

Montane Salamanders from the Costa Rica–Panamá Border Region, with Descriptions of Two New Species of *Bolitoglossa*

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Two new species of lungless salamanders (Plethodontidae) are described from montane habitats of eastern Costa Rica and adjacent western Panamá. *Bolitoglossa gomezi* and *B. bramei* are distinguished from each other and from other salamander species in this remote area 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*. A newly identified specimen of *Bolitoglossa anthracina*—only the fourth known specimen of this rare species in collections—is reported from the same region. Salamander species diversity along the border between Costa Rica and Panamá is exceptionally large, at present comprising 22 named and two unnamed forms.

Se describen dos especies nuevas de salamandras de la familia Plethodontidae de áreas montañosas del este de Costa Rica y zonas adyacentes del oeste de Panamá. *Bolitoglossa gomezi* y *B. bramei* se distinguen entre sí y de otras especies de salamandras de esta zona en el tamaño y proporciones corporales, palmeadura de las patas, número de dientes y/o coloración. Ambas especies nuevas se asignan al complejo *B. subpalmata*, del subgénero *Eladinea*. Se indica también el hallazgo de un espécimen de *Bolitoglossa anthracina*—el cuarto ejemplar que se conoce de esta especie—de la misma región. La diversidad de especies de salamandras a lo largo de la zona limítrofe entre Costa Rica y Panamá es excepcionalmente alta, cuenta con 22 especies descritas y dos más aún sin describir.

THE border region between Costa Rica and Panamá has a large and complex salamander fauna, one of the richest anywhere (Wake et al., 1973, 2005; Brame et al., 2001; Hanken et al., 2005; Wake, 2005). These salamanders, however, are difficult to find. Only a handful of species are reliably seen (e.g., *Bolitoglossa minutula*, *B. sombra*, and *Oedipina grandis*), and few specimens exist in museum collections. Most specimens were long forced into existing taxa known from other areas, although some endemic species were described from specimens collected long ago (e.g., *Bolitoglossa schizodactyla*). Fieldwork by C. W. Myers and associates in the Panamanian sector and J. M. Savage and associates in the Costa Rican sector yielded important specimens from the region. Several of the most morphologically distinct of these were described as new species in the 1970s (*O. grandis*, *B. compacta*, and *B. minutula*), but other likely new species remained undescribed. Additional fieldwork in recent years, combined with accumulating molecular data, led to the description of several new species (*O. savagei*, *B. magnifica*, and *B. sombra*), and one apparently rare but morphologically differentiated species was added as well (*B. anthracina*). Despite these efforts, the presence of several more species of *Bolitoglossa* has been signaled in several publica-

tions (García-París et al., 2000; Savage, 2002; Wake, 2005). Most of these claims are based on specimens that have been collected infrequently over many years, and none of the species is well known. Here we describe two new species and assign them to the *B. subpalmata* group, subgenus *Eladinea* (García-París et al., 2000; Parra-Olea et al., 2004). We also review some of the remaining undescribed forms and provide new information about previously named salamanders from this species-rich region.

MATERIALS 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 appressed fore- and hind limbs, measured in one-half increments (e.g., 3, 4.5). Radiographs were prepared for one or two specimens of each new species. 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

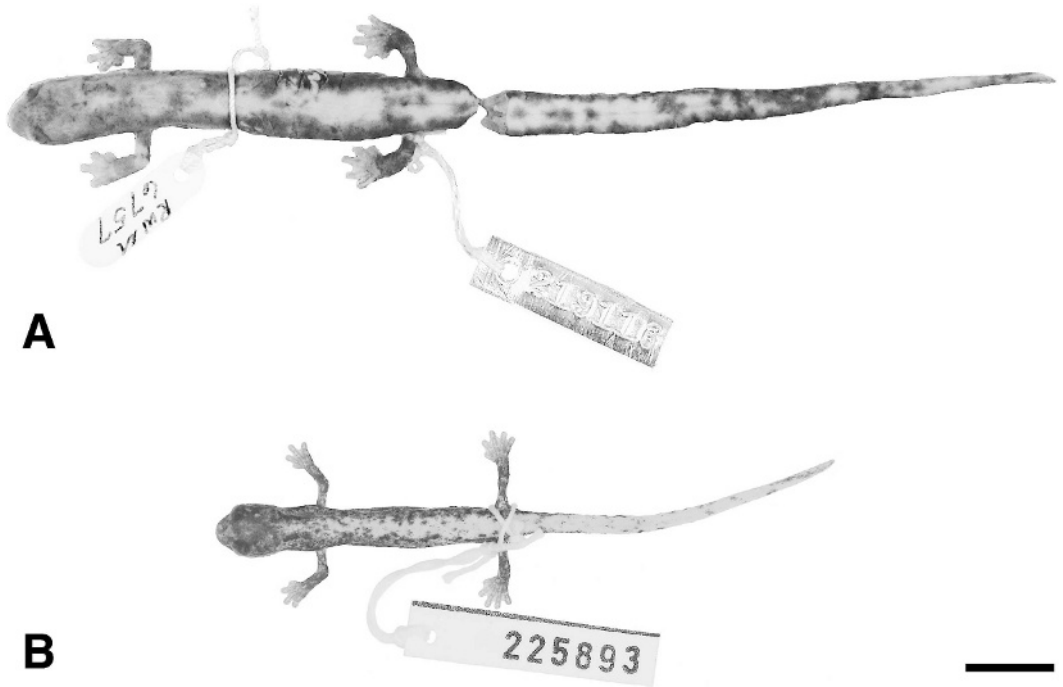


Fig. 1. Holotypes of new species. (A) *Bolitoglossa gomezi*, USNM 219116, an adult female from Las Cruces Biological Station, Costa Rica. The tail separated from the body following fixation. (B) *B. bramei*, MVZ 225893, an adult male from Las Tablas, Costa Rica. Scale bar, 1 cm.

are summed for other individuals. Institutional abbreviations are as listed in Leviton et al. (1985), except for CH-Ch (Circulo Herpetológico de Panamá) and MVUP (Museo de Vertebrados, Universidad de Panamá).

***Bolitoglossa gomezi*, new species**
Gómez's Web-footed Salamander
Figures 1A, 2, 3A, 3C, 3E

Bolitoglossa sp. 2.—Savage and Villa, 1986:9, 44, 48.

Bolitoglossa pesrubra.—Savage, 2002:135, map 6.11 (part).

Bolitoglossa sp. nov. 6.—Wake, 2005:76, fig. 3.2.

Holotype.—USNM 219116, adult female, Costa Rica, Provincia Puntarenas, Las Cruces Biological Station, 8°47'35"N, 82°57'30"W, 1250 m, 22 May 1971, R. W. McDiarmid.

Paratypes.—Costa Rica, Provincia Puntarenas: LACM 146323, 2 km SSW of Cañas Gordas at Finca Loma Linda, ca. 8°43.3'N, 82°54.3'W, 1170 m, 4 June 1964, J. M. Savage and others; MVZ 97811–12 (two specimens), same locality as the holotype, March 1971, P. Myers. Panamá, Provincia Chiriquí: UMMZ 173548, Rio Candela

Valley, ca. 8°54'N, 82°45'W, 1700 m, 22 June 1976, A. Jaslow; MVUP 929, Cotito, ca. 8°53'N, ca. 82°43'W, ca. 1800 m, 14 March 1990, F. Arosemena; SMF 85062, Cerro Jurutungo, 8°54'28.3"N, 82°42'59.5"W, 2120 m, 12 Jan. 2006, G. Köhler and J. Sunyer.

Diagnosis.—A moderately small, relatively stout salamander that resembles other members of the *B. subpalmata* group in general morphology. Limbs are moderately short; hands and feet have distinct, columnar digits with relatively little webbing (Fig. 2). *Bolitoglossa gomezi* is distinguished from its close relative *B. bramei* by its somewhat shorter limbs, fewer maxillary teeth, and narrower head, which is less distinct from the trunk. It is slightly smaller than *B. subpalmata* and *B. pesrubra* and appears to have a longer tail and shorter limbs, especially in males.

Description.—A moderately small species (Wake and Brame, 1972). Standard length 29.3–49.9 mm (mean 38.9) in five male paratypes, 42.3 and 54.5 (48.4) in the two females. Tails moderately long, frequently exceed standard length; SL divided by tail length 0.85–1.07 (mean 0.96) in males, 0.84–0.87 (0.86) in females. Head

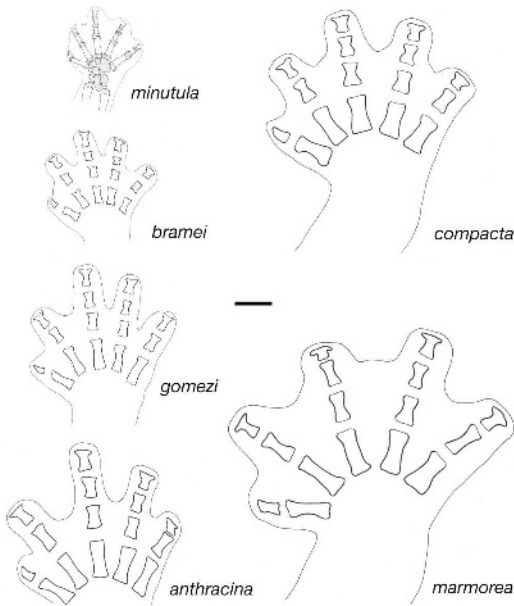


Fig. 2. Comparison of foot size, digital webbing, and phalangeal morphology among six species of *Bolitoglossa* from Costa Rica and Panamá. Each drawing is derived from a radiograph or cleared-and-stained specimen; all are depicted as right feet and at the same scale for ease of comparison. The foot of *B. minutula* also depicts cartilaginous mesopodials (ankle bones) and cartilaginous epiphyses on individual phalanges and lower limb bones (shaded). Specimens depicted: *B. anthracina*, KU 116671; *B. bramei*, MVZ 225893; *B. compacta*, MVZ 128635; *B. gomezi*, USNM 219116; *B. marmorea*, MVZ 210284; *B. minutula*, KU 104330. Scale bar, 1 cm.

moderately broad (Wake and Brame, 1972); SL divided by head width 6.2–7.1 (mean 6.6) in males, 6.6–7.0 (6.8) in females. Snout broadly rounded. Nostrils small, nasolabial protuberances modest. Eyes relatively small, do not protrude beyond lateral margins of head in dorsal view. Teeth moderate in number: premaxillary 2 or 3 (mean 2.6) in males, 5 in each female; maxillary 29–52 (mean 38.8) in males, 48–53 (50.5) in females; vomerine 17–30 (mean 20.8) in males, 18–29 (23.5) in females. Limbs relatively short; limb interval 1.5–3 (mean 2.4) in males, 2.5–3 (2.8) in females. Hands and feet relatively large (Fig. 2). Digits columnar, discrete, and bluntly tipped; three longest digits in

manus and pes bear well-developed subterminal pads. Webbing only moderate for the genus (Wake and Brame, 1969), with two or more distal phalanges free (unwebbed). Fingers, in order of decreasing length, 3–4–2–1; toes 3–4–2–5–1. Postiliac glands obscure.

Measurements of the holotype (in millimeters).—Head width 7.8; snout to gular fold (head length) 11.8; head depth at posterior angle of jaw 5.0; eyelid width 1.5; eyelid length 3.4; anterior rim of orbit to tip of snout 3.2; horizontal orbit diameter 0.3; interorbital distance between angle of eyes 4.2; interorbital distance between eyelids 3.2; length of groove extending posteriorly from eye 3.2; distance between nuchal groove and gular fold 4.4; snout to forelimb 15.6; distance separating external nares 2.3; snout projection beyond mandible 1.4; snout to posterior angle of vent (standard length) 54.5; snout to anterior angle of vent 50.1; axilla to groin 31.1; number of costal interspaces between appressed limbs 3.0; tail length 62.4; tail width at base 5.3; tail depth at base 5.0; forelimb length (to tip of longest finger) 11.1; hind limb length 12.0; hand width 4.6; foot width 5.4; length of fifth toe 1.0; length of third toe 1.8; distance between vomerine teeth and parasphenoid tooth patch 0.6. Numbers of teeth: premaxillary 5; maxillary 26–27; vomerine 14–15.

Coloration of the holotype in alcohol.—Ground color brownish tan. Throat and upper surface of head brown. Broad, light, irregular dorsal band invaded in some areas by large, dark brown spots. Band extends onto base of tail but is discontinuous posteriorly. Venter brown but lighter than flanks, as is underside of tail. Tail tip light.

Coloration in life.—LACM 146323 (based on field notes of J. M. Savage): Dorsum dark brown with reddish cast. Sides and belly dark chocolate brown with many white guanophores. Tail tip reddish-orange, as is dorsal and proximal portion of each forelimb (Fig. 3A, 3C, 3E).

Variation.—Two small paratypes from the type locality (MVZ 97811–12) both have a broad dorsal stripe or band with some darker streaking.

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Fig. 3. Salamanders in life. (A, C) Paratype of *Bolitoglossa gomezi*, SMF 85062, an adult female from Cerro Jurutungo, Panamá. Courtesy of G. Köhler. (B) Holotype of *B. bramei*, MVZ 225893, from Las Tablas, Costa Rica. Courtesy of M. García-París. (D) *B. anthracina*, AMNH A-94807, an adult male from Presa Fortuna, Panamá. Courtesy of C. Myers. (E) Paratype of *B. gomezi*, UMMZ 173548, an adult male from Rio Candela Valley, Panamá. Courtesy of A. Jaslow.



A



B



C



D



E

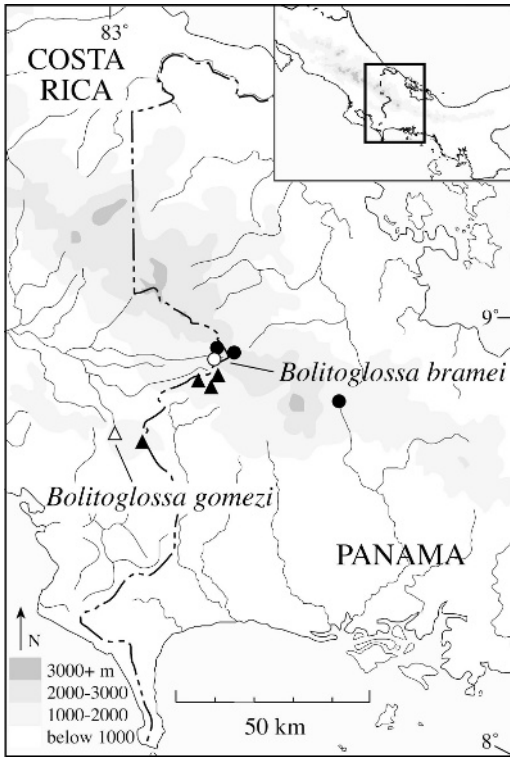


Fig. 4. Distribution of two new species of *Bolitoglossa* in the border region of eastern Costa Rica and western Panamá. Open symbols denote type localities.

The band was reddish in life and the tails of both animals were red to the tip. Ventrals of both are dark with numerous tiny white spots. SMF 85062 is a recently collected small adult female that has a relatively complicated pattern (Fig. 3A, 3C). The dark brown ground color is streaked with cream to reddish-brown from snout to tail tip. Pigment is prominent on the eyelids and is present on both distal and proximal limb segments. The entire venter is covered with light spots and blotches. These are especially large and prominent on the gular and anterior belly regions, become smaller and less prominent posteriorly, but reappear as larger spots on the underside of the tail. UMMZ 173548 is a relatively large male (49.5 mm SL) with 52 maxillary teeth. It has the longest limbs of any specimen assigned to this species (Fig. 3E). MVUP 929 is a male of moderate size (40.9 mm SL), but it has more hand and foot webbing than other specimens assigned to this species. A broad dorsal band extends from the shoulder region to near the tip of the tail. It contains scattered dark spots of varying size and shape and may have been reddish in life. There is a V-shaped light mark on the occiput.

Osteology.—The following account is based on digital radiographs of the holotype and one paratype (SMF 85062). Skull well ossified. Pre-maxillary bone stout but narrow; paired frontal processes arise and remain separate for their entire lengths. Nasal bones moderately large. Prefrontal bone evident only on left side of holotype; septomaxillary bones absent both sides. Paired parietal and frontal bones well ankylosed to one another, leaving no dorsal fontanelle. Maxillary bones only moderately long, extend posteriorly to a level about 80% through eyeball. Each bone extends rostrally as a spinous process lying anterior to dental process of premaxillary. Operculum lacks columella. Fourteen trunk vertebrae; all but the last bear ribs. Two caudosacral vertebrae. Transverse processes on first caudal vertebra of holotype are perpendicular to long axis; processes on second caudal vertebra sweep forward as curved, sharp spines. Thirty-seven caudal vertebrae in holotype; transverse processes present on only the first seven or eight. SMF 85062 has 36 vertebrae. Digits well developed on all four limbs. Slightly more than two distal-most phalanges of the longest fingers and toes free of basal webbing (Fig. 2). Phalangeal formulae 1-2-3-2 (hand), 1-2-3-3-2 (foot). Terminal phalanges of longer fingers and toes widely expanded distally so that they are T-shaped to Y-shaped. Tibial spur absent.

Habitat and range.—The species is known only from a small region along the Pacific slope on either side of the Costa Rica–Panamá border (Fig. 4). In Costa Rica it is known from the eastern end of the Fila Costeña at the Las Cruces Biological Station (Catherine and Robert Wilson Botanical Garden) and the relatively close Finca Loma Linda. These localities range in elevation from 1170 to about 1250 m. We also assign to this species specimens from the western slopes of the Cordillera de Talamanca in extreme western Panamá. These were collected at three separate sites ranging in elevation from 1700 to 2120 m, both in the vicinity and above and to the east of the valley of the Río Candela. The species is found in the Tropical Premontane Rainforest and Tropical Lower Montane Rainforest zones (*sensu* Holdridge, 1967). The holotype was collected from a bromeliad in the cloud forest along the Rio Java to the west of the Las Cruces Station headquarters. LACM 146323 was collected at night, along with a specimen of *B. colonneae*. MVZ 97811–12 were collected abroad at night in a cloud forest on a ridge just west of the Las Cruces Station. UMMZ 173548 was collected from a large green

bromeliad (1 m in diameter) 3 m up a tree on the forested ridge of a recently cleared field. MVUP 929 was found at night on a heliconia plant. SMF 85062 was found in a tree between two attached bromeliads about 2.5 m above-ground.

Etymology.—This species is named in honor of Dr. Luis Diego Gómez, Costa Rican botanist extraordinary, Director Emeritus of Las Cruces Biological Station and Wilson Botanical Garden, and recently retired as Director of the La Selva Biological Station of the Organization of Tropical Studies, in recognition of his many contributions to tropical biology.

***Bolitoglossa bramei*, new species**
Brame's Web-footed Salamander
Figures 1B, 2, 3B

Bolitoglossa sp. C.—García-París et al., 2000:1641, fig. 3.

Bolitoglossa pesrubra.—Savage, 2002:135, map 6.11 (part).

Bolitoglossa sp. nov. 3.—Wake, 2005:76, fig. 3.2.

Holotype.—MVZ 225893, adult male, Costa Rica, Provincia Puntarenas, trail to Cerro Pando, above Las Tablas, 8°56'N, 82°46'W, 2200 m, 22 May 1994, E. Jockusch and M. García-París.

Paratypes.—Panamá, Provincia Bocas del Toro: KU 116653–54 (two specimens), north slope of Cerro Pando, 2050–2100 m, 4 May 1966, C. W. Myers and T. Quintero; KU 116657, north slope of Cerro Pando, 1920 m, 7 May 1966, C. W. Myers and T. Quintero. Provincia Chiriquí: CH-Ch 1217, Bajo Mono, 4 km NW of Boquete, 8°48'N, 82°28'W, 2012 m, 31 Aug. 1982, R. Ibáñez, F. Crastz, F. Jaramillo, and C. Jaramillo. Costa Rica, Provincia Puntarenas: MVZ 219585, trail up W side of Cerro Pando, above La Casita, ca. 2–3 km SE of Las Tablas, 8°55'12.6"N, 82°43'22.1"W, 2100 m, 12 Aug. 1990, D. Wake and K. Lips.

Diagnosis.—A slender, long-legged species with a long, slender, prehensile tail that has a bright red or red-orange tip. It resembles other members of the *B. subpalmata* group in general morphology. Hands and feet are moderately wide and bear discrete, columnar digits that are slightly expanded distally and have moderate webbing for the genus (Fig. 2). *Bolitoglossa bramei* is distinguished from its somewhat larger close relative *B. gomezi* by its longer legs and many more maxillary teeth. It is distinguished

from both *B. pesrubra* and *B. subpalmata* by its smaller size, more gracile form, somewhat longer limbs, more numerous maxillary teeth, and brighter coloration (tail or tail tip usually reddish), and from *B. gracilis* by its longer legs and larger number of vomerine teeth. It is slightly smaller than *B. subpalmata* and *B. pesrubra*.

Description.—A relatively small, slender species. Standard length (SL) 37.6–39.1 (mean 38.1) in three males, 38.1–41.0 (39.6) in two females. Tails moderately to very long, typically exceed standard length; SL divided by tail length 0.93–1.10 (mean 1.0) in males, 0.89–0.99 (0.94) in females. Head narrow; SL divided by head width 6.1–6.5 (mean 6.3) in males, 5.9–6.2 (6.1) in females. Head relatively well demarcated from an even narrower neck. Snout broadly rounded, not prominent. Nostrils small, nasolabial protuberances poorly developed. Eyes moderately prominent, protrude slightly beyond lateral margins of head and are relatively frontal in orientation. Teeth numerous: premaxillary 3 or 4 (mean 3.7) in males, 6 in each female; maxillary 49–57 (mean 52.7) in males, 52–66 (59.0) in females; vomerine 24–27 (mean 25.3) in males, 24–28 (26.0) in females. Limbs long; limb interval 0–0.5 (mean 0.3) in males, 0–1.0 (0.5) in females. Hands and feet moderately wide with moderate webbing; fewer than two distal-most phalanges of the longest digits free. Toe tips truncate, bear well-developed subterminal pads. Fingers, in order of decreasing length, 3–4–2–1; toes 3–4–2–5–1. Postiliac glands not evident.

Measurements of the holotype (in millimeters).—Head width 6.0; snout to gular fold (head length) 9.1; head depth at posterior angle of jaw 3.1; eyelid width 1.6; eyelid length 3.0; anterior rim of orbit to tip of snout 2.1; horizontal orbit diameter 1.9; interorbital distance between angle of eyes 2.2; interorbital distance between eyelids 3.5; length of groove extending posteriorly from eye 1.5; distance between nuchal groove and gular fold 3.6; snout to forelimb 11.7; distance separating external nares 1.6; snout projection beyond mandible 0.6; snout to posterior angle of vent (standard length) 37.6; snout to anterior angle of vent 34.6; axilla to groin 19.6; number of costal interspaces between appressed limbs 0.5; tail length 34.1; tail width at base 2.2; tail depth at base 2.5; forelimb length (to tip of longest finger) 8.4; hind limb length 9.1; hand width 3.1; foot width 4.0; length of fifth toe 1.0; length of third toe 0.7; distance between vomerine teeth and parasphenoid tooth patch 0.6. Numbers of

teeth: premaxillary 4; maxillary 24–25; vomerine 12–13, arranged in a single row.

Coloration of the holotype in alcohol.—Dorsal surface yellowish, infiltrated with melanic patches. Yellow is more prominent posteriorly along trunk. Tail light yellowish to yellow-orange with scattered patches of punctate melanophores and occasional melanophore networks most prominent laterally. Head dark gray except for patches of dark yellow, which show through on snout and in irregular spots between and behind eyes. Throat region light gray, with irregular small patches and flecks of underlying yellow pigment showing through. Flanks have more continuous melanic network, with melanin-free areas interspersed with darker and very dark areas. Venter light gray overall as a result of mainly punctate melanophores, which leave yellowish gaps. Yellow most prominent in streaks and irregular spots on either side of midventral line. Limbs mainly melanic with subtle patches of yellow showing through, especially near limb bases.

Coloration in life.—Based on the field notes of D. Wake (22 May 1994) for the holotype (Fig. 3B): Ground color a rich dark brown. An irregularly edged dorsal band extends caudally from nuchal region and is brightest on tail. Its color ranges from red-orange, to orange, to tan-orange and includes highlights of bright copper. Tail mainly orange—bright and lively. Laterally, the band has some lively cream-colored streaks and flecks. Anteriorly, discrete black spots on dorsum coalesce on shoulders and head, yielding mottled black and tan-to-orange coloration. Tan patch on otherwise dark snout. Limbs dark, with some bright orange flecks on insertions. Venter generally gray, with some light streaks. Belly blackish, throat paler. Underside of tail orange with some darker mottling.

Based on the field notes of D. Wake (12 August 1990) for MVZ 219585: Lively reddish-brown dorsal stripe is bordered by a fine, bright, cream-colored line that becomes discontinuous on the tail. Trunk dark brown laterally, near stripe, but paler ventrally, with patchy guanophores on the flanks. Head somewhat darker brown; nasolabial protuberances tannish. Slender tail becomes extremely dark caudally before becoming red at tip. Venter mottled, with punctate melanophores overlain by larger, thin, pale guanophores. Pectoral region and throat yellow-green, with some small guanophores and melanophores. Limbs yellowish brown.

Based on the field notes of C. Myers (7 May 1966) for KU 116657: Brownish red dorsally with black head, nape mark, limbs, and flanks. Dorsal

and lateral black areas continuous with black venter; all black areas sparsely speckled with silver. Iris black with a few tiny brown areas.

Color notes for CH-Ch-1217 were recorded by Roberto Ibáñez at the time of collection: Dorsum brown; dorsal surface of tail reddish. Venter same color as dorsum, with white spots. Flanks with scattered white spots; white spots also on legs.

Osteology.—The following account is based on radiographs of KU 116653 and 116657 and digital radiographs of the holotype. Cranial anatomy generalized. A single premaxillary bone bears frontal processes that remain separate for their entire lengths and are not expanded distally. Nasal bones large. Prefrontal bone clearly evident on only one side of one paratype; no prefrontal seen in holotype. No septomaxillary bones. Dorsal fontanelle between paired frontal and parietal bones very small. Paired vomers have long, well-developed preorbital processes. Operculum lacks columella. Transverse processes of second caudosacral and first caudal vertebrae are swept forward and do not overlap. Phalangeal formulae 1–2–3–2 (hand), 1–2–3–3–2 (foot). Terminal phalanges of longest digits moderately to slightly expanded distally. In holotype, three outer fingers and four outer toes have terminal phalanges that are strongly T-shaped. Two phalanges of longest digit free of webbing. No tibial spur. Holotype has 29 caudal vertebrae and a shadow suggests that a 30th is developing.

Habitat and range.—*Bolitoglossa bramei* is known from both Pacific and Atlantic slopes of the southern Cordillera de Talamanca (Fig. 4). Localities range from the vicinity of Cerro Pando on the Costa Rica–Panamá border in the west, to the Pacific slope in Chiriquí Province, Panamá, as far east as the Boquete area, east of Volcán Barú. The species occurs in Tropical Lower Montane Rainforest zone (*sensu* Holdridge, 1967) at elevations between 1900 and 2300 m. It is nocturnal and frequently arboreal; whereas the holotype was found at night on the ground, others were found on low vegetation within a couple meters of the ground. It is a good climber; the tail is prehensile.

Remarks.—DNA sequence data (cytochrome *b* gene) for MVZ 225893 are reported in García-París et al. (2000; *B. sp. C*); GenBank accession AF212066.

Etymology.—The species is named in honor of the late Arden H. Brame, Jr., II, in recognition of his

many contributions to the study of neotropical salamanders. Arden first recognized that specimens of this *Bolitoglossa* from Cerro Pando represented an undescribed species.

DISCUSSION

Both new species described in this paper are members of the *subpalmata* group of *Bolitoglossa*, subgenus *Eladinea* (Parra-Olea et al., 2004). One mitochondrial DNA sample of *B. bramei* has been sequenced (García-París et al., 2000). Corrected divergence distances (K2p) are 0.081–0.085 to *B. gracilis*, 0.062–0.074 to *B. pesrubra*, and 0.080–0.087 to *B. subpalmata*. Some of these values differ slightly from those in García-París et al. (2000) because of transcription errors in that work. Phylogenetic analysis of these data clusters *B. bramei* with *B. pesrubra*, albeit with low bootstrap support. No molecular data are available for *B. gomezi*; we assign this species to the *B. subpalmata* species group on the basis of its morphological similarity to *B. bramei*.

Although Wake et al. (1973) were unable to separate what we have named *B. bramei* from *B. minutula*, these species are not close relatives. Morphological distinctions between them have become more evident after additional experience with both species in the field. Hands and feet of *B. minutula* are smaller and more extensively webbed (Fig. 2). Digits of *B. minutula* are somewhat conical and tapered, whereas those of *B. bramei* are better defined, somewhat columnar with expanded tips, and have very little basal webbing. Furthermore, the hands and feet of *B. bramei* are relatively larger than those of *B. minutula*. As Wake et al. (1973) suggested, *B. minutula* is a relative of *B. epimela* and it has since been assigned to the *B. epimela* species group (Parra-Olea et al., 2004), whereas *B. bramei* is allied to *B. pesrubra* and *B. subpalmata* (García-París et al., 2000).

While the ecological significance of subtle differences in foot morphology among species of the border region is not well understood, the combination of hand and foot morphology plus body size is the easiest way to distinguish co-occurring species (Fig. 2). Terminal phalanges of the longest digits are expanded in most of the species, but especially in *B. marmorea*. The largest (*B. marmorea*) and smallest (*B. minutula*) species have the most interdigital webbing, but digits of the former species are better defined than in the latter. The least webbing is found in *B. anthracina*, and *B. bramei* has more webbing than *B. gomezi*. In both *B. minutula* and *B. bramei*, the penultimate phalanges of the longest digits are shorter than the terminal phalanges.

Since Wake et al. (1973) first reported three species of *Bolitoglossa* from Cerro Pando and vicinity, five additional salamander species—*Oedipina grandis*, *B. anthracina*, *B. bramei*, *B. gomezi*, and *B. sombra*—have been described from this limited area on the Costa Rica–Panamá border. Although the Las Cruces area of Costa Rica, along the Fila Costeña, is only about 35 km to the southwest, terrain descends to about 800 m in the intervening region and there is considerable faunal change. At Las Cruces, *B. gomezi* co-occurs only with *O. pacificensis* and *O. savagei*. We have been hesitant to assign three salamanders (UMMZ 173548, MVUP 929, and SMF 85062) to *B. gomezi* because they occur at substantially higher elevations along the south slope of the Cordillera de Talamanca–Barú north and east of the Coto–Brus Valley. However, the Fila Costeña actually is a western spur of the Cordillera de Talamanca–Barú and is connected to it along the Costa Rica–Panamá border a few kilometers east of Las Cruces. Based on morphological similarities, we think it is best to assign them to a single taxon for the present.

Wake et al. (1973) decided not to describe *B. bramei* in part because of doubts that so many salamander species could occur in broad sympatry in the same region. The fact that experienced salamander systematists were unwilling to describe a species now known to be genetically well differentiated is an indication of the difficulties inherent in attempting to discriminate species represented by only a few specimens. Even though this border region is one of exceptional diversity—22 species were identified by Wake (2005)—we know of at least two unnamed species (see below) and expect additional species to be discovered when the isolated high peaks of the Talamancan range in this region are thoroughly explored.

Previous authors have signaled the presence of several unnamed taxa from the Costa Rica–Panamá border region and have given them different labels. *Bolitoglossa* sp. 2 of Savage and Villa (1986) is *B. gomezi*, as is *B. sp. nov. 6* of Wake (2005). García-París et al. (2000) designated *B. sp. C*, which we herein name *B. bramei*, and Wake's *B. sp. nov. 3* corresponds to that species as well. Wake's *sp. nov. 1* is *B. magnifica*, and *B. sp. nov. 2* of Parra-Olea et al. (2004) is *B. sombra*. Several unnamed forms remain, including Wake's *B. sp. nov. 4* (which may represent more than a single species) and *B. sp. nov. 5*, which occurs at high elevations along the crest of the Talamancan range. Both taxa are currently under study. There also are additional unnamed species in the lowlands.

Bolitoglossa anthracina is one of four species that occur on both sides of the Continental Divide. *Bolitoglossa colonnea* and *B. robusta* are relatively wide-ranging forms that occur over much of Costa Rica and western Panamá, whereas *B. anthracina* and *B. bramei* are known only from the border region. Until now, *B. anthracina* has been known from just three specimens—two from the Atlantic slopes of the Talamanca range (1450–1700 m) and a third from the Presa Fortuna area (Brame et al., 2001). Here we report a fourth specimen, AMNH A-94807, collected by C. W. Myers from Presa Fortuna on 22 February 1976, prior to construction of a dam at that locality (Myers and Duellman, 1982; Savage and Myers, 2002; Fig. 3D). According to Myers's field notes, the adult male salamander was uniform black above, grading imperceptibly to dark blackish brown on the head. The underside of the head was grayish brown, grading to grayish black on the rest of the ventral surfaces. There was no clear demarcation between the grayish black venter and the black sides. The iris was bright bronze. The salamander was found inside a bromeliad about 18 m aboveground, which also harbored a lizard (*Anadia ocellata*). Assignment of this specimen to *B. anthracina* makes it clear that this is a highly arboreal species with a long, whip-like tail, which most likely is prehensile as well. Typically, tails of *Bolitoglossa* are at least modestly prehensile. The tail in this specimen is much longer than the body (78.2 mm vs. 54.0 mm SL). The tail of the holotype was lost prior to capture.

There are several literature references to *Bolitoglossa subpalmata* from Panamá, but the species as presently understood does not occur anywhere near that country. The species as originally known was subdivided recently into a western *B. subpalmata*, which is restricted to the Cordillera Central and adjoining uplands in central and western Costa Rica, and *B. pesrubra* of the Cordillera de Talamanca and some adjoining uplands (García-París et al., 2000). Localities nearest the Panamanian border are some sites on and near Chirripó Grande (based on records in University of Costa Rica collections). Slevin (1946) and Walters (1953) report *B. subpalmata* from Volcán Chiriquí (Barú), but these specimens are known now as *B. marmorea* (Tanner and Brame, 1961). Brame (1965) referred two specimens from lower elevations on the same volcano to *B. subpalmata* (as *Magnadigita subpalmata*), but one is a juvenile and the other is too badly preserved to be identified to species. Neither should be regarded as *B. subpalmata*; they are unidentified *Bolitoglossa*.

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