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Author(s): Ana C. R. Alves, Luiz F. Ribeiro, Célio F. B. Haddad, and Sérgio F. dos Reis
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TWO NEW SPECIES OF *BRACHYCEPHALUS* (ANURA: BRACHYCEPHALIDAE) FROM THE ATLANTIC FOREST IN PARANÁ STATE, SOUTHERN BRAZIL

ANA C. R. ALVES[1], LUIZ F. RIBEIRO[2,3,4], CÉLIO F. B. HADDAD[1], AND SÉRGIO F. DOS REIS[5,6]

[1]*Departamento de Zoologia, Instituto de Biociências, Universidade Estadual Paulista, Caixa Postal 199, 13506-900, Rio Claro, SP, Brazil*
[2]*Universidade Tuiuti do Paraná, Rua Marcelino Champagnat, 505, 80710-250, Curitiba, PR, Brazil*
[3]*Mater Natura, Instituto de Estudos Ambientais, Rua Desembargador Westphalen, 15–16° andar, 80010-110, Curitiba, PR, Brazil*
[4]*Programa de Pós-Graduação em Genética e Biologia Molecular, Instituto de Biologia, Universidade Estadual de Campinas, Caixa Postal 6109, 13083-970, Campinas, SP, Brazil*
[5]*Departamento de Parasitologia, Instituto de Biologia, Universidade Estadual de Campinas, Caixa Postal 6109, 13083-970, Campinas, SP, Brazil*

ABSTRACT: Two new species of brachycephalid frogs are described from Pico Marumbi, municipality of Morretes, and Pico da Igreja, municipality of Guaratuba, Paraná State, southern Brazil. The new species share the following attributes: body bufoniform; skin on top of the head, and central part of the back body smooth with no dermal co-ossification; outer metatarsal tubercle distinct; dermal roofing bones of skull unornamented; all paired cranial bones distinct and not fused; quadratojugals, and maxillary odontoids present. The new species from Pico Marumbi is characterized by male SVL = 11.6–12.5 and female SVL = 13.0–14.5 mm; and general color orange with dorsal reddish-brown irregular markings, lateral surfaces with small dark brown spots, and belly with brownish spots and small dots. The new species from Pico da Igreja is characterized by male SVL = 12.6–13.9 and female SVL = 14.6–15.3 mm; and general color orange, lateral surfaces with small dark brown spots, and belly with brownish coalescent spots and small dots. Comparisons with other brachycephalid species and osteological data are provided.

Key words: Amphibia; Anura; Atlantic Forest; Brachycephalidae; *Brachycephalus*; New species; Osteology; Southern Brazil

THE FAMILY Brachycephalidae is monotypic (Frost, 2004). The species of the genus *Brachycephalus* have snout–vent length <1.8 cm, phalangeal loss, and reduced number of toes and are believed to have evolved by miniaturization (Yeh, 2002). These small frogs inhabit leaf litter and are endemic to the Atlantic rainforest of southeastern and southern Brazil (Giaretta and Sawaya, 1998; Izecksohn, 1971; Miranda-Ribeiro, 1920; Pombal, 2001; Pombal et al., 1998). Until recently, the known diversity of *Brachycephalus* included six species occurring in the States of Rio de Janeiro, São Paulo, and Paraná, namely, *Brachycephalus didactylus* (Izecksohn, 1971), *Brachycephalus ephippium* (Spix, 1824), *Brachycephalus hermogenesi* (Giaretta and Sawaya, 1998), *Brachycephalus nodoterga* Miranda-Ribeiro, 1920, *Brachycephalus pernix* Pombal, Wistuba and Bornschein, 1998, and *Brachycephalus vertebralis* Pombal, 2001.

As a result of recent herpetological surveys in the mountain slopes of the Serra do Mar, we discovered two undescribed species from the State of São Paulo and four undescribed species from the State of Paraná. These findings double the known diversity of *Brachycephalus*. We have already described two of the four new species from the State of Paraná, namely, *Brachycephalus brunneus* Ribeiro, Alves, Haddad, and Reis, 2005 and *Brachycephalus izecksohni* Ribeiro, Alves, Haddad, and Reis, 2005, and here we described the other two species. The diagnoses of the two new species are based on the color, external morphology, and ostelogy of adults. Additionally, we used continuous metric traits to characterize these two new species morphometrically and discriminate them from *B. brunneus*, *B. pernix*, and *B. izecksohni*, all of which are restricted in distribution to the Serra do Mar mountain range in the State of Paraná. We also provide morphological comparisons among species in the genus *Brachycephalus*.

[6] CORRESPONDENCE: e-mail, sfreis@unicamp.br

Materials and Methods

Specimens were anaesthetized and killed in 30% ethyl alcohol, fixed in 10% formalin, and preserved in 70% ethyl alcohol. The terminology used for the external morphology and texture of the skin followed Lynch and Duellman (1997). The color codes used in color descriptions were those of Smithe (1975). The bones and cartilages were cleared and double-stained with alizarin red and alcian blue according to Taylor and Van Dyke (1985). Specimens of *B. brunneus* ($n = 2$), *B. ephippium* ($n = 1$), *B. hermogenesi* ($n = 1$), *B. izecksohni* ($n = 2$), and *B. pernix* ($n = 1$) were used for osteological comparisons. Drawings were made using a Zeiss stereomicroscope fitted with a drawing tube.

Ten metric traits were measured with a micrometric ocular fitted to the stereomicroscope. The abbreviations used were: SVL (snout–vent length); HL (head length; from tip of snout to angle of jaw); HW (head width; greatest width of head located between angles of jaw); ND (nostril diameter); IND (internostril distance; between inner margins of nostrils); ED (eye diameter); IOD (interorbital distance; between anterior corners of the eyes); END (eye–nostril distance; from anterior corner of the eye to posterior margin of nostril); THL (thigh length); TBL (tibia length). All measurements were in millimeters.

Canonical variate analysis (CVA) was used to describe variation in metric traits within and among the five species of *Brachycephalus* from the State of Paraná. As noted by Rohlf et al. (1996:347), assumptions of multivariate normality and homogeneity of within-group covariance matrices underlie the construction of canonical axes and impose restrictions on inferential approaches to CVA (Krzanowski, 1989; Krzanowski and Radley, 1989). In the present analysis, we constructed confidence regions around sample centroids for canonical axes using parametric bootstrap theory developed for CVA by Ringrose (1996). The parametric bootstrap procedure is based on the $N(\bar{\mathbf{x}}_i, \hat{\Sigma})$ distribution, where $\bar{\mathbf{x}}_i$ is the vector of means for the i-th population group and $\hat{\Sigma}$ is the unbiased estimate of the pooled within-group covariance matrix. The Cholesky factorization was applied to $\hat{\Sigma}$ in the simulation of 1000 replicate data matrices (Von Zuben et al., 1998). For each replicate matrix, bootstrap analogs were obtained for the sample group vector means and for the within- and between-group sum of squares and product matrices. Canonical variate analysis was done to yield bootstrap eigenvalues and eigenvectors. The variances and covariances of sample centroids on canonical axes were estimated over all replicates and the χ^2 distribution was used to construct 95% confidence regions by applying formulas provided by Krzanowski (1989). Computations for the parametric bootstrap were numerically formulated and computationally implemented in MATLAB as described in Von Zuben et al. (1998). Vector correlations between original metric traits and canonical variate scores were calculated and were graphically displayed to portray the principal directions of variation of each metric trait in the reduced canonical variate space (Garavello et al., 1992). Sample sizes used for the morphometric analyses were as follows: *B. brunneus* ($n = 24$), *B. ferruginus* ($n = 13$), *B. izecksohni* ($n = 15$), *B. pernix* ($n = 12$), and *B. pombali* ($n = 8$).

The specimens used in the description or examined for comparisons are in AL-MN (Adolpho Lutz collection, deposited in the Museu Nacional, Rio de Janeiro, Rio de Janeiro, Brazil), CFBH (Célio F. B. Haddad collection, deposited in the Departamento de Zoologia, Universidade Estadual Paulista, Campus de Rio Claro, São Paulo, Brazil), MHNCI (Museu de História Natural do Capão da Imbuia, Curitiba, Paraná, Brazil), MNRJ (Museu Nacional, Rio de Janeiro, Rio de Janeiro, Brazil), MZUSP (Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil), and ZUEC (Museu de História Natural, Universidade Estadual de Campinas, Campinas, São Paulo, Brazil). The specimens examined in the comparisons are listed in Appendix I.

Results

Brachycephalus **ferruginus** *sp. nov*

Holotype.—CFBH 8024, adult male, one of a series collected at Pico Marumbi (25° 26′ S; 48° 55′ W), municipality of Morretes, Paraná State, southern Brazil, altitude 1200 m, on 17 December 2002 by L. F. Ribeiro (Fig. 1A,B).

Paratopotypes.—CFBH 8037, one male and, CFBH 8036, one female collected on 27

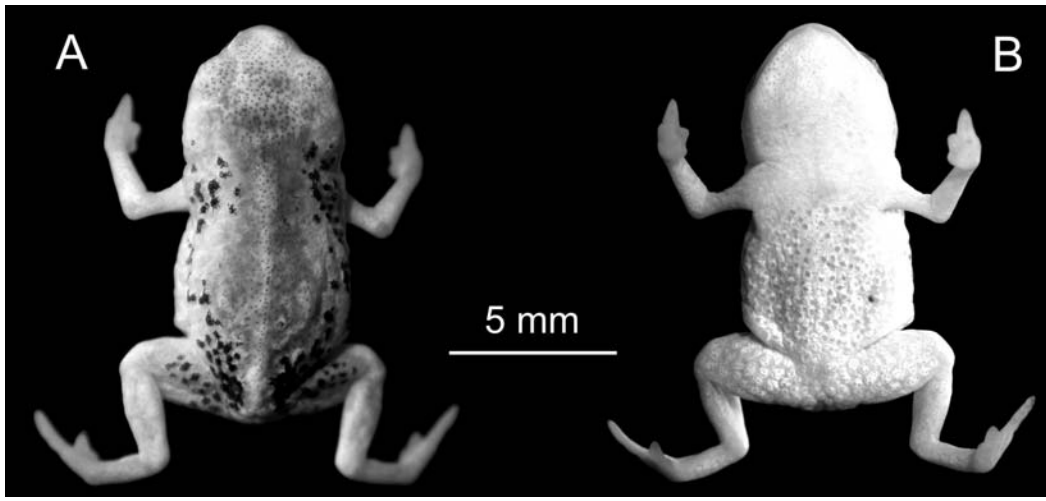

FIG. 1.—*Brachycephalus ferruginus*, CFBH 8024 (holotype), adult male from Pico Marumbi (25° 26′ S; 48° 5′ W), municipality of Morretes, Paraná State, southern Brazil. (A) Dorsal view, (B) ventral view. SVL = 12.0 mm.

March 2001 by L. F. Ribeiro; CFBH 8039, 8040, two males collected on 19 April 2001 by L. F. Ribeiro; CFBH 8041 (cleared and stained), one male collected on 18 January 2002 by L. F. Ribeiro; CFBH 8025–27, three males and, CFBH 8038, one female collected with the holotype on 17 December 2002 by L. F. Ribeiro; CFBH 8030, 8031, 8033, 8034, four males, CFBH 8029 (cleared and stained), 8035, two females and CFBH 8028, 8032, two juveniles collected on 24 April 2003 by L. F. Ribeiro.

Diagnosis.—(1) SVL in males 11.6–12.5 and SVL in females 13.0–14.5 mm; (2) body bufoniform; (3) skin on top of the head and central part of the back body smooth and without dermal co-ossification; (4) general color orange with dorsal reddish-brown irregular markings, lateral surfaces with small dark brown spots, and belly with brownish spots and small dots.

Like other species of the genus *Brachycephalus*, *B. ferruginus* is miniaturized (sensu Yeh, 2002) with loss of phalanges in the manus and pes; and has a completely ossified pectoral girdle with epicoracoids closely juxtaposed and articulating throughout their lengths, omosternum present, and sternum absent. The dorsal color pattern of *B. ferruginus* resembles *B. pernix* but is readily distinguished from the latter by the presence of dorsal reddish-brown irregular markings, and by the form and brownish color of the dorso-lateral spots. The relative larger size and the dorsal color pattern also distinguish *B. ferruginus* from *B. izecksohni*, which is smaller and without dorsal or lateral marks or spots. The general orange color and the rounded snout shape in dorsal view distinguish *B. ferruginus* from *B. brunneus*, which has a general brown color and a mucronate snout shape in dorsal view. *Brachycephalus ferruginus* has smooth skin texture with no dermal co-ossification on top of the head and central part of the back body, whereas *B. ephippium*, *B. nodoterga*, and *B. vertebralis* have dermal co-ossification on top of the head and central part of the back body. *Brachycephalus ferruginus* differs from *B. didactylus* and *B. hermogenesi* in having a bufoniform body shape, a rounded snout shape in dorsal view, and a general orange color; whereas *B. didactylus* and *B. hermogenesi* have a leptodactyliform body shape, a short and pointed with a rounded tip snout shape in dorsal view, and general brownish color.

Description of holotype.—Body robust, bufoniform (Figs. 1A, 2A). Head as wide as long, slightly narrower than body; head length 36% of snout–vent length; snout short with length almost equal to eye diameter, rounded in lateral and dorsal views (Fig. 2A,B); nostrils protuberant, directed anterolaterally; canthus rostralis not distinct; loreal region weakly concave; lips nearly sigmoid; eye slightly

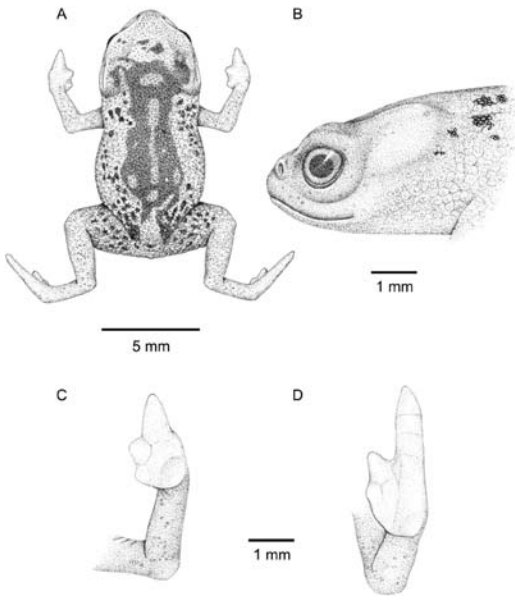

FIG. 2.—*Brachycephalus ferruginus*, CFBH 8024 (holotype). (A) Dorsal view of body, (B) lateral view of head, (C) left hand, and (D) left foot.

protruding in dorsal and lateral views, eye diameter 26% of head length; tympanum absent; vocal sac not expanded externally; vocal slits present; tongue longer than wide, posterior 1/2 not adherent to floor of mouth; choanae relatively small and round; vomerine odontophores absent. Upper arm and forearm relatively slender, upper arm approximately as long as forearm; fingers I–III robust, short and distinct; finger IV very reduced; tip of fingers I and II slightly rounded, tip of finger III pointed; relative lengths of fingers IV < I < II < III; subarticular tubercles and inner and outer metacarpal tubercles absent (Fig. 2C). Legs relatively short, thigh robust; thigh length 35% of SVL, tibia length 90% of thigh length; toe II very reduced, toe III short and relatively distinct, toe IV robust and distinct, toes I and V externally absent; relative lengths of toes II < III < IV; subarticular tubercles and inner metatarsal tubercles absent; outer metatarsal tubercle distinct, large, and ovoid (Fig. 2D).

Skin on top of the head and central part of the back body smooth and with no dermal coossification (Figs. 1A, 2A); skin on dorso-lateral surfaces of body, flanks, and dorsal surface of thighs granular; skin on venter and ventral surfaces of the legs smooth; skin on ventrolateral surfaces of body and area around the cloacal opening granular.

TABLE 1.—Measurements in millimeters of the type series *Brachycephalus ferruginus* ($\bar{x}$ = mean; SD = standard deviation). Character abbreviations are listed in the Material and Methods.

	Males (n = 9)			Females (n = 4)		
	$\bar{x}$	SD	Range	$\bar{x}$	SD	Range
SVL	12.2	0.3	11.6–12.5	13.8	0.6	13.0–14.5
HL	4.5	0.1	4.3–4.6	5.2	0.1	5.1–5.3
HW	4.8	0.3	4.0–5.0	5.5	0.1	5.4–5.8
ED	1.2	0.1	1.0–1.3	1.3	0.1	1.2–1.4
ND	0.2	0.0	0.1–0.2	0.2	0.0	0.2–0.2
IOD	2.4	0.1	2.2–2.6	2.7	0.0	2.6–2.7
IND	1.2	0.0	1.1–1.3	1.4	0.1	1.3–1.5
END	0.6	0.0	0.5–0.7	0.7	0.1	0.6–0.8
THL	4.4	0.1	4.2–4.6	4.8	0.3	4.5–5.3
TBL	4.0	0.1	3.8–4.2	4.4	0.1	4.3–4.6

Coloration of holotype in life.—Dorsum bright orange (orange yellow, #18); central area of body and head with reddish-brown (maroon, #31) irregular markings; light areas pale bright yellow (sulfur yellow, #157) with very small olive gray (#42) dots near or around the reddish-brown markings. Lateral areas of body, flanks, and thighs with small dark brown (sepia, #219) spots. Arms orange (spectrum orange, #17) and legs bright orange (orange yellow, #18). Throat and belly orange (spectrum orange, #17) with small greenish (olive gray, #42) dots. Belly with glandular aspect and with brownish (raw umber, #23) spots and small dots.

Coloration of holotype in preservative.—General color pale cream (cream color, #54); central area of body and head with markings orange-brown (amber, #36), lateral spots almost black (dusky brown, #19); small dots on belly pale greyish (smoke gray, #44).

Measurements of holotype.—SVL 12.0; HL 4.4; HW 4.8; IND 1.1; ED 1.1; IOD 2.2; END 0.6; THL 4.3; TBL 3.8.

Variation in the type series.—Measurements and proportions of nine males and four females are given in Tables 1 and 2. Color in life varying among specimens in the extension of reddish-brown markings on the central area of body and head (Fig. 3).

Distribution.—Brachycephalus ferruginus is known only from Pico Marumbi (25° 26′ S; 48° 55′ W), municipality of Morretes, Paraná State, southern Brazil.

TABLE 2.—Proportions (%) of the type series of *Brachycephalus ferruginus* ($\bar{x}$ = mean; SD = standard deviation). Character abbreviations are listed in the Material and Methods.

	Males (n = 9)			Females (n = 4)		
	$\bar{x}$	SD	Range	$\bar{x}$	SD	Range
THL/SVL	36	1	34–38	35	2	32–37
TBL/THL	92	3	85–96	93	7	93–100
HL/SVL	37	1	35–40	37	2	36–39
ED/HL	26	2	23–28	25	2	23–25

Etymology.—The specific epithet is a Latin noun meaning rust or reddish-brown. The name is used in allusion to the frog's dorsal reddish-brown irregular markings.

Remarks.—Individuals of the new species were found in leaf litter at approximately 1000 to 1200 m of altitude. *Brachycephalus ferruginus* is active by day and is locally abundant. Adult males were always exposed on the litter when calling. A female (CFBH 8029) that was dissected for osteological studies had three large, unpigmented maturing oocytes. Direct development of terrestrial eggs was described in detail for *B. ephippium* (Pombal, 1999) and probably also occurs in *B. ferruginus*.

Brachycephalus **pombali** *sp. nov*

Holotype.—CFBH 8042, adult male, one of a series collected at Morro dos Padres, Pico da Igreja (25° 39′ S; 48° 51′ W), municipality of Guaratuba, Paraná State, southern Brazil, altitude 1300 m, on 27 April 2003 by L. F. Ribeiro and A. Dalai (Fig. 4A,B).

Paratopotypes.—CFBH 8043 (cleared and stained), 8044, 8045, three males, CFBH 8046 (cleared and stained), 8047–49, four females and, CFBH 8050–53, four newly hatched collected with the holotype on 27 April 2003 by L. F. Ribeiro and A. Dalai.

Diagnosis.—(1) SVL in male 12.6–13.9 and SVL in female 14.6–15.3 mm; (2) body bufoniform; (3) skin on top of the head and central part of the back body smooth and without dermal co-ossification; (4) general color orange, lateral surfaces with small dark brown spots, and belly with brownish coalescent spots and small dots.

Like other species of the genus *Brachycephalus*, *B. pombali* is miniaturized (sensu Yeh, 2002) with loss of phalanges in the manus and pes; and has a completely ossified pectoral girdle with epicoracoids closely juxtaposed and articulating throughout their lengths, omosternum present, and sternum absent. The dorsal color pattern of *B. pombali* slightly resembles that of *B. pernix* but may be readily distinguished by the form and brownish color of the dorso-lateral spots and small dots. The relatively larger size and the dorso-lateral color pattern also distinguish *B. pombali* from *B. izecksohni*, which is smaller and without dorso-lateral marks or spots. The orange dorsal color and rounded snout shape in dorsal view in *B. pombali* distinguish this new species from *B. brunneus* which has brown dorsal color and mucronate snout shape in dorsal view. *Brachycephalus pombali* has smooth skin texture with no dermal co-ossification on top of the head and central part of the back body, whereas *B. ephippium*, *B. nodoterga*, and *B. vertebralis* have dermal co-ossification on top of the head and central part of the back body. *Brachycephalus pombali* differs from *B. didactylus* and *B. hermogenesi* in having a bufoniform body shape, a rounded snout shape in dorsal view, and a general orange color; whereas *B. didactylus* and *B. hermogenesi* have a leptodactyliform body shape, a short and pointed with a rounded tip snout shape in dorsal view, and general brownish color.

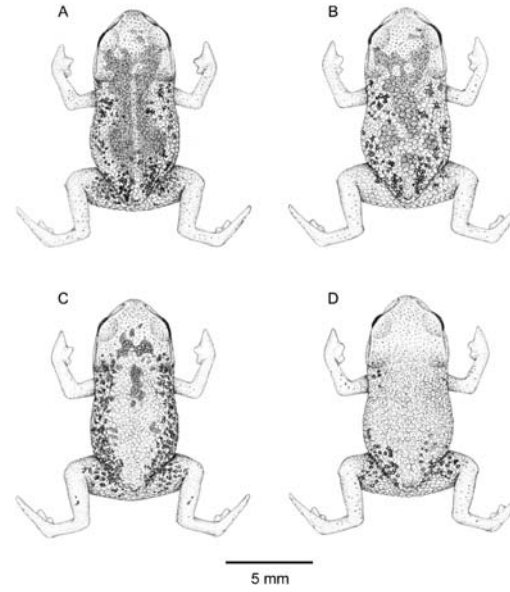

FIG. 3.—Pattern of dorsal variation in *Brachycephalus ferruginus*.

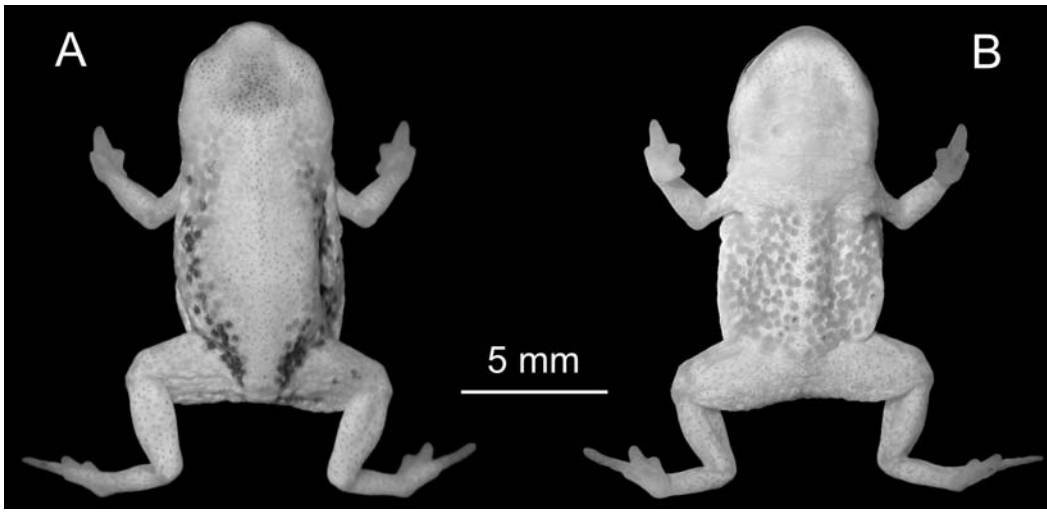

FIG. 4.—*Brachycephalus pombali*, CFBH 8042 (holotype), adult female from Pico da Igreja (25° 39′ S; 48° 51′ W), municipality of Guaratuba, Paraná State, southern Brazil. (A) Dorsal view, (B) ventral view. SVL = 13.1 mm.

Description of holotype.—Body robust, bufoniform (Figs. 4A, 5A). Head as wide as long, slightly narrower than body; head length 38% of SVL, snout short with length almost equal to eye diameter, rounded in lateral and dorsal views (Fig. 5A,B); nostrils protuberant, directed anterolaterally; canthus rostralis not distinct; loreal region weakly concave; lips nearly sigmoid; eye slightly protruding in dorsal and lateral views, eye diameter 26% of head length; tympanum absent; vocal sac not expanded externally; vocal slits present; tongue longer than wide, posterior 1/2 not adherent to floor of mouth; choanae relatively small and round; vomerine odonthophores absent. Upper arm and forearm relatively slender, upper arm approximately as long as forearm; fingers I–III robust, short and distinct; finger IV reduced; tip of fingers I and II slightly rounded, tip of finger III pointed; relative lengths of fingers IV < I < II < III; subarticular tubercles and inner and outer metacarpal tubercles absent (Fig. 5C). Legs relatively short, thigh robust; thigh length 37% of SVL, tibia length 97% of thigh length; toe I externally absent, toes II–III short and distinct; toe IV robust and distinct, toe V very reduced only visible as a slight bulge; relative lengths of toes V < II < III < IV; subarticular tubercles and inner metatarsal tubercles absent; outer metatarsal tubercle distinct, large, and ovoid (Fig. 5D).

Skin on top of the head and central part of the back body smooth and with no dermal coossification (Figs. 4A, 5A); skin on dorso-lateral surfaces of body, flanks, and dorsal surface of thighs granular; skin on venter and ventral surfaces of the legs smooth; skin on ventrolateral surfaces of body and area around the cloacal opening granular.

Coloration of holotype in life.—Dorsum orange (spectrum orange, #17); dorso-lateral skin covered with very weak dark orange (chrome orange, #16) tubercles, especially on flanks. Head with an approximately circular, central post-orbital spot and one inconspicuous spot above each eye. Head markings, dorso-vertebral stripe, and leg articulations pale bright yellow (sulfur yellow, # 157) with very small olive gray (#42) dots; central head marking more greenish (olive gray, #42) than the others. Lateral areas of body, flanks, and thighs with small dark brown (sepia, #219) spots. Limbs dark orange (chrome orange, #16). Throat dark orange (chrome orange, #16) and belly orange (spectrum orange, #17) with brownish (raw umber, #23) coalescent spots and small dots, and with a short, ventral pale bright yellow (sulfur yellow, #157) stripe.

Coloration of holotype in preservative.—General color pale cream (pale pinkish buff, #121D); lateral spots dark brown (raw umber, #223); coalescent spots and small dots on belly pale greyish (smoke gray, #44).

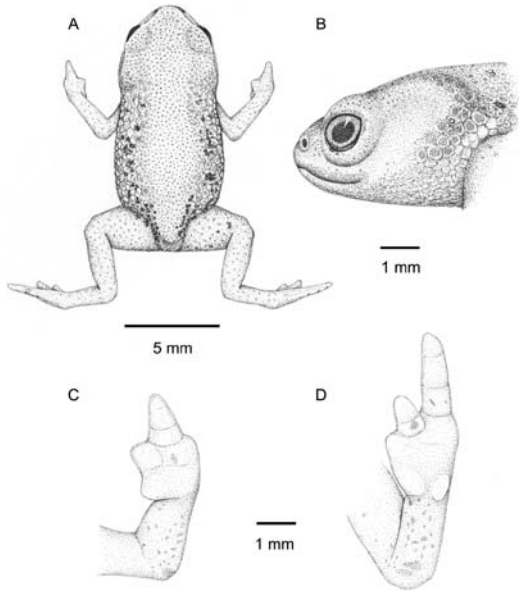

FIG. 5.—*Brachycephalus pombali*, CFBH 8042 (holotype). (A) Dorsal view of body, (B) lateral view of head, (C) left hand, and (D) left foot.

Measurements of holotype.—SVL 13.1; HL 5.0; HW 5.3; IND 1.3; ED 1.3; IOD 2.6; END 0.7; THL 4.8; TBL 4.7.

Variation in the type series.—Measurements and proportions of four males and four females are given in Tables 3 and 4. Color in life on dorsum orange varying from spectrum orange (#17) to chrome orange (#16); central head marking usually more greenish (olive gray, #42) than other head marks; lateral small glands dark orange (chrome orange, #16) or slightly brownish (raw umber, #23); lateral areas of body with different amounts of small dark brown (sepia, #219) spots (Fig. 6); belly of some specimens with a short, ventral pale bright yellow (sulfur yellow, # 157) stripe.

Distribution.—*Brachycephalus pombali* is known only from Morro dos Padres at Pico da Igreja (25° 39′ S; 48° 51′ W), municipality of Guaratuba, Paraná State, southern Brazil.

Etymology.—The specific epithet is a noun in the genitive case and honors José Perez Pombal, Jr., who has made invaluable contributions to our knowledge of the genus *Brachycephalus*.

Remarks.—Individuals of the new species were found in leaf litter at approximately 1300 m of altitude. *Brachycephalus pombali* is active by day and adult males were always exposed on the litter when calling.

TABLE 3.—Measurements in millimeters of the type series *Brachycephalus pombali* ($\bar{x}$ = mean; SD = standard deviation). Character abbreviations are listed in the Material and Methods.

	Males (n = 4)			Females (n = 4)		
	$\bar{x}$	SD	Range	$\bar{x}$	SD	Range
SVL	13.3	0.5	12.6–13.9	15.0	0.3	14.6–15.3
HL	4.9	0.4	4.5–5.4	5.6	0.1	5.5–5.6
HW	5.4	0.2	5.3–5.6	6.0	0.1	6.0–6.1
ED	1.3	0.0	1.2–1.3	1.4	0.0	1.3–1.4
ND	0.2	0.0	0.2–0.2	0.2	0.0	0.2–0.2
IOD	2.6	0.0	2.6–2.7	2.9	0.1	2.8–2.9
IND	1.3	0.1	1.2–1.4	1.5	0.0	1.5–1.6
END	0.7	0.0	0.7–0.7	0.8	0.0	0.8–0.8
THL	4.9	0.1	4.8–5.1	5.4	0.2	5.3–5.6
TBL	4.7	0.1	4.6–4.9	5.1	0.2	4.9–5.3

Osteology of B. ferruginus *and* B. pombali

Skull slightly wider than long in dorsal view; the greatest width at the level of the squamosals (Figs. 7A,B, 8A,B). Dermal roofing bones of the skull unornamented and without co-ossification of skin to bones. Premaxillae broad and triangular in dorsal view, not fused medially; pars dentalis of each premaxilla with five reduced odontoids in *B. ferruginus* (n = 2) and four in *B. pombali* (n = 1); alary process of premaxillae distinct, about twice the height of the pars dentalis and narrowly separated from the nasal; in ventral view, pars palatina with palatine process distinct and slightly pointed. Maxillae arched; pars dentalis of each maxilla with nine reduced odontoids in *B. ferruginus* (n = 2) and eight in *B. pombali* (n = 1) distributed in the anterior half of the bone; pars facialis modestly developed with very distinct and relatively long preorbital processes. Quadratojugals present (Figs. 7C,

TABLE 4.—Proportions (%) of the type series of *Brachycephalus pombali* ($\bar{x}$ = mean; SD = standard deviation). Character abbreviations are listed in the Material and Methods.

	Males (n = 4)			Females (n = 4)		
	$\bar{x}$	SD	Range	$\bar{x}$	SD	Range
THL/SVL	37	1	36–39	36	1	35–37
TBL/THL	96	1	95–97	96	2	94–98
HL/SVL	37	2	36–39	37	0	37–38
ED/HL	26	1	24–27	25	1	23–25

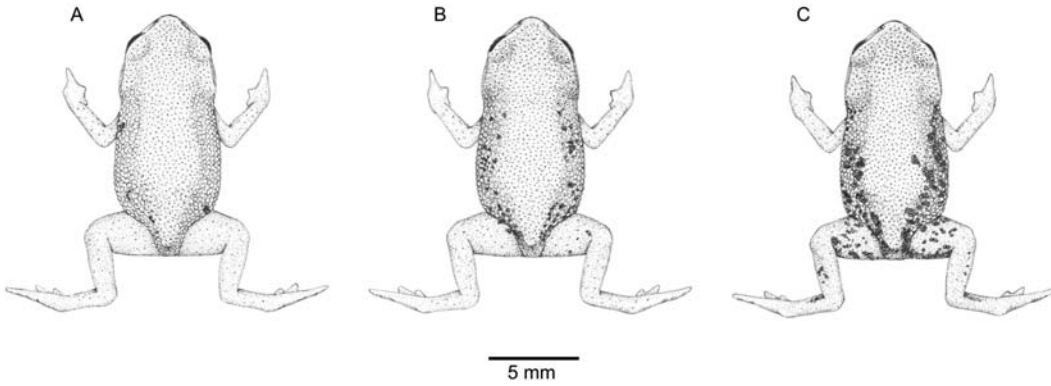

FIG. 6.—Pattern of dorsal variation in *Brachycephalus pombali*.

8C), slender, relatively long, and strongly deflected ventrally from the plane of the maxillae, completing the maxillary arcade posteriorly. Posterior ends of each quadratojugal articulate with the ventral ramus of squamosal. Anterior tips of quadratojugals narrowly overlapped by maxillae. Nasals approximately triangular in dorsal view, widely separated medially, and not fused to slightly articulate with surrounding elements; their anterior margins overlie the nasal capsule and their posterior margins barely overlap the sphenethmoid. Sphenethmoid thin, and poorly ossified, invested by the cultriform process of the parasphenoid ventrally. Frontoparietals paired, almost rectangular, narrowly separated medially, slightly articulate or fused with one another, and not fused to slightly fused with surrounding elements; frontoparietal fontanelle completely roofed; frontoparietal fenestra absent. Anteriorly, frontoparietals overlap the posterior margin of the sphenethmoid, and posteriorly they overlap part of the prootic and exoccipital. Vomers reduced; dentigerous process absent, prechoanal and postchoanal ramus reduced but distinct (Figs. 7B, 8B). Neopalatines absent. Parasphenoid robust; cultriform process broad; alary process broad and long. Squamosals T-shaped in lateral view, anterior zygomatic ramus short, with approximately 1/2 of posterior otic ramus length; posterior otic ramus articulates with distal portion of crista parotica (Figs. 7C, 8C). Pterygoids relatively robust; anterior ramus long and articulates with maxillary arch; posterior ramus short and articulates with the ventral ramus of squamosal; medial ramus short and articulates with the prootic. Exoccipitals and prootics fused, without visible sutures; occipital condyles well developed and widely separated from each other. Operculum, stapes, and tympanic annulus absent. Mandible edentate. Hyoid plate about twice as long as wide at midline; hyoglossal sinus U-shaped; hyales slender and long; anterior process of hyale slender and with approximately 1/3 of hyale length; lateral process of hyoid plate short; posteromedial process of hyoid plate bony and slender, its length approximately equal to hyoid plate length (Figs. 7D, 8D).

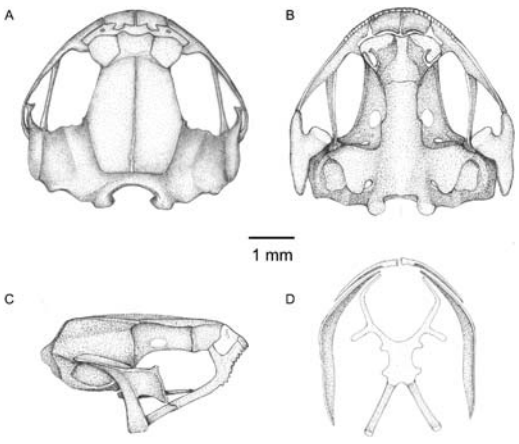

FIG. 7.—*Brachycephalus ferruginus* (CFBH 8029). (A) Dorsal, (B) ventral and (C) lateral views of skull, (D) ventral view of mandible and hyoid apparatus.

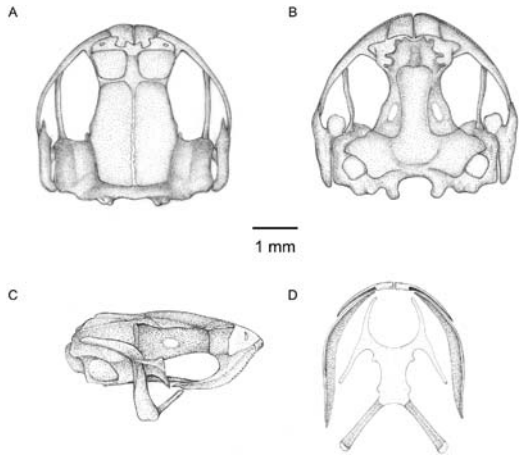

FIG. 8.—*Brachycephalus pombali* (CFBH 8046). (A) Dorsal, (B) ventral and (C) lateral views of skull, (D) ventral view of mandible and hyoid apparatus.

Pectoral girdle arciferal and robust; procoracoid and epicoracoid completely ossified; procoracoid and epicoracoid synosteotically united with clavicle, coracoid and scapula; suprascapula broadly expanded, anterior half ossified as cleithrum; omosternum developed, cartilaginous, its distal portion expanded; sternum absent (Figs. 9A, 10A). Vertebral column composed of eight presacral, procoelous, and non-imbricate vertebrae; first presacral vertebra (atlas) lacks transverse process, all other presacral vertebrae have slender transverse processes; transverse processes of presacrals III–VI perpendicular to the notochordal axis, those of the presacrals II, VII–VIII directed anteriorly. Lengths of the transverse process of presacrals along with that of the sacral diapophyses: SD > III > IV > II > V ≅ VI ≅ VII ≅ VIII in *B. ferruginus* and III ≅ SD > IV > II > V ≅ VI ≅ VII ≅ VIII in *B. pombali*. Sacral diapophyses moderately expanded and directed posteriorly, distal end of diapophyses with a flat, slightly calcified cartilage that articulates with the ilial shaft of the pelvic girdle. Urostyle with a dorsal flange and joined to the sacrum by a bicondylar articulation; urostyle length approximately 2/3 of the length of the presacral portion of the vertebral column. Pelvic girdle V-shaped in dorsal view; ilial shaft with a long crest; ischia fused to one another medially; pubis developed.

Forelimbs with humerus slightly curved and possessing a small crest at the proximal end of the ventral surface; radius and ulna not fused. Manus with distal carpals (I–IV) fused with centrale; radiale and ulnare about the same size; prepollex elements very reduced with one element; phalangeal formula 1-2-3-1; tips of the terminal phalangeal elements of fingers arrow-shaped (Figs. 9B, 10B). Hindlimbs with tibia and fibula fused forming the tibiofibula; femur and tibiofibula of approximately the same length; fibulare and tibiale fused, but distinguishable. Pes with distal tarsal element I absent, II–III fused, centrale present; one very reduced ossified prehallical element; toe I and V reduced, phalangeal formula 1-2-3-4-0 in *B. ferruginus* (Fig. 9C) and 0-2-3-4-0 in *B. pombali* (Fig. 10C); tips of the terminal phalangeal elements of toes II–IV arrow-shaped.

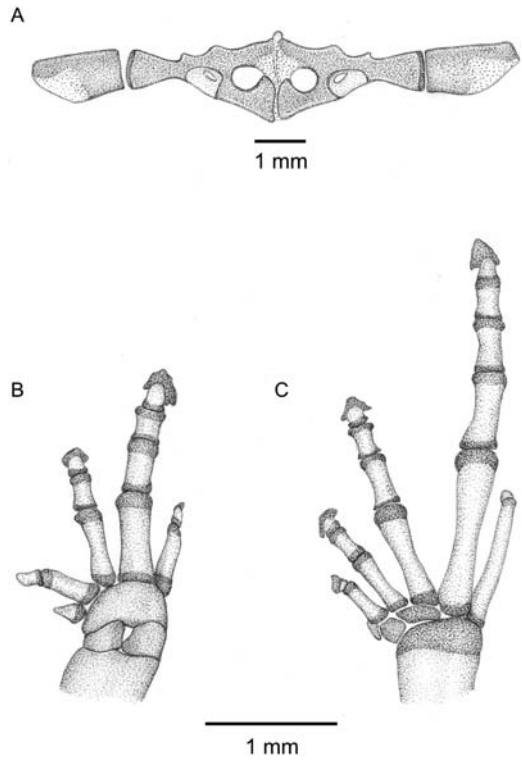

FIG. 9.—*Brachycephalus ferruginus* (CFBH 8029). (A) Ventral view of pectoral girdle with scapula and suprascapula deflected, (B) dorsal view of right hand, (C) dorsal view of right foot.

Morphometric variation

The dispersion of samples of the five species of *Brachycephalus* from the State of Paraná for

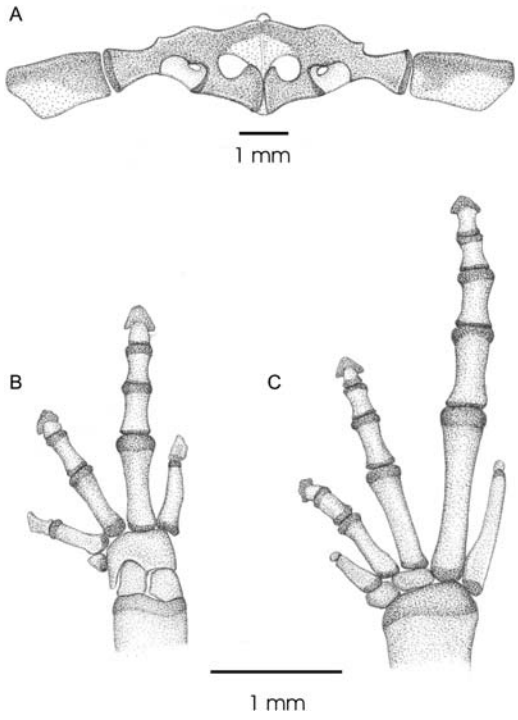

FIG. 10.—*Brachycephalus pombali* (CFBH 8046). (A) Ventral view of pectoral girdle with scapula and suprascapula deflected, (B) dorsal view of right hand, (C) dorsal view of right foot.

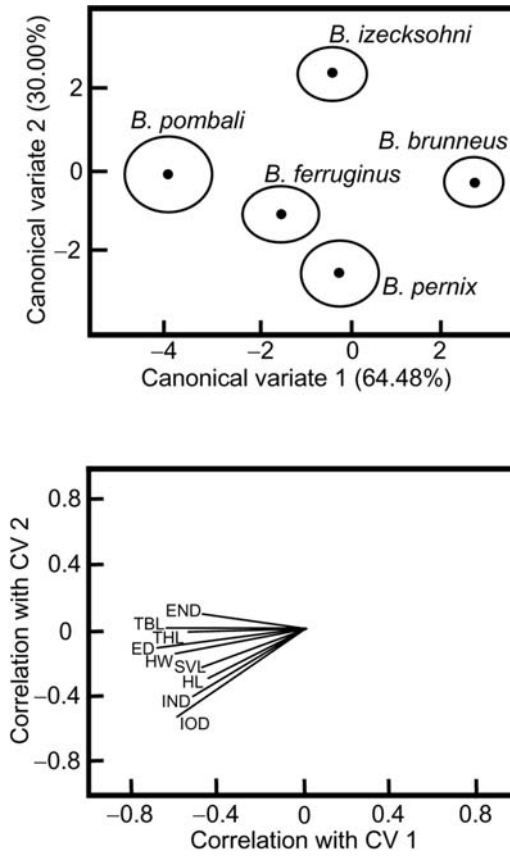

FIG. 11.—Canonical variate analysis of nine metric traits for five species of *Brachycephalus* from the State of Paraná, southern Brazil. (A) Bivariate plot of centroids (denoted as dots) and 95% confidence regions for canonical variates 1 and 2 (and percent variance explained), (B) Vectors portraying the principal directions of variation in metric traits in the plane of the first two canonical variates. Character abbreviations listed in the Material and Methods.

the first two canonical axes is shown in Fig. 11A. The first two canonical axes explained 94.48% of the total variation in the covariance matrix derived from the nine metric traits. The centroids (denoted by dots) for the five species of *Brachycephalus* were plotted for the first two canonical axes and the estimated bounds of variation were given by the 95% confidence ellipses, derived from a simulation of 1000 replicate data matrices used in the parametric bootstrap. *Brachycephalus ferruginus* and *B. pombali* were separated from *B. brunneus, B. izecksohni*, and *B. pernix* by the first canonical variate. *Brachycephalus ferruginus*, *B. izecksohni*, and *B. pernix* overlapped along the first canonical variate but were completely discriminated by the second canonical variate. Vector plots (Fig. 11B) indicated that all metric traits were correlated with canonical variate 1, although with different magnitudes.

DISCUSSION

A comparison of the external morphology of *B. ferruginus* and *B. pombali* with that of other brachycephalid species showed that the new species can be distinguished by: (1) Body shape—bufoniform in *B. ferruginus*, *B. pombali*, *B. brunneus*, *B. ephippium*, *B. izecksohni*, *B. nodoterga*, *B. pernix*, and *B. vertebralis*; leptodactyliform in *B. didactylus* and *B. hermogenesi*. (2) Texture of skin—top of the head and central part of the back body smooth with no dermal co-ossification; granular on the dorso-lateral surfaces of body, flanks, and dorsal surface of thighs in *B. ferruginus*, *B. pombali*, *B. brunneus*, *B. izecksohni*, and *B. pernix*; smooth, granular only on the ventral surface around the cloacal opening in *B.*

didactylus and *B. hermogenesi*; with dermal co-ossification on top of the head and central part of the back in *B. ephippium* and *B. vertebralis*; and with ossified warts in *B. nodoterga*. (3) Color in life—orange with dorsal reddish-brown irregular markings, lateral surfaces, flanks, and thighs with small dark brown spots, and belly with brownish spots and small dots in *B. ferruginus*; orange with lateral surfaces, flanks, and thighs with small dark brown spots, and belly with brownish coalescent spots and small dots in *B. pombali*; orange with black spots on dorso-lateral surfaces, flanks, and hind limbs in *B. pernix* (Pombal et al., 1998); orange without marks or spots in *B. ephippium* and *B. izecksohni*; orange greyish in *B. nodoterga* (Heyer et al., 1990); yellow in *B. vertebralis* (C. F. B. Haddad, unpublished data); brown with variable amount of orange markings and spots on belly, throat, and ventral surface of limbs in *B. brunneus*; brownish with a dorsal dark X mark, lateral surfaces dark brown in *B. didactylus* (Izecksohn, 1971); brownish yellow to pale brown, eventually with dark grey stripes on dorsal surfaces of hind limbs and a lateral dark brown stripe from the posterior edges of eye to flank in *B. hermogenesi* (Giaretta and Sawaya, 1998). (4) Snout shape in dorsal view—rounded in *B. ferruginus*, *B. pombali*, *B. ephippium*, *B. izecksohni*, *B. nodoterga*, *B. pernix*, and *B. vertebralis*; mucronate in *B. brunneus*; short and pointed with a rounded tip (subacuminate) in *B. didactylus* and *B. hermogenesi*. (5) Nostrils shape—protuberant in *B. ferruginus*, *B. pombali*, *B. brunneus*, and *B. izecksohni*; not protuberant in *B. didactylus*, *B. ephippium*, *B. hermogenesi*, *B. nodoterga*, *B. pernix*, and *B. vertebralis*. (6) Canthus rostralis shape—not distinct in *B. ferruginus*, *B. pombali*, *B. izecksohni*, *B. didactylus*, *B. ephippium*, *B. hermogenesi*, *B. nodoterga*, *B. pernix*, and *B. vertebralis*; distinct and sinuous in *B. brunneus*. (7) External trace of toe V—absent in *B. izecksohni* and *B. pernix*; present but reduced in *B. ferruginus*, *B. pombali*, *B. brunneus*, *B. didactylus*, *B. ephippium*, *B. nodoterga*, and *B. vertebralis*; present and functional in *B. hermogenesi*. (8) Outer metatarsal tubercle—present in *B. ferruginus, B. pombali, B. brunneus, B. didactylus, B. hermogenesi, B. izecksohni, B. nodoterga*, and *B. vertebralis*; absent in *B. ephippium* and *B. pernix*.

A comparison of the osteology of *B. ferruginus* and *B. pombali* with that of other brachycephalid species showed that the two new species can be distinguished by: (9) Skull dermal roofing bones—unornamented and with no co-ossification of skin to bones in *B. ferruginus*, *B. pombali*, *B. brunneus*, *B. hermogenesi*, *B. izecksohni*, and *B. pernix*; exostosis and co-ossification present in *B. ephippium*. (10) Paired skull bones—distinct, not fused with surrounding elements in *B. ferruginus*, *B. pombali*, *B. brunneus*, *B. hermogenesi*, *B. izecksohni*, and *B. pernix*; completely fused in *B. ephippium*. (11) Quadratojugals—present, slender in *B. ferruginus*, *B. pombali*, *B. brunneus*, *B. izecksohni*, and *B. pernix*; very slender in *B. hermogenesi*; absent in *B. ephippium*. (12) Neopalatines—absent in *B. ferruginus*, *B. pombali*, *B. ephippium*, *B. hermogenesi*, and *B. pernix*; present but reduced in *B. brunneus* and *B. izecksohni*. (13) Maxillary odontoids—present, few in number (6–8) in *B. ferruginus*, *B. pombali*, *B. brunneus*, *B. izecksohni*, and *B. pernix*; present, numerous in *B. hermogenesi*; absent in *B. ephippium*. (14) Vomers—reduced in *B. ferruginus*, *B. pombali*, *B. brunneus*, *B. hermogenesi*, *B. izecksohni*, and *B. pernix*; very reduced in *B. ephippium*. (15) Squamosals—complete in *B. ferruginus*, *B. pombali*, *B. brunneus*, *B. izecksohni*, and *B. pernix*; with anterior zygomatic ramus reduced and ramus ventral laterally expanded in *B. hermogenesi*; fused to prootic and with zygomatic ramus very reduced in *B. ephippium*. (16) Pterygoids—relatively robust in *B. ferruginus*, *B. pombali*, *B. brunneus*, *B. hermogenesi*, *B. izecksohni*, and *B. pernix*; very slender in *B. ephippium*. (17) Fusion of the cultriform process of parasphenoid to sphenethmoid—not fused in *B. ferruginus*, *B. pombali*, *B. brunneus*, *B. hermogenesi*, *B. izecksohni*, and *B. pernix*; fused in *B. ephippium*. (18) Fusion of IV–V and VI–VII presacral vertebrae—not fused in *B. ferruginus*, *B. pombali*, *B. brunneus*, *B. hermogenesi*, *B. izecksohni*, and *B. pernix*; fused in *B. ephippium*. (19) Tips of the terminal phalangeal elements—arrow-shaped in *B. ferruginus*, *B. pombali*, *B. brunneus*, *B. ephippium*, *B. izecksohni*, and *B. pernix*; claw-shaped in *B. hermogenesi*. (20) Hyoid—about twice as long as wide at midline, with lateral process of hyoid plate short in *B. ferruginus*,

B. pombali, *B. brunneus*, *B. ephippium*, *B. izecksohni*, and *B. pernix*; three times as long as wide, without lateral process of hyoid plate in *B. hermogenesi*.

The osteological data reviewed above show that the species of *Brachycephalus* that occur in the Serra do Mar in the State of Paraná share a set of similar osteological features. The main features shared by *B. brunneus*, *B. ferruginus*, *B. izecksohni*, *B. pernix*, and *B. pombali* include unornamented skull bones with no co-ossification of skin to bones, paired skull bones distinct and not fused with surrounding elements, quadratojugals present, odontoids present and few in number, squamosals complete and not fused to prootic, pterygoids relatively robust, cultriform process of the parasphenoid to sphenethmoid not fused, and presacral vertebrae not fused. Despite the similar osteological features shared by the species of *Brachycephalus* that occur in the State of Paraná (Pombal et al., 1998; Ribeiro et al., 2005; present study), these species can be distinguished from each other by a combination of morphological and osteological traits.

The species of *Brachycephalus* from the state of Paraná can also be uniquely characterized by multivariate patterns of covariation in metric traits, as revealed by nonoverlapping confidence regions around centroids for each species in the reduced space of the first and second canonical variates (Fig. 11A). The pattern of correlations of individual metric traits with the first canonical variate (Fig. 11B) suggests that discrimination is based on multivariate size (Garavello et al., 1992). This finding is relevant for the taxonomy of the *Brachycephalus* species of the state of Paraná because they overlap extensively in metric traits (Ribeiro et al., 2005; A. C. R. Alves, unpublished data; present study) and it is not possible to discriminate these species unambiguously on the basis of any single univariate metric trait. The addition of inferential information around sample centroids derived from multivariate procedures using resampling methods is an important development in statistics (Ringrose and Krzanowski, 1991; Ringrose, 1992) and proved to be relevant here for taxonomic characterization of *Brachycephalus*, as recently demonstrated for other taxonomic groups (Duarte et al., 2000; Reis et al., 2002*a*,*b*).

Although external morphological and osteological traits have traditionally been used to diagnose species of *Brachycephalus*, no studies have assessed the phylogenetic content of these traits. In relation to this, it should be remembered that the evolutionary conservatism of anurans may result in morphological traits not retaining phylogenetic signal (e.g., Austin et al., 2002). Therefore, analyses of the phylogenetic content of morphological traits will need to consider the potential limitations imposed by evolutionary conservatism. Additionally, phylogenetic information will need to be sought in DNA sequences in order to infer phylogenetic relationships of the taxa described from the State of Paraná and for other *Brachycephalus* species.

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APPENDIX I

Specimens Examined

Brachycephalus brunneus: **Paraná**, Campina Grande do Sul CFBH 7879 (holotype), 7880–7890 (paratopotypes), 7900, 7903–7904 (cleared and stained). *B. didactylus*: **Rio de Janeiro**, Rio de Janeiro, Ilha Grande MNRJ 31201; Sacra Família do Tinguá MNRJ 25402–25404, 25415–25421. *B. ephippium*: **Rio de Janeiro**, Rio de Janeiro MNRJ 25346, 27577–78, 30919–29; Itatiaia MNRJ 23581–86; **São Paulo**, Atibaia CFBH 7389 (cleared and stained). *B. hermogenesi*: **São Paulo**, Ubatuba CFBH 4041 (cleared and stained), MNRJ 18662–63 (paratopotypes), 18624–25 (paratypes). *B. izecksohni*: **Paraná**, between Guaratuba and Paranaguá CFBH 7388 (holotype), 7375–77, 7380–87 (paratopotypes), 7378–79 (cleared and stained). *B. nodoterga*: **São Paulo**, Serra da Cantareira MZUSP 0975 (holotype); Boracéia MUZUSP 30625–26, 30653; Ilha Bela MNRJ 23633–641. *B. pernix*: **Paraná**, Quatro Barras ZUEC 9433–37 (paratopotypes), MHNCI 1818–19 (paratopotypes), 3000–04, CFBH 7390 (cleared and stained). *B. vertebralis*: **Rio de Janeiro**, Parati MNRJ 11098 (holotype), 11094–96, 11106–11107, 11116–11118, 11120, 11131–1132 (paratopotypes).

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