Zootaxa 1981: 57–68 (2009)
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

Two new species of montane web-footed salamanders (Plethodontidae: *Bolitoglossa*) from the Costa Rica-Panamá border region

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Abstract

Two new species of lungless salamanders (Plethodontidae) are described from high montane habitats of the border region between Costa Rica and Panamá. *Bolitoglossa pygmaea* and *B. robinsoni* are distinguished from each other and from other salamander species in this remote area by differences in adult body size, external proportions, foot webbing, tooth counts and/or external coloration. Both new species are assigned to the *B. subpalmata* species group, subgenus *Eladinea*. The miniaturized *B. pygmaea* is remarkable in being extensively depigmented, yet having the peritoneum and stomach area heavily pigmented and visible through the body wall.

Key words: *Bolitoglossa pygmaea* **sp. nov.**, *B. robinsoni* **sp. nov.**, Cordillera de Talamanca, taxonomy, Central America, biogeography

Resumen

Se describen dos nuevas especies de salamandras sin pulmones (Plethodontidae) de hábitats montanos altos de la región fronteriza entre Costa Rica y Panamá: *Bolitoglossa pygmaea* y *B. robinsoni*. Se distinguen entre ellas y de otras especies de salamandras en esta remota área por el tamaño del cuerpo de los adultos, por las proporciones externas, por la membrana de los pies, por el número de dientes y por la coloración externa. Las dos especies se asignan al grupo de especies de *B. subpalmata*, subgénero *Eladinea*. La diminuta *B. pygmaea* es interesante por poseer poco pigmento y por tener el peritoneo y estómago con pigmento oscuro visible externamente.

Introduction

The high diversity of salamanders in Costa Rica and Panamá is due in part to a radiation in the Talamancan mountain range that remains poorly known. Costa Rica has 43 currently recognized species of salamanders (23% of the amphibians known from the country), and Panamá has 25 (12.7% of its amphibians) (salamanders are 8.9% of the World's amphibians, AmphibiaWeb 2008). While much larger countries, the United States and México, have larger numbers of species with 186 (65% of amphibians) and 131 (36.7%) salamanders, respectively, if one counts number of species per 10,000 km^2, Costa Rica (8.41) and Panamá (3.31) greatly exceed both the United States (0.19) and México (0.67). Other than Costa Rica, Panamá is exceeded only by Guatemala (3.67). The border region of Costa Rica and Panamá has a large and complex salamander fauna, one of the richest local salamander faunas anywhere (Brame *et al*. 2001; Hanken *et al*. 2005; Wake 2005; Wake *et al*. 1973, 2007). The area is in general difficult to access and has been rarely visited by herpetologists. The two species described in this paper, members of the subgenus *Eladinea* (as defined by Parra-Olea *et al*.

Accepted by M. Vences: 15 Dec. 2008; published: 16 Jan. 2009

2004), appear to represent the smallest and one of the larger species of the many salamanders that occur along the continental divide. The first species is known only from Panamá, while the second is known from localities in each country.

Material and methods

Measurements were made using digital or dial calipers or a dissecting microscope fitted with an ocular micrometer; standard length (SL) was measured from the anterior tip of the snout to the posterior angle of the vent. Limb interval equals the number of costal interspaces between the tips of adpressed fore- and hind limbs, measured in one-half increments (e.g., 3, 3.5). Radiographs were prepared for specimens of the first of the newly described species, and one specimen of that species was cleared-and-stained. Counts of presacral (trunk) vertebrae do not include the first, or atlas, vertebra. Tooth counts are based on direct counts of clearly ankylosed teeth. Numbers of maxillary and vomerine teeth in each holotype are provided for right and left sides; these counts are summed for other individuals. Institutional abbreviations are as listed in Leviton *et al.* (1985).

Descriptions of the new species

***Bolitoglossa pygmaea* sp. nov.**
Pygmy Web-footed Salamander
Figure 1

Holotype. UCR 11788, an adult female from Fábrega Massif (coordinates 9°07’00” N, 82°52’40” W) at 3100 m elevation, Provincia de Bocas del Toro, Panamá, collected 1-10 March, 1984 by Luis Diego Gómez.

Paratypes. Twenty-five individuals with the same collecting and locality data as holotype: UCR 17789–11799, MVZ 222490–222503.

Diagnosis. A very small species of *Bolitoglossa* (subgenus *Eladinea*) with a short tail and moderately webbed hands and feet that differs from all other species in the genus in its pale coloration and its black-pigmented stomach and peritoneum, which are apparent through the largely depigmented skin. Assigned to *Bolitoglossa* because it lacks a sublingual fold.

Description. This diminutive species is in the small size-class category for the genus (Wake & Brame 1972). Standard length ranges from 23.6-32.6 (mean 28.1) in fifteen male paratypes; SL is 23.5-36.8 (mean 29.8) in nine adult females. Tails are short and never exceed standard length; SL divided by tail length ranges from 1.25 to 1.54 in males and from 1.23 to 1.85 in females. The head is relatively broad (Wake & Brame, 1972); SL divided by head width equals 5.5–6.6 in males and 5.6–6.5 in females. The snout is broadly rounded and of moderate length. Nostrils are large for this genus, although nasolabial protuberances are slight, better developed in males than in females. Eyes are relatively large and prominent and protrude beyond the lateral margins of the head and are visible in ventral view. Teeth are relatively large and well developed, and moderate in number (but relatively numerous in relation to body size). There are 2 or 3 premaxillary teeth (mean 2.1) in males and 3-6 (mean 4) in females. Maxillary teeth number 27–44 (mean 34.6) in males and 18–60 (mean 39) in females. Vomerine teeth number 14–20 (mean 16.3) in males and 15–25 (18.9) in females. Limbs are relatively short; limb interval ranges from 2.0 to 3.0 in males and from 2.5 to 4.5 in females. Hands and feet are relatively large; foot width ranges from 2.1 to 3 (mean 2.6) in males and from 1.9 to 3.5 (mean 2.5) in females. Digits are well differentiated but broadly pointed and more joined basally than webbed (Fig. 2A). The first digit of the manus and the first and fifth of the pes are very small. The longer digits of the larger specimens bear small subterminal pads. About one and one-half phalanges of the longest digits are free of the basal digital fusion (which constitutes the webbing in this species). Fingers, in order of decreasing length, are

3-4-2-1; toes are 3-4-2-5-1. Postiliac glands are obscure, but collections of unicellular glands are prominent behind the hind limbs on the lateral sides of the body anterior to the vent.

FIGURE 1. Dorsal (A) and ventral (B) views of the adult female holotype (UCR 11788) of *Bolitoglossa pygmaea*, 33.7 mm SL.

Measurements (in mm), limb interval and tooth counts of the female holotype. Head width 5.3; snout to gular fold (head length) 8.2; head depth at posterior angle of jaw 3.7; eyelid width 1.2; eyelid length 2.1; anterior rim of orbit to tip of snout 2.0; horizontal orbit diameter 1.7; interorbital distance between angle of eyes 2.9; interorbital distance between eyelids 3.2; snout to forelimb 10.3; distance separating external nares 1.3; snout projection beyond mandible 0.9; shoulder width 3.7; snout to posterior angle of vent (standard length) 33.7; snout to anterior angle of vent 30.5; axilla to groin 18.2; limb interval (number of costal interspaces between adpressed limbs) 2.5; tail length 18.2; tail width at base 1.6; tail depth at base 2.4; forelimb length (to tip of longest finger) 7.4; hind limb length 7.2; hand width 2.4; foot width 2.9; length of fifth toe 0.8; length of third toe 1.1. Numbers of teeth: premaxillary 3; maxillary 27-28; vomerine 10-12.

Coloration of the holotype in alcohol (Fig. 1). Very pale general pigmentation, essentially transparent or translucent. Line of brown pigment from snout along canthus rostralis and through eye (one edge of eyelid) and behind eye in line over each shoulder, where it becomes a diffuse and irregular "line" that extends to the pelvic region. Pigment extends in a pair of weakly defined lines on tail nearly to tip. Scattering of brownish color on top of head, behind eye, and lightly on dorsum, but no evident ground color. Limb insertions, limbs, and hands and feet with lightly scattered brown pigment. Venter almost unpigmented with pale ventrolateral brownish color and some punctate melanophores thinly scattered over ventral surfaces. On the tail venter and behind hind limbs, transparent gland openings stand out as silvery circles. Internal black pigmentation in posterior abdomen and stomach shows through semitransparent ventral and lateral body wall, and heavily pigmented eyeball shows as very dark patch through eyelid. Iris dark brownish-black.

Osteology. The following account is based on radiographs of 12 paratypes, one of which (MVZ 222492) was cleared and stained. Although small, this species has a well developed, well articulated skull. The unpaired premaxilla is small but rather robust and is well articulated to the well-formed maxillary bones. An unpaired dorsal process rises from the dorsum of the tooth-bearing portion of the premaxillary between

FIGURE 2. Dorsal views of the left foot (width 2.9 mm) of the holotype of *Bolitoglossa pygmaea* (UCR 11788) (A), and of the right foot (width 7.4 mm) of the holotype of *Bolitoglossa robinsoni* (UCR 11216) (B).

the enlarged, cartilaginous nasal capsules; at the point where the nasal capsules diverge laterally the process splits into a pair that embraces a relatively large internasal fontanelle. These processes, well articulated to the nasals on their lateral borders, are slender and unexpanded distally. They end about half-way along the length of the fontanelle, where they articulate with the enlarged anterior parts of the frontals. The frontals articulate with each other, and the dorsal fontanelle often found in tropical plethodontids between the frontal and parietal bones is virtually absent. While well formed and relatively large, nasals are not protuberant anteriorly. A small lateral evacuation of the nasals expands internally and marks the passage of the nasolacrimal duct. Septomaxillaries and prefrontals are absent and the nasals form the anterior rim of the orbit. The nasals also articulate with the frontals. No otic crests are present. The operculum lacks a columella but has a minute anteroventral projection that contacts the otic capsule. The preorbital processes of the vomer are long and well developed, and bear teeth nearly to their tips. A large fontanelle separates the bodies of the vomers from each other medially. The 14 trunk vertebrae are well formed and bear bicipital ribs on the first 13. There are two caudosacral vertebrae. Tails are short, and several specimens have lost the tail. Six males have from 22 to 25 (mean 23) caudal vertebrae; two females have 22 and 24 caudal vertebrae. The first caudal vertebra has relatively stout, dorsoventrally expanded, rather short transverse processes that arise at the anterior end of the vertebra and are frontally oriented, but not at an acute angle. The limbs of the cleared and stained individual are in poor condition, but eight mesopodial elements are present in both the manus and pes (distal tarsal 3 is separate from a combined distal tarsal 4+5). Only digit 5 is complete on one limb and it contains two phalanges. The radiographs do not always display phalanges clearly, but when evident the phalangeal formulas are 1-2-3-2 and 1-2-3-3-2. All mesopodials are cartilaginous. No tibial spur is present. The hyoid apparatus is well stained and entirely cartilaginous. The basibranchial is relatively stout (diameter at midpoint about 14% of length) and bears two short cornua at the broad anterior end. No lingual cartilage is present. The first ceratobranchial is extraordinarily slender (diameter 2.5% of length and apparently discontinuous; it is strongly bowed). The second ceratobranchial, in contrast, is short and stout, with a length of about 50% that of the basibranchial and about 75% that of the first ceratobranchial. Its diameter at midpoint is 27% of its length. The epibranchial is elongated and slender, tapering to a pointed tip; it is 2.3 times the length of the basibranchial, 3.4 times the length of the first ceratobranchial, and 4.5 times the length of the second ceratobranchial. The ceratohyals are relatively short and lack a slender anterior extension, and they are relatively narrow. There is no urohyal.

Habitat and range. The species is known only from a small region called the Fábrega Massif, a general plateau with a mean elevation above 3000 m. The main peak, Cerro Fábrega, is 3335 m high (9º 07' N, 82º 53' W) and 3.5 km north of the Costa Rican border on the continental divide (the peak here is Cerro Biné, Fig. 3). The plateau is mainly to the north of the peak, and according to the collector the salamanders were found among grass tussocks in an open area.

Etymology. This species name is derived from *pygmaeus* (L.) and *pygmaios* (Gr.), in allusion to its miniature size, perhaps the smallest of any member of this large genus.

***Bolitoglossa robinsoni* sp. nov.**
Robinson's Web-footed Salamander
Figure 4

Holotype. UCR 11216, an adult male from Cerro Echandi (top of Cerro 3167 m), Prov. Puntarenas, Costa Rica, latitude 9°01'50" N (9.0306), longitude 82°49'20" W (-82.8222) (3.4 km max. error, WGS84 datum), elevation 3162 m, collected on 6 January 1992 by Eugenia Arguedas.

Paratypes. Three individuals: UCR 11217-11218, same data as holotype; UCR 10921, Cerro Burú, below Cerro Echandi, Prov. Puntarenas, Costa Rica, latitude 9°00' 45" N (9.0125, longitude 82° 49' 50" W (-82.8306), elevation 2300 m, collected 16 October 1991 by M. Zumbado and E. Arguedas.

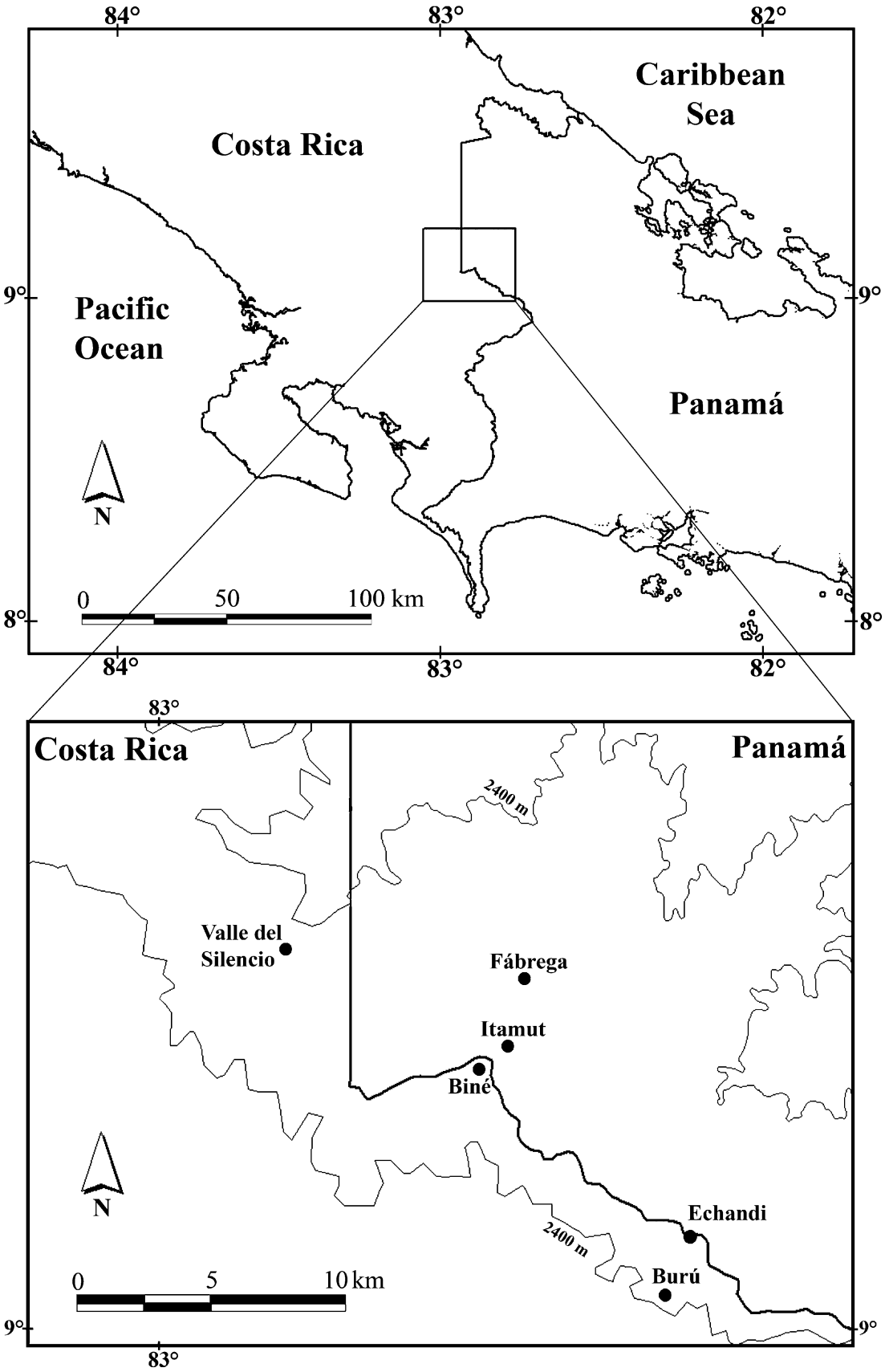

FIGURE 3. The border region between Costa Rica and Panamá showing the six localities from which species described in this paper have been collected. The two species are sympatric on the Fábrega Massif. The 2400 m contour line is indicated. Elevations within this contour are as high as 3335 m.

FIGURE 4. Dorsal (A) and ventral (B) views of the adult male holotype (UCR 11216) of *Bolitoglossa robinsoni*, 63.5 mm SL.

Referred material. We tentatively assign morphologically divergent populations from nearby peaks to this taxon. See section on variation for detailed comments.

Diagnosis. This is a relatively large, stout-bodied species assigned to *Bolitoglossa* because it lacks a sublingual fold. It resembles *B. cerroensis* in general form, but differs by having more slender habitus, more maxillary teeth and broader hands and feet, which however are less broad than those of the even larger *B. marmorea*. Differs from *B. sombra* by having more maxillary teeth, broader feet, shorter limbs, and lacking a uniform black coloration. Differs from *B. compacta* in having many more maxillary teeth and lacking extensive red or red-orange blotching or striping. Differs from all other salamanders in the region by its large size, relatively long and moderately webbed digits and extensive yellowish spotting on the body, limbs and tail.

Description. This is a relatively large, stout species. Standard length (SL) in two adult males is 45.9 and 63.5. Tails are moderate, shorter than SL; SL divided by tail length in two males is 1.34 and 1.06. The head is broad; SL divided by head width is 5.7 and 6.2. The head is well demarcated from the neck. The snout is broadly rounded and not prominent. Nostrils are small and nasolabial protuberances are poorly developed.

Eyes are moderately prominent; they protrude slightly beyond the lateral margins of the head and are relatively frontal in orientation. Teeth are numerous. There are 2 and 6 premaxillary teeth in males. Maxillary teeth are 50 and 65 in the two adult males, and vomerine teeth are 22 in each. Limbs are stout but moderate in length; limb interval is 1.5 and 2 in males. Hands and feet are broad (6.0 and 7.4) with little webbing; fewer than two distal-most phalanges of the longest digits are free of webbing (Fig. 2, B). Digital tips are truncate and bear well-developed subterminal pads. Fingers, in order of decreasing length, are 3-4-2-1; toes are 3-4-2-5-1. Postiliac glands are not evident.

Measurements (in mm), limb interval and tooth counts of the male holotype. Head width 10.2; snout to gular fold (head length) 13.9; head depth at posterior angle of jaw 6.6; eyelid width 2.0; eyelid length 4.4; anterior rim of orbit to tip of snout 3.4; horizontal orbit diameter 2.8; interorbital distance between angle of eyes 4.9; interorbital distance between eyelids 4.9; length of groove extending posteriorly from eye 5.8; distance between nuchal groove and gular fold 6.3; snout to forelimb 20.0; distance separating external nares 2.8; snout projection beyond mandible 0.8; snout to posterior angle of vent (standard length) 63.5; snout to anterior angle of vent 58.6; axilla to groin 34.0; limb interval 2.0; tail length 59.7; tail width at base 5.4; tail depth at base 5.6; forelimb length (to tip of longest finger) 16.1; hind limb length 16.6; hand width 6.0; foot width 7.4; length of fifth toe 1.2; length of third toe 2.7. Numbers of teeth: premaxillary 6; maxillary 31-34; vomerine 10-12, arranged in a single row.

Coloration of the holotype in alcohol (Fig. 4). Dorsal ground color dark brownish-black but with so much pale spotting that the animal appears light. Patches of light yellow have joined together along the trunk to produce a very complex pattern of light on dark. Costal grooves are mainly dark, and the intercostal folds are light. Limbs and tail are mottled dark brown and yellowish-gray. Venter mottled with dark and light but mainly pale because of spaces in the punctate melanophore background. Throat pale but with punctate melanophores. Tail venter dark with ragged light spots.

Variation. We tentatively assign specimens from four localities on or near the continental divide in Panamá and Costa Rica to this species (Fig. 3). However, these specimens differ in several respects from the type specimens and they may represent as many as four additional undescribed species. The four localities and the specimens associated with them are Valle del Silencio (Silencio in Fig. 3 and Table 1, elevation 2500 m, 9°06’30” [9.1083], 82°58’00” [-82.9667]), MVZ 193550–193559 (193550, 193553, 193556, 193558, 153550 used in morphometrical analysis, see below); Cerro Biné (3200 m, 9°05’12” [9.0867], 82°54’34” [-82.8928]), MVZ 222487–89 and UCR 11787 (MVZ specimens used in morphometrical analysis); Cerro Itamut (3000 m, 9°05’40” [9.0944], 82°53’00” [-82.8833]), MVZ 222485–86 and UCR 11783–11786 (all used in morphometrical analysis); Cerro Fábrega (3335 m, 9°07’00” [9.1167], 82°52’40” [-82.8778]); MVZ 222477–222483, 222484 and UCR 11775–11782 (MVZ 222478 and 222480, and UCR 11775–11778 used in morphometrical analysis). Specimens as indicated plus the type series of *B. robinsoni* were included in a discriminant function analysis. We conducted several slightly different analyses. In the first we used SL, tail length, head width, head length, forelimb and hind limb length, axilla-groin, shoulder width, foot width, and total numbers of maxillary, premaxillary and vomerine teeth as separate characters (Table 1, Fig. 5). A second analysis excluded tails, because we could not always be certain whether a tail had regenerated completely or in part from external morphology. A third analysis included the tail but excluded the teeth (on the grounds that they are counts rather than measurements). A final analysis included only teeth.

All specimens in the discriminant function analysis were classified in the appropriate group using all measurements (Wilks’ Lambda=0.0025, $F_{[60, 69]}$=2.9923 p=<0.000). Each of the populations is surprisingly well differentiated from the others although the samples are small. In the classification matrix (not shown) all specimens were correctly classified except a single specimen from Fábrega misclassified as from Silencio. In the analysis without the tail one specimen from Fábrega was again misclassified as from Silencio. In the analysis without teeth four specimens were misclassified, one of them a specimen from Echandi placed with Burú. A Biné specimen and two Fábrega specimens were classified as Silencio. In the analysis of teeth only, discrimination was far poorer than in the other analyses (Wilks’ Lambda=0.4095, $F_{[15, 88]}$=2.2400 p=0.0103)

and only 55% of the specimens were classified correctly. One specimen from Echandi was classified as Silencio and single specimens from Fábrega, Itamut and Silencio were classified as Burú.

TABLE 1. Morphometrical data (average ± standard deviation, range in parenthesis) for six samples assigned to *Bolitoglossa robinsoni*. The type locality is Echandi and one paratype is from Burú (cf. Figs. 3 and 5).

Locality	Echandi	Burú	Fábrega	Itamut	Biné	Silencio
n	3	1	9	6	3	9
Standard Length (SL, mm)	46.5 ± 16.7 (30.2–63.5)	30.2	55.4 ± 11.2 (34.4–72.5)	48.0 ± 6.5 (37.2–55.7)	53.3 ± 12.4 (39.0–60.6)	36.2 ± 7.4 (26.2–51.8)
Tail Length (mm)	37.3 ± 21.1 (17.8–59.7)	17.8	53.3 ± 13.8 (25.4–70.7)	45.8 ± 7.2 (33.5–52.8)	50.5 ± 17.1 (30.8–62.3)	29.9 ± 11.8 (16.3–55.1)
Head Width (mm)	7.7 ± 2.7 (4.8–10.2)	4.8	8.2 ± 1.3 (5.4–9.9)	8.1 ± 1.0 (6.6–9.3)	8.4 ± 2.2 (5.9–9.9)	6.0 ± 1.0 (4.6–8.2)
Head Length (mm)	10.6 ± 3.3 (7.3–13.9)	7.3	12.7 ± 2.0 (9.3–15.5)	11.8 ± 1.2 (9.7–13.0)	11.9 ± 3.0 (8.5–14.1)	9.0 ± 1.7 (6.7–12.6)
Hindlimb Length (mm)	12.4 ± 4.5 (7.7–16.6)	7.7	15.0 ± 3.3 (8.0–18.8)	13.2 ± 2.0 (10.3–15.2)	13.7 ± 3.1 (10.1–15.6)	9.4 ± 2.5 (6.0–14.3)
Forelimb Length (mm)	11.9 ± 4.7 (6.8–16.1)	6.8	13.4 ± 2.9 (6.6–16.7)	13.0 ± 1.9 (10.1–15.0)	13.1 ± 3.1 (9.5–15.3)	8.9 ± 2.5 (5.9–14.1)
Axilla to Groin Length (mm)	23.9 ± 9.5 (15.2–34.0)	15.2	29.8 ± 6.5 (16.8–37.4)	25.6 ± 3.7 (19.3–30.6)	29.0 ± 7.1 (20.8–33.9)	18.9 ± 4.2 (14.5–28.3)
Shoulder Width (mm)	5.8 ± 1.9 (4.1–7.9)	3.5	5.5 ± 1.2 (3.3–7.3)	5.8 ± 0.7 (4.8–6.6)	5.6 ± 1.8 (3.6–7.1)	4.0 ± 0.7 (3.1–5.1)
Foot Width (mm)	5.4 ± 2.3 (2.9–7.4)	2.9	5.7 ± 1.3 (3.3–8.0)	6.3 ± 1.1 (4.5–7.3)	5.7 ± 1.5 (4.1–6.9)	3.8 ± 1.2 (2.2–6.3)
Number of Maxillary Teeth	53 ± 11 (43–65)	43	49 ± 10 (30–64)	46 ± 9 (32–54)	41 ± 27 (9–58)	29 ± 14 (14–56)
Number of Premaxillary Teeth	4 ± 2 (2–6)	3	5 ± 1 (3–6)	4 ± 1 (3–5)	5 ± 3 (2–7)	2 ± 1 (0–4)
Number of Vomerine Teeth	18 ± 6 (11–22)	23	21 ± 5 (16–32)	20 ± 3 (17–25)	25 ± 10 (14–33)	16 ± 5 (11–25)
Number of Grooves when Limbs Adpressed *	(1.5–3.5)	(3.5)	(0.0–2.0)	(-1.5–1.0)	(1.0–1.5)	(0.5–2.0)

*Variable not included in discriminant function analysis

Despite the results of the discriminant function analysis there is little to distinguish these populations in particular characters. The number of costal folds between adpressed limbs gives an integrated measure (although inexact) that is useful for quick identification of many species of salamanders. In the small Echandi population this value ranges from 1.5-3.5, which is a value larger than for any of the other populations (total range of values from -1.5 to +1.5).

Habitat and range. *Bolitoglossa robinsoni* is known from a section of the Cordillera de Talamanca on the continental divide that forms the boundary between Costa Rica and Panamá, and in the high Fábrega Massif, which extends northward into Panamá (Fig. 3). Some specimens were obtained from areas of paramo, but others are from nearby montane forests.

Etymology. The species is named in honor of the late Douglas C. Robinson, who did a significant survey of amphibians and reptiles in Costa Rica, consolidated the UCR collection and was the mentor of most herpetologists still present in the country.

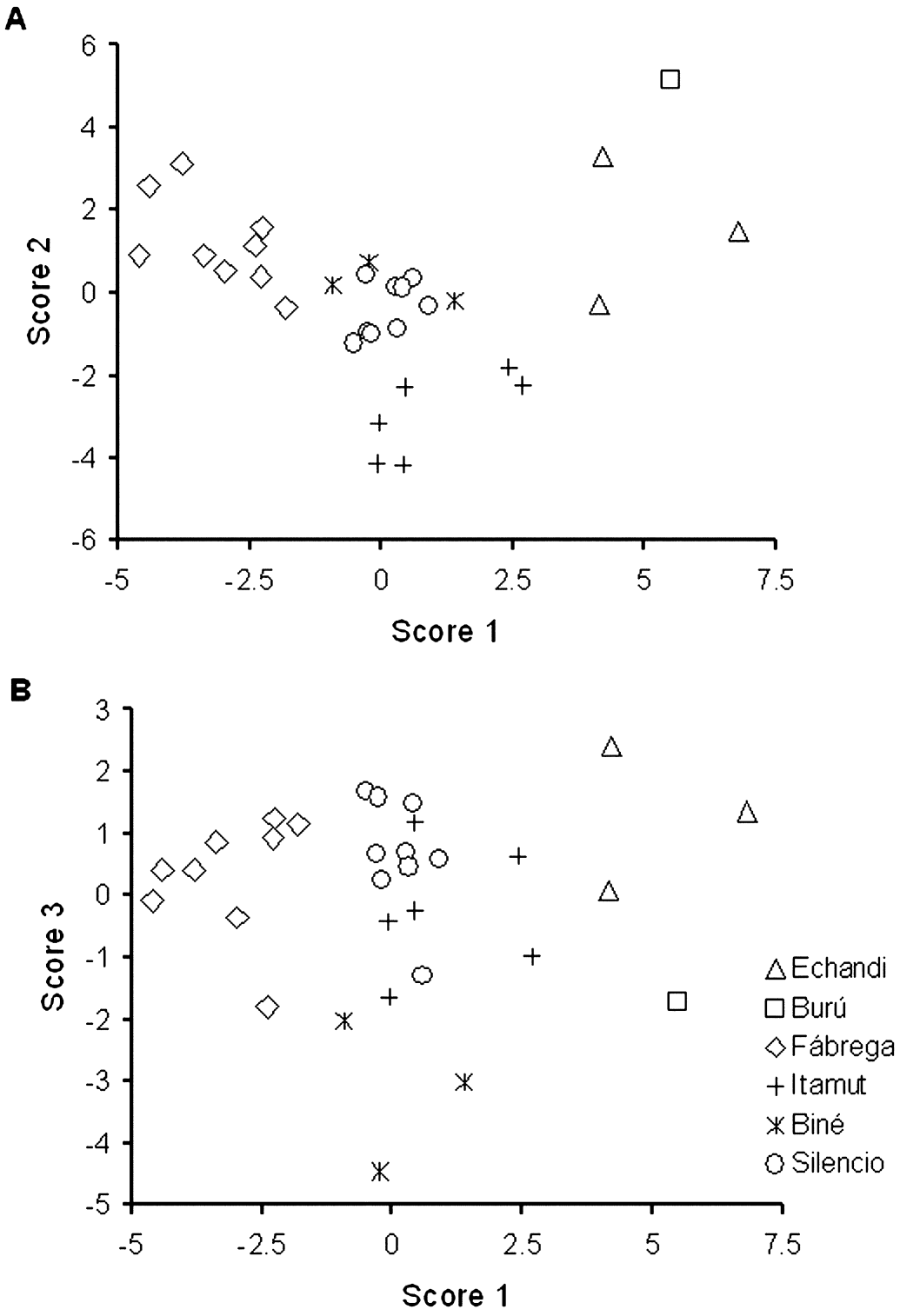

FIGURE 5. Results of a discriminant function analysis of morphometrical data for six samples of specimens assigned to *Bolitoglossa robinsoni*. A. Plot of individuals using the scores of the first two canonical axes. B. Plot of individuals with scores of canonical axis three plotted against canonical axis one.

Discussion

To the best of our knowledge, *B. pygmaea* is the smallest species in the large (90+ species) genus *Bolitoglossa*. Two other diminutive species are known from Costa Rica and Panamá. The species long thought to be the smallest, *B. minutula*, has an average size of 33.5 (males) and 33.7 (females) SL, and females are known to reach at least 41.7 SL. Only two adult *B. diminuta* are known to us, both adult females (each was attending a clutch of eggs when discovered) between 31 and 32 SL. Accordingly, *B. diminuta* is about the same size as *B. pygmaea*, whose average size is less than 30 SL (with the largest individual being a female 36.8 SL). Other small species (*B. chica*, *B. rufescens*, *B. occidentalis*) are all larger.

Despite its small size, *B. pygmaea* does not display many of the paedomorphic traits that are found in other tiny congeners (e.g., *B. occidentalis* and *B. rufescens*, Alberch & Alberch 1981, Alberch 1983). Prefrontals are absent, a paedomorphic trait, but these bones are absent from many species in the genus and one cannot exclude the possibility that the species belongs to a clade that lacks the bones. In contrast, skulls are relatively well formed and there is no dorsal fontanelle. A long, tooth-bearing preorbital process is present on the vomer. Limbs are typical for the genus and there are no special mesopodial fusions. Thus, the species appear to be miniaturized, as opposed to paedomorphic, using the contrasts proposed for *Parvimolge* versus *Thorius* (Wake, 1991).

The pigmentation of the peritoneum, testes and stomach of *B. pygmaea* is extraordinary and we can only speculate as to its significance. These salamanders are apparently active by day at very high elevations where the temperatures are typically low. The pigmentation might serve the dual role of protection from ultraviolet radiation (in which case, why is the skin almost unpigmented?), and increasing the temperature of the stomach, possibly speeding digestion.

Salamander diversity along the Costa Rica-Panamá border is high, with possibly as many as 20 species of two genera (Wake 2005, Wake *et al.* 2007). The new species described herein are sp. nov. 4 and 5 of Wake (2005, Fig. 3.2). Wake *et al.* (2007) refer to some additional species in the vicinity of Cerro Pando, at the eastern margin of Costa Rica, and we have pointed out the morphological distinctiveness (discriminant function analysis) of what we have named as *B. robinsoni*, which could be as many as four or five species. We do not have tissue samples for any of these, nor for *B. pygmaea*, and in the absence of molecular data we are reluctant to describe any but the most distinctive unidentified populations. Current exploratory work in the eastern mountains of Costa Rica has recently produced additional samples of other undetermined species, and tissue samples of many of these are available. They should help us determine whether the local morphological diversity reflects individual variation, geographic variation, or both, or more species that we have recognized so far. Fortunately much of the high elevation habitat in this region is in good condition, although almost all territory below 1800 m is heavily disturbed, especially along the Pacific coast.

Acknowledgments

Animal use was approved by the University of California, Berkeley, protocol #R093-0205 to DBW. Research support was provided by NSF grants DEB-9408347 and EF-0339439 (DBW). Gerardo (Cachi) Chaves helped determine the locality coordinates and Adrián García helped prepare the maps. We especially acknowledge the foresight and dedication of Luis Diego Gómez, who discovered these salamanders while conducting botanical work and recognized their value by collecting and preserving specimens and calling them to our attention. We thank Marvalee Wake for review of the manuscript and discussion. This is a contribution from the Museo de Zoología, Universidad de Costa Rica.

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