VARIAÇÃO GEOGRÁFICA E TAXONOMIA DO LAGARTO *PTYCHOGLOSSUS BREVIFRONTALIS* BOULENGER, 1912 (SQUAMATA, GYMNOPHTHALMIDAE)

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MUSEU PARAENSE EMÍLIO GOELDI
UNIVERSIDADE FEDERAL DO PARÁ
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Capa: *Ptychoglossus brevifrontalis* Boulenger, 1912 – Rio Xingu, Pará, Brasil (Foto: P.L.V. Peloso)

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Dissertação apresentada ao Programa de Pós-graduação em Zoologia, Curso de Mestrado, do Museu Paraense Emílio Goeldi e Universidade Federal do Pará como requisito parcial para obtenção do grau de mestre em Zoologia

Orientadora: Teresa C. S. de Ávila Pires

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Dissertação aprovada como requisito para obtenção do grau de Mestre no curso de Pós-graduação em Zoologia do Museu Paraense Emílio Goeldi e Universidade Federal do Pará, pela Comissão formada pelos professores:

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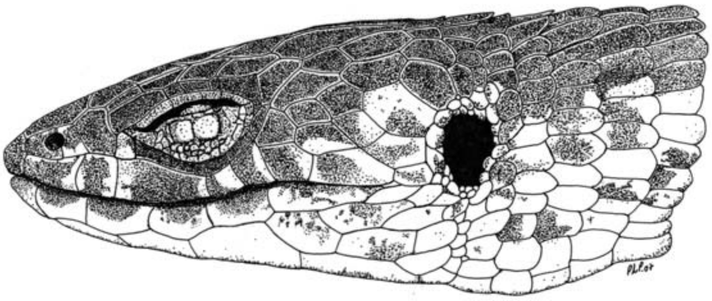
Belém, Pará, Maio de 2009

“Como um bom darwinista, é parte da minha religião acreditar que nada acontece na evolução sem ter sido autorizado pela seleção natural.”

Ernst Mayr

Aos lagartos e sapos...

...espero que consigam resistir à passagem humana na Terra!!!



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SUMÁRIO

RESUMO

O gênero *Ptychoglossus* está incluído na família Gymnophthalmidae e abriga atualmente 15 espécies distribuídas principalmente na Amazônia ocidental. *Ptychoglossus brevifrontalis*, inicialmente considerada como tendo uma distribuição peri-amazônica, nos últimos anos foi registrada em diversos pontos do interior da Amazônia, indicando ampla distribuição na região. Contudo, há poucas informações acerca da variação morfológica ao longo da distribuição da espécie. Neste trabalho foi estudada a variação intra- e interpopulacional na morfologia externa de *Ptychoglossus brevifrontalis*, analisando-se também a ocorrência de dimorfismo sexual e variação ontogenética. *Ptychoglossus nicefori* foi incluída no estudo, tendo em vista sua grande semelhança com *P. brevifrontalis* e o histórico de sinonímia entre as duas espécies. Observou-se variação geográfica em alguns caracteres, sem contudo justificar o reconhecimento de mais de um taxon. A validade de *P. nicefori* é questionada, porém estudos adicionais são necessários antes da proposição de novas alterações na taxonomia.

Palavras-chave: *Ptychoglossus*, taxonomia, microteídeo, *Anadia nicefori*, hemipenis

ABSTRACT

The genus *Ptychoglossus* is included in the family Gymnophthalmidae and currently comprises 15 species distributed principally in western Amazonia. *Ptychoglossus brevifrontalis*, initially thought to have a peripheral distribution in Amazonia, was recorded in recent years in several localities in the interior of the Amazon, indicating a wide distribution within the region. However, little information on the morphological variation along the species range is available. In this report intra- and interpopulational variation in the morphology of *Ptychoglossus brevifrontalis* was studied, including data on sexual dimorphism and ontogenetic variation. *Ptychoglossus nicefori* was included in the study, due to its resemblance to *P. brevifrontalis* and a history of synonymy between the two species. Geographic variation in some characters was found, without however justifying the recognition of additional taxa. The validity of *P. nicefori* is questionable but additional studies are needed before changes to the taxonomy of the group are proposed.

Keywords: *Ptychoglossus*, taxonomy, microteiid, *Anadia nicefori*, hemipenis

INTRODUÇÃO GERAL

Os lagartos da família Gymnophthalmidae estão representados por aproximadamente 40 gêneros e cerca de 180 espécies segundo as revisões mais recentes (Castoe et al., 2004; Rodrigues et al., 2005). No entanto, esses números estão longe da estabilidade, visto que muitas espécies e alguns novos gêneros têm sido descritos recentemente (e.g. Rodrigues, 1991a, b, c; Avila-Pires, 1995; Avila-Pires e Vitt, 1998; Rodrigues e Juncá, 2002; Kok, 2005, 2009; Rodrigues e Ávila-Pires, 2005; Rodrigues et al., 2005, 2007; Rodrigues e Santos 2008). Alguns grupos necessitam de revisões taxonômicas modernas e sabe-se de algumas novas espécies e gêneros que ainda aguardam descrição formal (Rodrigues et al., 2007; Rodrigues e Santos 2008).

A taxonomia dos gimnoftalmídeos é historicamente considerada difícil e é por algumas vezes bastante confusa (Presch, 1980; Rodrigues et al., 2005). Diversas espécies da família são conhecidas apenas das suas descrições originais, sem nenhuma informação adicional disponível sobre distribuição geográfica, variação morfológica, história natural e relações filogenéticas. Muitos gêneros são superficialmente semelhantes entre si o que torna a diagnose dos gêneros uma tarefa um tanto quanto complicada e mais da metade dos gêneros é monotípico ou possui no máximo duas espécies. Muitas das diagnoses genéricas em Gymnophthalmidae são baseadas em alguns poucos caracteres envolvendo número e formato de escamas e nos graus de alongamento do corpo e de redução dos membros.

Apesar dos problemas mencionados acima, o conhecimento acerca da taxonomia e história natural de diversos taxa da família cresceu consideravelmente nas últimas décadas. Três são os motivos para o avanço alcançado no conhecimento acerca das espécies de Gymnophthalmidae: **(1) inventários de fauna em áreas previamente não amostradas, além de novos inventários em áreas já amostradas.** Esses fatores permitiram a coleção de formas desconhecidas, além de aumento do número de exemplares de diversas espécies, outrora conhecidas de poucos exemplares. As novas amostragens permitiram também o aumento no conhecimento acerca da distribuição e da variação geográfica de algumas espécies; **(2) uso de armadilhas de interceptação e queda (pitfall traps).** O uso deste tipo de armadilha (ver revisão sobre a técnica em Cechin e Martins, 2000) mostrou-se bastante eficiente na coleção de algumas espécies de Gymnophthalmidae. Para se ter uma idéia, autores distintos mostraram que algumas espécies são capturadas exclusivamente nesse tipo de armadilha em alguns inventários (Pinto et al., 2008; Ribeiro-Júnior et al., 2008). A coleção de lagartos terrícolas e de pequeno porte, como é o caso da maioria dos Gymnophthalmidae, foi particularmente beneficiada por esse novo método; **(3) utilização de maior número de caracteres, incluindo morfologia interna e externa e dados moleculares nas revisões taxonômicas do grupo.** Neste último tópico as relações filogenéticas supraespecíficas entre os diversos grupos de Gymnophthalmidae foram as que mais avançaram. As relações genéricas dentro da família foram consideradas incertas por muito tempo, apesar de algumas tentativas de reconstrução dessas relações terem sido elaboradas principalmente baseadas em caracteres osteológicos (Presch, 1980). Recentemente o uso de técnicas moleculares (Pellegrino et al., 2001; Castoe et al., 2004), ou a análise conjunta de caracteres morfológicos e moleculares (Rodrigues et al., 2005), permitiram um avanço no entendimento da sistemática do grupo, principalmente no que se refere aos limites genéricos e às relações intergenéricas. Ainda assim, diversas dúvidas persistem quanto às relações de parentesco entre as espécies de gimnoftalmídeos.

As tentativas mais recentes de reconstrução filogenética de Gymnophthalmidae como um todo foram realizadas por Pellegrino et al. (2001) e Castoe et al. (2004). Esses trabalhos concordam com a divisão da família nas subfamílias Alopoglossinae, Rhachisaurinae, Cercosaurinae, e Gymnophthalminae. Castoe et al. (2004) reconhecem ainda Ecpleopinae como uma subfamília distinta, ao invés de uma tribo de Cercosaurinae como considerada por Pellegrino et al. (2001). Ademais, Castoe et al. (2004) propõem a tribo Bachini dentro de Cercosaurinae, para agrupar as formas do gênero *Bachia*, e não reconhecem a divisão de Gymnophthalminae em duas tribos, Gymnophthalmini e Heterodactylini, como proposto por Pellegrino et al. (2001).

Os dois esquemas foram subsequentemente mencionados na literatura, mas em termos gerais as filogenias são bastante semelhantes e uma discussão aprofundada acerca da filogenia da família está bem além do propósito deste trabalho. Por isso apenas ilustro na Fig. 1 as diferenças e semelhanças entre as duas propostas vigentes de classificação. Um ponto que vale menção especial é em relação ao posicionamento do gênero *Ptychoglossus* Boulenger, 1890 nas filogenias recentes.

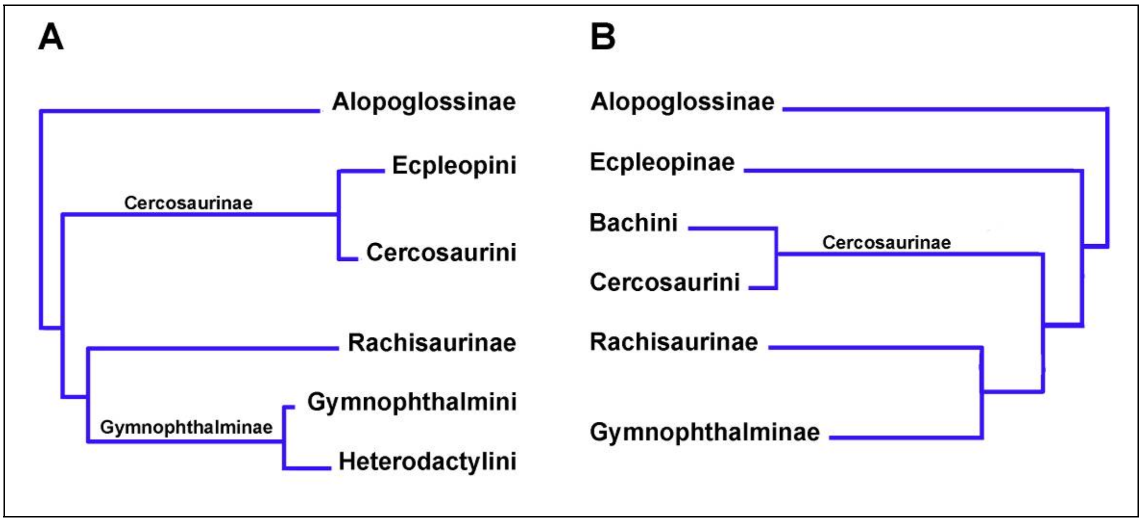

Figura 1. Duas principais propostas de relações filogenéticas dos táxons superiores reconhecidos dentro de Gymnophthalmidae. Modificado de (A) Pellegrino et al. (2001) e (B) Castoe et al. (2004).

Pellegrino et al. (2001) consideraram *Ptychoglossus* como pertencente à subfamília Cercosaurinae. Esse agrupamento foi subseqüentemente questionado por

Harris (2003), onde *Ptychoglossus* apareceu como grupo-irmão de *Alopoglossus*, no que formaria a subfamília Alopoglossinae. O trabalho de Harris (2003), no entanto, não buscou avaliar relações intergenéricas em Gymnophthalmidae e sim relações de táxons superiores ao nível genérico dentro dos Squamata. Castoe et al. (2004) concluíram que a alocação de *Ptychoglossus* em Cercosaurinae foi devido a uma troca acidental nos nomes de *P. brevifrontalis* e *Neusticurus juruazensis*, na hora da análise dos dados. Esse fato foi confirmado posteriormente por Rodrigues et al. (2005, 2007).

É consenso entre os autores que Alopoglossinae é basal em relação aos demais Gymnophthalmidae (Pellegrino et al., 2001; Castoe et al., 2004; Rodrigues et al., 2005, 2007). Embora *Ptychoglossus* não tenha sido amostrado nas filogenias que envolveram caracteres morfológicos (Rodrigues et al., 2005, 2007), onde somente *Alopoglossus* representou os Alopoglossinae, o grupo apresenta uma sinapomorfia bem documentada na literatura – a presença de pregas transversais em toda a língua (Harris, 1994; Castoe et al., 2004; Rodrigues et al., 2005), ao invés de papilas semelhantes a escamas, como presente nos demais membros de Gymnophthalmidae. Alguns gêneros da família possuem pregas na parte posterior ou anterior da língua (Kok, 2005), mas nunca em toda a língua, como em Alopoglossinae.

Como reconhecido atualmente o gênero *Ptychoglossus* compreende 15 espécies, sendo caracterizado por possuir, segundo Harris (1994) e Avila-Pires (1995), o corpo levemente achatado e cauda arredondada em secção transversal; membros bem desenvolvidos, com mãos e pés pentadáctilos e portadores de garra; a escama interparietal com aproximadamente o mesmo comprimento que as parietais e a margem posterior formada por essas três escamas praticamente reta; frontoparietais em contato medial; geralmente quatro supraoculares (três em duas espécies); gulares e ventrais quadrangulares (gulares retangulares em somente uma espécie), lisas, sub-imbricadas e organizadas em fileiras transversais bem definidas; língua recoberta por pregas transversais em toda a sua extensão e anteriormente bífida; dorsais geralmente alongadas e hexagonais (quase tão largas quanto longas em duas espécies), organizadas em fileiras transversais.

As espécies do gênero *Ptychoglossus* vivem na serrapilheira de áreas florestadas, em altitudes que variam do nível do mar até mais de 2100 m, e estão distribuídas desde a Costa Rica até o Peru (Harris, 1994). A maioria das espécies apresenta distribuição geográfica aparentemente restrita e três são conhecidas apenas pelo holótipo (*P. bilineatus*, *P. gradisquamatus* e *P. eurylepis*).

Ptychoglossus brevifrontalis (Fig. 3) é a espécie do gênero com a distribuição aparentemente mais ampla (Harris, 1994; Fig. 2) e foi a única espécie do gênero registrada no Brasil por Avila-Pires (1995), em sua extensa revisão sobre os lagartos da Amazônia Brasileira. É importante ressaltar que Avila-Pires (1995) não examinou nenhum espécime coletado efetivamente no Brasil, tendo examinado três exemplares do Equador, incluindo o holótipo. Na época, o único registro da espécie para o Brasil era o de Vanzolini (1986), o qual coletou um único exemplar no Estado de Rondônia (eu reexaminei o espécime, MZUSP 32329, e trata-se na verdade de um *Arthrosaura reticulata* juvenil).

Além disso, Hoogmoed (1979) registrou a ocorrência da espécie no Suriname, baseado em um espécime (BMNH 1939.1.1.75) coletado na localidade de “New River, 750 feet”, muito provavelmente correspondendo às cabeceiras do rio Kutari, nas montanhas do Acarai (Hoogmoed, 1973: 8,13-14). A localidade fica próxima à fronteira do Suriname com o Brasil.

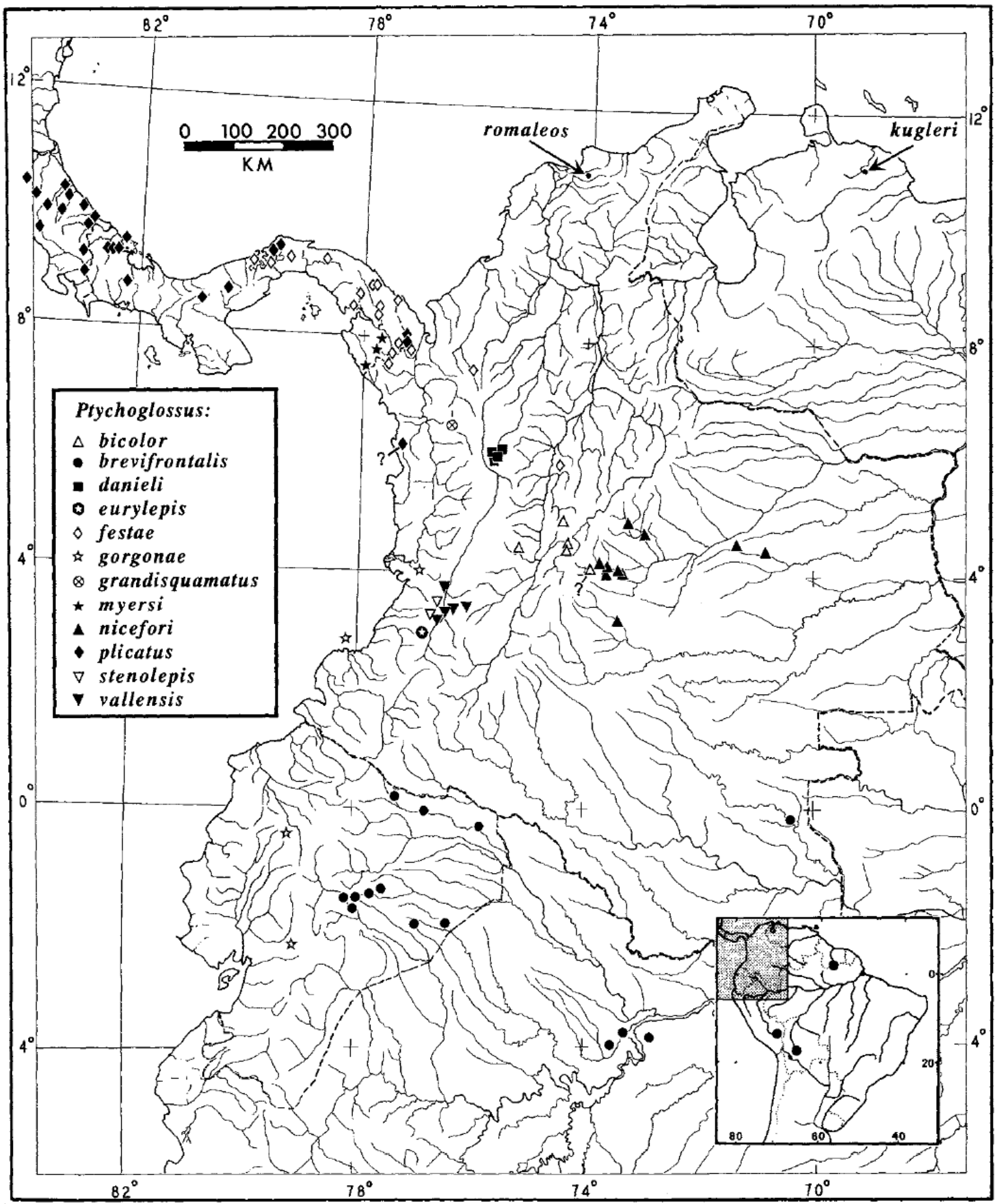

Figura 2. Reprodução do mapa da distribuição geográfica das espécies de *Ptychoglossus* apresentado por Harris (1994) na ocasião da revisão do gênero.

Com ocorrência registrada também para a Amazônia ocidental, da Colômbia ao Peru, considerava-se que a espécie era restrita à periferia da Amazônia (Avila-Pires, 1995; Hoogmoed, 1979). Desde então novos espécimes de *P. brevifrontalis* têm sido coletados em diversas localidades no Brasil, resultando em uma ampliação da distribuição geográfica da espécie em mais de 800 km (Vitt et al., 1998; Pinto and Quatman, 2005; exemplares nas coleções herpetológicas do Museu Paraense Emílio Goeldi e do Instituto Nacional de Pesquisas da Amazônia) e parecendo indicar uma ampla ocorrência na Amazônia.

Figura 3. *Ptychoglossus brevifrontalis* de Anapu, Rio Xingu, Pará, Brasil, em vida (MPEG 25642, fêmea). CRC = 49.5 mm.

À luz das novas coletas de *Ptychoglossus brevifrontalis* o presente trabalho buscou avaliar a variação geográfica em caracteres morfológicos na espécie. Ao longo da análise de exemplares coletados recentemente, alguns exemplares foram identificados como *Ptychoglossus nicefori*. Em vista de haver um histórico de sinonímia entre as duas espécies, o status de *P. nicefori* é também reavaliado neste trabalho.

Os métodos e os resultados encontrados durante o estudo são apresentados a seguir, em formato de artigo, em língua inglesa. A formatação segue aquela da revista Herpetologica.

Foram examinados 147 espécimes de *Ptychoglossus brevifrontalis* / *P. nicefori*, além de exemplares de outras espécies do gênero analisadas para comparação. Devido ao baixo número de exemplares coletados em uma mesma localidade para a maioria das localidades, amostras foram agrupadas e diferenças na morfologia foram analisadas entre esses agrupamentos através de análise da Função Discriminante.

Diversas diferenças morfológicas foram encontradas dentro e entre amostras e elas são apresentadas, ilustradas quando necessário, e discutidas.

A validade de *Ptychoglossus nicefori* é questionável, contudo consideramos que mais estudos deveriam ser feitos antes que nova alteração nomenclatural seja proposta para o grupo.

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

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RRH: Morphological variation in *Ptychoglossus brevifrontalis*

ABSTRACT

Intra- and interpopulational variation in the morphology of *Ptychoglossus brevifrontalis* 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 pre-cloacal and femoral pores, and to a lesser degree in body elongation. Hemipenial morphology is briefly discussed. The validity of *Ptychoglossus nicefori* is questionable and deserves further study. Brief comments on the species taxonomy are provided.

Keywords: *Ptychoglossus*, taxonomy, microteiid, *Anadia nicefori*, hemipenis

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 altitudes ranging from sea level up to 2100 m in some Andean localities. Most species are apparently restricted to small distribution ranges, although a few (*P. 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: 421) based on a single specimen (BMNH 1946.8.31.63) from El Topo, Rio Pastaza, Ecuador. Loveridge (1929: 99) described *Anadia nicefori* the basis of a specimen from Rio Garagoa, Boyacá, Colombia (MCZ 27340), which Dunn (1944: 67) soon transferred to the genus

Ptychoglossus. Both species were considered valid until Dixon and Soini (1975: 51) suggested that *P. nicefori* should be regarded as a junior synonym of *P. brevifrontalis*. This position was followed by Duellman (1978: 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 close 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, 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 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 & 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*.

MATERIAL AND METHODS

A total of 147 specimens of *Ptychoglossus 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, USA (AMNH); The Natural History Museum, formerly British Museum of Natural History, London, UK (BMNH); California Academy of Sciences, California, USA (CAS); The Field Museum, Illinois, USA (FMNH); Instituto Nacional de Pesquisas da Amazônia, Amazonas, Brazil (INPA); University of Kansas, Museum of Natural History, Kansas, USA (KU); Natural History Museum of Los Angeles County, California, USA (LACM); Louisiana State University, Museum of Natural Science, Louisiana, USA (LSU); Museum of Comparative Zoology, Massachusetts, USA (MCZ); Museu Paraense Emilio Goeldi, Pará, Brazil (MPEG); Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP); Texas Cooperative Wildlife Collection, Texas, USA (TCWC); University of Michigan, Museum of Zoology, Michigan, USA (UMMZ); National Museum of Natural History, District of Columbia, USA (USNM); University of Texas at 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 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), including them, to level of posterior margin of hind limbs), **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 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), were prepared and examined.

Non-geographic Variation

To examine non-geographic variation we analyzed samples from two relatively close localities (both included in operational unit "G" in Figure 2), totaling 51 specimens: Floresta Nacional de Caxiuanã, municipalities of Melgaço and Portel, Pará, Brazil, *n* = 38 (from now on referred to as Caxiuanã); and U.H.E. Belo Monte, Rio Xingu, Pará, *n* = 13 (from now on

Belo Monte). Samples from Belo Monte come from both sides of the Xingu river (municipalities of Anapu and Altamira), while 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 one 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 2005) two separate datasets 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 (Vanzolini, 2002; Heyer, 2005). 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 ten 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 (7 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 (7 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. brevifrontalis*) were examined from photographs and were not included in the analyses.

The record of *P. brevifrontalis* for the state of Rondônia, Brazil (Vanzolini 1986; Avila-Pires 1995) is apparently an identification error. I 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). Size-free 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 (Strauss, 1985; Reis et al., 1990). Since 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 OUs 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 using a Missing Value Analysis, based on the linear regression of the observed variables, while 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).

RESULTS

Non-geographic Variation

Male SVL in the two samples from central Pará, Brazil, ranged from 29.0 to 51.3 mm; female SVL ranged from 38.0 to 56.4 mm (Fig. 3). One juvenile of undetermined sex from Belo Monte had a SVL of 22.0 mm. 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 ($r = 0,856$, $df = 7$, $p < 0.05$) but no significant correlation was found for males ($r = 0.328$, $df = 12$, $P > 0.05$) (Fig. 4A). 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 4B–F). A summary of morphometric data is given in Table 1.

Number of supralabial scales seven in most specimens, but six in one specimen and eight in three others; occipitals 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; suboculars 1–5; supraciliaries 4–6 (usually five); temporals 8–13; gulars in 5–6, usually six, rows; dorsals arranged in 29–32 well defined transverse scale rows; ventrals in 17–20 transverse rows; scales around midbody 28–34; 10–13 lamellae under fourth finger, 16–20 under fourth toe. A summary of scale counts is available in Table 2. Numbers of pre-cloacal and femoral pores show sexual dimorphism (Fig. 5). 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 medial contact in all specimens of this sample, but contact line 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 3). 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 non geographic variation analysis (Figs. 3 and 6). However, there seems to be a shift in maximum size among OTUs. Males from OTU “A” present the smallest mean SVL, while females from OTU “F” present the smallest mean SVL (Fig 6). However, such differences may be related to the samples, not necessarily reflecting population differences. Variation in morphometric data among OTU´s are summarized in Table 4. Correlation between combined fore and hind limb lengths, on one side, and distance between limbs, on the other side, show no distinct variation among groups (Fig. 7).

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 while those from OTU “F” have lower counts of lamellae under toe IV. Differences in scale counts between OTUs are illustrated in Table 5.

We analyzed 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.* 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 7A), a condition not previously reported in *P. brevifrontalis* (Harris, 1994; Ávila-Pires, 1995) 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 (Fig. 10). Most specimens (over 70% of the sample) show the typical condition described for *P. brevifrontalis,* with five scales of nearly the same size (Fig. 9A). Fewer specimens show three scales, with lateral ones enlarged (Fig. 9C), the typical condition described for *P. nicefori,* 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), and in some individuals only one enlarged occipital, either on the left or the right side of the head, is present (Fig. 9B). Other variations are worth mentioning. In one specimen from Peru (KU 215000) the interparietal reaches the post-occipitals. One specimen from Faro, Pará (MPEG 25492), apparently shows a fusion of the three medial occipitals to form a transversely elongated scale.

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 Lambda = 0.145; F-ratio = 10, 304;

df = 30, 448; $p < 0.001$) and correctly classified 59% of the individuals (Table 6). 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 (Table 7).

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 is most influenced by number of occipitals and postoccipitals (Table 7) and promoted an almost complete separation between OTU “F” and the remaining groups (Fig. 12). Additionally OTU “A” is completely separated from OTU “B” and partially separated from the remaining 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 7). 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 7) and lacked any resolution in separating any of the groups in both canonical axes and the results of this analysis are not commented further because they provide no material for geographic variation analyses (Wilk’s Lambda 0.644; F-Ratio = 5, 205; df = 12, 225; $p < 0.001$).

Together with 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; OU “B” USNM 196259, examined by Harris; OTU “D” TCWC 41770, examined by Harris, and MPEG 25945, examined by us; OTU “E” MPEG 25948, examined by us; OTU “F” MPEG 24058, examined by us; OTU “G” MPEG 25948, examined by us). The four 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. 14). The number of apical fleshy protuberances is constantly six - three pairs as reported by Harris (1994), shown in Fig. 14.

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 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 (19–21) 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 5). 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 5 occipitals (3 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 correctly address the taxonomic status of the populations from the Tumucumaque mountain.

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 *Ptychoglossus* 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 (OU A) and eastern Amazonia (F and G), while higher counts were found in OUs from central Amazonia (D, E) and Ecuador (B) (Fig. 13, Table 5). Geographic variation is also found in other counts, such as temporals, with higher counts in Ecuador (B) and central Amazonia (D, 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, neither 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 shows 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 3B) 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. 10). 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 paper). 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. 11).

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 presented new evidence for recognizing both species. Harris (1994) argued that (1) enlargement of occipitals in *P. nicefori* (= post parietals 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 9), including individuals (INPA 13842, MPEG 26346) with one enlarged occipital on one side of the head while no enlarged scales are present on the other side (Figure 9B). Although usually fixed in a given population, the condition of the occipitals should be used with care to diagnose species since it showed to be a polymorphic trait, and possibly not linked to phylogenetic history (discussion in Wiens and Servedio 2000; Aleixo 2007). 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 25642) failed to meet by one dorsal, while in a male (MPEG 25643) limbs overlapped by one dorsal. As shown above body elongation varies among sexes and onthogenetically. Regarding relative length of tail, as shown in Fig. 4A, within two samples of close by localities used for the non-geographic 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 its 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 5 specimens of *P. brevifrontalis* and 9 *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 non-geographic 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 paper) 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 raise the possibility that *Ptychoglossus nicefori* (Loveridge, 1929) and *Ptychoglossus brevifrontalis* Boulenger 1912, might be conspecific, as originally proposed by Dixon & Soini (1975). Based on our results on the geographic variation of examined specimens, we could tentatively assign specimens from OTU “F” to *P. nicefori* but such action would be arbitrary and not based on conclusive evidence and would just add unwanted complications to the taxonomic history of the group. Additionally, the status of some populations is assessed tentatively (i.e. Itaituba and Tumucumaque) and the high degree of morphological variation may mask species diversity in the genus. As a result, we have not ruled out the possibility that *P. brevifrontalis* may actually represent a complex of similar and cryptic species. However, until further evidence is available for a concrete argument for considering or rejecting them as valid species we prefer to be conservative and do not propose taxonomic changes. To avoid further confusion we list all the material examined by us for geographic variation studies (Appendix I) together.

Redescription of the species treated here is unnecessary since the descriptions provided by Hoogmoed (1973), Harris (1994), and Avila-Pires (1995) together are sufficiently detailed.

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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 Azil, 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)**: **BRASIL: Pará**: Melgaço, Estação Científica Ferreira Penna, Caxiuanã, Melgaço (MPEG 17914-17); **Rondônia**: Nova Brasília (MZUSP 32329).

FIGURES

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

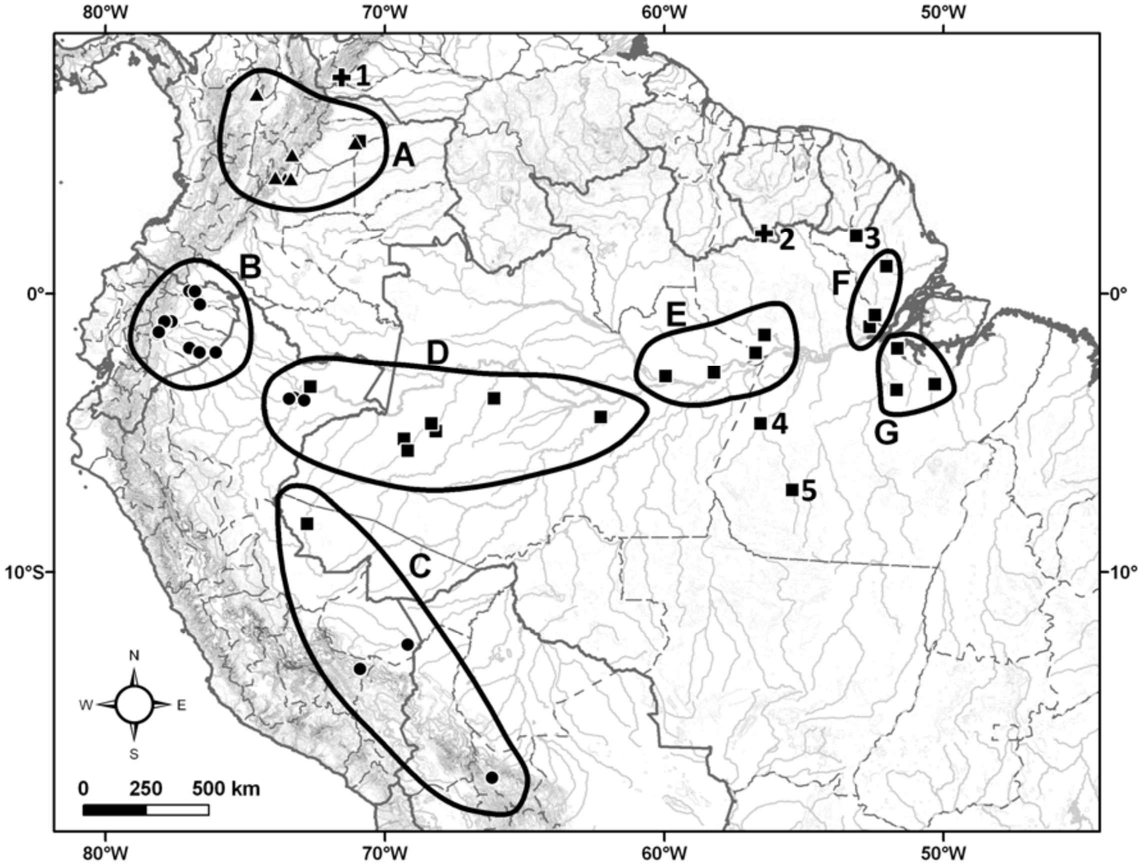

Fig. 2.—Distribution records of specimens examined during this study. Triangles and circles represent specimens also analyzed by Harris (1994) and identified respectively as *P. nicefori* and *P. brevifrontalis*; squares represent specimens examined by us but not by Harris (1994); crosses are records 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.

Fig. 3.—Snout vent length (SVL) distribution, separated by sex, in two samples of *Ptychoglossus brevifrontalis* from central Pará, Brazil. Belo Monte: n = 8 males and 4 females; Caxiuanã: n = 29 males and 9 females. A juvenile of undetermined sex from Belo Monte was excluded. Measurements are in millimeters. Central line is the mean value; the length of each box shows the range within which the central 50% of the values fall.

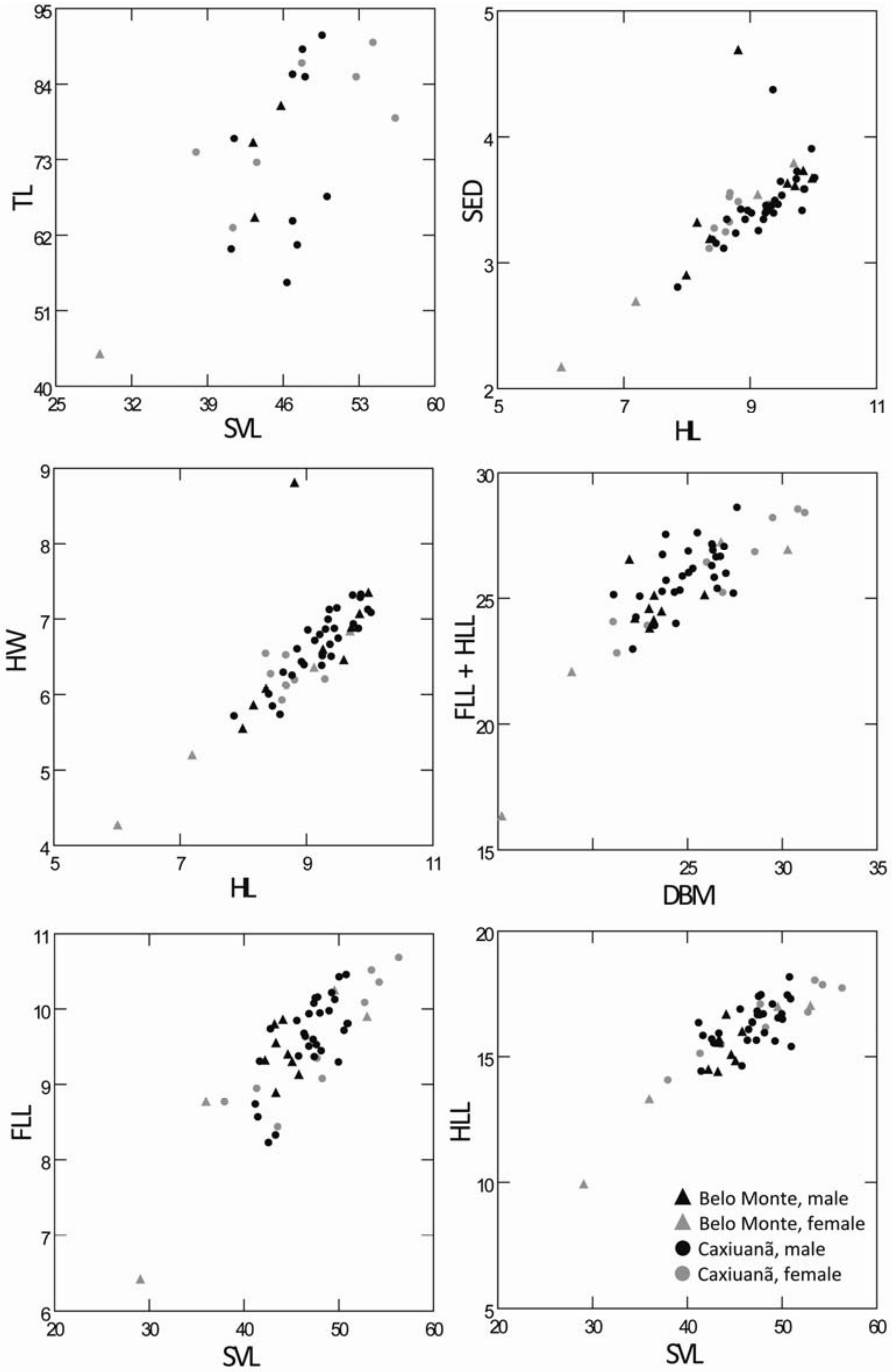

Fig. 4.—Correlation among several morphometric traits in two samples of *Ptychoglossus brevifrontalis* from central Pará, Brazil (DBM = distance between members, FLL = forelimb length, TL = tail length, HL = head length, HLL = hind limb length, HW = head width, SED = snout-eye distance, SVL = snout-vent length. Measurements in millimeters.

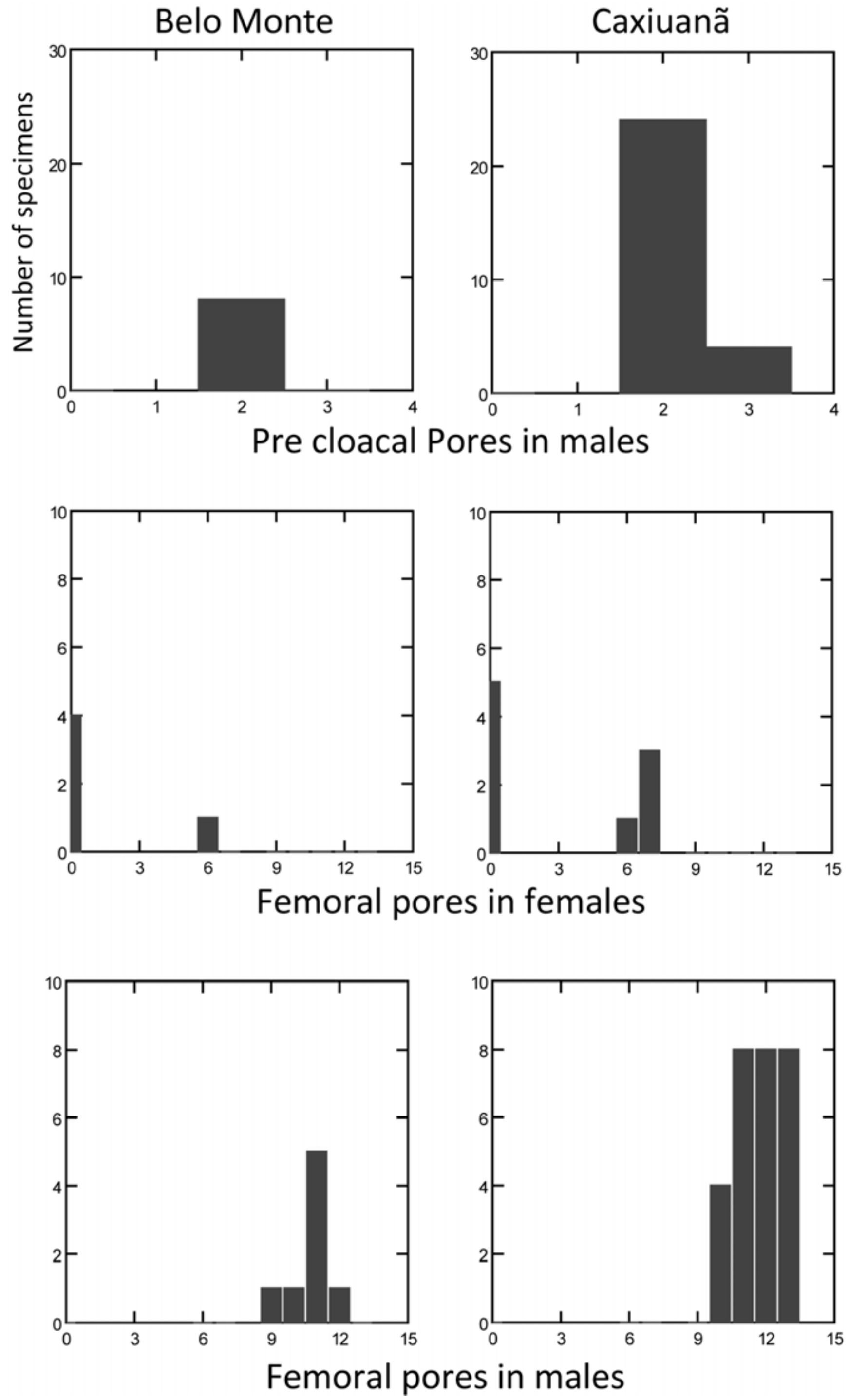

Fig. 5.—Distribution of precloacal and femoral pores among males and females in two samples of *Ptychoglossus brevifrontalis* from central Pará, Brazil. Left graphs are from Belo Monte and rigth graphs are from Caxiuanã.

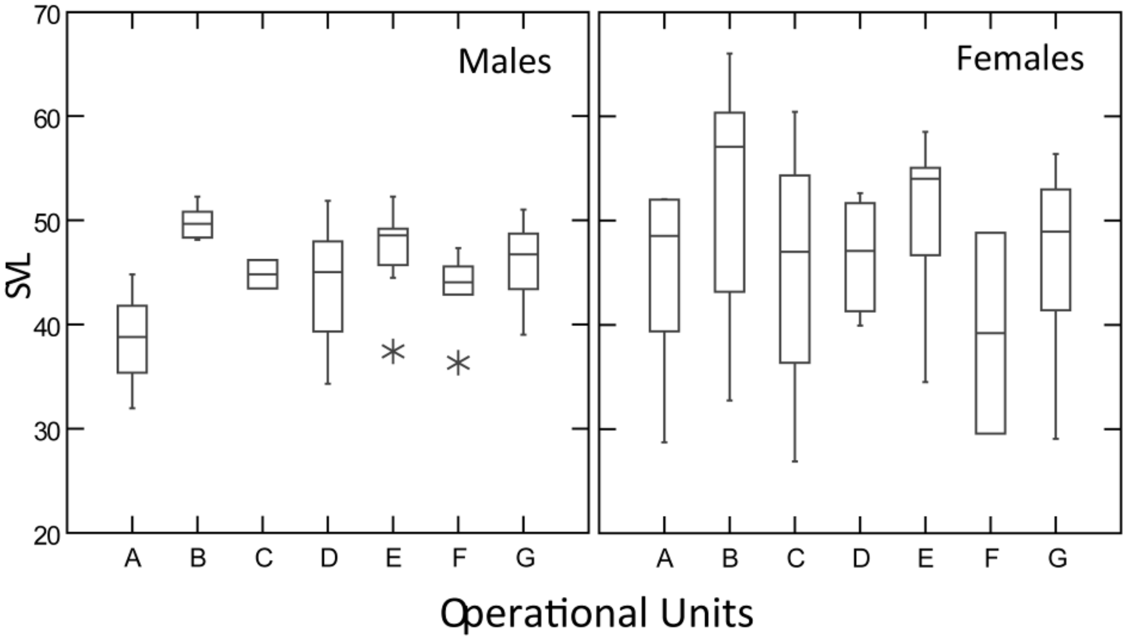

Fig. 6.—Variation in snout-vent length among sexes in the seven operational units evaluated in this study. Measurements are in millimeters. Asterisks are juveniles regarded here as sample outiers. Central line is the mean value; the length of each box shows the range within which the central 50% of the values fall.

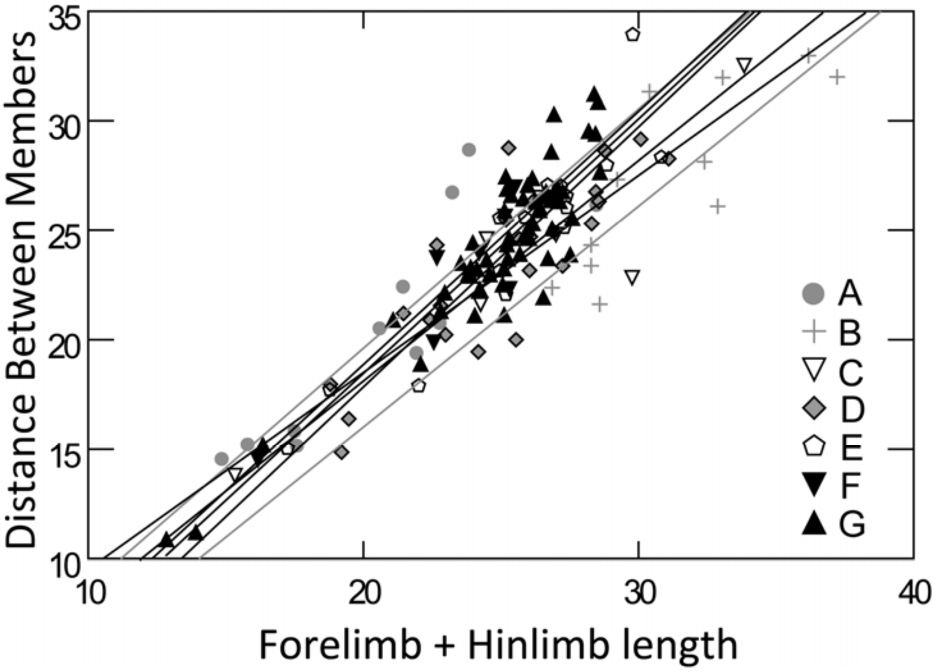

Fig. 7.—Relationship of combined limb length (FLL + HL) to distance between members (DBM) in the seven Operational Units evaluated in the present study.

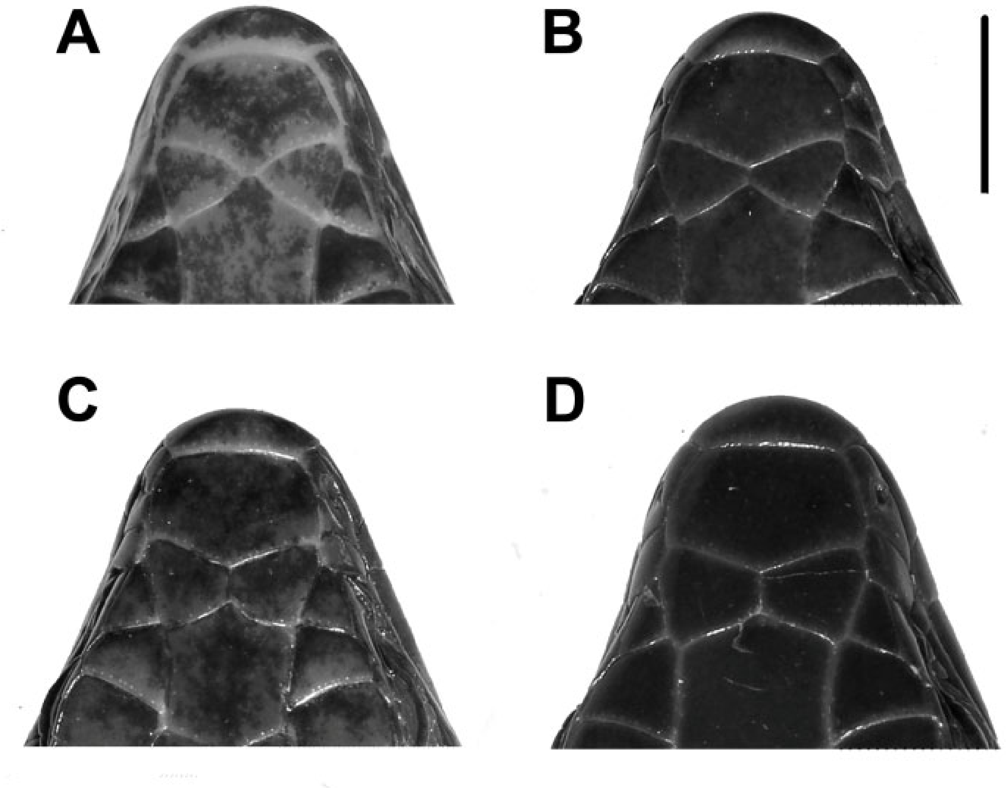

Fig. 8.—Dorsal view of the snout in *Ptychoglossus brevifrontalis* evidencing the degree of medial contact between prefrontal scales. (A) MPEG 24057; (B) MPEG 26346; (C) MPEG 25910; and (D) MPEG 22346. Scale bar 3 mm.

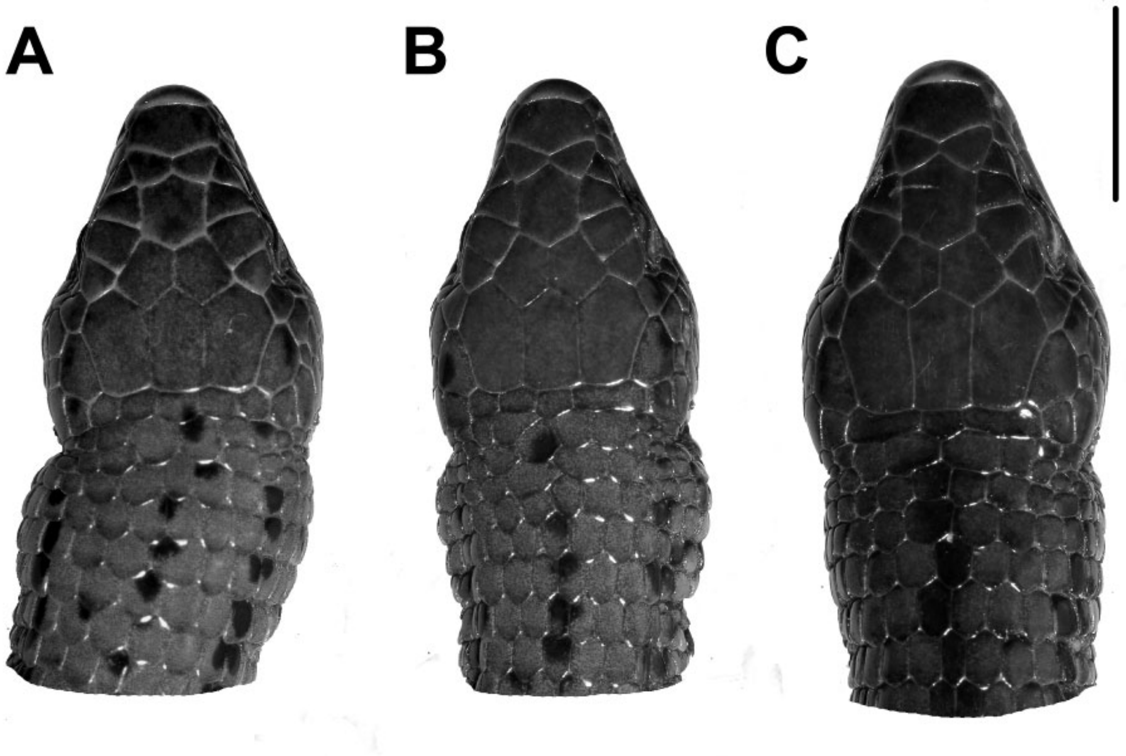

Fig. 9.—Dorsal view of the head of *Ptychoglossus brevifrontalis* from Caxiuanã, Pará, Brazil, showing variation in the condition of the occipitals. (A) MPEG 26435; (B) MPEG 26346 (note the different condition on each side of the head); and (C) MPEG 26429.

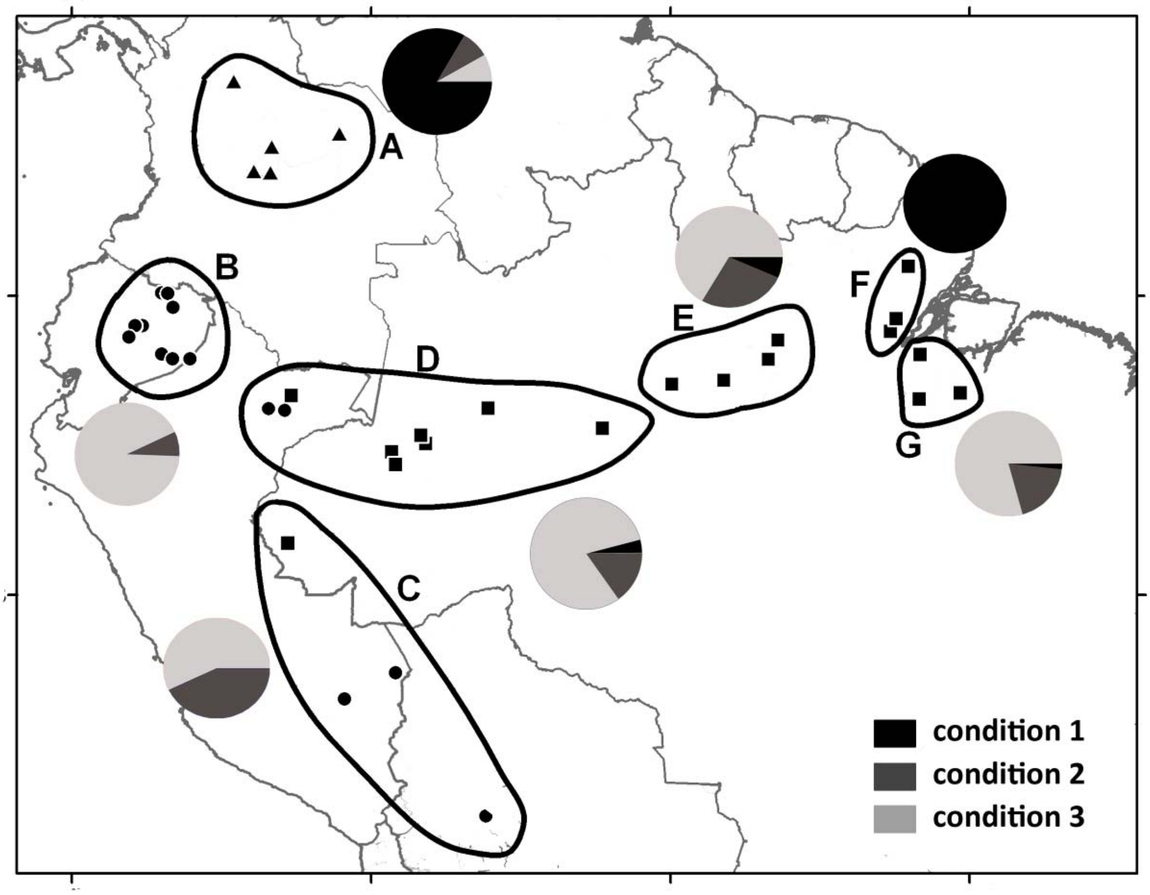

Fig. 10.—Relative frequencies of the states of organization of occipital scales among Operational Units studied. Conditions are as follows: (1) typical condition described for *P. nicefori* (represented in Fig. 9C); (2) intermediate condition or anomalous specimens, specimens that deviated from conditions A or C were included here; and (3) typical condition described for *P. brevifrontalis* (Fig. 9A).

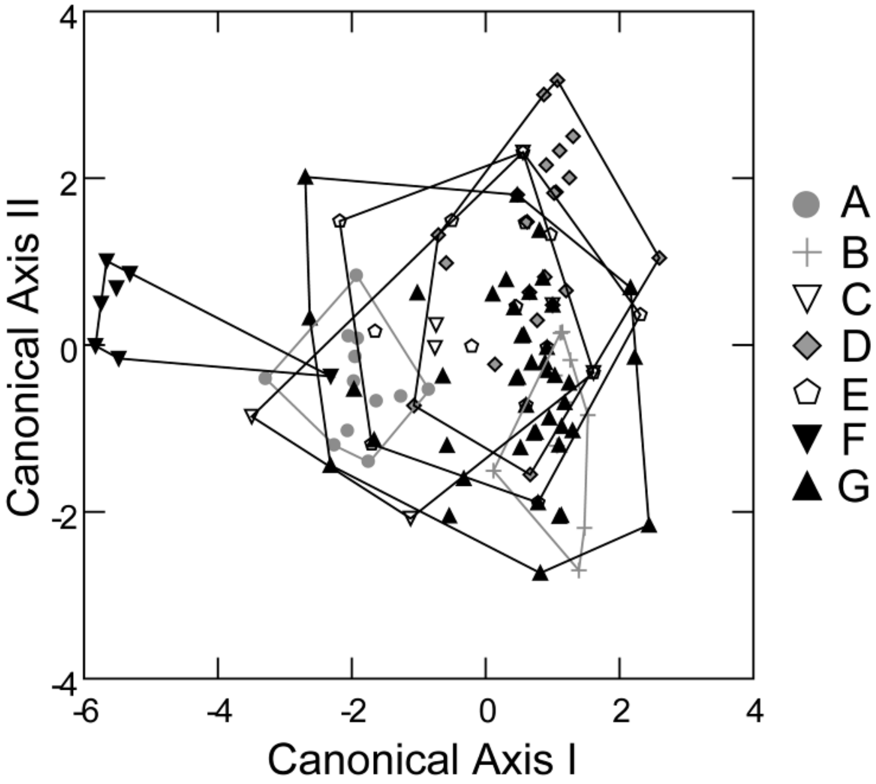

Fig. 11.—Graphical representation of scores of the first two axes of the Discriminant Functions Analyses performed with meristic characters for the seven operational units (A–G).

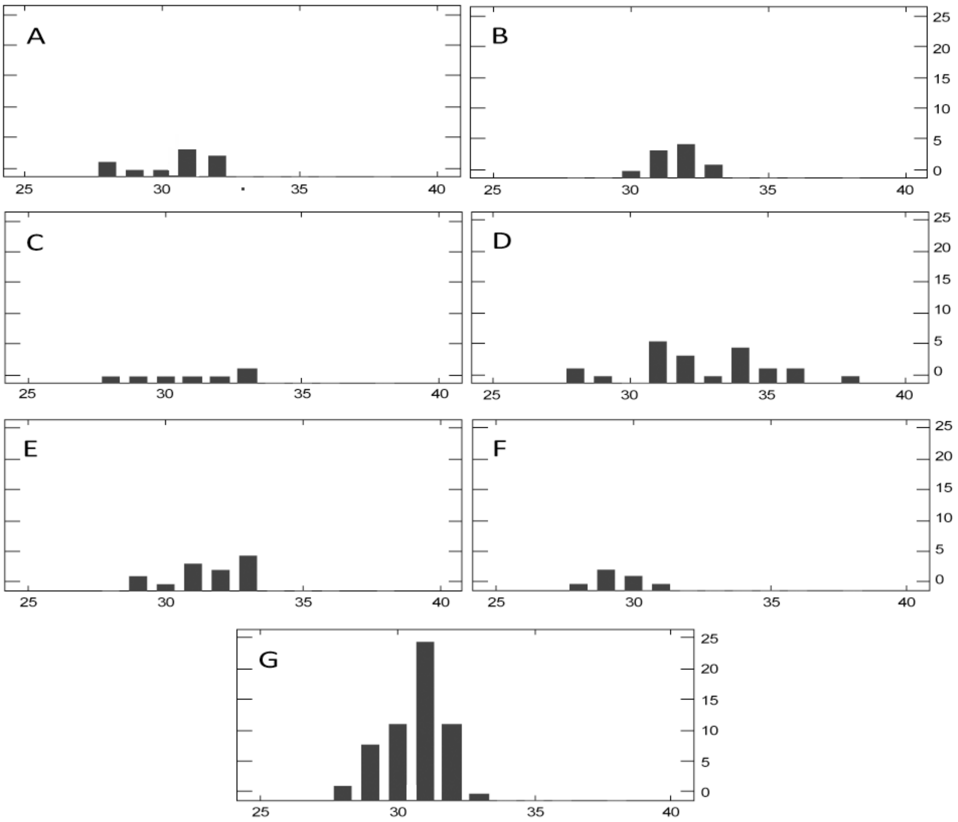

Fig. 12.—Variation on counts of scales around midbody in the the seven operational units evaluated in this study.

Fig. 13.—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.

TABLES

Table 1. Summary of descriptive statistics on morphometric data of males and females (in millimeters) of *Ptychoglossus brevifrontalis* from two samples, Belo Monte and Caxiuanã (combined for a higher sample size) from central state of Pará, Brazil. Abbreviations in Material and Methods.

	Males (n = 36) Range	Females (n = 13) Range
SVL	39.0–51.0	29.0–56.3
HL / SVL	0.19–0.21	0.17–0.21
HL / HW	1.32–1.50	1.00–1.49
HH / HL	0.41–0.81	0.44–0.73
SED / HL	0.34–0.47	0.36–0.53
DBM / SVL	0.48–0.57	0.51–0.58
FLL / SVL	0.20–0.23	0.19–0.24
HLL / SVL	0.34–0.40	0.31–0.37
LIMBS / DBM	0.93–1.21	0.89–1.17

Table 2. Scale count variation among two samples of *Ptychoglossus brevifrontalis* from central Pará, Brazil (combined for a higher sample size, N=50). SD = standard deviation. Abbreviations in Material and Methods.

	Range	Mean ± SD
SPL	7–8	7.0 ± 0.2
OCC	2–5	4.7 ± 0.6
POC	2–5	4.0 ± 0.6
SBO	1–5	3.3 ± 0.8
SPC	4–6	5.0 ± 0.3
PAL	1–3	2.2 ± 0.4
TEMP	8–13	11.2 ± 0.8
DOR	29–32	30.5 ± 0.6
VEN	17–20	18.3 ± 0.8
SAM	28–33	30.7 ± 1.1
GIL	5–6	6.0 ± 0.1
COL	7–11	8.4 ± 0.8
LFIV	10–13	11.4 ± 0.9
LTIV	16–20	17.4 ± 0.9

Table 3. Eigenvectors of covariance factor of the first component (PCI) of the Principal Components and Multivariate Coefficient of Allometry (MCA) for ten morphometric variables in two samples, males plus juveniles and females plus juveniles, of *Ptychoglossus brevifrontalis* from central Pará, Brazil. Abbreviations in Material and Methods.

	Males		Females	
	PCI	MCA	PCI	MCA
SVL	-0.361295	-1.14251	-0.377812	-1.19475
HL	-0.27428	-0.86735	-0.260345	-0.82328
HW	-0.280281	-0.88633	-0.284255	-0.89889
HH	-0.311918	-0.98637	-0.306537	-0.96935
SED	-0.270288	-0.85472	-0.292375	-0.92457
EED	-0.358553	-1.13384	-0.313069	-0.99001
VED	-0.281956	-0.89162	-0.259182	-0.81961
DBM	-0.391457	-1.2379	-0.420115	-1.32852
FLL	-0.296539	-0.93774	-0.283137	-0.89536
HLL	-0.309994	-0.98029	-0.327687	-1.03624

Table 4. Variation in morphometric traits between the seven Operational Units used for the study of geographical variation. Measurements in millimeters. M, males, F, females. Abbreviations in Material and Methods.

	Operational Unit A		Operational Unit B		Operational Unit C		Operational Unit D	
	M (n = 4)	F (n = 6)	M (n = 5)	F (n = 6)	M (n = 4)	F (n = 2)	M (n = 18)	F (n = 6)
	Range	Range	Range	Range	Range	Range	Range	Range
SVL	31.9–50.1	28.7–52.0	48.1–52.3	43.1–66.0	26.9–60.4	43.5–46.2	34.3–51.9	32.7–52.6
HL / SVL	0.19–0.21	0.14–0.20	0.13–0.21	0.18–0.20	0.17–0.22	0.19–0.20	0.19–0.21	0.18–0.20
HL / HW	1.40–1.56	1.42–1.50	1.00–1.47	1.36–1.50	1.37–1.47	1.37–1.43	1.24–1.46	1.33–1.45
HH / HL	0.50–0.54	0.46–0.53	0.46–0.72	0.47–0.57	0.46–0.53	0.51–0.52	0.46–0.60	0.41–0.53
SED / HL	0.37–0.41	0.37–0.99	0.36–0.55	0.36–0.40	0.37–0.39	0.36–0.38	0.34–0.39	0.36–0.41
DBM / SVL	0.46–0.52	0.39–0.57	0.48–0.55	0.49–0.54	0.47–0.54	0.49–0.53	0.41–0.56	0.50–0.57
FLL / SVL	0.19–0.21	0.15–0.20	0.20–0.23	0.18–0.25	0.21–0.24	0.19–0.20	0.16–0.23	0.18–0.23
HLL / SVL	0.31–0.36	0.24–0.35	0.36–0.41	0.32–0.40	0.33–0.37	0.33–0.35	0.32–0.42	0.32–0.40
LIMBS / DBM	1.09–1.13	0.83–1.04	1.07–1.26	0.97–1.32	1.04–1.30	0.99–1.12	0.93–1.29	0.87–1.18

Table 4 (continuation).

	Operational Unit E		Operational Unit F		Operational Unit G	
	M (n = 9)	F (n = 5)	M (n = 5)	F (n = 2)	M (n = 42)	F (n = 14)
	Range	Range	Range	Range	Range	Range
SVL	37.4–52.3	34.5–58.5	36.3–47.3	29.5–48.8	39.0–51.0	29.1–56.4
HL / SVL	0.19–0.20	0.18–0.20	0.19–0.20	0.17–0.21	0.18–0.21	0.17–0.21
HL / HW	1.30–1.45	1.27–1.45	1.33–1.50	1.34–1.52	1.27–1.50	1.00–1.48
HH / HL	0.46–0.60	0.45–0.50	0.48–0.60	0.50–0.53	0.38–0.81	0.43–0.73
SED / HL	0.35–0.40	0.35–0.41	0.35–0.37	0.37–0.38	0.34–0.46	0.36–0.53
DBM / SVL	0.47–0.54	0.50–0.58	0.50–0.55	0.49–0.55	0.49–0.56	0.51–0.57
FLL / SVL	0.19–0.22	0.18–0.22	0.17–0.23	0.17–0.19	0.18–0.22	0.18–0.24
HLL / SVL	0.31–0.36	0.31–0.36	0.32–0.38	0.33–0.37	0.30–0.39	0.31–0.37
LIMBS / DBM	0.97–1.20	0.87–1.08	0.95–1.13	0.94–1.11	0.91–1.21	0.88–1.16

Table 5. Variation in scale counts between the seven Operational Units (A–G) used for the study of geographic variation. Abbreviations in Material and Methods.

	A (n = 12) Range (Mean ± SD)	B (n = 11) Range (Mean ± SD)	C (n = 7) Range (Mean ± SD)	D (n = 25) Range (Mean ± SD)	E (n = 15) Range (Mean ± SD)	F (n = 7) Range (Mean ± SD)	G (n = 58) Range (Mean ± SD)
SPL	5–7	6–8	7–7	6–7	6–7	7–7	6–8
	(6.7 ± 0.6)	(7.0 ± 0.4)	(7.0 ± 0.0)	(6.9 ± 0.3)	(6.9 ± 0.3)	(7.0 ± 0.0)	(7.0 ± 0.3)
OCC	3–5	4–5	2–5	4–5	3–5	3–3	2–5
	(3.2 ± 0.6)	(4.9 ± 0.3)	(4.3 ± 1.1)	(4.9 ± 0.3)	(4.5 ± 0.8)	(3.0 ± 0.0)	(4.8 ± 0.6)
POC	3–4	4–4	3–4	4–5	4–5	2–4	2–5
	(3.8 ± 0.4)	(4.0 ± 0.0)	(3.9 ± 0.4)	(4.0 ± 0.2)	(4.1 ± 0.3)	(2.3 ± 0.8)	(4.0 ± 0.6)
SBO	3–4	2–5	2–4	2–5	3–5	3–5	1–5
	(3.6 ± 0.5)	(3.5 ± 0.8)	(3.7 ± 0.8)	(3.9 ± 0.9)	(3.8 ± 0.7)	(4.0 ± 0.6)	(3.3 ± 0.8)
SPC	5–5	5–5	5–5	5–5	4–5	5–6	4–6
	(5.0 ± 0.0)	(5.0 ± 0.0)	(5.0 ± 0.0)	(5.0 ± 0.0)	(4.9 ± 0.3)	(5.1 ± 0.4)	(5.0 ± 0.3)
PAL	2–3	2–3	2–3	2–3	2–4	2–3	1–3
	(2.3 ± 0.4)	(2.3 ± 0.4)	(2.4 ± 0.5)	(2.4 ± 0.5)	(2.5 ± 0.7)	(2.4 ± 0.5)	(2.2 ± 0.4)
TEMP	9–12	10–14	11–11	8–14	11–13	9–12	8–13
	(9.9 ± 1.0)	(11.5 ± 1.2)	(11.0 ± 0.0)	(11.6 ± 1.1)	(11.7 ± 0.6)	(9.7 ± 1.1)	(11.2 ± 0.8)
DOR	30–31	30–31	30–31	30–32	30–31	30–31	29–32
	(30.7 ± 0.40	(30.5 ± 0.5)	(30.9 ± 0.4)	(30.7 ± 0.5)	(30.9 ± 0.3)	(30.6 ± 0.5)	(30.5 ± 0.6)
VEN	17–20	17–21	18–19	17–19	17–20	17–19	16–20
	(18.6 ± 0.7)	(18.2 ± 1.1)	(18.3 ± 0.5)	(17.9 ± 0.8)	(18.1 ± 0.9)	(18.0 ± 0.6)	(18.2 ± 0.8)
SAM	28–32	30–33	28–33	28–38	29–33	28–31	28–33
	(30.4±1.4)	(31.6±0.9)	(30.9±2.0)	(32.6±2.5)	(31.5±1.4)	(29.4±1.0)	(30.6±1.1)
GUL	5–6	6–7	6–6	6–6	6–6	5–6	5–6

	(5.8±0.4)	(6.1±0.3)	(6.0±0.0)	(6.0±0.0)	(6.0±0.0)	(5.9±0.4)	(6.0±0.1)
COL	7–10	7–9	7–9	7–10	7–10	7–9	7–11
	(7.8±0.9)	(8.0±0.7)	(8.0±1.0)	(8.0±1.0)	(8.5±0.8)	(8.6±0.8)	(8.5±0.8)
LFIV	11–12	12–14	10–14	10–12	10–14	10–11	10–13
	(11.3±0.4)	(13±0.9)	(11.4±1.4)	(11.1±0.7)	(11.5±1.1)	(10.4±0.5)	(11.3±0.9)
LTIV	16–19	16–21	14–17	15–18	15–19	14–17	16–20
	(17.1±0.8)	(18.2±1.5)	(16.4±1.1)	(16.8±1.0)	(17.0±1.2)	(15.9±1.1)	(17.3±0.9)

Table 6. Summary of classification accuracy of samples within operational units used in the Discriminant Function analyses. Abbreviations in Material and Methods.

	Meristic		Morphometric	
Operational Unit	%	Jackniffed %	%	Jackniffed %
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

Table 7. Raw canonical functions of the five most powerful variables recovered from the stepwise Discriminant Analysis for meristic data. CA, Canonical Axis, number in parenthesis is the eigenvalue for each axis. Abbreviations in Material and Methods.

Variable	CA I (2.10)	CA II (0.44)
OCC	1.327	0.158
POC	1.657	-0.269
SBO	-0.033	0.845
SAM	0.084	0.508
LFIV	0.263	-0.661