# MORPHOLOGICAL VARIATION IN *PTYCHOGLOSSUS BREVIFRONTALIS* BOULENGER, 1912 AND THE STATUS OF *PTYCHOGLOSSUS NICEFORI* (LOVERIDGE, 1929) (SQUAMATA, GYMNOPHTHALMIDAE)

PEDRO L. V. PELOSO<sup>1,2,3</sup> AND TERESA C. S. AVILA-PIRES<sup>1</sup>

<sup>1</sup>Museu Paraense Emílio Goeldi/CZO, Avenida Perimetral 1901, Terra Firme, 66077-530, Belém, Pará, Brazil
<sup>2</sup>Programa de Pós-Graduação em Zoologia Universidade Federal do Pará—Museu Paraense Emílio Goeldi, Belém, Para, Brazil

ABSTRACT: Intra- and interpopulational variation in the morphology of *Ptychoglossus brevifrontalis* Boulenger, 1912 were studied. Differences in scale counts and morphometric traits among populations and between sexes are evaluated and described. Sexual dimorphism is evident in number of precloacal and femoral pores, and to a lesser degree in body elongation. Hemipenial morphology is briefly discussed. *Ptychoglossus nicefori* (Loveridge, 1929) is again considered a junior synonym of *P. brevifrontalis*. Brief comments on the species taxonomy are provided.

RESUMO: Estudamos a variação intra- e interpopulacional na morfologia de *Ptychoglossus brevifrontalis* Boulenger, 1912. Diferenças em contagens de escamas e na morfometria entre populações e entre os sexos foram avaliadas e descritas. Dimorfismo sexual é evidente no número de poros pré-cloacais e femorais e, em menor escala, no grau de alongamento do corpo. Morfologia hemipeniana é brevemente discutida. *Ptychoglossus nicefori* (Loveridge, 1929) é novamente considerada um sinônimo junior de *P. brevifrontalis*. Alguns comentários sobre a taxonomia da espécie são também fornecidos.

Key words: Anadia nicefori; Hemipenis; Microteiid; Ptychoglossus; Taxonomy

THE LIZARD genus Ptychoglossus Boulenger, 1890 comprises 15 valid species distributed from Costa Rica to Peru and Brazil (Avila-Pires, 1995; Harris, 1994; Savage, 2002). They are inhabitants of the forest floor, living in elevations ranging from sea level up to 2100 m in some Andean localities. Most species are apparently restricted to small distribution ranges, although a few (Ptychoglossus brevifrontalis, P. gorgonae Harris, 1994, P. nicefori Loveridge, 1929, and *P. plicatus* Taylor, 1949) have wider distributions (Harris, 1994). Ptychoglossus brevifrontalis presents the broadest geographic distribution within the genus and is the only species known from Brazilian Amazonia (Avila-Pires, 1995). Avila-Pires (1995) considered P. brevifrontalis to occur in Brazil based on literature records from Rondônia by Vanzolini (1986) and from the Suriname/Brazil border by Hoogmoed (1973).

Ptychoglossus brevifrontalis (Fig. 1) was described by Boulenger (1912, p. 421) based on a single specimen (BMNH 1946.8.31.63) from El Topo, Rio Pastaza, Ecuador. Loveridge (1929, p. 99) described Anadia nicefori

on the basis of a specimen from Rio Garagoa, Boyacá, Colombia (MCZ 27340), which Dunn (1944, p. 67) soon transferred to the genus Ptychoglossus. Both species were considered valid until Dixon and Soini (1975, p. 51) suggested that P. nicefori should be regarded as a junior synonym of *P. brevifrontalis*. This position was followed by Duellman (1978, p. 223), although explicitly by recommendation of J. R. Dixon. The two species were separated mainly by number of scales around midbody and color pattern, but Dixon and Soini (1975) argued that number of scales around midbody was very similar and all other characters overlapped, including color pattern. However, Harris (1994), in his review of Ptychoglossus, resurrected P. nicefori based on differences in the occipitals (=postparietal in his work), dorsal scale keels, number of tricuspid dentary teeth, body size, and relative length of body (in relation to limbs) and tail.

Harris (1994) analyzed 35 specimens of *P. brevifrontalis* and 38 of *P. nicefori*, most of them from western Amazonia. The only eastern specimen of *P. brevifrontalis* studied and known at that time was from the

<sup>&</sup>lt;sup>3</sup> CORRESPONDENCE: e-mail, pedropeloso@gmail.com



FIG. 1.—Ptychoglossus brevifrontalis from Anapu, Rio Xingu, Pará, Brazil, in life (MPEG 25642, female). SVL = 49.5 mm.

Suriname–Brazil border (BMNH 1939.1.1.75), already described in detail by Hoogmoed (1973). According to Harris (1994), specimens of *P. brevifrontalis* from southeastern Peru, Bolivia and the single known specimen from Suriname had fewer scales around midbody than those from Ecuador and Colombia. Besides, dorsal scale keels were also less pronounced in specimens from southeastern Peru and Bolivia. No geographic variation was mentioned in relation to *P. nicefori*.

Hoogmoed (1979) considered *P. brevifrontalis* as presenting a peripheral Amazonian distribution, which was still true at the time of the studies by Harris (1994) and Avila-Pires (1995). Since then, however, new specimens have been collected, especially in central and eastern Amazonia (Pinto and Quatman, 2005; Vitt et al., 1998; material in the collections of Museu Paraense Emílio Goeldi and Instituto de Pesquisas da Amazônia, Brazil), indicating that the species occurs apparently all over Amazonia. This new material allows a better evaluation of the geographic variation in the species and a reassessment of the validity of *P. nicefori*.

#### MATERIALS AND METHODS

A total of 147 specimens of *P. brevifrontalis* plus *P. nicefori* was examined, including the holotype of *P. nicefori* (that of *P. brevifrontalis* was examined through photographs). These specimens, as well as those of congeneric species examined for comparisons, are listed in Appendix I. Specimens deposited in the following institutions were studied: American Museum of Natural History, New York, New York, USA (AMNH); The Natural History Museum, formerly British Museum of Natural History, London, United Kingdom (BMNH); California Academy of Sciences, San Francisco, California, USA (CAS); The Field Museum, Chicago, Illinois, USA (FMNH); Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil (INPA); University of Kansas Museum of Natural History, Lawrence, Kansas, USA (KU); Natural History Museum of Los Angeles County, Los Angeles, California, USA (LACM); Louisiana State University Museum of Natural Science, Baton Rouge, Louisiana, USA (LSU); Museum of Comparative Zoology, Cambridge, Massachusetts, USA (MCZ); Museu Paraense Emilio Goeldi, Belém, Pará, Brazil (MPEG); Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP); Texas Cooperative Wildlife Collection, College Station, Texas, USA (TCWC); University of Michigan Museum of Zoology, Ann Arbor, Michigan, USA (UMMZ); National Museum of Natural History, Washington, DC, USA (USNM); University of Texas at Arlington, Arlington, Texas, USA (UTA).

Scale terminology follows Harris (1994), except for the two rows of postparietals, which are referred to as occipitals and postoccipitals. All measurements were taken with an electronic caliper under a stereomicroscope (to the nearest 0.1 mm) except for tail length, taken with a ruler (to the nearest 1.0 mm). The following measures were taken: DBM (distance between members: from posterior margin of forelimb to anterior margin of hind limb), EED (eye-ear-opening distance: from posterior corner of eye to anterior border of ear opening), FLL (forelimb length: from arm insertion to tip of longest finger), HH (head height: highest height), HL (head length: from tip of snout to anterior margin of tympanum), HLL (hind limb-length: from leg insertion to tip of longest toe), HW (head width: measured on the widest portion of the head), SED (snout-eye distance: from tip of snout to anterior corner of eye), SVL (snout-vent length: from tip of snout to cloaca), TL (tail length: from cloaca to tip of tail), and VED (vertical ear-opening diameter). Additionally, the following scale counts were performed: COL (total number of scales that form the

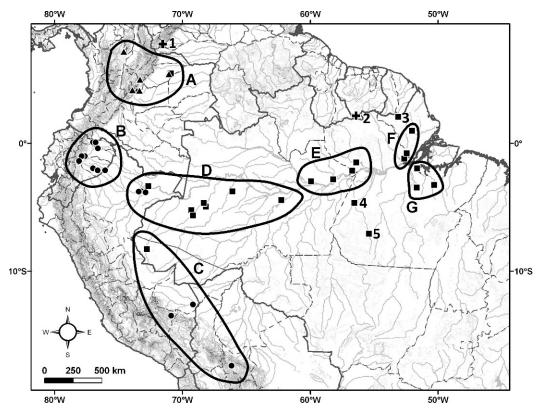


FIG. 2.—Distribution records of specimens examined during this study. Triangles and circles represent specimens also analyzed by Harris (1994) and identified respectively as *P. nicefori* and *P. brevifrontalis*; squares represent specimens examined by us but not by Harris (1994); crosses are records from literature. Grouped samples (A–G) represent the seven Operational Units used for statistical analysis of geographic variation. Numbers represent respectively; (1) record from Barrio et al. (2003); (2) Hoogmoed (1979); (3) Tumucumaque, Amapá; (4) Itaituba, Pará; (5) Novo Progresso, Pará.

collar), DOR (dorsal scale rows, counted along a mid-dorsal line from occipitals), FEM (number of femoral pores), GUL (transverse rows of gulars, including collar), LFIV (subdigital lamellae under fourth finger), LTIV (subdigital lamellae under fourth toe), OCC (occipitals), PAL (palpebrals), PCP (number of precloacal pores), POC (postoccipitals), SAM (scales around midbody; counted at half the distance between gular fold and posterior margin of hind limbs), SBO (suboculars), SPC (supraciliaries), SPL (supralabials), TCP (temporals in contact with parietal), TEMP (temporals), and VEN (transverse rows of ventrals). Counts and measurements were made on the left side; only when this was not possible the right side was used. Sex was determined by presence (males) and absence (females) of precloacal pores.

Pedro M. S. Nunes (IB-USP) kindly prepared and examined the hemipenes of four specimens (MPEG 24058, 25943, 24945, 25948) from four localities in Pará, Brazil (Almeirim, Faro, Novo Progresso and Caxiuanã, respectively). The retractor muscle was manually separated and the everted hemipenis was filled with stained petroleum jelly. The organ was then stained in alizarin red solution for 24 hours for observation of any mineralized structure (P. Nunes, personal communication).

# Nongeographic Variation

To examine nongeographic variation we analyzed samples from two relatively close localities (both included in Operational Unit G in Fig. 2), totaling 51 specimens: Floresta Nacional de Caxiuanã, municipalities of Melgaço and Portel, Pará, Brazil (from now on referred to as Caxiuanã), n = 38 (29 males, 9 females), and U.H.E. Belo Monte, Rio Xingu, Pará (from now on Belo Monte), n = 13 (8 males, 4 females, one juvenile). Samples from Belo Monte come from both sides of the Xingu river (municipalities of Anapu and Altamira), whereas Caxiuanã is located in the Xingu–Tocantins interfluvium.

We tested the role of allometric growth based on the multivariate allometric model of Jolicoeur (1963), where the multivariate coefficient of allometry (MCA) is calculated based on the coefficients of a principal component analysis (PCA) following the formula

MCA=
$$p/\sqrt{1/n}$$
,

where p is the principal component I (PCI) eigenvector of the covariance matrix for a given variable and n is the total number of variables. If MCA is equal to 1 this is considered as isometry (the parts grow at the same rate). Values higher than 1 mean positive allometry (variable grows in a faster rate than body size) and values lower than 1 mean negative allometry (variable grows in a lower rate than body size). On the assumption that males and females may show different growth rates (Pinto and Avila-Pires, 2004), two separate data sets were built for allometry tests, one with males and juveniles (sex undetermined) and one with females and juveniles. The PCA was performed with 10 log-transformed morphometric variables (SVL, HL, HW, HH, SED, EED, VED, DBM, FLL, HLL).

# Geographic Variation

A recurrent problem in studies on geographic variation is sample size. Vanzolini (2002) briefly discussed the subject and commented that "in characters with little variability samples of 6 or 8 specimens usually turn out quite well." However, from only four well-defined localities six or more specimens were available. We therefore used a common tactic in such cases, which is to group distinct localities into operational taxonomic units (OTUs, Heyer, 2005; Vanzolini, 2002). Groupings were based on geographic proximity and under the assumption of ecological homogeneity. This is, however, a subjective procedure and should be carefully evaluated before taxonomic decisions are made based on the results of statistical analysis using such groupings.

We grouped samples in the following OTUs (Fig. 2): Unit A (12 specimens from northern Colombia, including the holotype of Anadia *nicefori*; this sample contains 10 specimens examined by Harris (1994) and identified as P. nicefori, and two specimens not examined by him, tentatively identified as *P. nicefori*); Unit B (11 specimens from Ecuador); Unit C (seven specimens from the state of Acre, in Brazil, southern Peru, and Bolivia); Unit D (25 specimens from Departamento Loreto, Peru, and state of Amazonas, Brazil, south of the Amazon river); Unit E (15 specimens from eastern state of Amazonas and western state of Pará, Brazil, north of the Amazon river and east of the Negro river); Unit F (seven specimens from the Jari region in the states of Pará and Amapá, and one specimen from Serra do Navio, Amapá, Brazil); Unit G (58 specimens from central state of Pará, Brazil). Seven specimens (MPEG 22346-48, Itaituba, Pará, Brazil [represented by number 4 in Fig. 2]; MPEG 25946-48, Novo Progresso, Pará, Brazil [5]; TQ 312, Tumucumaque, Amapá, Brazil [3]) could not be confidently placed in any of the units, either because they are geographically isolated or because they show some singular features that did not allow us to confirm they represent the same lineage as those from other localities. These specimens are separately treated in the discussion of geographic variation. Two specimens from BMNH (including the holotype of *P. brevi*frontalis) were examined from photographs and were not included in the analyses.

The record of *P. brevifrontalis* for the state of Rondônia, Brazil (Avila-Pires, 1995; Vanzolini, 1986) is apparently an identification error. PLVP had access to the only specimen from Rondônia deposited in the MZUSP (where P. E. Vanzolini deposited most of the material he collected in Nova Brasília, Rondônia) and the specimen identified as *P. brevifrontalis* (MZUSP 32329) is in fact a juvenile *Arthrosaura reticulata*. We are not aware of additional records of any species of *Ptychoglossus* from Rondônia.

We compared OTUs through discriminant function analyses (DFA) of morphometric

(size-free) and meristic data (separately). Sizefree discriminant analysis consists of regressing each variable separately on the first principal component of a principal component analysis and then applying the DFA to the residuals obtained from the regressions (Reis et al., 1990; Strauss, 1985). Because meristic characters do not vary with size, the procedure explained above was only used for morphometric data. A forward stepwise DFA was used with both meristic and morphometric data in order to select the most powerful predictors for each analysis (Tabachnick and Fidell, 2001).

We lumped both sexes together in both analyses so we would not have to exclude one of the OTUs from the analysis due to small sample size after removal of one sex. We did this at the expense of two variables, number of precloacal pores and number of femoral pores, which were excluded from these analyses because they are highly sexually dimorphic. Missing morphometric values were estimated with the use of a missing value analysis, based on the linear regression of the observed variables, and missing meristic variables were filled with mean value of the missing variable in the OTU it belongs. Missing values never represented more than 14% of the total. All statistical analyses were performed in the software SYSTAT 12 for Windows (Systat Software, San Jose, California, USA).

We analyzed also some scale contacts on the head of almost every specimen examined. The contacts chosen to be evaluated are some of those used by Harris (1994) to diagnose species of *Ptychoglossus*.

# RESULTS

# Nongeographic Variation

Male SVL in the two combined samples from central Pará, Brazil, ranged from 29.0 to 51.3 mm (n = 37); female SVL ranged from 38.0 to 56.4 mm (n = 13). In specimens with a complete tail (no evident sign of regeneration) tail length is equivalent to 1.2–1.9 times the SVL in males (n = 13; mean 1.6) and 1.4–1.9 times the SVL in females (n = 8; mean 1.6). A significant correlation was found between TL and SVL in females (r = 0.86, df = 7, P < 0.05) but no significant correlation was found for males (r = 0.33, df = 12, P > 0.05; Fig. 3A). Visible correlations were found for all other morphometric data evaluated, such as between SED and HL, HW and HL, limbs (FLL + HLL) and DBM, FLL and SVL, and HLL and SVL (Figs. 3B–F).

Summary of measurements in millimeters/ ratios, among specimens are HL (males 6.0-10.0, females 7.5–10.1), HW (males 4.3–8.8, females 5.6-7.3), HH (males 2.7-6.4, females 3.4-7.7), SED (males 2.2-4.7, females 2.8-4.4), EED (males 2.1–4.1, females 2.7–5.5), VED (males 0.8–1.6, females 1.0–1.7), DBM (males 15.2–31.2, 20.9– females 27.6), FLL (males 6.4–10.7, females 7.1–10.5), HLL (males 9.9-18.1, females 14.0-18.2), HL/SVL (males 0.19-0.21, females 0.17-0.21), HL/HW (males 1.32-1.50, females 1.00-1.49), HH/HL (males 0.41–0.81, females 0.44–0.73), SED/ HL (males 0.34–0.47, females 0.36–0.53), DBM/SVL (males 0.48-0.57, females 0.51-0.58), FLL/SVL (males 0.20–0.23, females 0.19-0.24), HLL/SVL (males 0.34-0.40, females 0.31-0.37), limbs/DBM (males 0.93-1.21, females 0.89-1.17).

Number of supralabial scales seven in most specimens, but six in one specimen and eight in three others (range 7–8, mean 7  $\pm$  0.2); occipitals usually five, subequal in size in 84% of the specimens, four in seven specimens (possibly due to fusion of two scales) and three in one specimen (range 2–5, mean  $4.7 \pm 0.6$ ); postoccipitals 2-5 (mean  $4.0 \pm 0.6$ ); suboculars 1-5 (mean 3.3  $\pm$  0.8); suboculars 1-5 (mean  $3.3 \pm 0.8$ ; supraciliaries 4–6 (usually five; mean 5.0  $\pm$  0.3); palpebrals 1–3 (mean 2.2  $\pm$ 0.4); temporals 8–13 (mean 11.2  $\pm$  0.8); gulars in 5–6, usually six, rows (mean 6.0  $\pm$  0.1); dorsals arranged in 29-32 well-defined rows (mean  $30.5 \pm 0.6$ ); ventrals in 17–20 transverse rows (mean  $18.3 \pm 0.8$ ); scales around midbody 28-34 (mean  $30.7 \pm 1.1$ ); 10-13 lamellae under fourth finger (mean  $11.4 \pm 0.9$ ); 16–20 under fourth toe (mean  $17.4 \pm 0.9$ ). Numbers of precloacal and femoral pores show sexual dimorphism. Females lack precloacal pores and present none or 6–7 femoral pores on each side, while males present 2–3 precloacal and 9– 14 femoral pores on each side.

Prefrontals are in middle contact in all specimens of this sample, but contact line

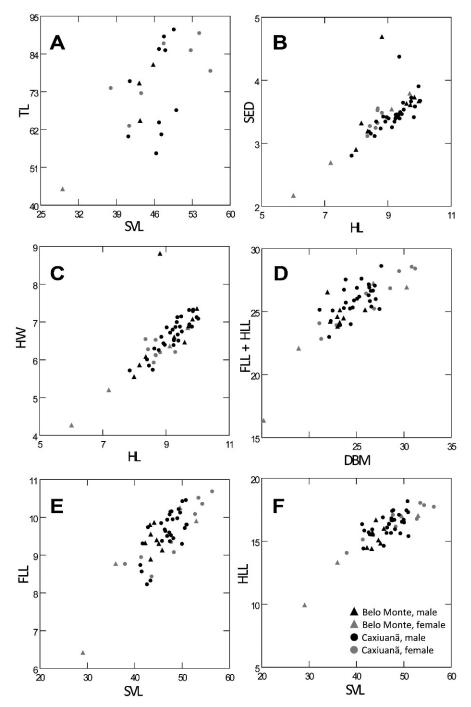


FIG. 3.—Correlation among several morphometric traits in two samples of *Ptychoglossus brevifrontalis* from central Pará. Measurements in millimeters. Abbreviations in Materials and Methods section.

	Males		Females		
	PCI	MCA	PCI	MCA	
SVL	-0.3613	-1.1425	-0.3778	-1.1948	
HL	-0.2743	-0.8674	-0.2603	-0.8233	
HW	-0.2803	-0.8863	-0.2843	-0.8989	
HH	-0.3119	-0.9864	-0.3065	-0.9694	
SED	-0.2703	-0.8547	-0.2924	-0.9246	
EED	-0.3586	-1.1338	-0.3131	-0.99	
VED	-0.282	-0.8916	-0.2592	-0.8196	
DBM	-0.3915	-1.2379	-0.4201	-1.3285	
FLL	-0.2965	-0.9377	-0.2831	-0.8954	
HLL	-0.31	-0.9803	-0.3277	-1.0362	

TABLE 1.—Eigenvectors of covariance factor of the first component (PCI) of the principal components and multivariate coefficient of allometry (MCA) for 10 morphometric variables in two samples, males plus juveniles and females plus juveniles, of *Ptychoglossus brevifrontalis* from central Pará, Brazil. Abbreviations in the Materials and Methods section.

varies from short to long. Loreal is either separated from supralabials by a contact between nasal and frenocular (85% of a subsample of 20 specimens examined for this character) or in contact with first or first and second supralabials (15% of the specimens examined).

Indications of allometric growth were found for some morphometric traits in both males and females (Table 1). Head length and head width showed negative allometry, meaning that juveniles have relatively longer and wider heads than adults. Distance between limbs and SVL showed positive allometry for both sexes, but with higher values for females than for males, indicating that adult females have proportionally longer bodies than males of similar size.

# Geographic Variation

Female specimens seem to attain a greater size (SVL) than males within all OTUs, as found in the nongeographic variation analysis (Fig. 4). However, there seems to be a shift in maximum size among OTUs. Males from OTU A present the smallest mean SVL, whereas females from OTU F present the smallest mean SVL (Fig. 4). However, such differences may be related to the samples, not necessarily reflecting population differences. Variations in morphometric data among OTUs are summarized in Table 2. Correlation between combined fore- and hindlimb lengths, on one side, and distance between limbs, on the other side, show no distinct variation among groups.

Supralabials in the whole sample vary from 6–8, but usually 7 scales are present; number of suboculars varies greatly, from just one enlarged scale to five smaller ones; temporals 9–14; rows of dorsals 29–32 (97% of the sample vary from 30–31); ventrals 16–21 (nearly 93%, 17–19); scales around midbody 28–38; gulars 5–7 (95%, 6); lamellae under fourth finger 9–14; under fourth toe 14–22.

Specimens from OTUS A and F show lower counts of occipitals and temporals, F also has lower counts of postoccipitals. Individuals from OTU B apparently have a higher number of lamellae under finger IV and toe IV, and those from OTU F have lower counts of lamellae under toe IV. Differences in scale counts between OTUs are illustrated in Table 3.

Two out of three specimens from Novo Progresso, Pará (MPEG 25946-47), and one out of four specimens from Almeirim, Pará (MPEG 24057), have separated prefrontals (Fig. 5A), a condition not previously reported in *P. brevifrontalis* (Ávila-Pires, 1995; Harris, 1994) and which is a diagnostic feature of *P. bilineatus*, *P. myersi*, and *P. stenolepis* (Harris, 1994). The shape of the loreal scale and its degree of contact with supralabials vary from completely separated to forming a relatively broad contact.

Occipitals showed marked variation. Most specimens (over 70% of the sample) show the typical condition described for *P. brevifronta-lis*, with five scales of nearly the same size (Fig. 5E). Fewer specimens show three scales, with lateral ones enlarged (Fig. 5G), the typical condition described for *P. nicefori*,

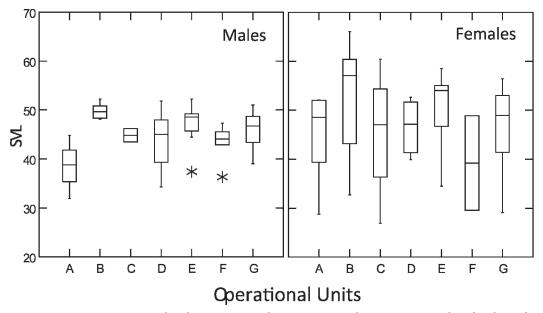


FIG. 4.—Variation in snout-vent length among sexes in the seven operational taxonomic units evaluated in this study. Measurements are in millimeters. Asterisks are juveniles regarded here as sample outliers. Central line is the mean value; the length of each box shows the range within which the central 50% of the values fall.

which predominates in specimens from Colombia (OTU A) and eastern Pará-Amapá (OTU F). There are, however, localities where both states of the occipitals are present (e.g., Caxiuanã and Faro, state of Pará; OTU G), and in some individuals only one enlarged occipital, either on the left or on the right side of the head, is present (Fig. 5F). Other variations of occipitals are worth mentioning. In one specimen from Peru (KU 215000) the interparietal reaches the postoccipitals. Harris (1994, p. 239) have already noted this anomaly and stated that "This anomalous departure from having a straight posterior parietal interparietal border is unique in the genus." One specimen from Faro, Pará (MPEG 25492), apparently shows a fusion of the three medial occipitals to form a transversely elongated scale. Geographic variation distribution of the occipital conditions is represented in Fig. 6.

We found lower counts of scales around midbody in samples from northern Colombia (OTU A), southern Peru and Bolivia (OTU C), and eastern Amazonia (OTUs F and G), whereas higher counts were found in OTUs from central Amazonia (D, E) and Ecuador (B) (Fig. 7).

The DFA results did not show strong regional differentiation of the Ptychoglossus samples included in the analyses. In the meristic DFA, the first two canonical discriminant variables accounted for 84% of the total variation (Wilks's lambda = 0.15;  $F_{30.448}$  = 10.30; P < 0.001) and correctly classified 59% of the individuals (Table 4). The stepwise DFA (F to enter = 3.0; F to remove = 2.9) performed with meristic data selected five variables, OCC, POC, SBO, SAM, LFIV, as the most powerful discriminators. Number of occipitals was selected first, correctly classifying 14% of the individuals. Postoccipitals and lamellae under finger IV were selected next, improving the classification percentage to 21 and 39%, respectively. The first canonical axis (eigenvalue = 2.10) is most influenced by POC (raw canonical function, RCF = 1.66), and OCC (RCF = 1.33), and the second canonical axis (eigenvalue = 0.44) is most influenced by SBO (RCF 0.85), LFIV (RCF = -0.66), and SAM (RCF = 0.51). The two first canonical axes promoted an almost complete separation between OTU F and the remaining groups (Fig. 8). Additionally OTU A is completely separated from OTU B and partially separated from the remaining

TABLE 2.— VARIATION IN MOPTIONICUE UARS DEWEEN HE SEVEN OPERATORIA UNIX USE AULY OF GEORGIAPTICAL VARIATION. MEASUREMENTS IN INTERESS, M, INARES, F, females. Abbreviations in the Materials and Methods section.	Operational Unit E Operational Unit F Operational Unit G	$ F(n = 6) \qquad M(n = 4) \qquad F(n = 2) \qquad M(n = 18) \qquad F(n = 6) \qquad M(n = 9) \qquad F(n = 5) \qquad M(n = 5) \qquad F(n = 2) \qquad M(n = 42) \qquad F(n = 14)  F(n = 14) $	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
or geograp ethods sect	Operati	M (n = 6	6 37.4-52 7 0.19-0.5 5 1.30-1.4 3 0.46-0.6 7 0.47-0.5 0 0.31-0.2 8 0.97-1.2 8 0.97-1.2
rials and M	Operational Unit D	) F $(n = 6)$	9 32.7-52. 1 0.18-0.22 6 1.33-1.4 0 0.41-0.5 9 0.36-0.4 6 0.50-0.5' 3 0.18-0.2' 0 0.32-0.41 9 0.87-1.1(
n the Mate	Operatic	M (n = 18)	2 34.3-51. 0 0.19-0.2 3 1.24-1.44 2 0.46-0.66 5 0.34-0.3 0 0.16-0.2 0 0.16-0.2 0 0.32-0.45 0 0.32-0.45 0 0.33-1.25 0 0.33-1.25
te seven Operational Units used for the source study of geographics females. Abbreviations in the Materials and Methods section	Operational Unit C	F $(n = 2)$	4     43.5-46.5       2     0.19-0.20       2     1.37-1.45       3     0.51-0.55       9     0.36-0.35       1     0.49-0.55       1     0.19-0.20       1     0.33-0.35       0     0.33-0.35       0     0.30-0.112
males. Abb	Operatio.	M (n = 4)	26.9-60.4 0.17-0.25 1.37-1.47 1.37-1.47 0.037-0.55 0.037-0.35 0.033-0.37 0.033-0.37 0.033-0.37 0.033-0.37 0.033-0.37 0.033-0.37
ferween me	Operational Unit B		$\begin{array}{cccccccccccccccccccccccccccccccccccc$
	Operation	$\mathbf{M}~(n~=5)$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$
шогрионе	Dperational Unit A	M $(n = 4)$ F $(n = 6)$ M $(n = 6)$	31.9-50.1 28.7-52.0 48.1 0.19-0.21 0.14-0.20 0.13 1.40-1.56 1.42-1.50 1.00 0.50-0.54 0.46-0.53 0.46 0.37-0.41 0.37-0.99 0.36 0.46-0.52 0.39-0.57 0.48 0.19-0.21 0.15-0.20 0.20 0.31-0.36 0.24-0.35 0.36 1.09-1.13 0.83-1.04 1.07
V di latuoli III	Operation	M ( $n = 4$ )	
1			SVL HL/SVL HL/HV HH/HL SED/HL DBM/SVL FLL/SVL Limbs/ DBM DBM

TABLE 3.—Variation in scale counts between the seven Operational Units (A–G) used for the study of geographic variation. Abbreviations in the Materials and Methods section.

	A $(n = 12)$	B $(n = 11)$	C $(n = 7)$	D $(n = 25)$	E(n = 15)	F(n = 7)	G $(n = 58)$
SPL	$5-7$ (6.7 $\pm$ 0.6)	$6-8$ $(7.0 \pm 0.4)$	$7-7$ (7.0 $\pm$ 0.0)	$6-7$ (6.9 $\pm$ 0.3)	$6-7$ $(6.9 \pm 0.3)$	$7-7$ (7.0 $\pm$ 0.0)	$6-8$ $(7.0 \pm 0.3)$
OCC	$3-5$ $(3.2 \pm 0.6)$		$2-5$ (4.3 $\pm$ 1.1)	$4-5(4.9\pm0.3)$	$3-5$ $(4.5 \pm 0.8)$	$3-3(3.0 \pm 0.0)$	$\pm 1$
POC	$3-4$ (3.8 $\pm$ 0.4)		$3-4$ (3.9 $\pm$ 0.4)	$4-5$ $(4.0 \pm 0.2)$	$4-5$ $(4.1 \pm 0.3)$	$2-4$ (2.3 $\pm$ 0.8)	2-5 (4.0 ± 0.6)
SBO	$3-4$ $(3.6 \pm 0.5)$	$2-5$ (3.5 $\pm$ 0.8)	$2-4$ (3.7 $\pm$ 0.8)	$2-5(3.9\pm0.9)$	$3-5$ (3.8 $\pm$ 0.7)	$3-5$ (4.0 $\pm$ 0.6)	+1
SPC	$5-5$ $(5.0 \pm 0.0)$		$5-5$ $(5.0 \pm 0.0)$	$5-5$ $(5.0 \pm 0.0)$	$4-5$ $(4.9 \pm 0.3)$	5-6 (5.1 ± 0.4)	$4-6$ (5.0 $\pm$ 0.3)
PAL	$2-3$ (2.3 $\pm$ 0.4)		$2-3$ (2.4 $\pm$ 0.5)	$2-3$ (2.4 $\pm$ 0.5)	$2-4$ (2.5 $\pm$ 0.7)	$2-3$ (2.4 $\pm$ 0.5)	$1-3 (2.2 \pm 0.4)$
TEMP	$9-12(9.9 \pm 1.0)$	$10-14 \ (11.5 \pm 1.2)$	$11-11 (11.0 \pm 0.0)$	$8-14(11.6 \pm 1.1)$	$11-13 (11.7 \pm 0.6)$	$9-12(9.7 \pm 1.1)$	(11.2 :
DOR	$30-31(30.7 \pm 0.40)$	$30-31 (30.5 \pm 0.5)$	$30-31$ ( $30.9 \pm 0.4$ )	$30-32(30.7 \pm 0.5)$	$30-31 (30.9 \pm 0.3)$	$30-31 (30.6 \pm 0.5)$	$29-32 (30.5 \pm 0.6)$
VEN	$17-20\ (18.6\ \pm\ 0.7)$	$17-21 \ (18.2 \pm 1.1)$	$18-19\ (18.3\pm0.5)$	$17-19(17.9 \pm 0.8)$	$17-20 \ (18.1 \pm 0.9)$	$17-19 (18.0 \pm 0.6)$	$16-20 \ (18.2 \pm 0.8)$
SAM	$28-32(30.4 \pm 1.4)$	$30-33$ $(31.6 \pm 0.9)$	28-33 (30.9 ± 2.0)	$28-38$ ( $32.6 \pm 2.5$ )	$29-33 (31.5 \pm 1.4)$	$28-31$ ( $29.4 \pm 1.0$ )	$28-33 (30.6 \pm 1.1)$
GUL	$5-6$ $(5.8 \pm 0.4)$	$6-7$ (6.1 $\pm$ 0.3)	6-6 (6.0 ± 0.0)	$6-6$ (6.0 $\pm$ 0.0)	6-6 (6.0 ± 0.0)	5-6 (5.9 ± 0.4)	$\sim$
COL	$7-10$ ( $7.8 \pm 0.9$ )	$7-9 (8.0 \pm 0.7)$	$7-9 (8.0 \pm 1.0)$	$7-10 (8.0 \pm 1.0)$	$7-10$ (8.5 $\pm$ 0.8)	$7-9$ (8.6 $\pm$ 0.8)	$7-11$ (8.5 $\pm$ 0.8)
LFIV	$11-12(11.3 \pm 0.4)$	$12-14 \ (13 \pm 0.9)$	$10-14 \ (11.4 \pm 1.4)$	$10-12(11.1 \pm 0.7)$	$10-14 \ (11.5 \pm 1.1)$	$10-11 (10.4 \pm 0.5)$	$10-13 (11.3 \pm 0.9)$
LTIV	$16-19(17.1 \pm 0.8)$	$16-21 \ (18.2 \pm 1.5)$	$14-17 (16.4 \pm 1.1)$	$15-18 (16.8 \pm 1.0)$	$15-19 \ (17.0 \pm 1.2)$	$14-17(15.9 \pm 1.1)$	$16-20\ (17.3\pm0.9)$

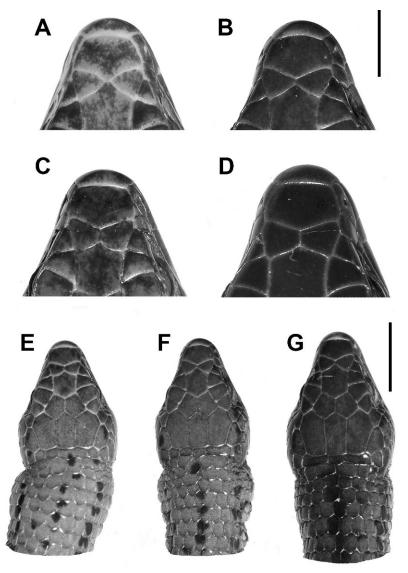


FIG. 5.—Head scales variation in *Ptychoglossus brevifrontalis*. Dorsal view of the snout of (A) MPEG 24057, (B) MPEG 26346, (C) MPEG 25910, and (D) MPEG 22346, evidencing the degree of medial contact between prefrontal scales. Dorsal view of the head of (E) MPEG 26435, (F) MPEG 26346 (note the different condition on each side of the head), and (G) MPEG 26429, showing variation in the condition of the occipitals. Scale bars = 3 mm.

groups. OTUS A and F showed smaller scores on the first axis, meaning they have lower counts of occipitals and postoccipitals; respectively, 83 and 86% of the individuals from these groups were correctly classified (Table 4). The second canonical axis, most influenced by number of suboculars, scales around midbody, and lamellae under fourth finger, lacked any resolution. The DFA with morphometric data produced a very low index of correctly classified individuals (24% of the total; Table 4) and lacked any resolution in separating any of the groups in both canonical axes. The results of this analysis are not commented upon further because they provide no material for geographic variation analyses (Wilks's lambda 0.64;  $F_{12,225} = 5.21$ ; P < 0.001).

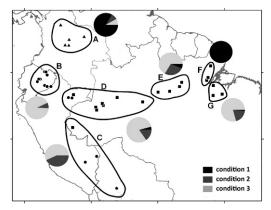


FIG. 6.—Relative frequencies of the states of organization of occipital scales among Operational Units studied. Conditions are as follows: (1) typical condition described for *Ptychoglossus nicefori* (represented in Fig. 5G); (2) intermediate condition or anomalous specimens, specimens that deviated from conditions A or C were included here; and (3) typical condition described for *Ptychoglossus brevifrontalis* (Fig. 5E).

Including the material studied by Harris (1994), at least one hemipenis from each of the OTUs (except OTU C) used in this work have been examined (OTU A MCZ 141221, 154336, examined solely by Harris; OTU B USNM 196259, examined by Harris; OTU D TCWC 41770, examined by Harris, and MPEG 25945, examined by us; OTU E MPEG 25943, examined by us; OTU F MPEG 24058, examined by us; OTU G MPEG 25948, examined by us). The four

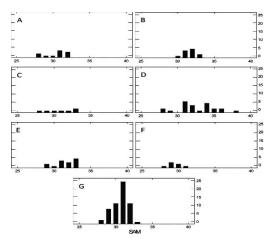


FIG. 7.—Variation on counts of scales around midbody in the seven Operational Units evaluated in this study.

TABLE 4.—Summary of classification accuracy of samples within Operational Units used in the discriminant function analyses. Abbreviations in the Materials and Methods section.

	Meristic		Morphometric	
Operational Unit	%	Jackknifed %	%	Jackknifed %
A $(n = 12)$	83	83	58	58
B(n = 11)	82	64	73	73
C(n = 07)	29	14	0	0
D $(n = 25)$	68	64	12	12
E(n = 15)	33	13	33	33
F(n = 07)	86	86	0	0
G(n = 58)	52	52	16	16
Total $(n = 135)$	59	53	24	24

hemipenes examined by us are very similar to that already reported for the species by Harris (1994). Hemipenial flounces 18–20 (MPEG 24058, 18 flounces; MPEG 25943, 20; MPEG 24945, 19; and MPEG 25948, 18), with distal ones continuous on asulcal and lateral faces, proximal ones continuous on asulcal face and interrupted laterally (Fig. 9). The number of apical fleshy protuberances is constantly six three pairs as reported by Harris (1994), shown in Fig. 9.

Seven specimens were not included in any of the Operational Units proposed. The only three specimens (MPEG 22346–48) available from Itaituba, Rio Tapajós, Pará, have two temporals in contact with the parietals on each

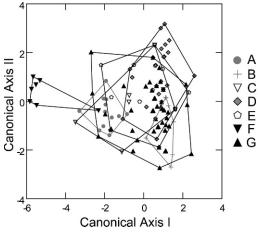


FIG. 8.—Graphical representation of scores of the first two axes of the discriminant functions analyses performed with meristic characters for the seven Operational Units (A–G).

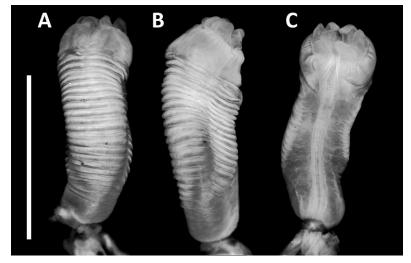


FIG. 9.—The hemipenis of *Ptychoglossus brevifrontalis* from Faro, Pará, Brazil (MPEG 25943). (A) asulcate, (B) lateral, and (C) sulcate side views. Photos by Pedro Nunes. Scale bar 5 mm.

side (one specimen has only one temporal in contact with the parietal on the left side), in contrast to only one temporal in contact with parietal in almost all but two other specimens. In these two latter specimens two temporals are in contact with the parietals, but one of them only punctually. The number of rows of gulars (6–7), transverse rows of ventrals (19–  $\overline{21}$ ), and lamellae under toe IV (18–22) are on the higher end of variation within the species, although there is a considerable amount of overlap in all counts (Table 3). Scales are smooth and with a nearly round posterior margin. These specimens are presently referable to P. brevifrontalis, but additional material is needed to confirm the taxonomic position of the population from Itaituba.

Three specimens (MPEG 25946–48) from Novo Progresso, southern Pará, show widened occipital scales and two of them present separated prefrontals. However, the remaining features of these specimens agree with the diagnosis of *P. brevifrontalis* and therefore they are referred to this species with a considerable degree of confidence.

The specimen from Tumucumaque (TQ 312) was not included in the OTU F, to which it is geographically closer, because unlike all specimens in that OTU, it has five occipitals (three in the remaining specimens), apparently less imbricated dorsal scales, 12–14 lamellae under fourth finger (versus 10–11). This

specimen is tentatively assigned to *P. brevifrontalis*. Additional material is needed to address the taxonomic status of the populations from the Tumucumaque mountain correctly.

Based on photographs and on available description and scale counts (Hoogmoed, 1973) the specimen from Suriname (BMNH 139.1.1.75) agrees in all features with *P. brevifrontalis* and this specimen is included in *P. brevifrontalis* without hesitation.

# DISCUSSION

Harris (1994) mentioned that female *Pty-choglossus* have longer bodies than males. Our data on allometric growth seems to support the idea of a proportionally longer body in females than in males, based on higher values of multivariate coefficient of allometry for DBM in females. Such a difference may be related to reproduction or other ecological aspects (Harris, 1994).

A lower count (28–30) of SAM was found by Harris (1994) in specimens from southern Peru. Besides southern Peru, we found lower counts of SAM also in samples from northern Colombia and eastern Amazonia (OTUs A, F, and G), whereas higher counts were found in OTUs from central Amazonia and Ecuador (OTUs B, D, and E) (Fig. 7, Table 3). Geographic variation is also found in other counts, such as temporals, with higher counts in OTUs from Ecuador (B) and central Amazonia (D and E) and lower counts in Colombia (A) and northeastern Amazonia (F). It is unclear what could be influencing these differences, but they do not follow a geographic pattern, nor do they seem to indicate specific differentiation.

The medial contact between prefrontals, contact of the loreal with the supralabials, and condition of the occipitals were considered by Harris (1994) as diagnostic features of some of the species recognized by him. Our data, however, show that these characters are polymorphic in *P. brevifrontalis*; therefore they should be used with care. *Ptychoglossus bilineatus* Boulenger, 1890, the type species of the genus, for instance, was considered to be distinguishable from P. brevifrontalis because the latter has "longer bodies, medially connected prefrontals, larger loreals that contact the supralabials, larger lateral neck scales, more flounces and bilaterally symmetrical hemipenial tips" (Harris, 1994). We found three specimens of *P. brevifrontalis* with separated prefrontals (Fig. 5A) and many (26% of specimens examined; not all specimens examined for this trait) with smaller loreals that do not contact the supralabials. On the other hand, significant differences in the hemipenis morphology are a good argument for proposing and diagnosing distinct species. The hemipenis of P. *bilineatus* is not bilaterally symmetric (Harris, 1994), while the organ is bilaterally symmetric in P. brevifrontalis (Fig. 9). However, the only available hemipenis of *P. bilineatus* was prepared in situ (Harris, 1994) and such preparations might affect the correct evaluation of the organ structure (Dowling, 2004). Additional specimens of P. bilineatus should be examined, especially a good hemipenis preparation. Unfortunately, as far as we are aware of, P. bilineatus is only known from the holotype.

Harris (1994) reported that he examined the hemipenis of specimen KU 41770; however, this specimen does not exist in his list of examined specimens (appendix I of his article). He does indeed list a TCWC specimen with that catalog number (which we also examined and is a male). We therefore assume the hemipenis examined by him was from specimen TCWC 41770, from Centro Union, Departamento Loreto, Peru.

Overall hemipenis morphology seems conservative in the entire range of *P. brevifrontalis* and *P. nicefori*, with a small variation in number of flounces. Harris (1994) mentioned variation in the number of hemipenial flounces in *P. nicefori* (18–20, n = 5), here represented by OTU A, and an exact number of 19 flounces in *P. brevifrontalis* (n = 2). We have found a variation of 18–20 flounces in the four hemipenes examined in samples assigned to *P. brevifrontalis*.

# The status of Anadia nicefori Loveridge 1929

Harris (1994) mentioned a slightly smaller SVL in *P. nicefori* than in *P. brevifrontalis*, and our samples indicate that indeed specimens from OTU A (referable to *P. nicefori*) have relatively small SVL in relation to the other samples. That same sample, along with OTU F, showed a tendency to segregate from all other groupings in the DFA (Fig. 8).

Dixon and Soini (1975) mentioned that no diagnostic characters were present for recognizing *P. nicefori* as a valid species and placed it under the synonymy of *P. brevifrontalis*. However, Harris (1994) later showed new evidence for recognizing both species. Harris (1994) argued that (1) enlargement of occipitals in P. nicefori (= postparietals in his work), (2) body/limb length proportions, (3) body/tail proportion, and (4) number of tricuspid teeth in the dentary were useful characters for distinguishing both species. We disagree with Harris (1994) for the following reasons: during the course of the examination of specimens of P. brevifrontalis from Brazil we found samples from the same locality with both states of the occipitals (Lago Ayapuá, in the state of Amazonas; Caxiuanã and Faro, state of Pará; Fig. 5), including individuals (INPA 13842, MPEG 26346) with one enlarged occipital on one side of the head and no enlarged scales on the other side (Fig. 5F). Although usually fixed in a given population, the condition of the occipitals should be used with care to diagnose species, because this has been shown to be a polymorphic trait, possibly not linked to phylogenetic history (discussion) in Aleixo, 2007; Wiens and Servedio, 2000). Harris (1994) argued that *P. nicefori* presents

a proportionally longer body and tail than P. *brevifrontalis*. According to him the adpressed limbs fail to meet by the distance of four dorsals or are just in contact, but do not overlap, in P. nicefori, whereas the limbs overlap a distance of 1-2 dorsals in *P*. *brevifrontalis*. However, during fieldwork at Belo Monte the senior author tested this with recently killed (not yet preserved in formalin) specimens and found that adpressed limbs of a female specimen (MPEG  $\overline{2}5642$ ) failed to meet by one dorsal, whereas in a male (MPEG 25643) limbs overlapped by one dorsal. As shown above, body elongation varies among sexes and ontogenetically. Regarding relative length of tail, as shown in Fig. 3A, within two samples of nearby localities used for the nongeographic evaluation we found no correlation between SVL and TL in males (although we did find it for females). Lack of correlation, however, could also be due to regenerated tails. Although we took extra care in removing all specimens with any sign of regeneration, if tails regenerate to the point of being indistinguishable from the original tail, except for length, they could be responsible for the observed result. We did not evaluate the condition of the teeth in either P. brevifrontalis or P. nicefori.

Additionally, we reexamined part of the material of *P. brevifrontalis* and *P. nicefori* seen by Harris (1994) and found that there are many juveniles in the sample, many specimens have their tails broken (Harris, 1994, examined only five specimens of *P. brevifrontalis* and nine *P. nicefori* for tail–body proportions) and fixation prevents examination of the condition of the adpressed limbs with the proper amount of confidence for most specimens. All this raises doubts about the conclusions reached by Harris (1994) related to the differentiation of the two species.

Harris (1994) also mentioned, although with less emphasis, minor scale count differences between *P. nicefori* and *P. brevifrontalis*, including number of femoral pores (males: 9–14 in *P. nicefori* and 10–14 in *P. brevifrontalis*/females: 0–4 in *P. nicefori* and 0–8 in *P. brevifrontalis*), scales around midbody (26– 33 in *P. nicefori* and 28–36 in *P. brevifrontalis*) and number of lamellae under toe IV (13–20 in *P. nicefori* and 15–22 in *P. brevifrontalis*). None of the female *P. nicefori* we examined have femoral pores. There is considerable overlap in the counts just given and almost all the variability is comprised in our OTU G, here used, in part, to evaluate nongeographic variation.

There seems to be no difference at all in the hemipenial morphology among *P. brevifrontalis* and *P. nicefori*. Harris (1994) mentions W-shaped flounces for *P. nicefori* (fig. 16 in his article) but this may be due to preservation and should be examined further in additional specimens.

Therefore, in light of the new morphological evidence shown above, we consider P. nicefori (Loveridge, 1929) a junior synonym of P. brevifrontalis Boulenger, 1912, as previously proposed by Dixon and Soini (1975). Some characters show geographic variation, but there is no evidence of independent lineages that could be recognized as distinct species. On the other hand, the identification of some specimens (e.g., from Itaituba and Tumucumaque) is done tentatively. More material from these localities would be necessary to ascertain their identification. Redescription of P. brevifrontalis is unnecessary at this point, because the descriptions provided by Hoogmoed (1973), Harris (1994), and Avila-Pires (1995) together are sufficiently detailed.

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#### LITERATURE CITED

- ALEIXO, A. 2007. Conceitos de espécie e o eterno conflito entre continuidade e operacionalidade: uma proposta de normatização de critérios para o reconhecimento de espécies pelo Comitê Brasileiro de Registros Ornitológicos. Ararajuba, Revista Brasileira de Ornitologia 15:297–310.
- ÁVILA-PIRES, T. C. S. 1995. Lizards of Brazilian Amazonia. Zoologische Verhandelingen 299:1–706.
- BARRIO, C. L., A. D. PASCUAL, AND A. CHACÓN-ORTIZ. 2003. Geographic distribution: *Ptychoglossus nicefori*. Herpetological Review 34:167.
- BOULENGER, G. A. 1890. First report on additions to the lizard collection in the British Museum (Natural History). Proceedings of the Zoological Society of London 1890:7786.
- BOULENGER, G. A. 1912. Descriptions of new reptiles from the Andes of South America, preserved in the British Museum. Annals and Magazine of Natural History 10:420–424.
- DIXON, J. R., AND P. SOINI. 1975. The reptiles of the upper Amazon Basin, Iquitos region, Peru. I. Lizards and amphisbaenians. Contributions in Biology and Geology, Milwaukee Publications Museum 41:1–58.
- DOWLING, H. G. 2004. On the structure of snake hemipenes with comments on their proper preparation for analysis: A reply to Cadle, Myers, Prudente, and Zaher. Herpetological Review 35:320–328.
- DUELLMAN, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. University of Kansas Museum of Natural History Miscellaneous Publications 65:1–352.
- DUNN, E. R. 1944. The lizard genus *Anadia* and *Ptychoglossus* in Colombia. Caldasia 3:63–68.
- HARRIS, D. M. 1994. Review of the Teiid genus Ptychoglossus. Herpetological Monographs 8:226–275.
- HEYER, W. R. 2005. Variation and taxonomic clarification of the large species of the *Leptodactylus pentadactylus* species group (Amphibia: Leptodactylidae) from Middle America, northern South America, and Amazonia. Arquivos de Zoologia 37:269–348.
- HOOGMOED, M. S. 1973. Notes on the herpetofauna of Surinam. IV. The lizards and Amphisbaenians of Surinam. Biogeographica 4:1–419.
- HOOGMOED, M. S. 1979. The herpetofauna of the Guianan Region. Pp. 241–279. *In* W. E. Duellman (Ed.), The South American Herpetofauna: Its Origin, Evolution, and Dispersal. Monographs of the University of Kansas Museum of Natural History 7.
- JOLICOEUR, P. 1963. The multivariate generalization of the allometry equation. Biometrics, 19:497–499.
- LOVERIDCE, A. 1929. A new *Anadia* from Colombia with remarks on other members of the genus. Proceedings of the Biological Society of Washington 42:99–102.
- PINTO, G. S., AND T. C. AVILA-PIRES. 2004. Crescimento alométrico, morfologia e uso do hábitat em cinco

espécies de *Mabuya* Fitzinger (Reptilia, Scincidae). Revista Brasileira de Zoologia 21:161–168.

- PINTO, M. G. M., AND W. E. QUATMAN. 2005. Ptychoglossus brevifrontalis (Boulenger's large-scaled lizard). Herpetological Review 36:202.
- REIS, S. F., L. M. PESSÓA, AND R. E. STRAUSS. 1990. Application of sizefree canonical discriminant analysis to studies of geographic differentiation. Revista Brasileira de Genética 13:509–520.
- SAVAGE, J. M. 2002. The Amphibians and Reptiles of Costa Rica. A Herpetofauna Between Two Continents, Between Two Seas. University of Chicago Press, Chicago, Illinois, USA.
- STRAUSS, R. E. 1985. Evolutionary allometry and variation in body form in the South American catfish genus *Corydoras* (Callichthyidae). Systematic Zoology 34:381–396.
- TABACHNICK, B. G., AND L. S. FIDELL. 2001. Using Multivariate Statistics. Fourth Edition. Allyn and Bacon, Boston, Massachusetts, USA.
- VANZOLINI, P. E. 1986. Levantamento herpetológico da area do Estado de Rondônia sob a influência da rodovia BR 364. Programa Polonoroeste, subprograma Ecologia Animal, Relatório de Pesquisa no. 1. Ministério da Ciencia e tecnologia/Conselho Nacional de Desenvolvimento Científico e Tecnológico, Brazil.
- VANZOLINI, P. E. 2002. A second note on the geographical differentiation of *Amphisbaena fuliginosa* L., 1758 (Squamata, Amphisbaenidae), with a consideration of the forest refuge model of speciation. Anais da Academia Brasileira de Ciências 74:609–648.
- VITT, L. J., T. C. AVILA-PIRES, J. P. CALDWELL, AND V. R. L. OLIVEIRA. 1998. The impact of individual tree harvesting on thermal environments of lizards in Amazonian rain forest. Conservation Biology 12:654–664.
- WIENS, J. J., AND M. R. SERVEDIO. 2000. Species delimitation in systematics: Inferring diagnostic differences between species. Proceedings of the Royal Society of London, Series B 267:631–636.

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#### Appendix I

#### Specimens Examined

*Ptychochoglossus bilineatus* Boulenger, 1890.—Ecuador (BMNH 1946.8.2.3, holotype, examined from photographs).

Ptychoglossus brevifrontalis Boulenger, 1912/Ptychoglossus nicefori Loveridge, 1929.—Brazil: Acre: ca. 5 km north of Porto Walter, Rio Juruá (MPEG 20612–13); Amapá: Laranjal do Jari (MPEG 26458–59); Parque Nacional Montanhas do Tumucumaque (IEPA, not catalogued; field number TQ 0312); Serra do Navio (MPEG 19615); Amazonas: Cachoeirinha, Rio Madeira (INPA 12176, 12376–77); Comunidade Antonina, Rio Juruá, Juruá (INPA 16244); Comunidade Botafogo, Reserva Extrativista Baixo Juruá, Juruá (INPA 15938– 39); Lago Ayapuá, Rio Purus (INPA 13842–44); Silves (INPA 20087); Reserva Florestal Adolpho Ducke, Manaus (INPA 12477-81); Rio Curuena, Jutaí (MPEG 25946-47); Comunidade Pirarucu, Rio Jutaí, Jutaí (MPEG 25937); Boa Vista, Rio Jutaí, Jutaí (MPEG 25938–39); Rio Velho, Jutaí (MPEG 25940); Pará: BR-163, 9 km south of Novo Progresso, Novo Progresso (MPEG 25945-47); Floresta Estadual de Faro, Faro (MPEG 25941-44); Estação Científica Ferreira Pena, Floresta Nacional de Caxiuanã, Rio Curuá, Melgaço (MPEG 21827); Parque Nacional da Amazônia, Acampamento Base Sapopema, Rio Tapajós, Itaituba (MPEG 22346–48); PPBio, Floresta Nacional de Caxiuanã, Portel (MPEG 25903-13, 25948, 26416-41); Fazenda Riacho Monte Verde, Portel (MPEG 24420-26); Platô Almeidas, Porto Trombetas, Oriximiná (MPEG 22195); Monte Dourado, Bituba, Almeirim (MPEG 24055-58); U.H.E. Belo Monte, Bom Jardim, Rio Xingu, Vitória do Xingu (MPEG 24968); U.H.E. Belo Monte, Fazenda Caracol, Altamira (MPEG 24969-73, 25638-44). Bolivia: Cochabamba: Cochabamba Valley (UMMZ 69548). Colombia: Boyaca: Rio Garagoa, Macanal (MCZ 27340, holotype of Anadia nicefori); Meta: 28 km East of Aplay (KU 110585-87); Peralonzo (MZUSP 44854); Rio Cainarache, 33 km Northeast Tarapoto (KU 209539) Carimagua (MCZ 141221, MZUSP 49201); Lomalinda (UTA 3617, 3619, 9333-34). Ecuador: Napo: Limoncocha (LACM 74453-56); Puerto Libre, Rio Aguarico (KU 122197); Cabeceras del Rio Arajuno, tributary of Rio Napo (USNM 196261); Pastaza: Abitagua (FMNH 28058, UMMZ 90778); Mera (UMMZ 90777); Rio Corrientes (USNM 196259, 248258); Rio Pastaza watershed (FMNH 27675); Rio Pucayacu (USNM 196258); Upper Rio Oglan (USNM 196260); Sucumbios: Santa Cecilia, Sucumbios (KU 175381); Tungurahua: El Topo, Rio Pastaza (BMNH 1946.8.31.63, holotype, examined from photographs). Peru: Cuzco: Hacienda Cadena, Marcapata (FMNH 62123); Loreto: Centro Union (TCWC 41770–71, 43346, 44246); Moropon, Rio Nanay (TCWC 38145, 41396–97), no specific locality (TCWC 38145, 41397); Rio Calleria, Colonia Calleria (CAS 93233); Madre de Dios: 15 km East of Puerto Maldonado (KU 214998–5000). Suriname/Guyana: New River, 750 feet (BMNH 139.1.1.75, examined from photographs).

*Ptychoglossus danieli* Harris, 1994.—Colombia: Antioquia: El Clara, Angelopolis (AMNH 38819, paratype).

Ptychoglossus festae (Peracca, 1896).—Panama: Panama: Cerro Azul, Rio Piedra (AMNH 119874).

Ptychoglossus kugleri Roux, 1927.—Venezuela: Falem: Pauji (MZUSP 7631).

Ptychoglossus plicatus (Taylor, 1949).—Costa Rica: Moravia (UTA 1534); Panama: Coclé: Coclé (AMNH 115919–20); Derién: Cerro Malí (AMNH 119371–73).

*Ptychoglossus vallensis* Harris, 1994.—Colombia: Valle: Lago de Calima (AMNH 119239, paratype).

Arthrosaura reticulata (O'Shaughnessy, 1881).—Brazil: Pará: Melgaço, Estação Científica Ferreira Penna, Caxiuanã, Melgaço (MPEG 17914–17); Rondônia: Nova Brasília (MZUSP 32329).

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Allen Press, Inc., 810 East 10th Street, Lawrence, KS 66044, USA emueller@allenpress.com

COVER ART: The neotropical lizard genus *Ptychoglossus* (in the family Gymnophthalmidae) comprises approximately 15 species that occur in forested environments from Costa Rica to Peru and Brazil. Most of the species appear to have small distributions, although a few have large ranges. *Ptychoglossus brevifrontalis* has the largest geographic distribution within the genus; it is the only species known from Brazilian Amazonia and formerly was thought to have peripheral Amazonian distribution. However, recent collections have shown that species occurs more widely throughout Amazonia, and have provided material for a thorough study of the species. In this issue, Pedro Peloso and Teresa Avila-Pires studied the morphological variation within and among populations of the *Ptychoglossus brevifrontalis* and related species. They found limited geographic variation in the morphometrics and most aspects of scalation, except for the temporal and occipital scales and the midbody scale rows, which showed moderate to high variation. In addition, they found considerable overlap in morphology and scalation between *Ptychoglossus brevifrontalis* and *P. nicefori*. The authors found no evidence indicating that these taxa represent independent lineages that can be recognized as two distinct species, and concluded that *Ptychoglossus nicefori* is a junior synonym of *Ptychoglossus brevifrontalis*. The specimen of *Ptychoglossus brevifrontalis* on the cover was from Rio Xingu, Pará, Brazil, and was photographed by Pedro L. V. Peloso.

> FUTURE MEETING 6–11 July 2011—Minneapolis, Minnesota