also presented definitions of the subfamily Phyllomedusinae (a hylid subfamily at this time) and its then-recognized genera: *Agalychnis*, *Hylomantis*, *Pachymedusa*, *Phasmahyla*, *Phrynomedusa*, and *Phyllomedusa*.

Some of the traits included in these definitions of *Phrynomedusa* are shared with other Phyllomedusidae and so do not help in diagnosing *Phrynomedusa*. Due to recent advances in understanding the systematics of Phyllomedusidae (e.g., Faivovich et al. 2005, 2010; Pyron and Wiens 2011), new, more-precise morphological diagnoses are needed for its genera. Therefore, we present here a reappraisal of the diagnosis of the genus *Phrynomedusa* with some remarks about the species that belong to this genus.

Phrynomedusa Miranda-Ribeiro, 1923
(Tables 1, 2; Figs. 1–12)

Phrynomedusa Miranda-Ribeiro, 1923: Miranda-Ribeiro (1923:3–5), species description; Miranda-Ribeiro (1926:63, 105–106 [his Fig. 62]); A. Lutz and B. Lutz (1939:219–221, 223, Plate VIII [their Fig. 3]); Bokermann (1966:81–83); Izecksohn and Cruz (1976:261); Cruz (1982:148); Weygoldt (1984:250); Cruz (1990:711, 713 [his Figs. 3, 4], 715 [his Figs. 8, 11], 718–724 [his Figs. 14, 19]), revalidated; Cruz (1991:271–275); Duellman (1993:110); Duellman and Trueb (1994:539); De La Riva (1999:123); Duellman (1999:269, 309 [his Appendix 5]); Altig and McDiarmid (1999b:311); McDiarmid and Altig (1999:13 [their Table 2.2]); Caramaschi and Cruz (2002:6–8, 10 [their Appendix 1]); Cruz and Caramaschi (2004:e.T55826A11374546 [IUCN Red List website]); Cruz and Carvalho-e-Silva (2004:e.T55828A11375261 [IUCN Red List website]) in part; Cruz and Pimenta (2004:e.T17078A6797217 [IUCN Red List website]); Garcia et al. (2004:e.T55825A11374203 [IUCN Red List website]); Faivovich et al. (2005:19, 112–116); Haddad and Prado (2005:209 [their Box 1], 216); Pimenta et al. (2005:supporting information [their Table S3 and Appendix S2–S3]); Cruz and Feio (2007:118, 123); Gasparini et al. (2007:76, 78, 80 [their Table 6.1], 86–87 [their Photo], 133 [their Appendix]); Pombal and Haddad (2007:109 [their Box 1]); Wiens et al. (2005:720 [their Table 1], 733 [their Fig. 5], 737 [their Fig. 8], their Appendix 3–5); Barrio-Amóros (2006:56); Caramaschi (2006:159–160); Wiens et al. (2006: supporting information [11, his Fig. A1; 26, his Table A2]); Carvalho-e-Silva et al. (2007:476); Wells (2007:478); Haddad (2008:290 [his Table2], 291 [his Table 3], 303–304); Haddad et al. (2008:155); Nunes and Fagundes (2008:22); Garcia et al. (2009:331, 333–334 [their Table 10], 346); Moen and Wiens (2009: supporting information [their Fig. A1]); Moen et al. (2009: supporting information [19, their Fig. S1]); Cruz and Carvalho-e-Silva (2010:e.T55827A11374868 [IUCN Red List website]); Faivovich et al. (2010:227–231 [their Figs. 1, 2B–D], 233–236 [their Fig. 4], 244–247 [their Fig. 6], 249, 251–252, 261 [their Appendix 3]); Araújo et al. (2010:201 [their Table 1], 208); Pontes et al. (2010:161); Almeida et al. (2011:544, 547 [their Table 2], 557 [their Fig. 3H], 559 [their Appendix 1]); Faivovich et al. (2011:355 [their Fig. 1], 357–358, their supporting information); Pyron and Wiens (2011:568 [their Fig. 2], their Appendix B.3 [481], their supporting information); Rossa-Feres et al. (2011:52 [their Table 1]); Luna et al. (2012:714 [their Table 1], 716–720 [their Figs. 2A, 3B, 4C], 722, their supporting information); Rivera-Correa et al. (2013:89 [their Fig. 1], 100 [their Appendix II]); Haddad et al. (2013:379); Barth et al. (2014:795); Borteiro et al. (2014:393); Segalla et al. (2014:44); Silva et al. (2014:5, supporting information [their Data S1 and Appendix S4]); Toledo et al. (2014:59 [their Fig. 3], supporting information [their Tables A1, A2]); Trevine et al. (2014:130 [their Table 1], 140, 146 [their Appendix 1]); Vilela et al. (2014:716); Machado et al. (2015:467); Wan et al. (2015:5182); Duellman et al. (2016:9 [their Fig. 2], 16 [their Fig. 4], 49 [their Fig. 17], 51, 91 [their Appendix 1], 108 [their Appendix1]); Ruiz-Monachesi et al. (2016:557); IUCN (2016: Red List website); Duellman et al. (2016:9 [their Fig. 2], 16 [their Fig. 4], 49 [their Fig. 17], 51, 91 [their Appendix 1], 108 [their Appendix 1]).

Phyllomedusa Wagler, 1830: A. Lutz (1925:137); A. Lutz (1926:8, 15); A. Lutz and B. Lutz (1939:219–221, 223–224, 236–238, 253, 259–260, 262–263, Plate I [their Fig. 4], Plate III [their Figs. 1–7], Plate IV [their Figs. 5, 6], Plate VII [their Figs. 5, 6]), in part; B. Lutz (1950:600–601 [her Table I], 618–619 [her Table I], in part [incertae sedis, consider a possible *Agalychnis*]); Cochran (1955: frontispiece, 196–198, Plate 18 [her Figs. J, K]), in part; Funkhouser (1957:8 [her Fig. 7], 11 [her Map 2], 14, 20, 27–28, 70 [her Fig. 15]), in part; Cochran (1961:70); Bokermann (1966:82); Duellman (1968:5–8), in part; Izecksohn and Cruz (1976:257–261); Tyler (1971:326

TABLE 2.—Selected morphometric characters (range [mean ± standard deviation]) in mm for of tadpoles of *Phrynomedusa dryade* from Núcleo Santa Virgínia, Parque Estadual da Serra do Mar, município de São Luiz do Paraitinga, São Paulo, Brazil. Developmental stages 25–39 (Gosner 1960).

Stage	25 ($n = 1$)	26 ($n = 3$)	27 ($n = 2$)	28 ($n = 2$)	31 ($n = 1$)	33 ($n = 1$)	34 ($n = 1$)	35 ($n = 2$)	36 ($n = 1$)	37 ($n = 1$)	39 ($n = 1$)
Total length	21.8	21.9–23.9 (22.8 ± 1.0)	21.5–24.0 (22.7 ± 1.8)	26.4–28.0 (27.2 ± 1.1)	34.4	45.5	37.3	44.0–44.2 (44.1 ± 0.1)	46.9	49.8	39.1
Body length	8.1	7.4–8.7 (8 ± 0.7)	7.9–8.1 (8 ± 0.1)	9.2–9.4 (9.3 ± 0.1)	11.3	14.7	13.1	15.2–18.5 (16.9 ± 2.3)	15.6	16.6	14.0
Body height	4.4	3.8–4.3 (4.0 ± 0.3)	4.0–4.3 (4.2 ± 0.2)	4.4–4.9 (4.7 ± 0.4)	6.1	8.6	7.8	6.5–9.4 (8 ± 2.1)	8.8	9.6	8.0
Body width	4.4	4.4–4.8 (4.6 ± 0.2)	4.3–4.4 (4.4 ± 0.2)	4.7–5.4 (5.1 ± 0.5)	6.5	8.2	8.2	6.7–9.1 (7.9 ± 1.7)	9.7	10.1	8.2
Tail length	13.8	13.9–16.5 (14.8 ± 1.4)	13.6–15.9 (14.8 ± 1.6)	17.2–18.6 (17.9 ± 1.0)	23.1	30.8	24.2	25.7–28.8 (27.3 ± 2.2)	31.3	33.2	25
Maximum tail height	4.3	3.7–7.3 (5.1 ± 1.9)	4.2–4.4 (4.3 ± 0.1)	4.2–5.0 (4.6 ± 0.6)	5.2	8.1	6.9	7.3–8.2 (7.8 ± 0.6)	8.9	8.9	5.8
Tail maximum height	2.1	2.5–3.7 (3.3 ± 0.7)	2.1–2.3 (2.2 ± 0.1)	2.6–3.4 (3 ± 0.6)	3.5	5,8	4.5	6.1–6.2 (6.2 ± 0.1)	6.4	6.5	4.4
Tail maximum width	1.8	1.8–2.5 (2.1 ± 0.3)	2.2–2.7 (2.5 ± 0.4)	2–2.8 (2.4 ± 0.6)	3.1	5.0	6.7	5.3–5.5 (5.4 ± 0.1)	6.0	6.1	4.3
Interorbital distance	2.7	2.4–2.9 (2.6 ± 0.2)	2.6–2.9 (2.8 ± 0.2)	2.4–3.0 (2.7 ± 0.6)	3.7	6,8	4.4	6.3–6.4 (6.4 ± 0.1)	4.6	5.3	4.8
Internarial distance	2.2	1.9–2.3 (2.0 ± 0.2)	1.9–2.0 (2.0 ± 0.1)	2.1–2.2 (2.1 ± 0.1)	2.4	3.4	2.9	3.4–4.7 (4.1 ± 0.9)	3.5	3.3	3.0
Eye-diameter	1.3	1.2–1.4 (1.3 ± 0.1)	1.3–1.4 (1.4 ± 0.2)	0.8–1.4 (1.1 ± 0.4)	1.6	2.1	2.0	2–2.3 (2.2 ± 0.2)	2.3	2.3	2.2
Eye–snout distance	2.4	2.2–2.4 (2.3 ± 0.1)	2.5–2.6 (2.6 ± 0.1)	2.4–2.8 (2.6 ± 0.3)	3.2	4.3	3.8	4.4–4.8 (4.6 ± 0.3)	4.3	4.8	3.7
Eye–nostril distance	1.4	1.3–1.5 (1.4 ± 0.1)	1.3–1.4 (1.4 ± 0.1)	1.4–1.7 (1.5 ± 0.2)	2.0	2,5	2.0	2.5–2.6 (2.6 ± 0.1)	2.8	2.6	2.9
Nostril–snout distance	0.7	0.7–0.8 (0.8 ± 0.1)	1–1.1 (1.1 ± 0.1)	0.8–1.2 (1 ± 0.3)	0.9	1.4	1.4	1.7–1.9 (1.8 ± 0.1)	1.5	2.2	1.2
Oral disc width	2.2	2.3–2.6 (2.4 ± 0.2)	2.3–2.4 (2.4 ± 0.1)	2.6–2.7 (2.6 ± 0.1)	3.5	3.7	3.5	4.4–4.5 (4.2 ± 0.5)	3.8	3.9	3.5

[his Table 1], 331–332, 350, 357 [his Appendix]), in part; B. Lutz (1972:95) in part; Tyler and Davies (1978:220–222), in part; Lynch (1979:200, 215 [his Appendix 8.4]); Cruz (1982:148–151 [his Figs. 1–8], 166, 168–170), in part; Weygoldt (1984:248–251); Cruz (1985:93–98); Cruz (1990:711–717); Weygoldt (1991:83–96); Heyer et al. (1990:284, 323–324, 326, 330 [their Table3], 333–334 [their Table 4–5], 337 [their Table 6], 350, 383 [their Fig. 27]), in part; Duellman and Trueb (1994:538).

Type species.—*Phrynomedusa fimbriata* Miranda-Ribeiro, 1923 (3–5), by monotypy.

Diagnosis.—*Phrynomedusa* can be distinguished and diagnosed from the other genera of Phyllomedusidae by the following combinations of characters: (1) small Treefrogs (combined SVL 26.0–46.6 in males and 28.0–45.0 mm in females); (2) iris bicolored, dark yellow in upper and lower surfaces with horizontal diffuse dark stripe in middle of eye; (3) palpebral reticulation absent; (4) vocal sacs and vocal slits present; (5) U-shaped aponeurosis of musculus intermandibularis and musculus interhyoideus; (6) posterolateral elements of musculus intermandibularis inserting on aponeurosis; (7) posterolateral elements of m. intermandibularis triangular; (8) third ramus of depressor mandibulae absent; (9) dorsum smooth; (10) parotoid glands absent; (11) dorsolateral glands absent; (12) nuptial pads keratinized and cover metacarpus and proximal phalanx; (13) digital webbing absent between Fingers I and II, reduced between others; (14) flanks, medial, and lateral regions of thighs without flash color ornamentation; (15) cloacal opening at upper level of thighs; (16) calcar triangular on tarsus; (17) digital webbing reduced between toes; (18) tadpoles with complete row of marginal papillae in oral disc.

Among these 18 diagnostic characteristics, six of them are putative synapomorphies of *Phrynomedusa*: (1) iris bicolored; (2) palpebral reticulation absent; (3) posterolateral elements of musculus intermandibularis inserting on aponeurosis; (4) third ramus of depressor mandibulae absent; (5) nuptial pads keratinized and cover metacarpus and proximal phalanx; (6) tadpoles with complete row of marginal papillae in oral disc. The value of these characteristics as putative synapomorphies of *Phrynomedusa* needs to be confirmed in a broad phylogenetic analysis with morphology and molecular characters.

Comparison with other genera of Phyllomedusidae.—*Phrynomedusa* may be distinguished from all other genera of Phyllomedusidae (characters in parenthesis) by the absence of flash colors on flanks, preaxial, and postaxial margins of thighs (present in *Agalychnis*, *Cruziohyla*, *Callimedusa*, *Hylomantis*, *Pithecopus*, *Phasmahyla*, and *Phyllomedusa*); iris bicolored, dark yellow in upper and lower surfaces with vertical diffuse dark stripe in middle of eye (diffuse stripe not present in *Agalychnis*, *Callimedusa*, *Hylomantis*, *Pithecopus*, *Phasmahyla*, and *Phyllomedusa*); vocal sacs and vocal slits present (absent in *Phasmahyla*); U-shaped aponeurosis (oval with small constriction anteriorly in *Cruziohyla* and *Phasmahyla*); posterolateral elements of musculus intermandibularis inserts on aponeurosis (posterolateral elements inserts in musculus intermandibularis and aponeurosis in *Phasmahyla* and *Agalychnis* [except in *Agalychnis annae* and *Agalychnis granulosa*]); triangular posterolateral elements of musculus

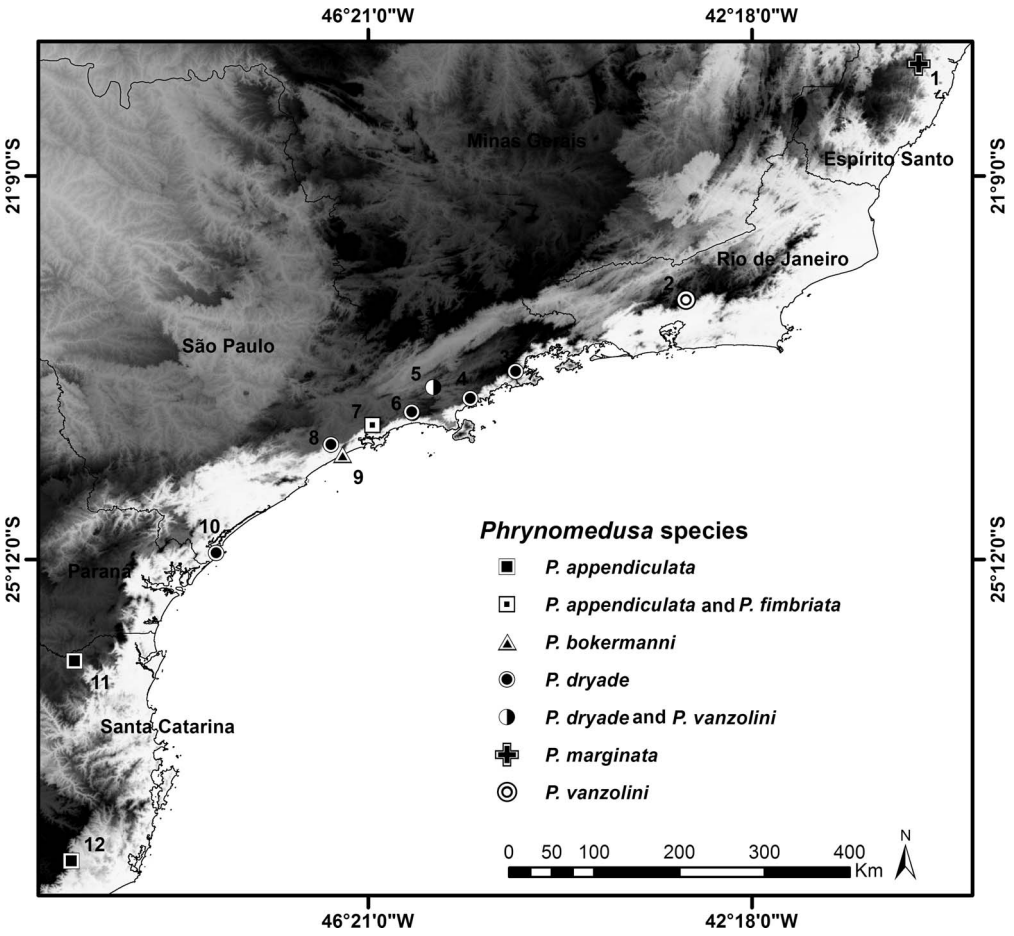

FIG. 1.—Geographic distribution from species of *Phrynomedusa* from southeastern to south regions of Brazil: (1) Santa Teresa, (2) Teresópolis, (3) Paraty, (4) São Luiz do Paraitinga, (5) Salesópolis, (6) Paraibuna, (7) Santo André, (8) Mongaguá, (9) Itanhaém, (10) Cananéia, (11) São Bento do Sul, and (12) Lauro Muller.

intermandibularis (rectangular in *Phasmahyla*); third ramus of depressor mandibulae absent (present in *Phyllomedusa*); dorsum smooth (rugose in *Phasmahyla*); parotoid glands absent (present in *Callimedusa*, *Pithecopus*, and *Phyllomedusa*); dorsolateral glands absent (present in *Phasmahyla*); keratinized nuptial pad covers metacarpus and proximal phalanx in *Phrynomedusa* (covers only the metacarpus in *Phasmahyla*); digital webbing absent between Fingers I–II, reduced between others (well developed between all fingers in *Cruziohyla*, absent in all fingers in *Callimedusa*, *Pithecopus*, *Phasmahyla*, and *Phyllomedusa*); cloacal opening positioned at upper level of thighs (ventral in *Agalychnis*, *Cruziohyla*, and *Hylomantis*); triangular calcar on tarsus (absent in *Pithecopus* and *Phyllomedusa*); digital webbing reduced between toes (absent in *Pithecopus*, *Phasmahyla*, and *Phyllomedusa*, well developed in *Cruziohyla*); tadpole with complete marginal papillae on oral disc without gaps (gaps present in *Agalychnis*, *Callimedusa*, *Pithecopus*, and *Phyllomedusa*).

Distribution.—Species of the genus *Phrynomedusa* are rare and restricted to 12 localities in the Atlantic Forest of Brazil, more specifically in the highlands of the Serra do Mar and Serra da Mantiqueira mountain ranges (Fig. 1).

Natural history.—Species of the genus are found in mountain streams and their associated ponds in the Atlantic Forest. Egg clutches are laid as several rows of eggs and are deposited outside of the water in rock crevices above the water; eggless capsules were present in the egg clutch. After hatching, tadpoles develop in these water bodies until metamorphosis (A. Lutz and B. Lutz 1939; Izecksohn and Cruz 1976; Heyer et al. 1990).

Remarks on the genus *Phrynomedusa*.—With the addition of the new species described herein, the genus *Phrynomedusa* is currently comprised of six species: *P. appendiculata*, *P. bokermanni*, *Phrynomedusa dryade*, *P. fimbriata*, *P. marginata*, and *P. vanzolinii*.

Phrynomedusa fimbriata was described from a single specimen collected by Hermann Lüderwaldt at the locality called "Alto da Serra" (currently Paranapiacaba, município de Santo André, state of São Paulo [SP]; Bokermann 1966). The second species of *Phrynomedusa* that was described was *Phrynomedusa appendiculata* by Adolpho Lutz (1925; who considered it as *Phyllomedusa* at the time), based on a specimen collected by Jonathan Nahderer from município de São Bento do Sul, state of Santa Catarina (SC). Not until 51 yr later was the third species of the genus, *Phrynomedusa marginata*, described by Izecksohn and Cruz (1976) from município de Santa Teresa, state of Espírito Santo (ES). The remaining two known species, *P. bokermanni* and *P. vanzolinii*, were described by Cruz (1991) 15 yr after the discovery of *P. marginata*. *Phrynomedusa bokermanni* was described from a single specimen collected by J.C. Oliveira

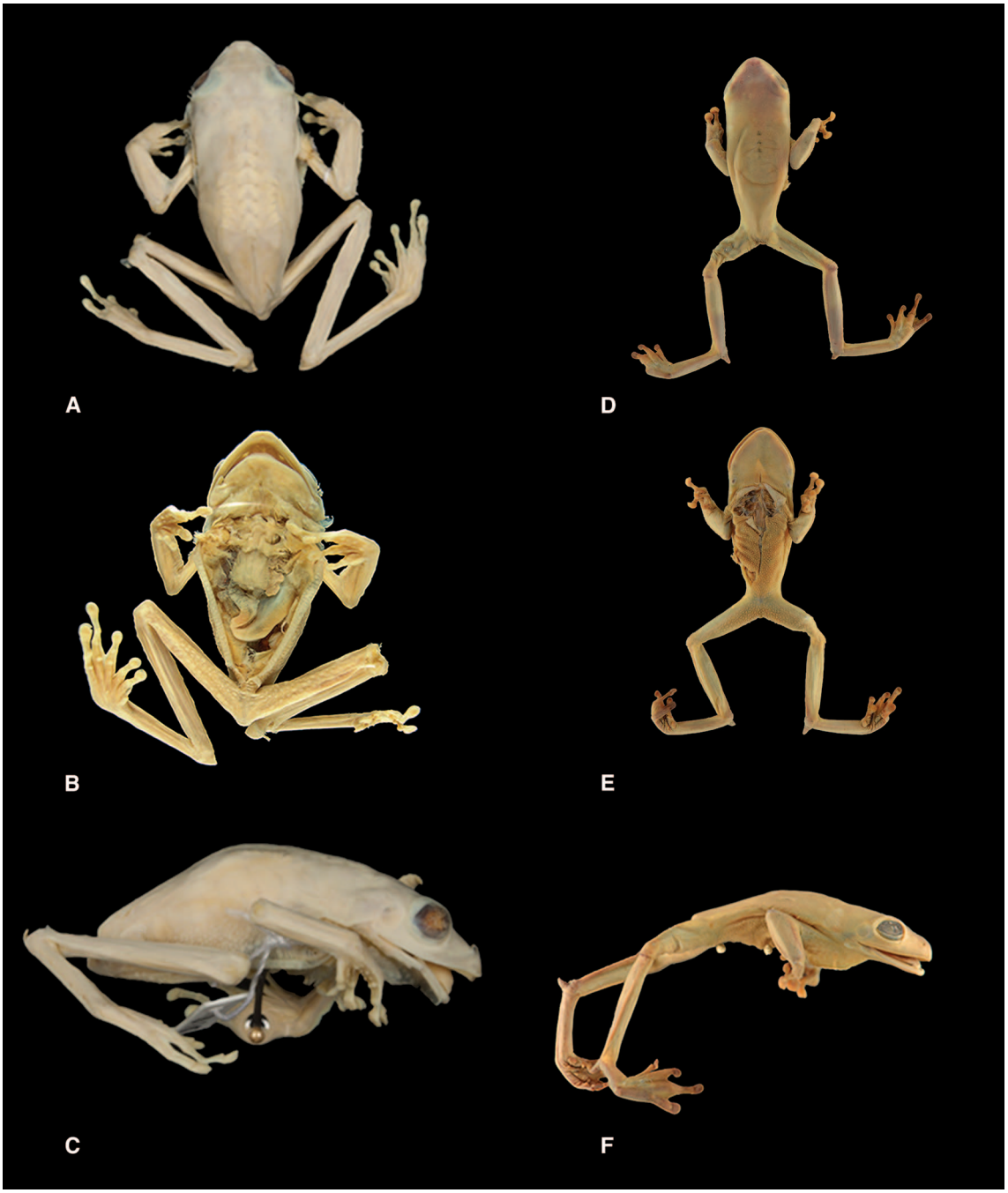

Fig. 2.—Holotypes of *Phrynomedusa fimbriata* (A–C) MZUSP 316, female, SVL = 45.6 mm, and *Phrynomedusa appendiculata*. (D–F) MNRJ 770, male, SVL = 33.0 mm. A color version of this figure is available online.

in the município de Mongaguá, state of São Paulo (SP), while *P. vanzolinii* was described from five specimens from Estação Biológica de Boracéia, município de Salesópolis, state of São Paulo (SP) and from município de Teresópolis, state of Rio de Janeiro (RJ).

Species Accounts

Phrynomedusa fimbriata Miranda-Ribeiro, 1923 (Fig. 2A–C)

Phrynomedusa fimbriata Miranda-Ribeiro (1923:4–5), species description; Miranda-Ribeiro (1926:63, 105–106 [his Fig. 62]); A. Lutz and B. Lutz (1939:219–221, 223, Plate VIII [their Fig. 3]); Bokermann (1966:81–83); Cruz (1990:711, 715 [his Figs. 8, 11], 719–721 [his Fig. 19], 723–724), in part; Duellman (1993:110); Duellman (1999:269, 309 [his Appendix 5]); Caramaschi and Cruz (2002:6–8, 10 [his Appendix 1]); Cruz and Pimenta (2004:e.T17078A6797217 [IUCN Red List website]); Faivovich et al. (2005:19, 116); Pimenta et al. (2005: their Table S3); Wiens et al. (2005: their Appendix 5); Wells (2007:478); Haddad (2008:290–291 [his Tables 2–3], 303–304); Garcia et al. (2009:331, 333 [their Table 10], 346); Araújo et al. (2010:201 [their Table 1], 208); Faivovich et

al. (2010:231); Pontes et al. (2010:161); Faivovich et al. (2011: supporting information); Rossa-Feres et al. (2011:52 [their Table 1]); Segalla et al. (2014:44); Toledo et al. (2014: supporting information [their Table A1]); Trevine et al. (2014:130 [their Table 1], 140, 146 [their Appendix 1]).

Phyllomedusa appendiculata: Cochran (1955:196).

Phyllomedusa fimbriata: B. Lutz (1950:601 [her Table I], 619 [her Table I]; incertae sedis, consider a possible *Agalychnis*); Funkhouser (1957:8 [her Fig. 7], 11 [her Map 2], 14, 20, 27–28), in part; Bokermann (1966:81, 83); Duellman (1968:5); Izecksohn and Cruz (1976:261); Lynch (1979:200, 215 [his Appendix 8.4]); Cannatella (1980:3); Weygoldt (1984:250); Cruz (1985:93–98 [his Fig. 2]); Cruz (1990:711–717), in part; Ruiz-Carranza et al. (1988:379); Heyer et al. (1990:324); Weygoldt (1991:83, 92); Duellman (1993:110).

Holotype.—Adult female (MZUSP 316), collected at "Alto da Serra" on November 1898 by H. Lüderwaldt (Fig. 2A–C). Currently "Alto da Serra" corresponds to Paranapiacaba, município de Santo André, state of São Paulo, Brazil (Bokermann 1966).

Diagnosis.—*Phrynomedusa fimbriata* is distinguishable from all congeners by the following combination of characters: (1) SVL = 45.6 mm of only known female; (2) snout acuminate in dorsal view and markedly oblique in lateral view; (3) canthus rostralis straight and loreal region concave; (4) dentigerous processes of vomer absent; (5) upper lip dermal fringe present; (6) dermal folds with sparse papillae on forearm postaxial margin, from elbow to adhesive disc of Finger IV; (7) triangular calcar large and well developed, parallel with tarsus sagittal axis; (8) calcar covering entire heel; (9) dermal folds with sparse papillae on tarsus postaxial margin, from calcar to adhesive disc of Toe V.

Comparisons with congeners.—*Phrynomedusa fimbriata* may be distinguished from its congeners (characters in parenthesis) by females with a large sized SVL = 45.6 mm (maximum SVL = 35.8 in *P. appendiculata*; SVL = 28.0 mm in *P. marginata*; SVL = 36.5 mm in *P. vanzolinii*); snout acuminate in dorsal view (rounded with a small medial projection in *P. marginata* and *P. dryade*); snout markedly oblique in lateral view (oblique in *P. appendiculata*, *P. bokermanni*, and *P. vanzolinii*; rounded with small medial projection in *P. marginata* and *P. dryade*); canthus rostralis concave (oblique in *P. appendiculata*, *P. bokermanni*, and *P. vanzolinii*; straight in *P. marginata* and *P. dryade*); loreal region straight (curved in *P. appendiculata*, *P. bokermanni*, and *P. vanzolinii*); dentigerous processes of vomer absent (present in *P. bokermanni* and *P. vanzolinii*); upper lip dermal fringe present (absent in all species of *Phrynomedusa*); dermal folds with sparse papillae on forearm postaxial margin (smooth in *P. appendiculata*, *P. marginata*, and *P. vanzolinii*; small tubercles in series in *P. bokermanni* and *P. dryade*); triangular calcar parallel with tarsus sagittal axis (calcar oblique with tarsus sagittal axis, at postaxial margin in *P. dryade*); triangular calcar covering entire heel (triangular calcar covering half of heel in *P. appendiculata* and *P. dryade*; calcar covering one-third of heel in *P. bokermanni*, *P. marginata*, and *P. vanzolinii*); dermal folds with sparse papillae on tarsus postaxial margins (absent in *P. bokermanni* and *P. dryade*; smooth in *P. appendiculata*, *P. marginata*, and *P. vanzolinii*).

Description of holotype.—Body robust for the genus; head wider than long (32% of SVL); snout acuminate in dorsal view, markedly oblique in lateral view; nostrils lateral and protruding, located on slight projection nearest to tip of snout; internarial distance 44.6% of interorbital distance; canthus rostralis concave; loreal region straight without flaring on lips; upper lip dermal fringe present; eye large, its posterior margin in contact with anterior margin of tympanum; palpebral membrane not reticulated; eye diameter 89.3% of interorbital distance; tympanum visible and rounded; tympanic annulus visible; tympanum diameter smaller than width of Finger III disc; supratympanic fold present and oblique, from posterior margin of tympanum to insertion of arm; tongue cordiform, anteriorly attached, laterally and posteriorly free, posteriorly with shallow notch; dentigerous process of vomer absent; choanae large and elliptical, widely separated.

Upper limbs slender, not hypertrophied; dermal folds with sparse papillae on forearm postaxial margin, from elbow to adhesive disc of Finger IV; fingers slender; finger length: I < II < IV < III; subarticular tubercles single, rounded; supernumerary tubercles single, rounded, their diameter less than or equal to subarticular tubercles; supernumerary tubercles present only in finger ventral surfaces; one supernumerary tubercle in palmar surface, below Finger III; inner metacarpal tubercle single and elliptical; outer metacarpal tubercle absent; adhesive discs rounded; reduced webbing between fingers, with formula: I absent – absent II $1^{1/2}$ – 2 III 2 – 2 IV.

Hind limbs slender; tibia length 55.7% of SVL; dermal folds with sparse papillae on tarsus postaxial margin, from calcar to adhesive disc Toe V; triangular calcar large and well developed on tarsus, parallel oriented with tarsus sagittal axis and covering entire heel width; toes slender, in following order of length: I < II < III < V < IV; subarticular tubercles single and rounded; supernumerary tubercles rounded and smaller than subarticular tubercles, more evident in toes and absent in plantar surface; one supernumerary tubercle on plantar surface, below fourth toe; inner metatarsal tubercle elliptical; outer metatarsal tubercle absent; adhesive discs rounded; reduced webbing between toes with formula: $I2^{+}$ – $1^{1/2}$ II 2 – $2^{1/2}$ III 2^{-} – 3^{+} IV 3^{+} – 2 V.

Skin on dorsum of body and limbs smooth; gular region and venter areolate; limbs ventral surface smooth; skin of distal and proximal surface of femur slightly areolate; osteoderms, parotoid, and dorsolateral glands absent; pterorhodin pigment present in the skin; cloacal opening at upper level of thighs.

Measurements of the holotype (in mm).—Snout–vent length 45.6; head length 14.6; head width 15.4; internarial distance 2.5; interorbital distance 5.6; eye diameter 5.0; eye–nostril distance 5.8, tympanum diameter 2.5; tibia length 25.4; foot length 14.6.

Coloration in life.—Unknown.

Coloration of holotype in preservative.—Miranda-Ribeiro presented a succinct description of the color of the fixed holotype 25 yr after it was collected (Miranda-Ribeiro 1923). According to this author the dorsal surfaces are pale blue and reddish yellow ("amarelo miniáceo" in the original description) on the ventral surfaces; the upper lip and the postaxial margin of the fourth finger and forearm have a

white line; the arm is totally white; gular region, preaxial region of thigh, ventral surfaces of hands, ventral surfaces of foot, and subcloacal region yellow ocre ("terra de Sienne" in the original description) with white dots; adhesive discs white dorsally; iris silver. The holotype has become completely white and no color pattern remains visible.

Distribution.—Known only from the type locality at Paranapiacaba, município de Santo André, state of São Paulo, Brazil (Fig. 1).

Advertisement call.—Unknown.

Tadpole.—Unknown.

Natural history.—Unknown.

Remarks.—The holotype of *P. fimbriata* is a female in bad condition. The skin of the tip of the snout is cut and deflected, exposing some of the musculature. There is an incision in the left tympanum that exposes the musculature associated with depressor mandibulae. There is a large medial incision from the posterior region of the gular region to the inguinal region, exposing the superficial gular musculature, pectoral girdle, and the internal organs. Only a very thin skin supports the articulation between the left femur and tibia. There are other small incisions on the dorsum and venter.

Phrynomedusa fimbriata is known only from the holotype collected in 1898 and, in spite of efforts to recover this species, no new records have been obtained (Trevine et al. 2014). Due to its rarity, *P. fimbriata* is considered the first and the only Brazilian amphibian to become extinct according to Conservation International and the official Brazilian Red List (Cruz and Pimenta 2004; BRASIL Portaria ICMBio no. 444 de 17 de Dezembro de 2014).

Phrynomedusa appendiculata (A. Lutz, 1925)
(Figs. 2D–F)

Phyllomedusa appendiculata A. Lutz (1925:139) species description: A. Lutz (1926:8, 15); A. Lutz and B. Lutz (1939:219–221, 223–224, 236–238, 253), in part; Cochran (1955:196–198 [her Plate 18J, K]), in part; B. Lutz (1950:601 [her Table I], 619 [her Table I]) [incertae sedis, considered a possible *Agalychnis*]); Cochran (1961:70); Bokermann (1966:82); Tyler (1971:326 [his Table 1], 331–332, 350, 357 [his Appendix]), in part; Tyler and Davies (1978:220–222), in part; Cruz (1985:93–98 [his Fig. 1]); Cruz (1990:711–717, in part); Weygoldt (1991:83); Duellman (1993:110).

Phyllomedusa fimbriata: Funkhouser (1957:8 [her Fig. 7], 11 [her Map 2], 14, 20, 27–28, 70 [her Fig. 15]), in part; Duellman (1968:5); Tyler (1971:326 [his Table 1], 331–332, 350, 357 [his Appendix]), in part; Tyler and Davies (1978:220–222), in part.

Phrynomedusa appendiculata: Cruz (1990:713 [his Figs. 3–4], 719 [his Fig. 19], 721, 723–724) in part; Duellman (1993:110); Caramaschi and Cruz (2002:6–8, 10 [their Appendix 1]); Garcia et al. (2004:e.T55825A11374203 [IUCN Red List website]); Faivovich et al. (2005:19, 116); Wiens et al. (2005: their Appendix 5); Faivovich et al. (2010:231, 246); Faivovich et al. (2011:355 [their Fig. 1], 357–358, their supporting information); Luna et al. (2012:714 [their Table1], 716– 720 [their Figs. 2A, 3B, 4C], 722); Segalla et al. (2014:44); Toledo et al. (2014:59 [their Fig. 3], their Table A1); Trevine et al. (2014:130 [their Table 1]).

Holotype.—Adult male (AL-MN 770) collected at município de São Bento do Sul, state of Santa Catarina, Brazil on February 1924 by J. Nahderer (Fig. 2D–F).

Diagnosis.—*Phrynomedusa appendiculata* is distinguishable from all congeners by the following combination of characters: (1) SVL = 26.3–34.9 mm in males (n = 42) and 35.8 mm in females (n = 1); (2) snout acuminate in dorsal view and oblique in lateral view; (3) canthus rostralis curved (concave) and loreal region oblique; (4) head lateral surface and tympanum green; (5) dentigerous processes of vomer absent; (6) upper lip dermal fringe absent; (7) nuptial pad keratinized, not extending to hand ventral surface; (8) dermal folds smooth on forearm postaxial margins, from elbow to adhesive disc of Finger IV; (9) forearm and fingers not hypertrophied in males; (10) triangular calcar parallel with tarsus sagittal axis; (11) calcar covering only half of heel; (12) dermal folds smooth on tarsus postaxial margins, from calcar to adhesive disc of Toe V.

Comparisons with congeners.—*Phrynomedusa appendiculata* may be distinguished from its congeners (characters in parenthesis) by male sizes SVL = 26.3–44.9 mm (SVL = 46.0 mm in *P. bokermanni*); female size SVL = 35.8 mm in female (SVL = 45.6 mm in *P. fimbriata*, SVL = 28.0 mm in *P. marginata*); snout acuminate in dorsal view (rounded with a small medial projection in *P. marginata* and *P. dryade*); oblique snout in lateral view (markedly oblique in *P. fimbriata*, rounded with small medial projection in *P. marginata* and *P. dryade*); canthus rostralis curved (straight in *P. fimbriata*, *P. marginata*, and *P. dryade*); loreal region oblique (concave in *P. fimbriata*; straight in *P. marginata* and *P. dryade*); head lateral surface and tympanum green (head lateral surface and tympanum cream-white in *P. bokermanni*; large marbled black and white stripe in *P. marginata* and *P. dryade*; narrow, oblique orange stripe from posterior border of eye to arm insertion in *P. vanzolinii*); dentigerous processes of the vomer absent (present in *P. bokermanni* and *P. vanzolinii*); upper lip dermal fringe absent (present in *P. fimbriata*); nuptial pad not reaching inner metacarpal tubercle and first subarticular tubercle (keratinized nuptial pad reaches its tubercles in *P. dryade*); dermal folds smooth on forearm postaxial margins (small tubercles in series in *P. bokermanni* and *P. dryade*; sparse papillae in *P. fimbriata*); forearms and fingers not hypertrophied in males (hypertrophied in males of *P. bokermanni*); triangular calcar parallel with tarsus sagittal axis (calcar oblique with tarsus sagittal axis, at postaxial margin in *P. dryade*); triangular calcar covering half heel (calcar covers entire heel in *P. fimbriata*; calcar covers one third of heel in *P. bokermanni*, *P. marginata*, and *P. vanzolinii*); dermal folds smooth on postaxial margins of tarsus (absent in *P. bokermanni* and *P. dryade*; sparse papillae in *P. fimbriata*).

Description of holotype.—Body slender for the genus; head wider than longer (31.1% of SVL); snout acuminate in dorsal view, oblique in lateral view; nostrils lateral and not protruded; internarial distance 66.2% of interorbital distance; canthus rostralis curved (concave) and loreal region oblique; upper lip dermal fringe absent; eye large, its posterior margin in contact with anterior margin of tympanum; palpebral membrane not reticulated; eye diameter 91.1% of interorbital distance; tympanum visible and

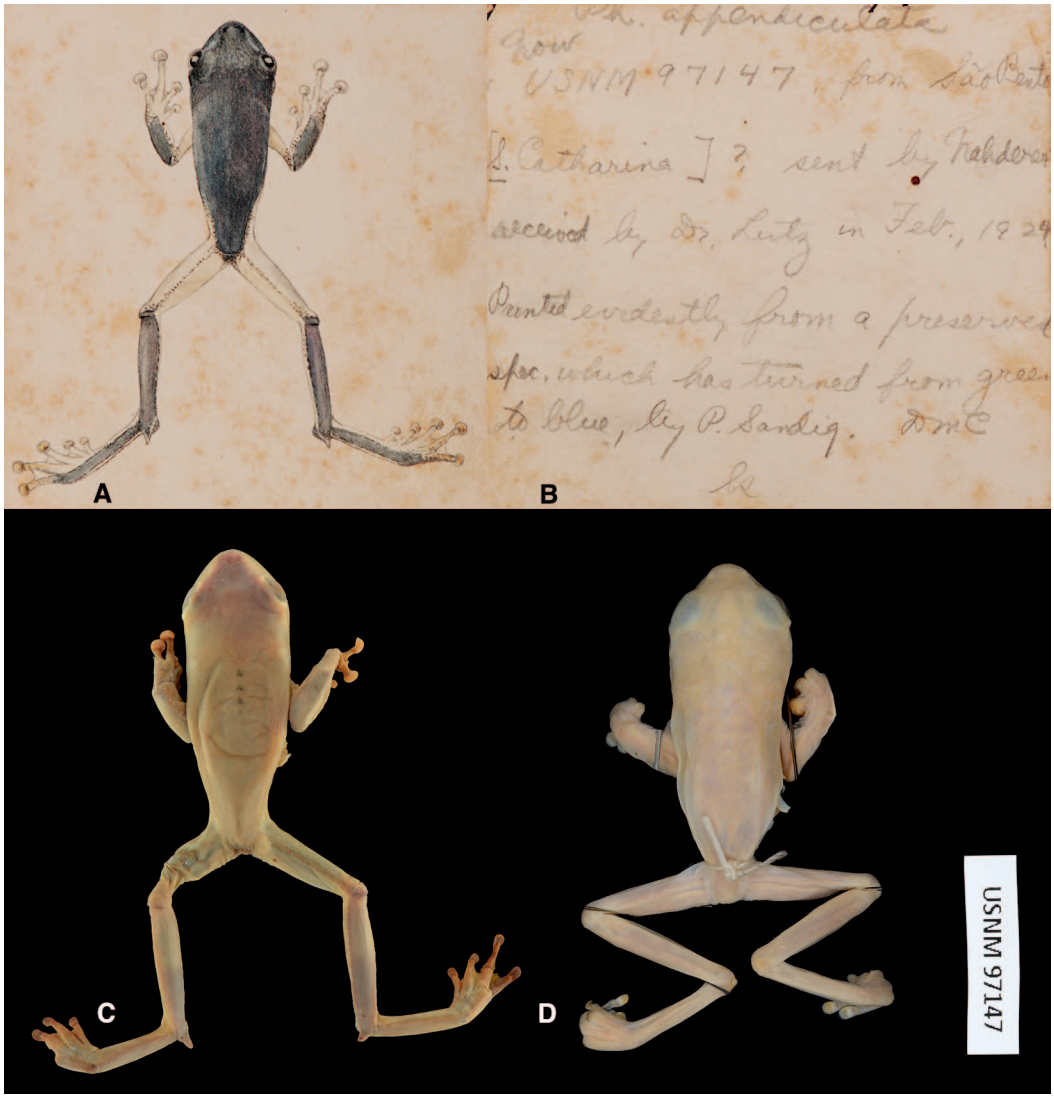

FIG. 3.—Colored sketch of *Phrynomedusa appendiculata* (A) AL-MN 770 (made by Paul Sandig), annotations of Dóris M. Cochran from the reverse side of the sketch (B), holotype of *P. appendiculata* (C) MNRJ 770, male, SVL = 33.0 mm, and topotype (USNM 97147, male SVL = 35.0 mm) from São Bento do Sul, Santa Catarina, Brazil. A color version of this figure is available online.

rounded; tympanic annulus visible; tympanum diameter about width of Finger III disc; supratympanic fold present, from posterior margin of eye passing over tympanum and oblique to insertion of arm; tongue cordiform, anteriorly attached, laterally and posteriorly free, posteriorly with shallow notch; dentigerous process of vomer absent; choanae large and elliptical widely separated from each other; vocal slits lateral and long, from middle of mandible to buccal commissure; vocal sac subgular, not externally evident.

Upper limbs robust, not hypertrophied; dermal folds smooth on forearm postaxial margins, from elbow to adhesive disc of Finger IV; fingers slender; finger length: I < II < IV < III; subarticular tubercles single, rounded; supernumerary tubercles single, rounded, their diameter less than or equal to subarticular tubercles; supernumerary tubercles sparse on fingers and hand ventral surfaces; inner metacarpal tubercle single and elliptical; outer metacarpal tubercle absent; adhesive discs rounded, adhesive disc of Finger I smaller than others; reduced webbing between fingers, with formula: I absent – absent II $1^{1/2}$ – $2^{1/2}$ III 2^{-} – $1^{1/2}$ IV; keratinized nuptial pad covers entire dorsal and preaxial surface at Finger I, not extending ventrally.

Hind limbs robust; tibia length 50.9% of SVL; dermal folds smooth on tarsus postaxial margin, from calcar to adhesive disc of Toe V; triangular calcar parallel with tarsus sagittal axis, covering only half of heel; toes slender, in following order of length: I < II < III < V < IV; subarticular tubercles single and rounded; supernumerary tubercles rounded and smaller than subarticular tubercles, more evident in toes and absent in plantar surface; one supernumerary tubercle on plantar surface, below fourth toe; inner metatarsal tubercle single and elliptical; outer metatarsal tubercle absent; adhesive discs rounded; reduced webbing between toes with formula: $I2^{+}$ – $1^{1/2}$ II 2^{-} – $1^{1/2}$ III 2^{-} – 2^{+} IV $2^{1/2}$ – 2^{+} V.

Skin on dorsum of body and limbs smooth, gular region and venter areolate; limbs ventral surface smooth; skin of distal and proximal surface of femur areolate, increasing in

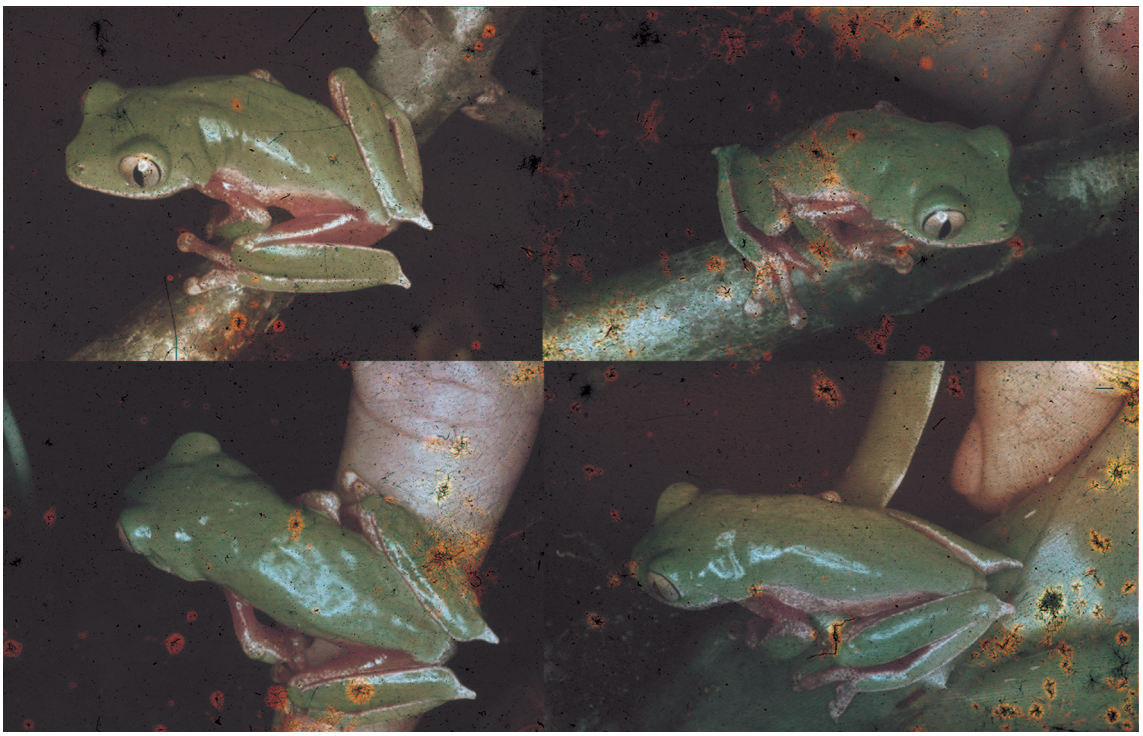

FIG. 4.—Live specimen of *Phrynomedusa appendiculata* from Paranapiacaba, município de Santo André, São Paulo, Brazil (Photos by Gualter Lutz, Gualter Lutz Slide Collection, MNRJ). A color version of this figure is available online.

density below to cloaca; osteoderms, parotoid, and dorsolateral glands absent; pterorhodin pigment present in the skin; cloacal opening at upper level of thighs.

Measurements of the holotype (in mm).—Snout–vent length 33.4; head length 10.4; head width 11.4; internarial distance 2.8; interorbital distance 4.5; eye diameter 4.1; eye–nostril distance 3.8; tympanum diameter 1.7; tibia length 17.0; foot length 11.8.

Coloration in life.—Cochran (1955) described the color in life based on a sketch from Paul Sandig, scientific illustrator of Museu Nacional – Universidade Federal do Rio de Janeiro (herein referred to as MNRJ), probably made shortly after it was preserved (Fig. 3A, B). The reverse side of Paul Sandig illustration has an annotation made by Doris M. Cochran that the sketch was made from a fixed specimen (USNM 97147) proceeding from the São Bento do Sul, SC collected by J. Nahderer on February 1924 (Fig. 3A, B; see Remarks above).

All surfaces of this specimen are dull indigo, with the exception of the arms, legs, fingers and toes, which are whitish cream; the ventral surfaces are whitish cream. This specimen has lost all of its coloration and has become completely white.

In the MNRJ there is a collection of 35-mm color photographic slides taken by Gualter Lutz (son of Adolpho Lutz) which included 13 slides of a live specimen of *P. appendiculata* from "Alto da Serra, SP" (Paranapiacaba, município de Santo André, SP; Fig. 4). Based on these slides we can see that the dorsal and lateral surfaces of the head of *P. appendiculata* are green; the same color is present on the dorsal surfaces of the body, forearm, and tibia. A marbled black and white line borders this green color. Hands and fingers are vivid orange, except for the fourth finger and the fourth and fifth toe, which have a marbled black and white color that is continuous with the medial borderline of the forearm. Apparently the arms and thighs are vivid orange on all surfaces, the same color as found on the flanks. There is a straight, marbled black and white line on the dorsal surfaces of the thighs from the knee to the body; the dorsal surface of the calcar is marbled black and white, cloacal region is marbled black and white. The eye is bicolored as in all species of *Phrynomedusa*; the iris is dark yellow with a diffuse dark stripe in the medial region of the eye. Unfortunately, we were not able to locate the voucher specimen for this photo.

Coloration in preservative.—In the original description, A. Lutz (1925) indicated that the dorsal surface is slate-colored in the holotype but most probably green in life, and the forelimbs above the elbow, thighs, hands, feet, and belly are cream white. The holotype has since completely lost its color pattern and is completely white; no evidence of any color pattern can be seen.

The other preserved specimens have the same color pattern described above from the slide photos of Gualter Lutz, with the following differences: the green regions have become pale blue, the orange regions have become cream colored and almost transparent, and the marbled black and white regions more cream colored.

Distribution.—Known only from three localities: the type locality in the município de São Bento do Sul and Novo Horizonte, município de Lauro Müller, both in the state of Santa Catarina and at Paranapiacaba, município de Santo André, state of São Paulo, in south and southeastern Brazil, respectively (Fig. 1).

Advertisement call.—Unknown.

Tadpole.—Unknown.

Natural history.—Unknown.

Remarks.—Since its original description there has been some confusion regarding the composition of the type series of *Phrynomedusa appendiculata*. Cochran (1955, 1961) referred to USNM 97147 as a cotype of *P. appendiculata*. Bokermann (1966) discussed problems about the precedence of the type and stated that AL-MN 770, from São Bento do Sul, SC, collected by J. Nahderer in February 1924, is probably the holotype. Cruz (1985), when resurrecting *P. appendicultada* (as *Phyllomedusa*) from synonymy of *P. fimbriata*, considered the type series of *P. appendiculada* to be composed only of the specimen AL-MN 770. However, the digital catalog of the USNM has the following taxonomic information about the specimen cited by Cochran (1961) as cotype USNM 97147: "Questionable syntype of *Phyllomedusa appendiculata* A. Lutz, 1925."

Adolpho Lutz did not define any specimen as the type of *Phyllomedusa appendiculata* in the original description (A. Lutz 1925) or in later reports (A. Lutz 1926). However, the original description (see below) clearly indicates that the author based his description on only one specimen having an SVL = 33 mm: "10° *Phyllomedusa appendiculata*. Espèce petite, L. 33 mm – Le dessus est bien ardoisé vert, pendant la vie. Le membre antérieur au-dessus du coude, la cuisse, les pattes antérieures et postérieures, le ventre, sont blanc-crême. Le talon présente un appendice conique" (A. Lutz 1925:139).

Subsequently, A. Lutz (1926) published both English and Portuguese versions of these communications with the title "Nota prévia sobre espécies novas de batrachios Brasileiros. New species of Brasilian batrachians. Preliminary note." In this note he added, in English, the following information to the description of *P. appendiculata*: "Of this very peculiar species one specimen in alcohol was obtained from São Bento, State of Santa Catarina" (A. Lutz 1926:15).

Clearly the type series of *Phrynomedusa appendiculata* is composed of only one exemplar from São Bento do Sul, SC. However two specimens (AL-MN 770 and USNM 97147) agree with this information; both were collected on February 1924 by J. Nahderer at São Bento do Sul, SC. Based on the collection date, collector, and locality, both specimens could be the holotype of *P. appendiculata*; however, Bokermann (1966) arbitrarily defines AL-MN 770 as the holotype. The comparison of SVL from these specimens shows that AL-MN 770 has the same SVL of the A. Lutz's holotype (SVL = 33.0 mm; A. Lutz 1925) and USNM 97147 as SVL = 35.0 mm. Thus the specimen USNM 97147 is not the holotype and should not be considered as part of the type series of *P. appendiculata*.

The rediscovery of Paul Sandig's illustration and the information present on its reverse side also must be clarified. On the reverse side of this sketch (Fig. 3A, B), we find the following annotation made by Doris M. Cochran: "Phy appendiculata: 'Now USNM 97147 from São Bento [S. Catharina] ? sent by J. Nahderer received by Dr. Lutz in Feb. 1924. Painted evidently from a preserved spec. which has turned from green to blue, by P. Sandig, DMC."

By the information written by Doris M. Cochran on the reverse side of P. Sandig's sketch, the figured specimen is USNM 97147; however, the position of arms and legs in this sketch does not agree with the USNM specimen (Fig. 3A–D). The position of the arms and legs of the sketch is coincident with the holotype, thus the association made by Doris Cochran is incorrect. Sandig's specimen is the holotype AL-MN 770.

Werner C. A. Bokermann collected a series of *P. appendiculata* specimens at Paranapiacaba, from 24 October 1963 to 1 October 1966 (MZUSP 81423–81424, 81426–81431). Sometimes these specimens were identified as *P. fimbriata* in the MZUSP herpetological collection or have this identity as considered to be doubtful. Confusion with *P. fimbriata* may be due to the historical taxonomic confusion between *P. appendiculata* and *P. fimbriata*, which led several authors to consider them the same species (B. Lutz 1950; Cochran 1955; Funkhouser 1957; Duellman 1968; Izecksohn and Cruz 1976; Cruz 1982). Despite the fact that *P. fimbriata* is known only from the female holotype (MZUSP 316), there are several characters that distinguish both species (see above Comparisons with congeners), thus there are no doubts that there are two species of *Phrynomedusa* in Paranapiacaba: *P. fimbriata* and *P. appendiculata*.

Phrynomedusa marginata Izecksohn and Cruz, 1976 (Figs. 5A, B; 8C, D)

Phyllomedusa marginata Izecksohn and Cruz (1976:257–261), species description: Lynch (1979:215 [his Appendix 8.4]); Cannatella (1980:3); Cruz (1982:148–151 [his Figs. 5–8], 166, 168–170); Weygoldt (1984:248–251); Cruz (1985:97); Ruiz-Carranza et al. (1988:379); Weygoldt (1991:83–96); Cruz (1990:711–717), in part; Duellman (1993:110); Duellman (1999:269, 309 [his Appendix 5]).

Phrynomedusa marginata: Cruz (1990:718–719 [his Figs. 14, 19], 721–724); Duellman (1993:110); Altig and McDiarmid (1999b:311); Caramaschi and Cruz (2002:6–8, 10 [their Appendix 1]); Haddad and Prado (2005:209 [their Box 1]); Faivovich et al. (2005:19, 116); Pimenta et al. (2005: their Appendix S2); Pombal and Haddad (2007:109 [their Box 1]); Wiens et al. (2005:720 [their Table 1], 733 [their Fig. 5], 737 [their Fig. 8], their Appendix 3–5); Wiens et al. (2006: supporting information [11, their Fig. A1, 26 their Table A2]); Gasparini et al. (2007:76, 78, 80 [their Table 6.1], 86–87 [their Photo], 133 [their Appendix]); Wells (2007:478); Moen and Wiens (2009: supporting information [their Fig. A1]); Moen et al. (2009: supporting information [19, their Fig. S1]); Cruz and Carvalho-e-Silva (2010:e.T55827A11374868 [IUCN Red List website]) in part; Faivovich et al. (2010:227, 230 [their Figs. 1, 2B–D], 234–236 [their Fig. 4], 244–247 [their Fig. 6], 261 [their Appendix 3]); Almeida et al. (2011:544, 547 [their Table 2], 557 [their Fig. 3H], 559 [their Appendix 1]); Faivovich et al. (2011:355 [their Fig. 1], 357–358, their supporting information); Pyron and Wiens (2011:568 [their Fig. 2], their Appendix B.3 [481], their supporting information), in part; Haddad et al. (2013:379); Borteiro et al. (2014:393) in part; Segalla et al. (2014:44); Toledo et al. (2014: supporting information [their Tables A1, A2]), in part; Duellman et al. (2016:9 [their Fig. 2], 16 [their Fig. 4], 49 [their Fig. 17], 51, 91 [their Appendix 1], 108 [their Appendix 1]), in part.

Holotype.—Adult male (EI 5177) collected at município de Santa Teresa, state of Espírito Santo, Brazil on 24 August 1974, by E. Izecksohn, C.A.G. Cruz, S.T. Albuquerque, and J.G. Silva (Fig. 5A, B).

FIG. 5.—Holotype of *Phrynomedusa marginata* (A–B) EI 5177, male, SVL = 28.0 mm. A color version of this figure is available online.

Paratopotypes.—Adult males (EI 5178, 5181–5182, 5184–5186; MNRJ 4100–4101; MZUSP 74149 [ex-EI 5183]), adult female (EI 5180), collected on 24 August 1974; adult male (EI 5179) collected on 26 October 1974. All specimens collected by E. Izecksohn, C.A.G. Cruz, S.T. Albuquerque, and J.G. Silva.

Diagnosis.—*Phrynomedusa marginata* is distinguishable from all congeners by the following combination of characters: (1) SVL = 26.0–30.0 mm in males (n = 19) and 28.0 mm in female (n = 1); (2) snout rounded with a small medial projection in dorsal view and rounded with small medial projection in lateral view; (3) canthus rostralis and loreal region straight; (4) lateral marbled black and white stripe from snout to inguinal region; (5) dentigerous processes of vomer absent; (6) upper lip dermal fringe absent; (7) nuptial pad keratinized, not extending to hand ventral surface; (8) dermal folds smooth on forearm postaxial margins, from elbow to adhesive disc of Finger IV; (9) forearm and fingers not hypertrophied in males; (10) triangular calcar parallel with tarsus sagittal axis; (11) calcar covering one third of heel; (12) dermal folds smooth on tarsus postaxial margins, from calcar to adhesive disc of Toe V.

Comparisons with congeners.—*Phrynomedusa marginata* may be distinguished from its congeners (characters in parenthesis) by male size SVL = 26.0–30.0 mm (SVL = 46.0 mm in *P. bokermanni*); female size SVL = 28.0 mm (SVL = 35.8 mm in *P. appendiculata*; SVL = 45.6 mm in *P. fimbriata*); snout rounded with a small medial projection in dorsal view (acuminate in *P. appendiculata*, *P. bokermanni*, *P. fimbriata*, and *P. vanzolinii*); rounded with small medial projection in lateral view (markedly oblique in *P. fimbriata*; oblique in *P. appendiculata*, *P. bokermanni*, and *P. vanzolinii*); canthus rostralis straight (curved in *P. appendiculata*, *P. bokermanni*, and *P. vanzolinii*); loreal region straight (concave in *P. fimbriata*; oblique in *P. appendiculata*, *P. bokermanni*, and *P. vanzolinii*); lateral marbled black and white stripe from snout to inguinal region (head lateral surface and tympanum green in *P. appendiculata*; cream-white in *P. bokermanni*; oblique orange stripe from posterior border of eye to arm insertion in *P. vanzolinii*); marbled black and white stripe extends over dorsum only in posterior third of body (marbled black and white stripe extends over dorsum in entire length of body in *P. dryade*); dentigerous processes of vomer absent (present in *P. bokermanni* and *P. vanzolinii*); upper lip dermal fringe absent (present in *P. fimbriata*); keratinized nuptial does not reach inner metacarpal tubercle and first subarticular tubercle (keratinized nuptial pad reaches tubercles in *P. dryade*); dermal folds smooth on forearm postaxial margins (small tubercles in series in *P. bokermanni* and *P. dryade*; sparse papillae in *P. fimbriata*); arms and fingers not hypertrophied in males (hypertrophied in males of *P. bokermanni*); triangular calcar parallel with tarsus sagittal axis (calcar oblique with tarsus sagittal axis, at postaxial margin in *P. dryade*); calcar covering one third of heel (calcar covering half of heel in *P. appendiculata* and *P. dryade*; calcar covering entire heel in *P. fimbriata*); dermal folds smooth on tarsus postaxial margins (absent in *P. bokermanni* and *P. dryade*; sparces papillae in *P. fimbriata*).

Description of holotype (based on Izecksohn and Cruz 1976 and holotype photos).—Body robust for the genus; head wider than long (32.1% of SVL); snout rounded with a small medial projection in dorsal view, rounded with small medial projection in lateral view; nostrils lateral and not protruded, located on slight projection nearest to tip of snout; canthus rostralis and loreal region straight without flaring on lips; upper lip dermal fringe absent; eye large, eye diameter 88% of interorbital distance; tympanum visible and rounded; tympanic annulus visible; supratympanic fold present, from posterior margin of eye passing over tympanum and oblique to insertion of arm; tongue cordiform, anteriorly attached, laterally and posteriorly free, posteriorly with shallow notch; dentigerous process of vomer absent.

Upper limbs robust and not hypertrophied; dermal folds smooth on forearm postaxial margins, from elbow to adhesive disc of Finger IV; fingers slender with small fringes; finger length: I < II < IV < III; subarticular tubercles single, rounded; supernumerary tubercles single, rounded, their diameter less than or equal to subarticular tubercles; inner metacarpal tubercle elliptical; outer meta-

carpal tubercle absent; adhesive discs rounded, disc on Finger I rounded, smaller than other fingers; reduced webbing between fingers, with formula: I absent – absent II 2 – $2^{1/2}$ III $2^{1/2}$ – 2^{+} IV; keratinized nuptial pad covering entire dorsal and medial surface at Finger I, extending from preaxial margin of finger to adhesive disc base.

Hind limbs robust; tibia length 44.4% of SVL; dermal folds smooth on tarsus postaxial margins, from calcar to adhesive disc of Toe V; triangular calcar parallel with tarsus sagittal axis, covering one third of heel; toes slender, in following order of length: I < II < III < V < IV; subarticular tubercles single and rounded; supernumerary tubercles rounded and smaller than subarticular tubercles, more evident in toes; adhesive discs rounded; reduced webbing between toes with formula: I absent – absent II 2 – 3 III 2^{-} – 3 IV $2^{1/2}$ – $1^{1/2}$ V.

Skin on dorsum of body and limbs smooth, gular region and venter areolate; limbs ventral surface smooth; skin of distal and proximal surface of femur areolate, increasing in density below to cloaca; osteoderms, parotoid, and dorsolateral glands absent; pterorhodin pigment present in the skin; cloacal opening at upper level of thighs.

Measurements of the holotype (in mm, from Izecksohn and Cruz 1976).—Snout–vent length 28.0; head length 9.0; head width 11.0; interorbital distance 4.5; eye diameter 4.0; eye–nostril distance 3.0; tympanum diameter 1.5; tibia length 13.0.

Coloration in life.—Based on the original description (Izecksohn and Cruz 1976) and color photographs (Fig. 8C, D) the color in life is as follows: dorsal surfaces of the head, body, forearm, and tibia are green with a white line on the margins; preaxial and postaxial margins of forearm orange colored and ventrally cream colored; marbled black and white stripe on flanks, from the tip of the snout passing over the eye and tympanum to the groin and reaching the cloacal region; marbled black and white stripe darker near midline of flanks, limited anterodorsally by loreal region and extending over dorsum only in the final third of the body; gular and pectoral region white; venter light orange; hands and fingers light orange, except the fourth finger, which is marbled black and white from the adhesive disc to the hand and extending to the postaxial margin of the forearm to the elbow; arm and femur are bright orange; toes are bright orange except the fifth toe, which has a marbled black and white stripe from the adhesive disc, extending over the dorsum and the postaxial margin of the tarsus, to the knee; ventral surface of the tarsus dark brown. Dorsal surface of the calcar marbled black and white. The iris is bicolored dark yellow in upper and lower surfaces with horizontal diffuse dark stripe in middle of eye.

Coloration in preservative.—The holotype has the same color pattern as described by Izecksohn and Cruz (1976), but the colors have since faded, mainly on the arms and legs. The green regions are pale blue, the orange colored regions are an almost transparent cream and the marbled black and white regions are marbled black and cream. The dorsum has lost color in some regions, but mainly between the eyes.

Distribution.—Known only for the type locality in the município de Santa Teresa, state of Espírito Santo, Brazil (Fig. 1).

Advertisement call.—Izecksohn and Cruz (1976) indicated that the call is difficult to define, not resembling the call of other Phyllomedusidae from southeast Brazil, being formed of a faint sound, with not much bass, pulsed, and of a short duration. Weygoldt (1991) presented a succinct description of *P. marginata* advertisement call from specimens in a terrarium. The advertisement call is a simple note emitted in intervals of 2–9 s ($\bar{X}$ = 4 s, n = 13), the call durations are 0.094–0.096 s (n = 14), the main frequencies are 1500–2500 Hz.

Tadpole.—The tadpole was described in the original description of *P. marginata* (Izeckson and Cruz 1976) based on a specimen (EI 5187) in the Stage 35 of Gosner (1960). There is no information about the number of tadpoles present in the lot EI 5187. However, in the description the authors clearly cite the presence of more than one tadpole in the lot. Cruz (1982) based his redescription on two lots of tadpoles from the type locality: a lot of 12 tadpoles (EI 5187) collected on 26 October 1974 and a lot of 36 tadpoles collected on 31 March 1978 (EI 5530).

From the original description and subsequent works (Izeckson and Cruz 1976; Cruz 1982), the tadpole of *P. marginata* may be described as follows: elliptical body, snout rounded in dorsal and lateral views; eyes positioned and directed laterally; oral disc anteroventral; two rows of marginal papillae on upper and lower lips and five rows laterally; dorsal gap on marginal papillae absent; a few scattered submarginal papillae present; labial tooth row formula 2(2)/3(1); A1 and A2 of equal length; P1, P2, and P3 of equal length; jaw sheaths finely serrate; spiracle ventral and directed posteriorly; vent tube dextral, short, and attached to the ventral fin; dorsal fin emerging on the first third of the tail musculature.

Natural history.—In the original description the authors reported that the specimens were collected at night on vegetation over artificial ponds dug by miners (Izecksohn and Cruz 1976). One adult male (MNRJ 57954) was found in similar conditions at the type locality by J.P. Pombal, Jr. Weygoldt (1984, 1991) provided some succinct information about specimens in the terrarium.

Remarks.—Unfortunately, we could not examine the type series deposited in the Eugênio Izecksohn collection (EI), deposited at Universidade Federal Rural do Rio de Janeiro. However, we examined three paratypes deposited in the Museu Nacional – Universidade Federal do Rio de Janeiro (MNRJ 4001–4002) and Museu de Zoologia – Universidade de São Paulo (MZUSP 74147, ex-EI 5183) and a series of topotypes (see examined material). Although the holotype of *Phrynomedusa marginata* was examined only from a photo, it was possible to observe the characters that differentiate *P. marginata* from *P. dryade*, the most-closely related species.

Carvalho-e-Silva et al. (2007) provided distribution records for *Phrynomedusa marginata* from municípios de Paraibuna (ZUFRJ 312–315, 603–605) and Paraty (ZUFRJ 10019–10021, 10046, 10066, 10073–10074), both in the state of Rio de Janeiro. We examined a specimen (MNRJ 32861) from município de Paraty that agrees with the diagnosis of *P. dryade*. Thus, at least one of the records of Carvalho-e-Silva et al. (2007) probably corresponds to the new species described herein, and the distribution of the new species and

FIG. 6.—Holotypes of *Phrynomedusa vanzolinii* (A–C) MZUSP 37669, male, SVL = 36.0 mm and *Phrynomedusa bokermanni* (D–F) MZUSP 81340, male, SVL = 46.0 mm. A color version of this figure is available online.

P. marginata must be re-evaluated based on the specimens used by Carvalho-e-Silva et al. (2007).

Phrynomedusa vanzolinii Cruz, 1991
(Figs. 1, 6A–C, 7)

Phyllomedusa appendiculata: A. Lutz and B. Lutz (1939:219–221, 223–224, 236–238, 253, Plate I [their Fig. 4], Plate III [their Figs. 1–7], Plate IV [their Figs. 5, 6], Plate VII [their Figs. 5, 6]), in part; Cochran (1955: frontispiece, 196–198, 379), in part; Heyer et al. (1990:284, 323, 326, 330 [their Table 3], 333–334 [their Table 4, 5], 337 [their Table 6], 350, 383 [their Fig. 27]).

Phyllomedusa fimbriata: B. Lutz (1972:95) in part; Cruz (1982:148–150 [his Figs. 1–4], 166, 168–170); Altig and

Fig. 7.—Colored sketches of *Phrynomedusa vanzolinii* (MNRJ collection). A color version of this figure is available online.

McDiarmid (1999b:311); McDiarmid and Altig (1999:13 [their Table 2.2]).

Phrynomedusa appendiculata: Duellman (1999:269, 309 [his Appendix 5].

Phrynomedusa vanzolinii Cruz (1991:272–274 [his Fig. 1]), species description; Caramaschi and Cruz (2002: 6–8, 10 [their Appendix 1]); Cruz and Carvalho-e-Silva (2004:e.T55828A11375261 [IUCN Red List website]), in part; Faivovich et al. (2005:19, 116); Haddad and Prado (2005:209 [their Box 1], 216); Pombal and Haddad (2007:109 [their Box 1]); Wiens et al. (2005: their Appendix 5); Wells (2007:478); Haddad (2008:290 [his Table 2]); Garcia et al. (2009:334 [their Table 10]); Araújo et al. (2010:201 [their Table 1]); Faivovich et al. (2010:231, 246); Rossa-Feres et al. (2011:52 [their Table 1]); Segalla et al. (2014:44); Toledo et al. (2014: supporting information [their Table A1]); Silva et al. (2014:5, supporting information [their data S1 and Appendix S4]).

Holotype.—Adult female (MZUSP 37699) collected at Estação Biológica de Boracéia, município de Salesópolis, state of São Paulo, Brazil, between 31 January to 4 February 1973 by G.R. Kloss and M. Mazzilli (Fig. 6A–C).

Paratopotypes.—Adult male (MZUSP 3998) collected on 15 January 1950 by W.C.A. Bokermann; juvenile (MZUSP 9387) collected on 1 December 1951 by L. Travassos Filho and H. Camargo.

Paratypes.—Adult males (AL-MN 1983, USNM 96447) collected at município de Teresópolis, state of Rio de Janeiro, Brazil, on November 1929 by J. Venâncio.

Diagnosis.—*Phrynomedusa vanzolinii* is distinguishable from all congeners by the following combination of characters: (1) SVL = 32.6–35.3 mm in males ($n = 4$) and 36.5 mm for the only known female; (2) snout acuminate in dorsal view and oblique in lateral view; (3) canthus rostralis curved and loreal region oblique; (4) lateral narrow oblique orange stripe from posterior border of eye to arm insertion; (5) dentigerous processes of vomer present; (6) upper lip dermal fringe absent; (7) nuptial pad keratinized does not extend to ventral surface of hand; (8) dermal folds smooth on forearm postaxial margins, from elbow to adhesive disc of Finger IV; (9) forearm and fingers not hypertrophied in males; (10) triangular calcar parallel with tarsus sagittal axis; (11) calcar covering one third of heel; (12) dermal folds smooth on tarsus postaxial margins, from calcar to adhesive disc of Toe V.

Comparisons with congeners.—*Phrynomedusa vanzolinii* may be distinguished from its congeners (characters in parenthesis) by male size SVL = 32.6–35.3 mm (SVL = 46.0 mm in *P. bokermanni*) and female size SVL = 36.5 mm (SVL = 45.6 mm in *P. fimbriata*; SVL = 28.0 mm in *P. marginata*); snout acuminate in dorsal view (rounded with a small medial projection in *P. marginata* and *P. dryade*); snout oblique in lateral view (markedly oblique in *P. fimbriata*; rounded with small medial projection in *P. marginata* and *P. dryade*); canthus rostralis curved (straight in *P. fimbriata*, *P. marginata*, and *P. dryade*); loreal region oblique (concave in *P. fimbriata*; straight in *P. marginata* and *P. dryade*); oblique orange stripe from posterior border of eye to arm insertion (head lateral surface and tympanum green in *P. appendiculata*, cream-white in *P. bokermanni*; large marbled black and white stripe in *P. marginata* and *P. dryade*); dentigerous processes of vomer present (absent in *P. appendiculata*, *P. fimbriata*, *P. marginata*, and *P. dryade*); upper lip dermal fringe absent (present in *P. fimbriata*); keratinized nuptial pad does not reach inner metacarpal tubercle and first subarticular tubercle (keratinized nuptial pad reaches its tubercles in *P. dryade*); dermal folds smooth on forearm postaxial margins (small tubercles in series in *P. bokermanni* and *P. dryade*; sparse papillae in *P. fimbriata*); forearm and fingers not hypertrophied in males (hypertrophied in males of *P. bokermanni*); triangular calcar parallel with tarsus sagittal axis (calcar oblique with tarsus sagittal axis, at postaxial margin in *P. dryade*); calcar covering one third of heel (calcar covering entire heel in *P. fimbriata*; calcar covering half heel in *P. appendiculata* and *P. dryade*); dermal folds smooth on tarsus postaxial margins (absent in *P. bokermanni* and *P. dryade*; sparse papillae in *P. fimbriata*).

Description of holotype.—Body slender for the genus; head wider than long (head length 32% of SVL); snout acuminate in dorsal view, oblique in profile; nostrils lateral and not protruded; internarial distance 54.3% of interorbital distance; canthus rostralis curved and loreal region oblique without flaring on lips; upper lip dermal fringe absent; eye large, its posterior margin in contact with anterior margin of tympanum; palpebral membrane not reticulated; eye diameter 89.1% of interorbital distance; tympanum visible and rounded; tympanic annulus visible in ventral region; tympanum diameter almost equal to width of Finger III disc; supratympanic fold present, from dorsal margin of tympanum and oblique to insertion of arm; tongue cordiform, anteriorly attached, laterally and posteriorly free, posteriorly with shallow notch; dentigerous process of vomer present; choanae large and elliptical, widely separated.

Upper limbs not hypertrophied; dermal folds smooth on forearm postaxial margins; fingers robust; finger length: I < II < IV < III; subarticular tubercles single, rounded; supernumerary tubercles single, rounded, their diameter less than or equal to subarticular tubercles, restricted to fingers ventral surfaces; one supernumerary tubercle in palmar surface, below Finger III; inner metacarpal tubercle elliptical; outer metacarpal tubercle absent; adhesive discs rounded; reduced webbing between fingers, with formula: I absent – absent II 2^{+} – 3^{-} III $2^{1/2}$ – 2^{+} IV.

Hind limbs slender; tibia length 49.4% of SVL; dermal folds smooth on tarsus postaxial margin; triangular calcar parallel with tarsus sagittal axis, covering one third of heel width; toes slender, in following order of length: I < II < III < V < IV; subarticular tubercles single and rounded; supernumerary tubercles rounded and smaller than sub-

articular tubercles, more evident in toe ventral surfaces, small tubercles scattered on plantar surface; one supernumerary tubercle in palmar surface, below Toe IV; inner metatarsal tubercle elliptical; outer metatarsal tubercle absent; adhesive discs rounded; reduced webbing between toes with formula: $I2^{+} - 2^{+}$ II $2^{-} - 2^{1/2}$ III $2^{-} - 2^{+}$ IV $2^{+} - 2^{+}$ V.

Skin on dorsum of body and limbs smooth, gular region and venter areolate; limbs ventral surface smooth; skin of distal and proximal surface of femur areolate, increasing in density below to cloaca, with some white granular tubercles near the articulation of femur with body, increasing in density below to cloaca; osteoderms, parotoid, and dorsolateral glands absent; pterorhodin pigment present in the skin; cloacal opening at upper level of thighs, with no ornamentation.

Measurements of the holotype (in mm).—Snout–vent length 36.0; head length 11.7; head width 12.9; internarial distance 2.5; interorbital distance 4.6; eye diameter 4.1; eye–nostril distance 2.5; tympanum diameter 2.0; tibia length 17.8; foot length 11.2.

Coloration in life.—The color of a live specimen, probably USNM 96447, was described by A. Lutz and B. Lutz (1939). The dorsal surfaces of head, body, forearms, thighs, tarsus, and the lateral margins of hands are green or violet brown; the flanks, arms, medial surface of forearms, hands, feet, fingers, and toes are transparent orange to yellowish orange; venter is immaculate; a longitudinal line of brown darker dots is present along the middle of the upper surface of the thigh.

Coloration in preservative.—The color of the holotype is faded, but we can observe that it agrees with the succinct description in life by A. Lutz and B. Lutz (1939). The green dorsal surface is pale blue; flanks, hands, feet, and ventral surfaces are cream; arms and thighs have lost their color and are transparent. We also found in the MNRJ two illustrations of a specimen of *Phrynomedusa vanzolinii* (probably the same specimen mentioned by A. Lutz and B. Lutz (1939) from município de Teresópolis, RJ and made by an unknown artist (Fig. 7). The color of this illustration agrees with the description in life of A. Lutz and B. Lutz (1939).

Distribution.—Known only for two localities: Estação Biológica de Boracéia, município de Salesópolis, state of São Paulo, and município de Teresópolis, state of Rio de Janeiro, southeastern Brazil (Fig. 1).

Advertisement call.—Unknown.

Tadpole.—Adolpho Lutz and B. Lutz (1939) described the tadpoles as *Phyllomedusa appendiculata* based on a lot of tadpoles collected by Joaquim Venâncio on 9 November 1929 in the município de Teresópolis, RJ. Cruz (1982) redescribed these tadpoles (AL-MN 4311–4312) under the name *Phyllomedusa fimbriata*. Subsequently, Heyer et al. (1990) described the tadpoles from the type locality under the name *Phyllomedusa appendiculata* (MZUSP 36559). Unfortunately, we could not locate these tadpoles and cannot add additional data to these accounts.

Based on the original description and subsequent publications (A. Lutz and B. Lutz 1939; Cruz 1982; Heyer et al. 1990), the tadpole of *P. vanzolinii* may be described as follows: elliptical body, snout rounded in dorsal and lateral views; nostrils slightly laterally positioned, oblique in relation to sagittal axis of body; eyes rounded and positioned closer to tip of snout than eyes; eyes laterally positioned and directed; oral disc anteroventral; two rows of marginal papillae on upper and lower lips, and five rows laterally; dorsal gap on marginal papillae absent; a few scattered submarginal papillae present; labial tooth row formula 2(2)/3(1); A1 and A2 of equal length; P1, P2, and P3 of equal length; jaw sheaths finely serrate; spiracle ventral and directed posteriorly; vent tube dextral, short, and attached to ventral fin; tail musculature slightly higher than body; dorsal fin emerging at junction of body and tail musculature.

Natural history.—Adolpho Lutz and B. Lutz (1939) presented notes on the eggs, embryos, and tadpoles of *Phrynomedusa vanzolinii* (as *P. appendiculata* from the population at município de Teresópolis, RJ). These notes were based on field observations made by Joaquim Venâncio (employee in the Adolpho Lutz's laboratory) on 9 November 1929, early in the dawn at a mountain brook. The egg clutch was laid as several rows of eggs, forming some layers, and was deposited outside of the water in a hollow in a rock covered by a fallen trunk in the middle of a mountain brook. Eggless capsules were present in the egg clutch. Heyer et al. (1990) presented short notes about the environment where two adults and the tadpoles of *P. vanzolinii* (as *P. appendiculata*) were found at the type locality Estação Biológica de Boracéia, município de Salesópolis, SP.

Remarks.—Cruz (1991) suggested that *Phrynomedusa vanzolinii* and *P. appendiculata* are related based on their great similarity. According to him, the only known difference between these two species is the presence of a narrow, oblique, orange stripe that extends from the posterior border of the eye to the insertion of the arm in *P. vanzolinii* that is absent in *P. appendiculata*. Unfortunately, due to the loss of coloration of the type series of *P. vanzolinii* and due to the absence of photographs in life of this species, this character cannot be observed in the specimens available. It is possible that *P. vanzolinii* is a synonym of *P. appendiculata*; however, the illustration of *P. vanzolinii* from município de Teresópolis, RJ (Fig. 7) and the pictures of *P. appendiculata* from Paranapiacaba, município de Santo André, SP (Fig. 4) show the presence of these diagnostic color characters that differentiated both species.

Phrynomedusa bokermanni Cruz, 1991
(Figs. 1, 6D–F)

Phrynomedusa bokermanii Cruz (1991:273–274 [his Fig. 2]), species description; Caramaschi and Cruz (2002:6–8, 10 [their Appendix 1]); Cruz and Caramaschi (2004:e.T55826A11374546 [IUCN Red List website]); Cruz and Feio (2007:123); Faivovich et al. (2005:19, 116); Pimenta et al. (2005: supporting information [their Appendix 3]); Wiens et al. (2005: supporting information [their Appendix 5]); Haddad (2008:290 [his Table 2]); Garcia et al. (2009:334 [their Table 10]); Araújo et al. (2010:201 [their Table 1]); Faivovich et al. (2010:231, 246); Rossa-Feres et al. (2011:52 [their Table 1]); Segalla et al. (2014:44); Toledo et al. (2014: supporting information [their Table A1]).

Holotype.—Adult male (MZUSP 81340, ex-WCAB 49654) collected at the município de Mongaguá, state of São Paulo, Brazil on October 1978 by J.C. Oliveira (Fig. 6D–F).

Diagnosis.—*Phrynomedusa bokermanni* is distinguishable from all congeners by the following combination of characters: (1) SVL = 46.0 mm in only known male; (2) snout acuminate in dorsal view and oblique in lateral view; (3) canthus rostralis curved and loreal region oblique; (4) head lateral surface and tympanum cream white; (5) dentigerous processes of vomer present; (6) upper lip dermal fringe absent; (7) nuptial pad keratinized, does not extend to ventral surface of hand; (8) dermal folds with tubercles in series on forearm postaxial margin; (9) forearm and fingers hypertrophied in male; (10) triangular calcar parallel with tarsus sagittal axis; (11) calcar covering only one third of heel; (12) dermal folds absent on tarsus postaxial margin.

Comparisons with congeners.—*Phrynomedusa bokermanni* is distinguished from its congeners (characters in parenthesis) by male size, SVL = 46.0 mm (SVL = 26.3–44.9 in *P. appendiculata*; SVL = 26.0–30.0 mm in *P. marginata*; SVL = 32.6–35.3 in *P. vanzolinii*; SVL = 29.4–31.7 mm in *P. dryade*); acuminate snout in dorsal view (rounded with a small medial projection in *P. marginata* and *P. dryade*); oblique snout in lateral view (markedly oblique in *P. fimbriata*; rounded with small medial projection in *P. marginata* and *P. dryade*); canthus rostralis curved (straight in *P. fimbriata*, *P. marginata*, and *P. dryade*); loreal region oblique (concave in *P. fimbriata*, straight in *P. marginata* and *P. dryade*); lateral region of head and tympanum cream white (head lateral surface and tympanum green in *P. appendiculata*; large marbled black and white stripe from snout to inguinal region in *P. marginata* and *P. dryade*; oblique orange stripe from posterior border of eye to arm insertion in *P. vanzolinii*); dentigerous processes of vomer present (absent in *P. appendiculata*, *P. fimbriata*, *P. marginata*, and *P. dryade*); upper lip dermal fringe absent (present in *P. fimbriata*); keratinized nuptial pad not reaching inner metacarpal tubercle and first subarticular tubercle (keratinized nuptial pad reaches its tubercles in *P. dryade*); small tubercles in series on forearm postaxial margin (smooth in *P. appendiculata*, *P. marginata*, and *P. vanzolinii*; sparse papillae in *P. fimbriata*); forearms and fingers hypertrophied in males (not hypertrophied in *P. appendiculata*, *P. marginata*, *P. vanzolinii*, and *P. dryade*); triangular calcar parallel with tarsus sagittal axis (calcar oblique with tarsus sagittal axis, at postaxial margin in *P. dryade*); calcar covering one third of heel (calcar covering entire heel in *P. fimbriata*; calcar covering half of heel in *P. appendiculata* and *P. dryade*); dermal folds absent on postaxial margins of tarsus (smoth in *P. appendiculata*, *P. marginata*, and *P. vanzolinii*; sparse papillae in *P. fimbriata*).

Description of holotype.—Body robust for genus; head wider than long (33.2% of SVL); snout acuminate in dorsal view, oblique in lateral view; nostrils lateral and not protruded; internarial distance 64.3% of interorbital distance; canthus rostralis curved; loreal region oblique without flaring on lips; upper lip dermal fringe absent; eye large, its posterior margin not in contact with anterior margin of tympanum; palpebral membrane not reticulated; eye diameter 89.3% of interorbital distance; tympanum visible and rounded; tympanic annulus visible in ventral region; tympanum diameter equal to disc width of Finger III; supratympanic fold present and oblique, from tympanum dorsal margin to arm insertion; tongue cordiform, anteriorly attached, laterally and posteriorly free, posteriorly with shallow notch; dentigerous process of vomer present; choanae large and elliptical widely separated; vocal slits present and small, nearest to buccal commissure; vocal sac subgular, not externally evident.

Upper limbs hypertrophied; small tubercles in series on forearm postaxial margins; fingers hypertrophied with small fringes; finger length: I < II < IV < III; subarticular tubercles single, rounded; supernumerary tubercles single, rounded, their diameter less than or equal to subarticular tubercles; supernumerary tubercles cover all ventral surfaces of hand and fingers; inner metacarpal tubercle single and elliptical; outer metacarpal tubercle elliptical and double; adhesive discs rounded; reduced webbing between fingers, with the following formula: I absent – absent II 2^{+} – 3 III $2^{1/2}$ – 2 IV; keratinized nuptial pad covering entire dorsal and medial surface at Finger I, extending from medial margin of finger to adhesive disc base.

Hind limbs robust; tibia length 50% of SVL; tubercles or dermal folds on tarsus postaxial margin absent; triangular calcar parallel with tarsus sagittal axis, covering one third of heel width; toes robust, in following order of length: I < II < III < V < IV; subarticular tubercles single and rounded; supernumerary tubercles rounded, smaller than subarticular tubercles and sparse in toes and foot surfaces; one supernumerary tubercle in plantar surface, below Toe IV; inner metatarsal tubercle elliptical; outer metatarsal tubercle absent; adhesive discs rounded; reduced webbing between toes with formula: I2 – 2^{+} II $1^{1/2}$ – $2^{1/2}$ III $1^{1/2}$ – $2^{1/2}$ IV 2^{+} – $1^{1/2}$ V.

Skin on dorsum of body and limbs smooth, gular region and venter areolate; limbs ventral surface smooth; skin of distal and proximal surface of femur areolate, increasing in density below to cloaca, with some white granular tubercles near the articulation of femur with body, increasing in density below to cloaca; osteoderms, parotoid, and dorsolateral glands absent; pterorhodin pigment present in the skin; cloacal opening at upper level of thighs, with no ornamentation.

Measurements of the holotype (in mm).—Snout–vent length 46.0; head length 14.3; head width 16.0; internarial distance 3.6; interorbital distance 5.6; eye diameter 5.0; eye–nostril distance 4.0, tympanum diameter 2.3; tibia length 23.0; foot length 16.1.

Coloration in preservative.—According to Cruz (1991), the holotype has the following color pattern: dorsal surfaces of head and body pale blue; head lateral surfaces and venter cream white; gular region with dark brown pigmentation extending onto flanks until inguinal region, more concentrated close to mandibulae and posterior half of flanks; dorsal surfaces of forearm, femur, tibia, and tarsus with pale blue blotches ("escudos" in the original), delimited by white line on its margins; dorsal surfaces of fingers, hands, and arms dark brown pigmented; ventral surfaces of forearm, tarsus, and toes dark brown pigmented; preaxial and postaxial surfaces of femur and tarsus dark pigmented; calcar dark pigmented; cloacal region dark brown pigmented, its brown pigment extends over posterior ventral surfaces of femur.

The holotype has lost most of its colors, mainly the pale blue colors, but we can see vestiges of the color pattern described by Cruz (1991). Most differences are in the dorsal surfaces of the head, body, forearm, femur, tibia, and tarsus.

FIG. 8.—Holotype (A) CFBH 16026, male, SVL = 30.9 mm (photo by C.F.B. Haddad) and paratype (B) CFBH 7684, SVL = 29.5 mm (photo by L.O.M. Giasson) of *Phrynomedusa dryade*, adult males from Núcleo Santa Virgínia, Parque Estadual da Serra do Mar, município de São Luiz do Paraitinga, São Paulo, Brazil. Topotypes (C) MNRJ 57954; male SVL = 27.6 mm (photo by J.P. Pombal, Jr.), (D) specimen not specified (photo by I. Sazima) of *Phrynomedusa marginata*, males from município de Santa Teresa, Espírito Santo, Brazil. A color version of this figure is available online.

The dorsal blue color of head and body has darkened with age. The dorsal pale blue color of forearm, femur, tibia, and tarsus have faded almost to cream, but we can see vestiges of the pale blue blotches described by Cruz (1991). All others surfaces become cream, but the dark brown regions described by Cruz (1991) are visible.

Distribution.—Known only for the type locality in the município de Mongaguá, state of São Paulo, Brazil (Fig. 1). Mongaguá is a coastal municipality with approximately 142,000 km^2 which includes lowlands and highlands that reach 1000 m above sea level (m a.s.l.). The type locality can be accessed by the coastal road Padre Manoel da Nóbrega (SP-055) from the north (leaving from município de Praia Grande) or south (leaving from município de Itanhaém). The exact point of collection is unknown and efforts to identify the collector identity were unsuccessful; as for all other *Phrynomedusa*, we suspect that *P. bokermanni* occurs in mountain streams.

Advertisement call.—Unknown.

Tadpole.—Unknown.

Natural history.—Unknown.

Remarks.—This species is known only from the holotype, an adult male in a good condition of preservation (Fig. 7D–F). The sex of the specimen is confirmed by the presence of vocal slits, extending from the middle of the mandible to the buccal commissure and by the presence of well-developed keratinized nuptial pads covering the preaxial and dorsal surfaces of the metacarpus and the preaxial surface of the basal phalanx. Cruz (1991) pointed out that *Phrynomedusa bokermanni* may be most-closely related to *P. fimbriata*, differing from this species by having the postaxial margins of the femur, tibia, and foot smooth and by the shape of the snout in lateral view. Both species share a large SVL, but until more systematic information becomes available from all species of *Phrynomedusa* we prefer not to consider the relation pointed to by Cruz (1991).

NEW SPECIES DESCRIPTION

Phrynomedusa ***dryade*** sp. nov.
(Tables 1, 2; Figs. 1, 8A B, 9–12)

Phrynomedusa cf. *marginata*: Toledo et al. (2014: supporting information [their Tables A1, A2]), in part; [misidentification].

Phrynomedusa marginata: Haddad et al. (2008:1550); Araújo et al. (2010: 201 [their Table 1], 208); Cruz and Carvalho-e-Silva (2010:e.T55827A11374868 [IUCN Red List website]) in part; Faivovich et al. (2010:234–236 [their Fig. 4], 244–247 [their Fig. 6], 249, 251–252, 261 [their Appendix 3]); Faivovich et al. (2011:355 [their Fig. 1], 357–358, their supporting information); Pyron and Wiens (2011:568 [their Fig. 2], their Appendix B.3 [481], their supporting information), in part; Rossa-Feres et al. (2011:52 [their Table 1]); Rivera-Correa et al. (2013:89 [their Fig. 1], 100 [their Appendix II]); Borteiro et al. (2014:393) in part; Duellman et al. (2016:9 [their Fig. 2], 16 [their Fig. 4], 49 [their Fig. 17], 51, 91 [their Appendix 1], 108 [their Appendix 1]), in part [misidentification].

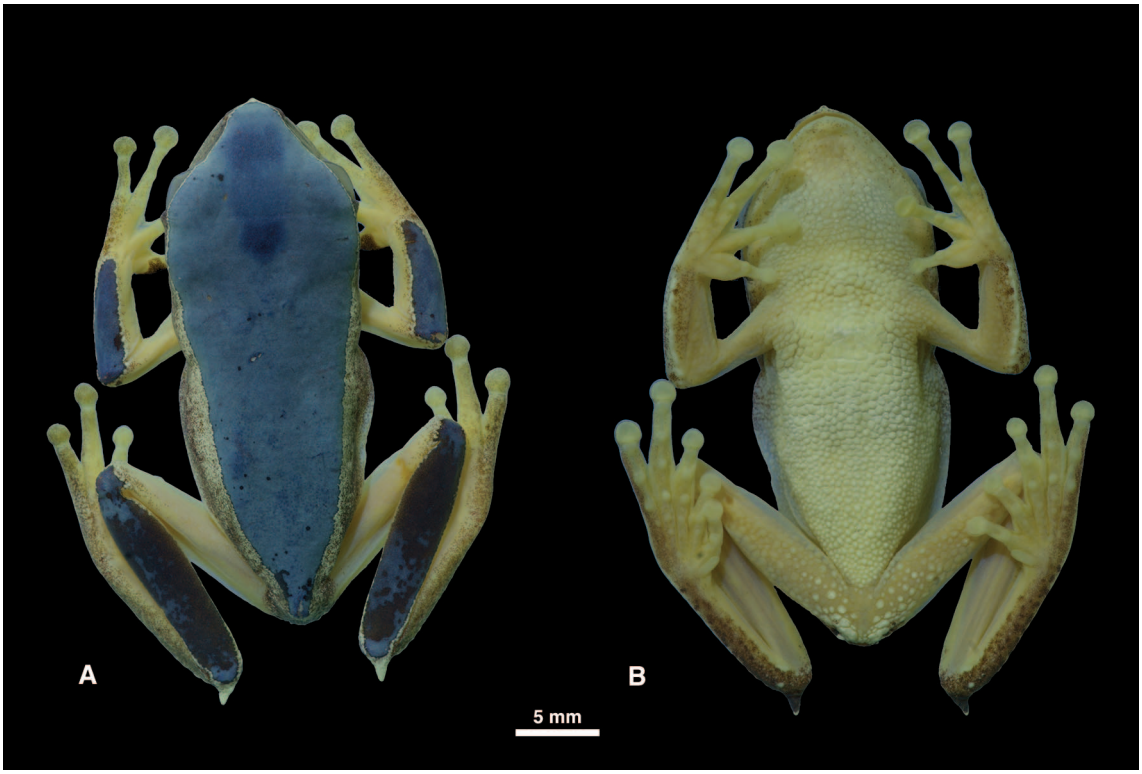

Fig. 9.—Dorsal (A) and ventral (B) views of the holotype of *Phrynomedusa dryade* (CFBH 16026). Adult male from Núcleo Santa Virgínia, Parque Estadual da Serra do Mar, município de São Luiz do Paraitinga, São Paulo, Brazil (SVL 30.9 mm).

Holotype.—Adult male (CFBH 16026) collected at Núcleo Santa Virgínia, Parque Estadual da Serra do Mar, município de São Luiz do Paraitinga, state of São Paulo, Brazil (23°19′55.92″S, 45°5′48.58″W, 979 m a.s.l., datum = WGS84) on 1 October 2005 by L.O.M. Giasson.

Paratopotypes.—Two adult males (CFBH 7613, 7684) collected on 18 October 2004; three adult males (CFBH 7716, 7722, and 7177 [cleared and stained]) collected on 18 November 2004; an adult female (CFBH 16025) collected on 10 December 2004, all specimens were collected in the same pond by L.O.M. Giasson; an adult male (CFBH 38749) collected on 23 January 2015 by F.R. Silva and A.Z. Boaratti.

Paratypes.—One adult male (MNRJ 32861) collected at Cachoeira dos Penha, município de Paraty, state of Rio de Janeiro, Brazil, on 9 March 1979 by S.P. Carvalho-e-Silva and G.N. Silveira; one adult male (MZUSP 137423) collected at Estação Ecológica de Boracéia, município de Salesópolis, state of São Paulo, on 25 September 2004 by M.T. Rodrigues et al.; one adult male (CFBH 22576) collected at Ilha do Cardoso, município de Cananéia, state of São Paulo, Brazil on 10 December 2007 by J. Zina.

Referred specimens.—Juvenile (CFBH 8244), four juveniles metamorphosed from tadpoles kept in the laboratory (CFBH 11386–11389), lot of three tadpoles (CFBH 29573), lot of one tadpole (CFBH 29574), lot of three tadpoles (CFBH 36926), all tadpole lots collected in the same pond at Núcleo Santa Virgínia, Parque Estadual da Serra do Mar, município de São Luiz do Paraitinga, state of São Paulo, Brazil; lot of nine tadpoles (CFBH 38056) collected at Núcleo Curucutu, Parque Estadual da Serra do Mar, município de Itanhaém, state of São Paulo, Brazil on 2 March 2014.

Diagnosis.—A medium-sized phyllomedusine (SVL = 28.4–31.7 mm) associated with the genus *Phrynomedusa* on the basis of phylogenetic placement (see Faivovich et al. 2010) and by the presence of a bicolored iris; a reduced webbing on fingers and toes; presence of a triangular calcar oblique with tarsus sagittal axis, at postaxial margin and covering half the heel; and a tadpole with a complete row of marginal papillae in the oral disc.

Phrynomedusa dryade is distinguishable from all congeners by the following combination of characters: (1) male SVL = 28.4–31.7 mm (n = 8), female SVL = 36.1 mm (n = 1); (2) snout round with a small medial projection in dorsal view and rounded with small medial projection in lateral view; (3) canthus rostralis and loreal region straight; (4) lateral marbled black and white stripe from snout to inguinal region; (5) dentigerous processes of vomer absent; (6) upper lip dermal fringe absent; (7) nuptial pad keratinized, extending to ventral surface of hand, reaching preaxial margin of inner metacarpal tubercle and proximal subarticular tubercle; (8) forearm postaxial margin with small tubercles in series; (9) forearm and fingers not hypertrophied in males; (10) triangular calcar oblique with tarsus sagittal axis, at postaxial margin; (11) calcar covering half of heel; (12) dermal folds or tubercles absent on tarsus postaxial margin.

Comparisons with congeners.—*Phrynomedusa dryade* may be distinguished from its congeners (characters in parenthesis) by male SVL = 28.4–31.7 mm (SVL = 46 mm in *P. bokermanni*); female SVL = 36.1 mm (SVL = 45.6 mm in *P. fimbriata*; SVL = 28 mm in *P. marginata*), snout rounded with a small medial projection in dorsal view (acuminate in *P. appendiculata*, *P. fimbriata*, *P. bokermanni*,

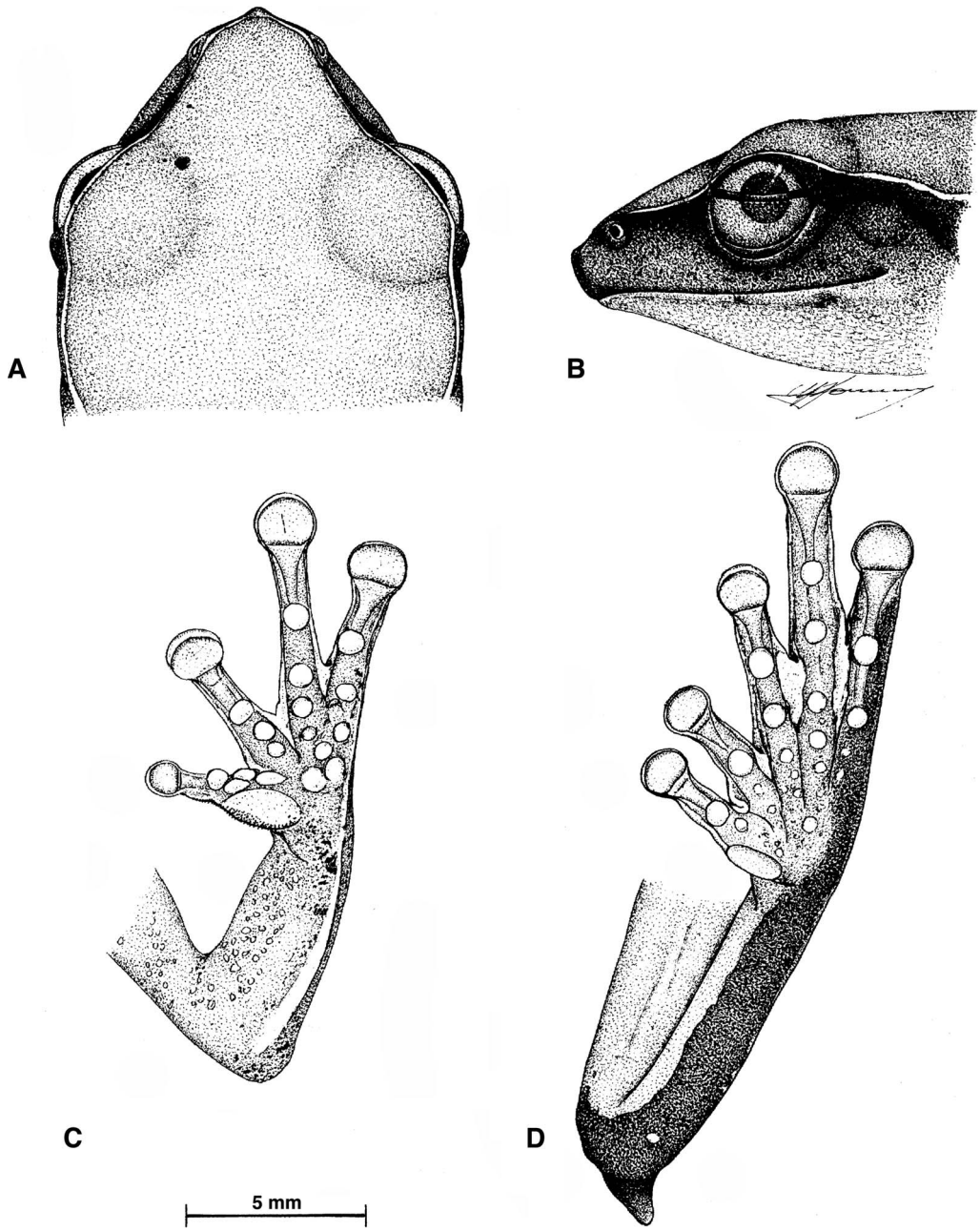

Fig. 10.—Holotype of *Phrynomedusa dryade* (CFBH16026). (A) Head in dorsal view, (B) head in lateral view, (C) left hand in ventral view, (D) left foot in ventral view. A color version of this figure is available online.

and *P. vanzolinii*); rounded with small medial projection (markedly oblique in *P. fimbriata*; oblique in *P. appendiculata*, *P. bokermanni*, and *P. vanzolinii*); canthus rostralis straight (curved in *P. appendiculata*, *P. bokermanni*, and *P. vanzolinii*); loreal region straight (oblique in *P. appendiculata*, *P. bokermanni*, *P. fimbriata*, and *P. vanzolinii*); marbled black and white stripe from the snout to inguinal region (head lateral surface and tympanum green in *P. appendiculata*; cream white in *P. bokermanni*; oblique orange stripe from posterior border of eye to arm insertion in *P. vanzolinii*); marbled black and white stripe extends over dorsum in entire length of body in *P. dryade* (marbled black and white stripe extends over dorsum only in posterior third of body in *P. marginata*); dentigerous processes of vomer absent (present in *P. bokermanni* and *P. vanzolinii*); upper lip dermal fringe absent (present in *P. fimbriata*); keratinized nuptial pads reach ventral surface of hand over first metacarpal and first phalanx and are in contact with the inner metacarpal tubercle and first subarticular tubercle (keratinized nuptial pad does not reach subarticular tubercles in any other species of *Phrynomedusa*); small tubercles in series on forearm postaxial margins (smooth in *P. appendiculata*, *P. marginata*, and *P. vanzolinii*; sparse papillae in *P. fimbriata*); arms and fingers not hypertrophied in males (hypertrophied in males of *P. bokermanni*); triangular calcar oblique with tarsus sagittal axis, at postaxial margin in *P. dryade* (parallel oriented with tarsus sagittal axis in all other species of *Phrynomedusa*); calcar covering half of

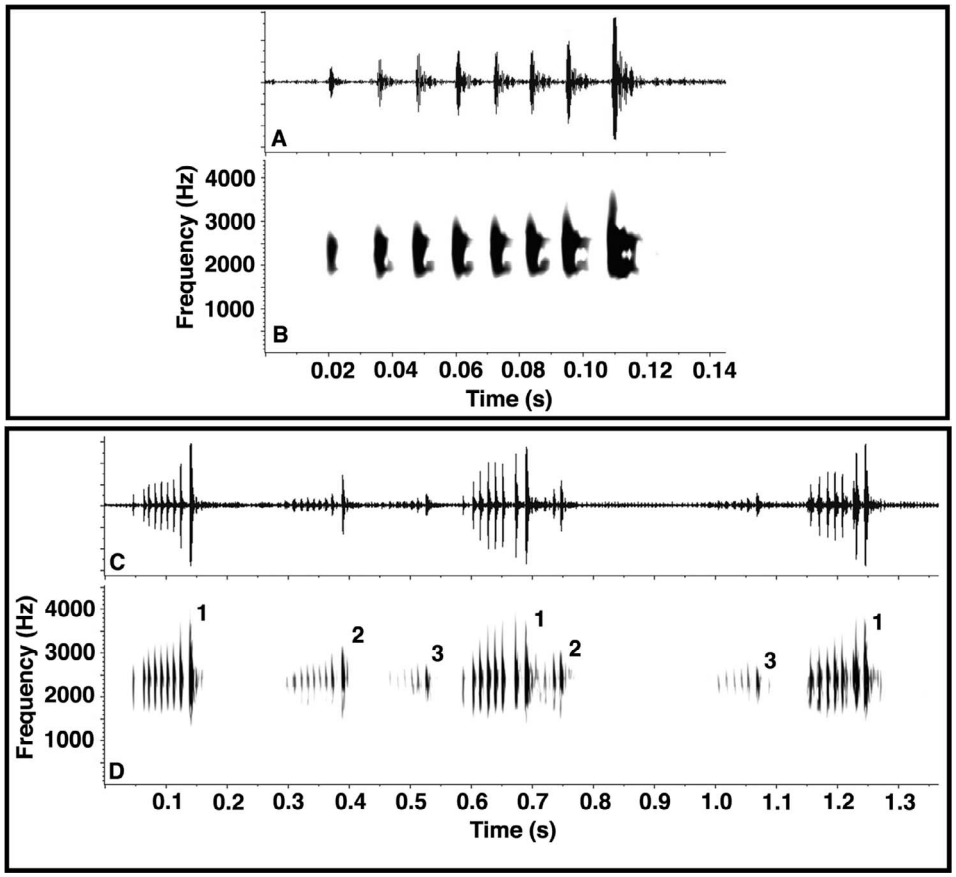

FIG. 11.—Advertisement call of *Phrynomedusa dryade*: (A) Waveform and (B) spectrogram of one note with eight pulses; (C) waveform and (D) spectrogram of advertisement call of three males (indicated by 1, 2, and 3). Vocalization from male paratopotype CFBH 7684 recorded on 18 October 2004, air temperature 17°C.

heel (calcar covering entire heel in *P. fimbriata*; calcar covering one third of heel in *P. bokermanni*, *P. marginata*, and *P. vanzolinii*); dermal folds absent on tarsus postaxial margin (sparse papillae in *P. fimbriata*; smooth in *P. appendiculata*, *P. marginata*, and *P. vanzolinii*).

Description of holotype.—Body robust for genus; head longer than wide (head length 35.3% of SVL); snout rounded with small medial projection in dorsal view, rounded with small medial projection in lateral view; nostrils lateral and not protruded, located on slight projection nearest to tip of snout; internarial distance 93.9% of interorbital distance; canthus rostralis and loreal region straight without flaring on lips; upper lip dermal fringe absent; eye large, its posterior margin in contact with anterior margin of tympanum; palpebral membrane not reticulated; eye diameter 97% of interorbital distance; tympanum visible and rounded; tympanic annulus visible; tympanum diameter equal to width of Finger III disc; supratympanic fold present, from posterior margin of eye passing over tympanum and oblique to insertion of arm; tongue cordiform, anteriorly attached, laterally and posteriorly free, posteriorly with shallow notch; dentigerous process of vomer absent; choanae large and elliptical widely separated; vocal slits lateral and long, from middle of mandible to buccal commissure; vocal sac subgular, not externally evident.

Upper limbs not hypertrophied; forearm with small tubercles in series on postaxial margins; fingers slender; length of Finger I < II < IV < III; subarticular tubercles single, rounded; supernumerary tubercles single, rounded, their diameter less than or equal to subarticular tubercles; inner metacarpal tubercle elliptical, same length as metacarpus and half of metacarpus width; outer metacarpal tubercle absent; adhesive discs elliptical, wider than long; disc on Finger I rounded, smaller than other fingers; reduced webbing between fingers, with the following formula: I absent – absent II 2^{+} – $3^{1/3}$ III 3^{-} – 2^{+} IV; keratinized nuptial pad covers entire dorsal and preaxial surface of Finger I, extending from preaxial margin of finger to adhesive disc base and extending ventrally to preaxial margin of inner metacarpal tubercle and proximal subarticular tubercle.

Hind limbs robust; tibia length 47.5% of SVL; white rounded tubercle on ventral surface of heel; dermal folds absent on tarsus postaxial margins, from calcar to adhesive disc of Toe V; triangular calcar oblique with tarsus sagittal axis, at postaxial margin, covering half of heel width; toes slender, in following order of length: I < II < III < V < IV; subarticular tubercles single and rounded; supernumerary tubercles rounded and smaller than subarticular tubercles; supernumerary tubercles scattered on toes and foot ventral surfaces; inner metatarsal tubercle elliptical; outer metatarsal tubercle absent; adhesive discs rounded; reduced webbing between toes with formula: I2 – 2 II 2 – 3 III 2^{-} – 3 IV $2^{1/2}$ – 2^{+} V.

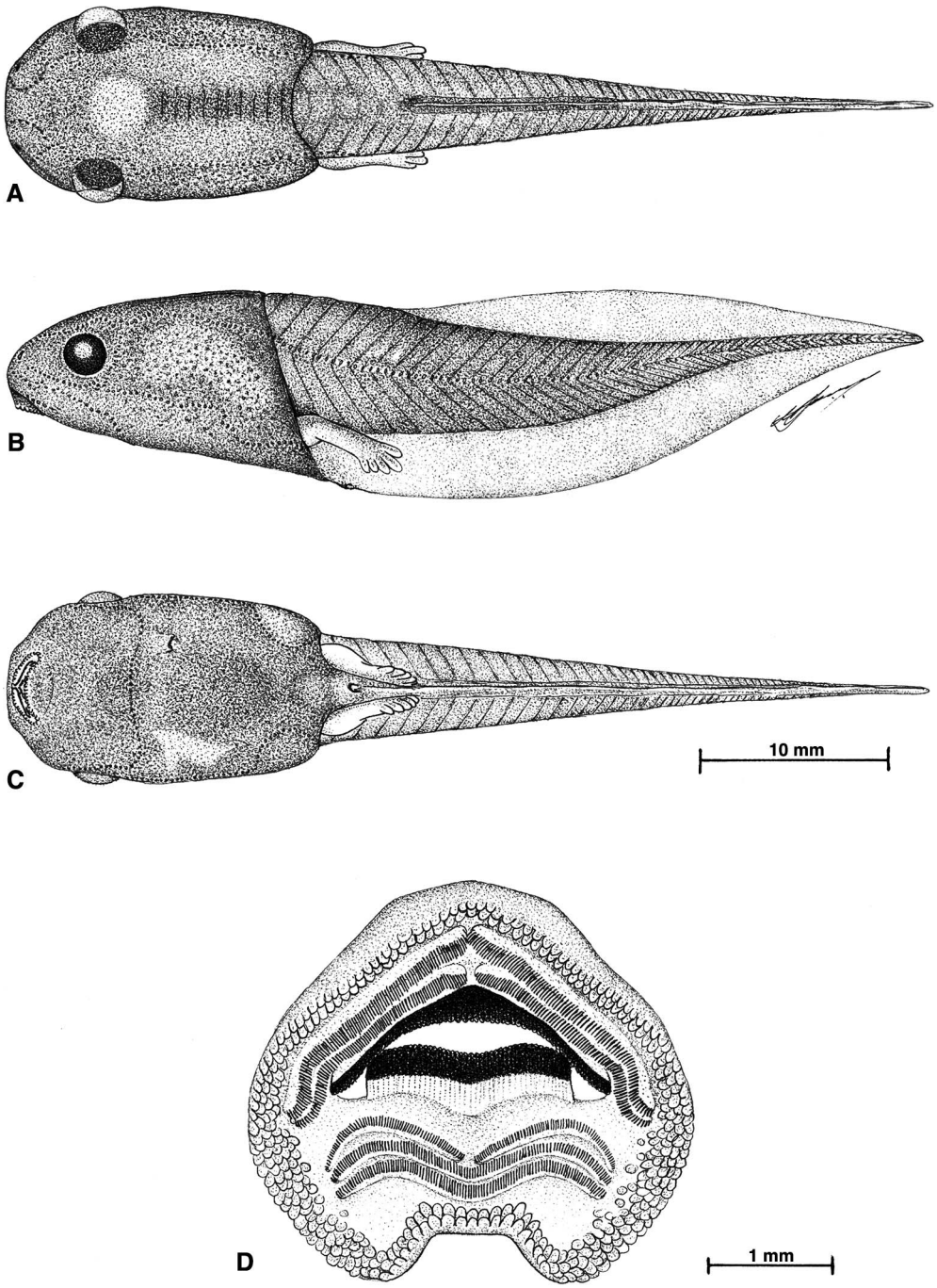

Fig. 12.—Tadpole of *Phrynomedusa dryade* (CFBH29573) and detail of its oral disc.

Skin on dorsum of body and limbs smooth, gular region and venter areolate; ventral surface of limbs smooth; skin of anterior and posterior surface of limbs areolate, some white granular tubercles near articulation of femur with body, increasing in density below cloaca; osteoderms, parotoid, and dorsolateral glands absent; pterorhodin pigment present in skin; cloacal opening at upper level of thighs, with some small tubercles around cloaca, but with no evident ornamentation.

Measurements of holotype (in mm).—Snout–vent length 30.9; head length 10.9; head width 10.4; internarial distance 3.1; interorbital distance 3.3; eye diameter 3.2; eye–nostril distance 2.8; tympanum diameter 1.6; tibia length 14.7; foot length 11.6.

Coloration of holotype in life.—Dorsal surfaces of head, body, forearm, and tibia green, delimited by white line; gular, pectoral region, and venter cream white, with small gray dots on anterior gular region; iris bicolored, dark yellow in upper and lower surfaces, with horizontal diffuse dark stripe in middle of eye; marbled black and white stripe on flanks from tip of snout to inguinal region, less dark near dorsal region; marbled black and white stripe limited anterodorsally by loreal region and dorsal margin of eye and tympanum, extending over dorsum reaching dorsal

cloacal region; Fingers I–III light orange; Finger IV marbled black and white from adhesive disc to forearm; hands light orange; postaxial margin of forearm marbled black and white; arm dorsal surfaces bright orange; Toes I–IV bright orange; Toe V marbled black and white, from adhesive disc to tarsus; dorsum and postaxial margin of tarsus marbled black and white; tarsus ventral surface dark brown pigmented from heel to Toe V; calcar white dorsally, marbled black and white ventrally; femur dorsal surfaces bright orange, with spaced white tubercles concentrated near cloacal region; cloacal region marbled black and white, continuous with color of flanks; white line below cloacal opening.

Coloration of holotype in preservative.—After 11 yr of preservation, the holotype is more faded. The most significant difference is that the green regions are pale blue and the bright orange regions are an almost transparent orange cream coloration.

Etymology.—The specific epithet "dryade" is in the genitive case and is derived from the Ancient Greek "dryas" (tree) and the suffix "ades" (from trees). The new name is a noun in apposition. In Greek mythology, dryads were the rare guardian deities of forests and woods. The German naturalist K.F.P. Martius (Martius et al. 1840) used the term 'Dryads' in the first phytogeographic division of Brazilian territory into five floristic regions, in which Dryads was the term used to refer to Atlantic Coastal Forest. The name of this new species refers to the occurrence of this beautiful Monkey Frog in the Atlantic Forest Domain.

Distribution.—*Phrynomedusa dryade* is known only from five localities in southeastern Brazil: four localities in state of São Paulo (municípios de Cananéia, Salesópolis, Itanhaém, and São Luiz do Paraitinga) and one locality in state of Rio de Janeiro (município de Paraty; Fig. 1).

Advertisement call.—The advertisement call of *Phrynomedusa dryade* consists of a series of pulsed notes with 6–12 pulses ($\bar{X} = 9 \pm 1.478$ pulses, $n = 67$; Fig. 10). The note durations are 0.079–0.148 s ($\bar{X} = 0.114 \pm 0.015$ s, $n = 68$), with a note interval of 0.261–0.588 s ($\bar{X} = 0.386 \pm 0.081$ s, $n = 32$). The pulses durations are 0.003–0.017 s ($\bar{X} = 0.008 \pm 0.002$ s, $n = 485$) and have a pulse rate of 55.556–94.340 s ($\bar{X} = 75.397 \pm 9.565$ s, $n = 67$). The pulse intervals between its upper limits of frequency are 0.004–0.026 s ($\bar{X} = 0.013 \pm 0.003$ s, $n = 429$) and the spacing between pulses is regular, though irregularly spaced pulses also occur. There is a gradual increase in the amplitude of the pulses; the last pulse has the upper limits of frequency 3–15 times greater than the first pulse, which can be observed in the oscilogram and spectrogram (Fig. 10 A–D). The lower limits of frequency bands are 1083–1483 Hz ($\bar{X} = 1333 \pm 94$ Hz, $n = 35$) and the upper limits of frequency bands are 3285–5448 Hz ($\bar{X} = 4515 \pm 548$ Hz, $n = 35$). The dominant frequencies are 1723–2412 Hz ($\bar{X} = 2225 \pm 297$ Hz, $n = 35$).

Tadpole external morphology (CFBH 29573, Stage 36 of Gosner 1960).—Body depressed (height of body 90% of its width), elliptical in dorsal view and oval in lateral view (Fig. 11 A, B); body length 30% of total length; body high 60% of body length; snout rounded in dorsal and lateral views; nostrils oval, slightly lateral (oblique to body sagittal axis); nostril positioned closer to tip of snout than eyes; eyes laterally positioned and directed; interorbital distance 50% of body width; interorbital distance 2× eye diameter; oral disc anteroventral (Fig. 11C); oral disc width 40% of body width; two rows of marginal papillae on upper and lower lips; dorsal gap on marginal papillae absent; a few scattered submarginal papillae on ventrolateral portions of posterior labium; labial tooth row formula 2(2)/3(1); A1 and A2 of equal length; P1, P2, and P3 of equal length; jaw sheaths darkly brown pigmented and finely serrated on margins; upper jaw sheath U-shaped; lower sheath V-shaped (Fig. 11D).

Spiracle ventral and sinistral; spiracle not expanded externally, with its inner wall absent; spiracle directed posteriorly, opening at middle third of body; spiracle opening visible only by presence of small, crescent-shaped slit in skin (Fig. 11C); spiracle inner wall absent; vent tube dextral, medial, short, and narrow; ventral tube opening directed posteriorly; ventral tube attached to ventral fin via an intervening fleshy membrane; tail length about 70% of total length; tail musculature well developed; dorsal fin emerging at first third of caudal musculature; ventral fin beginning anterior to vent tube.

Lateral line system visible as series of elliptical, vertical, whitish stitches, sometimes difficult to see; supraorbital lines consisting of irregular series of neuromasts from anteromedial region between nares, above eyes, to posteromedial region of body; posterior supraorbital lines consisting of irregular series of neuromasts from anteromedial region between nares, above eyes to posteromedial region of body; posterior supraorbital line continuous with middle ventral line in tail; infraorbital line curves from anterolateral region, above nares to insertion of posterior limbs (Fig. 11A–C); anterior oral neuromasts curve above infraorbital line from anterolateral region to ventral region, anterior to spiracle opening (Fig. 11B, C).

Color of tadpoles in preservative.—Coloration of the body and tail musculature is predominantly brown, with a few small white spots that vary in size and distribution, thereby giving the tadpole a marbled brown and cream appearance. The tail musculature has a well-marked, median lateral brown line, originating near the middle region of the body and extending posteriorly for the length of the tail. Some tadpoles also have a dorsal brown line on the tail, from the junction with the body to the tip of the tail. The coloration of the body and tail musculature is more evident in tadpoles of more-advanced stages of development (Stage 39 and later). Dorsal and ventral fins are unpigmented. Tadpoles in Stages 25–36 may be transparent; however, the dorsal and lateral median brown lines of the tail are always present. The abdomen has the same marbled coloration as the rest of the body except in the region of the visceral mass, which is unpigmented; iris black.

Natural history.—The new species was found in the município de São Luiz do Paraitinga, only in one pond located next to the Ipiranga river trail near the crossing of the Angelim River. The pond is located in forest and is shaded by the canopy. The pond retains water throughout the year, but the level changes according to season and rainfall. The bottom of the pond is rocky and covered by leaf litter. During monthly samples, vocalization activity of *Phrynomedusa dryade* was recorded during field trips from October 2004 to February 2005 and August 2005 to February 2006, with the exception of December 2005 when no field trips occurred. The greatest number of calling males, about five, was recorded in October and November 2004; in

December 2004 only a female was found in a bromeliad and in August 2005 only sparse vocalizations were heard from a single male. In the remaining months (January, February, September, October, and November 2005; January and February 2006), two to four individuals were actively vocalizing. Vocalizations started at sunset and intensified between 1 and 2 h after sunset. Males called from shrubs and trees while perched directly on the branches and trunks or in bromeliads. Males were perched at lower heights (0.4–2.0 m) above the ground when calling activity was more intense. On these occasions there were vocal interactions, and vocalizations had up to five pulsed notes emitted at regular spacing (Fig. 10). Once on 18 November 2004, we observed two males close to each other on a perch, interacting with aggressive vocalizations (the recordings were not analyzed due to their low quality) and pursuits with quick jumps, but we did not observe fights. When collected, individuals displayed remarkable agility with fast movements and jumps, an unusual behavior for Phyllomedusidae. During the more-dry or more-cold months (August and September), the vocalizations were more sporadic, and males were at higher perches (about 3 m), apparently calling from inside bromeliads. Amplectant pairs and egg clutches were not observed. Tadpoles were recorded throughout most of the year and were usually observed swimming with head upward in an almost vertical position (more than 45°), vibrating the terminal portion of the tail near the water surface. The pattern of coloration in metamorphosing specimens is the same as that of the adults. However, the dorsal surface of the body is faded green and the surfaces of the flanks and limbs are cream white. Other species that vocalized in the same pond were *Physalaemus olfersii*, *Aplastodiscus leucopygius*, *Dendropsophus microps*, and *Scinax hayii*.

Remarks.—In an extensive phylogenetic analysis of the subfamily Phyllomedusinae, Faivovich et al. (2010) employed a pairwise comparison of the 12S mitochondrial DNA sequences between one sample of a topotype of *Phrynomedusa marginata* (USNM 217827) and two samples of *P. dryade* (misidentified as *P. marginata* in Faivovich et al. 2010) from the municípios de São Luiz do Paraitinga (CFBH 7613, paratype of *P. dryade*) and Salesópolis (MZUSP 137423 paratype of *P. dryade*), both in the Serra do Mar of SP. The percentage of uncorrected pairwise *p*-distances between the overlapping regions 12S from specimens of Espírito Santo and São Paulo was 3.0%. Based on this result, these authors suggested that the divergence warranted a careful taxonomic revision of the material assigned to *P. marginata*. We examined the vouchers of these samples and found that besides the molecular differences, the specimens differ morphologically and can be recognized as two distinct taxa. The specimen from Santa Teresa, ES (USNM 217827) clearly is a topotype of *P. marginata*; however, the specimens from the municípios de São Luiz do Paraitinga and Salesópolis, SP (CFBH 7613 and MZUSP 137423) belong to the new species described herein, thereby corroborating the molecular differences obtained by Faivovich et al. (2010).

Weygoldt (1991) presented a succinct description of the call of *P. marginata* from specimens in a terrarium and only presented information about call duration, call interval, and dominant frequency. The comparison of Weygoldt's (1991) call description and the advertisement call of the new species reveal similarities between the call of *P. dryade* and *P. marginata*. Most importantly, the call interval is shorter in *P. dryade* (0.261–0.588 s) than in *P. marginata* (2.0–9.0 s). Ranges for the call durations and main dominant frequencies overlap in these two species.

Heyer et al. (1990) described the tadpole of *P. vanzolinii* from Estação Biológica de Boracéia, SP (MZUSP 36559) where *P. dryade* also occurs. Known tadpoles of *Phrynomedusa* have similar characters in external morphologies; however, origin of the dorsal fin can be used to differentiate tadpoles of *P. dryade* from those of *P. vanzolinii*. Tadpoles of *P. dryade* have the dorsal fin emerging above the first third of caudal musculature whereas the fin emerges at the junction of the body and tail musculature in tadpoles of *P. vanzolinii*.

Phrynomedusa marginata and *P. dryade* are morphologically similar, but the similarities are primitive characters found among other species of Phyllomedusidae, mainly among species of the genera *Phasmahyla* and *Pithecopus*. We examined almost all known specimens (with exception of specimens from municípios de Paraty and Paraibuna, RJ) of these two species, and the characteristics that we found to distinguish both are consistent in the examined material.

Diversity and Conservation of *Phrynomedusa*

Phrynomedusa can be considered the rarest hylid genus of the Brazilian Atlantic Forest and constant efforts must be made to re-encounter these rare Tree Frogs. Species of the genus *Phrynomedusa* are known from only 61 specimens since the first description in 1898. Except by *P. appendiculata* and *P. marginata*, which are known from 24 and 19 specimens respectively, all other species are known from only a few specimens. *Phrynomedusa bokermanni* and *P. fimbriata* remain known only from their holotypes, whereas *P. vanzolinii* is known from five specimens and *P. dryade* from 11 specimens. Until the last 30 yr, only eight specimens of *Phrynomedusa* were found at município de Paraibuna, RJ (Carvalho-e-Silva et al. 2007) and Santa Teresa, ES (MNRJ 57954).

Only two species of *Phrynomedusa* occur with certainty in protected areas: *P. vanzolinii* was found at Parque Nacional da Serra dos Órgãos (município de Teresópolis, RJ) and at Estação Biológica de Boracéia (município de Salesópolis, SP) whereas *P. dryade* was found at Estação Biológica de Boracéia (município de Salesópolis, SP) and at Núcleo Santa Virgínia and Núcleo Curucutu of Parque Estadual da Serra do Mar (municípios de São Luiz do Paraitinga and Itanhaém, SP). *Phrynomedusa appendiculata* and *P. fimbriata* may occur in protected areas at Paranapiacaba, município de Santo André, SP; however, due to the uncertainty concerning the collection localities of these species, it does not allow us to unequivocally report them from these protected areas. Both specimens were collected in Paranapiacaba without a more-precise locality.

Rodriguez et al. (2014) made a retrospective analysis of preserved Atlantic Forest anurans collected over a span of 116 yr to determine spatial and temporal evolutionary dynamics of *Batrachochytrium dendrobatidis* lineages in the Atlantic Forests. Besides their large sample, Rodriguez et al. (2014) do not include any *Phrynomedusa* species in this

analysis. It is an interesting issue because Jenkinson et al. (2016) found that *B. dendrobatidis* occurs in two localities were *Phrynomedusa* presumably disappeared, Santa Teresa, ES and at Parque Nacional da Serra dos Órgãos, RJ. At these two localities, Heyer et al. (1988) and Weygoldt (1989) reported amphibian declines. Thus, the potential effect of *B. dendrobatidis* on *Phrynomedusa* certainly warrants further study.

Another important issue is the phylogenetic position of *Phrynomedusa* in Phyllomedusidae systematics. *Phrynomedusa* and *Cruziohyla* are the most-basal genera of Phyllomedusidae. Thus, better knowledge about its morphological characteristics (e.g., musculature, osteology, tadpoles, natural history) is important to understand some issues about morphological evolution in Phyllomedusidae.

In spite of the rarity of specimens of this genus, it was still possible to identify a new species of *Phrynomedusa*, thereby demonstrating how anuran biodiversity in the Brazilian Atlantic Forest remains underestimated. The discovery of new specimens of *Phrynomedusa* and the addition of more morphological and molecular information is fundamental to a better understanding of the diversity in this genus.

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Appendix

Specimens Examined

Agalychnis annae.—**COSTA RICA**: CARTAGO: Cartago, bridge over Rio Grande (MNRJ 3638, 14633–14634, MZUSP 8040); **HONDURAS**: GRAÇAS A DIOS: Warunta (USNM 563935–563936).

Agalycnis buckleyi.—**ECUADOR**: NAPO: Santo Inecel, Rio Quijos, San Rafael waterfall (MZUSP 55616–55617).

Agalychnis callidryas.—**PANAMÁ**: Canal Zone (MNRJ 49218).

Agalychnis dacnicolor.—**MÉXICO**: MICHOACÁN: unknown locality (MNRJ 2792, 2794, 12498, 12500, 50065–50066).

Agalychnis hulli.—**ECUADOR**: PASTAZA: Santa Clara, San José, Centro Ecológico Sancha Arajuno (MNRJ 74777–74779).

Agalychnis lemur.—**COSTA RICA**: ALAJUELA: Cariblanco, 2.4 mi (by road) S and 1.6 mi (by road) E of, on road to Colonia Virgen del Socorro, along Rio Sarapaqui (USNM 219913–219915); CARTAGO: Tapanti, at bridge across Rio Grande de Orosi (USNM 219950–219951), Tapanti (MNRJ 4083, 15390); PUNTARENAS: La Palma (USNM 75066); SAN JOSE: San Jose, ca. 17 km (airline) NE of Alto La Palma (USNM 219974, 219979); **PANAMÁ**: DÁRIEN: Cerro Malí, head of Rio Pucuro (USNM 151079).

Agalychnis moreletii.—**GUATEMALA**: ALTA VERAPAZ: Senahu (USNM 35923); unknown locality (USNM 63004); **MÉXICO**: OAXACO: Mirador (MNRJ 49228); VERACRUZ: Finca Juarez (MZUSP 5120).

Agalychnis spurrelli.—**EQUADOR**: ESMERALDAS: Durango (MNRJ 74783–74785).

Callimedusa atelopoides.—**BRAZIL**: ACRE: município de Cruzeiro do Sul, Parque Nacional da Serra do Divisor (UFAC 1805, 3819).

Callimedusa perinesos.—**EQUADOR**: CHINCHIPE: Zamora, Las Penas, Los Encontros (MNRJ 74786, 74788–74789); NAPO: 14.7Km N Rio Salado (MZUSP 56389).

Callimedusa tomopterna.—**BRAZIL**: AMAZONAS: município de Manaus, Reserva Florestal Adolpho Ducke (MNRJ 4558, 57955); município de Manicoré (MPEG 17370–17375); município de Presidente Figueiredo, UHE Balbina (MNRJ 32887); PARÁ: Belém, EMBRAPA, (MNRJ 51031, 51032); município de Oriximiná, Jatuarava (MNRJ 51030), Porto Trombetas (MPEG 11157–11162); RONDÔNIA: município de Alto Paraíso (MZUSP 61145–61153); **EQUADOR**: ORELLANA: Francisco de Orellana, Estación Científica Yasuni (MNRJ 74795–74797).

Cruziohyla calcarifer.—**EQUADOR**: ESMERALDAS: São Francisco (MNRJ 74789–74791).

Hylomantis aspera.—**BRAZIL**: BAHIA: município de Camamu, Projeto de Assentamento Zumbi dos Palmares (MNRJ 27204–27205), Fazenda Canavieiras (MNRJ 27206); município de Ilhéus, Sede Regional da Comissão Executiva do Plano da Lavoura Cacaueira (UFBA 8293); município de Porto Seguro, Reserva Particular do Patrimônio Natural Estação Veracel (CFBH 36780–36784; MNRJ 25591, 28891–28893, 42550–42554, 44582); município de Prado, Parque Nacional do Descobrimento (MNRJ 29200); município de Uruçá, Parque Estadual da Serra do Conduru (MNRJ 35370–35376, MZUSP 81484).

Hylomantis granulosa.—**BRAZIL**: BAHIA: município de Amargosa, Serra do Timbó, (UFBA 7300–7302).

Phasmahyla cochranae.—**BRAZIL**: MINAS GERAIS: município de Lima Duarte, Parque Estadual do Ibitipoca (MNRJ 24839); SÃO PAULO: município de Campos do Jordão, Fazenda Lagoinha (paratype: MNRJ 74152); município de Jundiaí, Serra do Japi (JPPJ 240–241, 768, 797, 1047, MNRJ 4175, 57956–57957); município de São José do Barreiro, Serra da Bocaina, Campo de Fruticultura (holotype MZUSP 74448; paratypes: 74042–74048, 74449, 75619); Ponte Alta (MNRJ 4027, 49248–49249); município de Ribeirão Grande, Parque Estadual Intervales, Trilha roda d'água (MNRJ 28021).

Phasmahyla cruzi.—**BRAZIL**: SÃO PAULO: Ubatuba (CFBH 4286, 5704); RIO DE JANEIRO: município de Angra dos Reis (MNRJ 53769–53770).

Phasmahyla exilis.—**BRAZIL**: ESPÍRITO SANTO: município de Cariacica, Reserva Biológica Duas Bocas (MBML 1267, 4859, 4894, 5489–

5491, 5493, 6344, 6346–6348; MNRJ 24633); município de Santa Teresa (holotype EI 5584, paratypes: EI 5586, MNRJ 4120).

Phasmahyla guttata.—**BRAZIL**: RIO DE JANEIRO: município de Duque de Caxias (MNRJ 671, 677, 2253, 54588); município do Rio de Janeiro (syntypes: AL-MN, 983, 447–0449, 1118; topotypes: Al-MN 1973, 2767, 2768, 3233, 3624, 3625, 3685–3690, 3714, 3715, MNRJ 1840, 3866–3867, 41687–41692, 49229, 49231–49232, 49237–49238, 49243, 49244, 49247, 49252–49253, 49254, 49290, 49324), Jacarepaguá (MNRJ 27636, 27728); município de Saquarema (MNRJ 30285); município de Santa Maria Madalena (MNRJ 51811); município de Teresópolis (MNRJ 49231–49232, 49235–49236, 49250, 54016).

Phasmahyla jandaia.—**BRAZIL**: MINAS GERAIS: município de Barão de Cocais (MCNAM 4420); município de Caeté (MCNAM 1347); município de Cardeal Mota (MNRJ 6337, 6354); município de Catas Altas, Reserva Particular do Patrimônio Natural Santuário do Caraça, banho do Belchior (MNRJ 49708–49710, 55004, 60476–60478, 71955–71956, 73710); município de Conceição do Mato Dentro, Alto Palácio (MNRJ 39980–39981), (MCNAM 7861–7863; MNRJ 49461–49463, 49480, 49481); município de Congonhas do Campo, Mascate (LZV 11325A–11327A); município de Nova Lima (MCNAM 3202; MNRJ 49464–49469); município de Santa Bárbara (MNRJ 49708–49710, 55004); município de Santana do Riacho (Jaboticatubas in original description; holotype: MZUSP 74443; paratypes: MNRJ 4104, MZUSP 73730–73731, 73734–73735), Serra do Cipó, km 126 (MNRJ 71955–71956).

Phasmahyla spectabilis.—**BRAZIL**: BAHIA: município de Jussari (paratype: MNRJ 28425); município de Camacan (UFBA 9222–9223); MINAS GERAIS: município de Santa Maria do Salto (holotype: MNRJ 43078; paratypes: 43076–43077, 43079, 43080–43082).

Phasmahyla timbo.—**BRAZIL**: BAHIA: município de Amargosa (paratypes: MNRJ 52061–52065; topotypes UFBA 7987–7988, 8335).

Phrynomedusa appendiculata.—**BRAZIL**: SANTA CATARINA: município de Lauro Muller, Novo Horizonte (MZUSP 35182 [cleared and stained], MZUSP 35183–35194); município de São Bento do Sul (holotype: AL-MN 770); SÃO PAULO: município de Santo André, Paranapiacaba (MZUSP 4094, 9678, 81423–81424, 81426–81431).

Phrynomedusa bokermanni.—**BRAZIL**: SÃO PAULO: município de Mongaguá (holotype: MZUSP 81340 [ex-WCAB 49654]).

Phrynomedusa fimbriata.—**BRAZIL**: SÃO PAULO: município de Santo André, Paranapiacaba, alto da Serra de Cubatão (holotype: MZUSP 316).

Phrynomedusa marginata.—**BRAZIL**: ESPÍRITO SANTO: município de Santa Teresa (paratypes: MNRJ 4100–4101, 60139; MZUSP 74149 [ex-EI 5183]. Topotypes: MNRJ 46881, 57954, USNM 217823–217829.

Phrynomedusa vanzolinii.—**BRAZIL**: RIO DE JANEIRO: município de Teresópolis (paratype: AL-MN 1983), Parque Nacional da Serra dos Órgãos (topotype: MZUSP 81421 [ex-WCAB 37134]); SÃO PAULO: município de Salesópolis, Estação Biológica de Boracéia (holotype: MZUSP 37669; paratypes: MZUSP 3998, 9387).

Phyllomedusa bahiana.—**BRAZIL**: BAHIA: município de Belmonte, Mata da Elmasa (MNRJ 46864–46865); município de Caetité (MNRJ 25019–25520, 27454); município de Feira de Santana (MNRJ 478289–47830); município de Guaratinga, Fazenda Bela Vista (MNRJ 29785); município de Ilhéus (MNRJ 252, 67424); município de Itapetinga (MNRJ 16876); município de Itagiba, Fazenda Pedra Branca (MNRJ 65362–65365); município de Ituberá, Reserva da Michelin (MNRJ 51723); município de Jiquiriça, Fazenda Encobal (MNRJ 44980); município de Jussari, Reserva Particular do Patrimônio Natural Serra do Teimoso (MNRJ 27236, 44968–449690); município de Maracás, Nascente do Rio Jiquiriça, (MNRJ 50209–50212); município de Mascote, Fazenda São José (MNRJ 40453–40454); município de Porto Seguro, Reserva Particulara do Patrimônio Natural Estação Vera Céu (MNRJ 25595, 42660–42661); município de Santa Cruz Cabrália, Mata Cara Branca (MNRJ 27237); município de São José da Vitória (MNRJ 47793–47794); município de Valença (MNRJ 36961); ESPÍRITO SANTO: município de Conceição da Barra, Floresta Nacional do Rio Preto (MNRJ 30054–30055); SERGIPE: município de Indiaroba, Povoado do Retiro, Fazenda Sabão (MNRJ 46750–46753; 49740–49742); município de Salgado, Sítio do Jagarane (MNRJ 17987).

Phyllomedusa bicolor.—**BRAZIL**: AMAZONAS: Fonte Boa, Alto Solimões (MNRJ 255); PARÁ: município de Belém, Utinga (MNRJ 254, 2556); município de Oriximiná (MNRJ 49661–49665, 56668), Porto Trombetas, Floresta Nacional Saracá-Taquera, Platô Aviso (MNRJ 52970–52972).

Phyllomedusa boliviana.—**ARGENTINA**: ORAN: unknown locality (MNRJ 53651); **BOLÍVIA**: SANTA CRUZ: El Pailón (paratypes MZUSP 74177–74178); **BRAZIL**: MATO GROSSO: município de Aripuanã (MNRJ 44204–44207); município de Juína (UFMT 6199, 6201, 6204–6205, 6208), Reserva do Cabaçal (UFMT 2127), Vale de São Domingos (UFMT 1908–1910, 2363, 6216–6220).

Phyllomedusa burmeisteri.—**BRAZIL**: ESPÍRITO SANTO: município de Aracruz, Microbacias (MNRJ 17764–17771); município de Baixo Guandú (MNRJ 53649–53650); Barra Seca (MNRJ 3069); município de Conceição da Barra, Floresta Nacional do Rio Preto (MNRJ 20894–20898, 29825–29834, 30051–30055); município de Linhares (MNRJ 36059–36093, 36273), Fazenda Pirajá (MNRJ 29082), Reserva da Vale do Rio Doce (MNRJ 22721–22723, 32316–32317), Reserva Biológica Sooretama (MNRJ 35007); município de Mimoso do Sul (MNRJ 65310); município de Muniz Freire, Fazenda Recanto da Mata (MNRJ 26024–26027); município de Muniz Freire, São Simão (MNRJ 51929); município de Santa Teresa, Reserva Biológica Melo Leitão (MNRJ 34931), São Lourenço (MNRJ 30434), Sítio do Popota (MNRJ 56011–56013), Sooretama, Parque Sooretama (MNRJ 1683–1700; 8849–8860); MINAS GERAIS: município de Barão de Cocais (MNRJ 67421); município de Belmiro Braga, São José (MNRJ 27494, 27526); município de Belo Horizonte (MNRJ 10085–10086, 67311); município de Carmo do Rio Claro (MNRJ 3129); município de Catas Altas, Reserva Particular do Patrimônio Natural Santuário do Caraça (MNRJ 38481–38482, 49667–49668, 55084–55090, 60353–60359, 61346); município de Chiador (MNRJ 37210–212); município de Congonhas do Campo (LZV 1268A, 1315A–1316A); município de Cristália (MNRJ 32318–32319); município de Juiz de Fora, Água Limpa Estação Agrícola (MNRJ 10080), Privilégio (MNRJ 43656); município de Ouro Branco (LZV 1275A, 1345A, 1526A); município de Ouro Preto (LZV 189A, 196A, 1286A–1287A, 1329A), Estacão Ecológica do Tripuí (LZV 386A–387A); município de Paula Cândido (MNRJ 60315–60318); município de Pitangui (MNRJ 834, 5840); município de Santana do Deserto, Mata da Gruta (MNRJ 50322); município de Santana do Jacaré (MNRJ 36993–36995); município de Timóteo, Recanto Verde (LZV 205); município de Turmalina, Peixe Cru (MNRJ 33206–33207); município de Viçosa (MNRJ 65311); município de Volta Grande (MNRJ 56961–56962); RIO DE JANEIRO: município de Angra dos Reis (MNRJ 250, 5237–5238); município de Araruama (MNRJ 10078); município de Barra Mansa (MNRJ 34538–34541); município de Cachoeiras de Macacu, Reserva Ecológica de Guapiaçu (MNRJ 47954); município de Duque de Caxias (MNRJ 1538, 1667, 1772, 2343, 2426, 2480, 3079, 10069, 10070), Barro Branco (MNRJ 1429, 1586, 3083, 13297, 67493), Pilar (MNRJ 4397), Taquara (MNRJ 54770); município de Iguaba Grande, Núcleo Experimental Iguaba Grande (MNRJ 57805); município de Itaperuna (MNRJ 54020); município de Itatiaia (MNRJ 10087–10088, 67499); município de Niteroi (MNRJ 31316, 31562, 51540); município de Nova Iguaçu (MNRJ 67422–67423); município de Engenheiro Paulo de Frontim, Sítio Pau Ferro, Morro Azul (MNRJ 2100, 21005); município do Rio de Janeiro (MNRJ 251, 1433, 11286, 2164, 56841, 60678, 67308–67310, 67494, 67496, 67500), Campo Belo (MNRJ 1319), Campo Grande (MNRJ 10084); município de Saquarema, Palmital (MNRJ 30324); município de São Gonçalo (MNRJ 67495); município de São Pedro da Aldeia (MNRJ 21729, 21730); município de Tanguá (MNRJ 55610); município de Teresópolis (MNRJ 776, 5233–5235, 67492); município de Trajano de Morais (MNRJ 63725); município de Três Rios (MNRJ 37214–37216); SÃO PAULO: município de Botucatu (MNRJ 65155–65159), Rubião Júnior (MNRJ 10094, 10095); município de Pardinho, Fazenda Santo Antônio (MNRJ 65154).

Phyllomedusa camba.—**PERU**: UCAYALI:Pucallpa (MNRJ 53647).

Phyllomedusa distincta.—**BRAZIL**: PARANÁ: município de Bituruna (MNRJ 3719, 10071–10072, 19318); município de Guaraqueçaba (MNRJ 10090, 10093, 33759, 54652); SANTA CATARINA: município de Brusque, Mata do Müller (MNRJ 10077); município de Joinvile (MNRJ 2146); município de Porto Belo (MNRJ 19314–19315, 61510–61522); município de Santa Luzia (MNRJ 10079); município de São Bento do Sul (MNRJ 44496); Rio Vermelho (MNRJ 61529–61534); SÃO PAULO: município de Eldorado Paulista, Sítio das Nascentes (MNRJ 4732, 47743); município de Jacupiranga (MNRJ 61494–61504, 61505–61508, 61526–61528, MNRJ 61535–61541), Fazenda Seara (MNRJ 61484–61493), Juréia (MNRJ 39920, 39929); município de Periquera-Açu (MNRJ 61866–61867); município de Pedro de Toledo (MNRJ 10081–10083, 67425–67427); município de Ribeirão Branco, Fazendinha São Luís (MNRJ 17640, 17643–17647, 18703), Fazenda Mathedi (MNRJ 18246); município de Ribeirão Grande, Lago Negro, Parque Estadual Intervales (MNRJ 28032–28037).

Phyllomedusa sauvagii.—**ARGENTINA**: SALTA: Güemes (MNRJ 50965–50966), El Rey, Parque Nacional Fiuca (MNRJ 50924), Manancial (MNRJ 50963); TUCUMÁN (MNRJ 3483). **BRAZIL**: MATO GROSSO DO SUL: município de Ponta Porã (MNRJ 51521–51523); **PARAGUAI**:

PRESIDENTE HAYES: Plazo Colorado, Hotel Kai, Ruta Transchaco, km 222 (MNRJ 19385–19389, 61315–61341, 61325, 61542–61547).

Phyllomedusa tarsius.—**BRAZIL**: ACRE: Rio Branco (MPEG 5681–5684). AMAZONAS: Manaus, Reserva Florestal Adolpho Ducke (MNRJ 53647).

Phyllomedusa tetraploidea.—**BRAZIL**: SÃO PAULO: Paranapanema, Fazenda Holambra II (paratypes MNRJ 10787–10788, MZUSP 74175–74176); município de Pardinho, Fazenda Santo Antônio (MNRJ 66564); município de Pirajú (MNRJ 19407, 19409–19413); município de Ribeirão Branco (MNRJ 17641–17642, 18704). SANTA CATARINA: município de Xanxerê, Santa Manella waterfall (MNRJ 42287); PARANÁ: município de Bituruna, Rio Iguaçu (MNRJ 10073, 35525).

Phyllomedusa trinitatis.—**TRINIDAD**: TUNAPUNA/PIARCO: between Piarco and Port Spain, lowlands nearest Fischer Station (MNRJ 32964–32965); **VENEZUELA**: SUCRE: Guiria, Pica de Mango (MNRJ 61343–61344).

Phyllomedusa vaillantii.—**BRAZIL**: AMAPÁ: Serra do Navio (MNRJ 2328, 32871, MPEG 11078–11084); AMAZONAS: município de Benjamin Constant, Rio Itacoary, Km 30 (MNRJ 2664); Comunidade São Joaquim (MNRJ 42728); município de Humaitá, Iguaraé Banheiro (MNRJ 61400); MATO GROSSO: município de Querência, Fazenda Tanguro (MPEG 20841–20846); PARÁ: município de Belém, Utinga (MNRJ 253); município de Oriximiná, Porto Trombetas, Floresta Nacional Saracá-Taquera, Platô Aviso (MNRJ 52813, 52858); município de Parauapebas, Serra dos Carajás (MNRJ 58856); **EQUADOR**: PICHINCHA: Quito (MNRJ 74780–74782).

Pithecopus azureus.—**ARGENTINA**: FORMOSA: Pilcomayo (AL-MN 4884). CORRIENTES: Dr. Montana (MNRJ 39995); **BOLÍVIA**: SANTA CRUZ: San José de Chiquitos (MZUSP 21317–21318); **BRAZIL**: MATO GROSSO: (MNRJ 2773); município de Alto Araguaia (MZUSP 66784); município de Bela Vista (EI 1129–1131); município de Carandasal (MNRJ 13647–13648); Chapada dos Guimarães, Serra da Esperança (CFBH 0169); município de Cuiabá (MZUSP 22937–22938, 22940); município de Nioaque (EI 7458–7596); município de Poconé (CFBH 0202); município de Porto Esperança (MNRJ 634, 13650–13656; MZUSP 3617); município de Porto Esperidião (MZUSP 60553–60554, 59756–59757); unknown locality (MZUSP 52098); GOIÁS: município de Alto Paraíso de Goiás (MNRJ 27787); município de Mambaí (MNRJ 27839–27841); município de Minaçu, Serra da Mesa (MNRJ 17060–17067, 20251–20255); município de Monte Alegre de Goiás (MZUSP 66461–66471); município de Paranã (ZUEC 2687); município de Silvânia, EFLEX (MNRJ 18242–18243, 34472); MATO GROSSO DO SUL: município de Corumbá (CFBH 2575–2576), Passo do Lontra (MNRJ 17861–17879); município de Miranda (MNRJ 17861–17879; MZUSP 65156–65160); município de Santa Luzia (MZUSP 33785); MINAS GERAIS: município de Cabeceira Grande, Distrito de Palmital de Minas (MNRJ 40406–40408); **PARAGUAI**: DISTRITO CAPITAL: Assunción (AL-MN 5054–5067; MNRJ 262, 13649, 13657–13670, MZUSP 3614).

Pithecopus ayeaye.—**BRAZIL**: MINAS GERAIS: município de Arantina, Reserva Particular do Patrimônio Natural Ovídio Pires (MCNAM 11427); município de Ouro Preto, Parque Estadual do Itacolomi, Lagoa Seca (holotype of *P. itacolomi* MNRJ 34650; paratypes de *Phyllomedusa itacolomi* MCNAM 7807, 7811; MNRJ 30602, 34651–34657, 34662–34663; LZV 86A, 119A, 172A, 209A, 332A, 463A–465A, 602A–604A, 630A, 1101A, 1103A, 1569A, MCNAM 6012–6014; MNRJ 68697); município de Ouro Branco (LZV 630A, 658A, 1103A); município de Poços de Caldas, Morro do Ferro (holotype MNRJ 3722; paratypes MNRJ 3723, 3726–3727; CFBH 850; MNRJ 50614, 57655–57656); município de São Roque de Minas, Parque Nacional da Serra da Canastra (CFBH 2952–2953, 9356); SÃO PAULO: município de Pedregulho, Parque Estadual do Bom Jesus (CFBH 15672–15673).

Pithecopus centralis.—**BRAZIL**: MATO GROSSO: Chapada dos Guimarães (paratype MNRJ 3984; MNRJ 23681, MZUSP 37465–37466, 81341, UFMT 6221).

Pithecopus hypochondrialis.—**COLOMBIA**: META: Villavicencio (MNRJ 13676). BRAZIL: RORAIMA: município de Amari, Tepequém (MZUSP 66026), Igarapé Cocal (MZUSP 67023), Marco da Fronteira, BV-8 (MZUSP 65787–65789, 65762–65764, 67065–67066); PARÁ: (MNRJ 713, 5796); município de Altamira (MZUSP 66208–66209, ZUEC 7221–7222, 7379); município de Belém (MNRJ 13671–13675), Cachoeira do Espelho, Rio Xingu (MZUSP 63407); município de Canaã dos Carajás, entorno da FLONA Carajás (MNRJ 40401–40404); município de Canindé, Rio Gurupi (MZUSP 32081); município de Juruá, Rio Xingu (MZUSP 66183, 64273–64278); município de Marabá, Carajás, Serra Norte (MZUSP 61072); município de Uruá, Parque Nacional da Amazônia (MZUSP 53940–53964); município de Viseu, Bela Vista (MPEG 2707–2708); MARANHÃO: município de Bacabal (MNRJ 36631); município de Barra do Corda (MZUSP 21220); município de Bom Jesus das Selvas (MNRJ 33554); município de Carolina (MNRJ 261), Posto Gonçalves Dias, Médio Pindaré (MNRJ 1799, 10022–10024); MATO GROSSO: Chapada dos Guimarães, Serra da Esperança (CFBH 169); RONDÔNIA: município de Porto Velho (MNRJ 36154, EI 5629–5631); SURINAME: MARA-WIJNE: Langamankondre (MZUSP 32079); SIPALIWINI: Rio Lawa (MZUSP 32857).

Pithecopus megacephalus.—**BRAZIL**: unknown locality (holotype MNRJ 257). MINAS GERAIS: Jaboticatubas, Serra do Cipó (MNRJ 11307–11308, MZUSP 56889–56891); Santana do Riacho, Serra do Cipó (CFBH 793).

Pithecopus nordestinus.—**BRAZIL**: ALAGOAS: município de Maceió (MNRJ 3526–3529, 13628); município de Passo do Camaragibe, Fazenda Santa Justina (MNRJ 9845–9846, 9880–9889); município de Rio Largo (MNRJ 38630); município de São Miguel dos Campos, Fazenda Prata (MNRJ 9550–9551); município de São Miguel dos Campos e Pilar, Fazenda Varela (MNRJ 36725–36727, 36744). BAHIA: município de Barreiras (MNRJ 1412, 7917–7919, MZUFV 2025); município de Bom Jesus da Lapa (MNRJ 3138, 13474); município de Caetité (MNRJ 13621); município de Campo Formoso (MZUSP 38845–38846); município de Cocorobó (MZUSP 38426–38427); município de Conde (MNRJ 13619–13620); município de Gandu (ZUEC 8703–8704); município de Ibirapitanga (MNRJ 27257); município de Irecê (ZUEC 3320); município de Itamari, Fazenda Alto São Roque (MNRJ 28949); município de Itiuba (MZUSP 38768–38779); município de Jeremoabo (MZUSP 38212–38215); município de Juazeiro (MNRJ 1732, 9311); município de Paulo Afonso (MNRJ 3530–3531); município de Uruçuca, Serra Grande (MNRJ 35571); município de Valença (MNRJ 13612–13618); unknown locality (MNRJ 823); MINAS GERAIS: município de Itacarambi (MNRJ 17074–17075); município de Porteirinha, Mocambinho (MNRJ 13631–13646, MZUFV 2847–2849, 2933); município de Januária (MNRJ 1807, 10125); município de Jequitinhonha (MZUFV 8961); município de Nova Ponte, UHE de Miranda (MNRJ 39641–39642); município de Salto da Divisa, Fazenda Santana (MNRJ 35138–35147); município de Unaí, UHE Queimado (MNRJ 40405); PARAÍBA: município de Cabaceiras (MZUSP 63128); município de Gurinhém (MZUSP 63015–63016); município de Juazeirinho, Soledade (MNRJ 13629); PERNAMBUCO: município de Bom Conselho (MZUSP 51698); município de Caruaru, Serra dos Pintos (MNRJ 38571–38580); município de Casinhas (MNRJ 263, 5247–5248); município de Exu (MZUSP 51759–51765, 51959– 51960, 54529, 58789, 58835); município de Floresta, Fazenda Campos Bons (MZUSP 36857); município de Limoeiro (MNRJ 3040); município de Poção (MNRJ 264, 5249–5251); município de Recife (CFBH 2530, MNRJ 3032, 13039–13040), Rio Branco (MNRJ 265), São Gonçalo (MNRJ 3025), Tapera (AL-MN 1601–1604); PIAUÍ: município do Crato, Araripe (MNRJ 13630, 32870); município de Maranguape, Açude Amanari (MZUSP 13574–13575); município de Santana do Cariri (MZUSP 54751, EI 7452–7457); município de Tianguá (MNRJ 36645); RIO GRANDE DO NORTE: município de Natal (AL-MN 1687–1688); município de São Paulo do Potengi (MNRJ 13622–13627, MZUSP 3613); SERGIPE: município de Areia Branca (MZUSP 38040–38049); município de Santo Amaro das Brotas (MZUSP 63183–63184), Fazenda Capivara (MNRJ 17072–17073).

Pithecopus oreades.—**BRAZIL**: DISTRITO FEDERAL: Brasília (paratype: MNRJ 23680), Reserva Ecológica do IBGE (paratype: MNRJ 23679).

Pithecopus palliatus.—**ECUADOR**: NAPO: Santa Cecilia (MNRJ 32018); BRAZIL: ACRE: município de Cruzeiro do Sul (ZUEC 5388, 5392, 8490); município de Marechal Thaumaturgo (ZUEC 9519); município de Xapuri (ZUEC 5685–5695, 5741, 5754, 5760).

Pithecopus rohdei.—**BRAZIL**: ESPÍRITO SANTO: (MNRJ 3080, 13285); município de Linhares (MNRJ 40413–40419, 40858–40868), Estação Experimental de Linhares (MNRJ 13594–13596); município de Santa Teresa (MNRJ 1293, 40409–40412; 40869–40873), São Lourenço (MNRJ 30436–30438), Sítio do Bozza (MNRJ 30450–30451); município de Vargem Alta (MNRJ 26035); MINAS GERAIS: município de Marliéria, Parque Florestal Estadual do Rio Doce (MNRJ 17880–17882, MZUFV 1557, 1559, 1723); município de Santana do Paraíso, Fazenda Macedônia (MNRJ 17068–17071); RIO DE JANEIRO: Baixada Fluminense (MNRJ 561, 691, 2225, 5763–5766, 10883–10884, 13591); município de Duque de Caxias (AL-MN 2984; MNRJ 591, 1425, 1437–1438, 1571, 1642, 1646, 1935, 2208, 3118, 7079, 8000–8029, 8223–8224, 8495–8497, 10373–10383, 10843–10845, 1341–13420, 13589–13590); município de São Gonçalo (MNRJ 17052–17058); município de Nova Iguaçu (EI 6074–6092), Tinguá (EI 6460–6462); município do Rio de Janeiro (MNRJ 259, 560, 1455, 2067,

2220, 2315; 2888, 7139, 10868–10869, 13588); municipío de São Pedro d'Aldeia (MNRJ 17059); município de Saquarema, Palmital (MNRJ 30281, 30282–30284); município de Seropédica, FLONA Mário Xavier (CFBH 0135); município de Tanguá, Ipitangas (MNRJ 34890); município de Teresópolis (*Bradymedusa moschata* syntypes: MNRJ 258, 5239–5244; MNRJ 260, 5245–5246); SÃO PAULO: município de São Sebastião, Barequeçaba (MNRJ 17043–17051); município de Ubatuba, Itaguá (CFBH 766–767, 1232, 2097, 1073–1081, 1272–1275), Praia do Lázaro (CFBH 119, ZUEC 549–550, 5163–5164, 1757–1766, 2928–2935, 3609, 3611–3614).