

A Solution to the Large Black Salamander Problem (Genus *Bolitoglossa*) in Costa Rica and Panamá

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Several populations of large (adult standard length, 43–134 mm) black salamanders of the widespread neotropical genus *Bolitoglossa* (Plethodontidae) are known from the cordilleras of western Panamá and Costa Rica. These populations constitute at least seven species, including two recently described (*B. anthracina*, *B. copia*), one described long ago that remains poorly known (*B. nigrescens*), and three described herein as new. The long-recognized, wide-ranging *B. robusta*, which is distinguished by a pale, pigmented ring around the tail base and a unique combination of maxillary and vomerine tooth counts, may occur sympatrically with four of the other taxa. Differences in head and body form, adult size, cranial osteology, and maxillary and vomerine tooth counts separate all recognized taxa from one another. These results confirm and indeed increase the exceedingly high diversity of salamander species known from the Cordillera Talamanca-Barú of Costa Rica and Panamá, diversity that now rivals that found anywhere else in the tropics.

En las cordilleras de oeste de Panamá y de Costa Rica, se conocen varias poblaciones de salamandras de color negro y de tamaño grande (longitud estandar del adulto, 43–134 mm). Estas salamandras son parte de *Bolitoglossa* (Plethodontidae), un género de amplia distribución neotropical. Estas poblaciones se incluyen en al menos siete especies, una descrita recientemente (*B. anthracina*, *B. copia*), una descrita desde hace tiempo y que permanece poco conocida (*B. nigrescens*) y otras tres nuevas que se describen aquí. La especie *B. robusta* conocida desde hace tiempo y de amplia distribución se distingue por la presencia de un anillo de color claro alrededor de la base de la cola y una combinación exclusiva de número de dientes maxilares y del vómer. Esta especie puede encontrarse en simpatria con cuatro de las otras especies. Todos los taxa reconocidos se diferencian entre sí por caracteres osteología del cráneo, así como por la forma de la cabeza y del cuerpo, tamaño de adulto, y número de dientes maxilares y vomerinos. Estos resultados confirman y además incrementan la extremadamente alta diversidad de especies de salamandras conocidas en la Cordillera Talamanca-Barú de Costa Rica y Panamá, una diversidad que no es equiparable con la de ningún otro lugar de los trópicos.

THE best-known species of large black *Bolitoglossa* is *B. robusta* (Cope, 1894). It also is the most widely distributed species, occurring from northern Costa Rica (Volcán Cacao, Prov. Guanacaste) to western Panamá (near the Fortuna Dam, Prov. Chiriquí) at elevations usually below 1800 m. It is one of the two or three largest species of neotropical salamanders; adult standard length frequently exceeds 100 mm. The typical coloration is solid black with a distinct, pale, pigmented ring around the tail base. Some specimens, however, have only a faint, lightly pigmented basal tail ring whereas others, especially those from Panamá, have subdued or even prominent white dorsal spotting. Preliminary biochemical analyses based on limited samples show that populations of *B. robusta* in Costa Rica are only slightly differentiated genetically from those in Panamá, suggesting a single taxon; maximum pairwise Nei genetic

distances (D_N ; Nei, 1972) are less than 0.09 (Good and Wake, unpubl. data).

Bolitoglossa nigrescens was described from the high Cordillera de Talamanca in central Costa Rica (Taylor, 1949; Fig. 1). Because its description was based on a single specimen, an inconspicuous black juvenile sporting a small regenerating tail, this species was not fully characterized, and virtually all large black specimens that did not conform to the “stereotype” of *B. robusta* were identified as *B. nigrescens*. This includes specimens from the slopes of Volcán de Chiriquí (Barú), western Panamá (e.g., Hanken and Wake, 1982), and others from southwestern Costa Rica (Lips, 1993), but the species has never been reported again from anywhere near the type locality. Based on a small number of museum specimens, the elevational range of the species in the Cordillera de Talamanca, Costa Rica, was plotted between 1300 and 2700 m

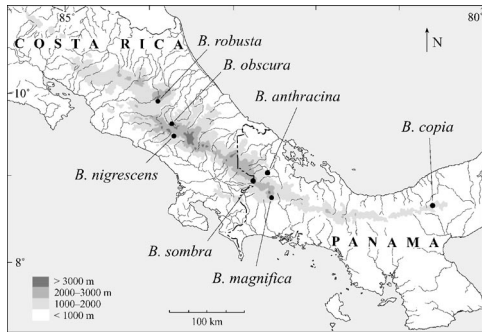


Fig. 1. Type localities of the seven species of large black *Bolitoglossa* found in Costa Rica and Panamá. *Bolitoglossa copia* and *B. obscura* are known only from their respective type localities.

(Wake, 1987), and 1650 and 3000 m (García-París et al., 2000). We demonstrate below that several morphologically discrete and geographically distinct units can be recognized from among specimens that were provisionally assigned to *B. nigrescens*. We choose to recognize these units as separate species, even though samples for all of them are small, because the current taxonomy is unsatisfactory and because it substantially underestimates diversity within the group.

MATERIALS AND METHODS

Measurements were made using digital or dial calipers or with an ocular micrometer in a dissecting microscope; 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, 3.5). Whole-mount skeletal preparations were stained for bone and cartilage using alizarin red S and Alcian blue 8GX, respectively (Klymkowsky and Hanken, 1991), or just alizarin red S. Counts of presacral (trunk) vertebrae do not include the first vertebra (atlas). Tooth counts are based on cleared and stained specimens when available. Numbers of maxillary and vomerine teeth in each holotype are provided for right and left sides; these counts are summed for other individuals. Geographic coordinates of collecting localities were estimated from topographic maps. Institutional abbreviations are as listed in Leviton et al. (1985), except for MVUP (Museo de Vertebrados, Universidad de Panamá).

DESCRIPTIONS OF NEW SPECIES

Bolitoglossa magnifica, new species Magnificent Web-Footed Salamander Figure 2

Bolitoglossa nigrescens: Hanken and Wake (1982): 275.

Holotype.—MVZ 128619, adult female, Panamá, from the southeast slope of Volcán Chiriquí, 7.8 km W and 2.5 km N (airline) of Boquete, Prov. Chiriquí, 8°47.6'N, 82°30.05'W, 2400 m elevation, J. F. Lynch and J. Hanken, 9 August 1975.

Paratypes.—MVZ 128620–30 (11 specimens; MVZ 128622 is cleared and stained), same data as the holotype except for MVZ 128630, which was collected 8.0 km W and 2.5 km N (by air) of Boquete, 2450 m elevation.

Referred specimens.—All from Panamá: Prov. Chiriquí: ANSP 22571, lower slopes of Volcán Barú, 1250 m elevation; FMNH 121217, Cerro Punta, 1982 m elevation; AMNH 69624, 3.2 km NW of Boquete.

Diagnosis.—A large black salamander with whitish flecks on the dorsum and larger whitish patches on the dorsal surface of the tail. It is one of the largest species in the genus; some specimens exceed 100 mm SL. The head is relatively narrow, especially in large specimens (females). The species is distinguished from other large black *Bolitoglossa* by the following combinations of traits (Tables 1, 2; Figs. 3, 4): from *B. robusta* by lacking a cream-colored ring about the base of the tail, in averaging fewer maxillary teeth, and by the very long nasal bones; from *B. nigrescens* by having a more slender trunk (SL averages 9.6 times the width across the shoulders in adult female *B. magnifica*, vs. 7.8 in adult female *B. nigrescens*), relatively shorter limbs, and on average fewer maxillary and vomerine teeth; from *B. sombra* by having a larger adult size and fewer maxillary and vomerine teeth; and from *B. obscura* by having many more maxillary and vomerine teeth. Newly recognized *B. anthracina* (Brame et al., 2001) has more maxillary and vomerine teeth than *B. magnifica*, whereas recently described *B. copia* has more extensive digital webbing and white pigment along the jaws and throat (Wake et al., 2004).

Description.—This very large species displays strong sexual dimorphism: mean adult SL 58.6 mm (range 50.9–69.6) in three males and 90.1 (61.5–104.0) in six females. Head broader in males—SL 6.2 times head width (6.1–6.3)—than

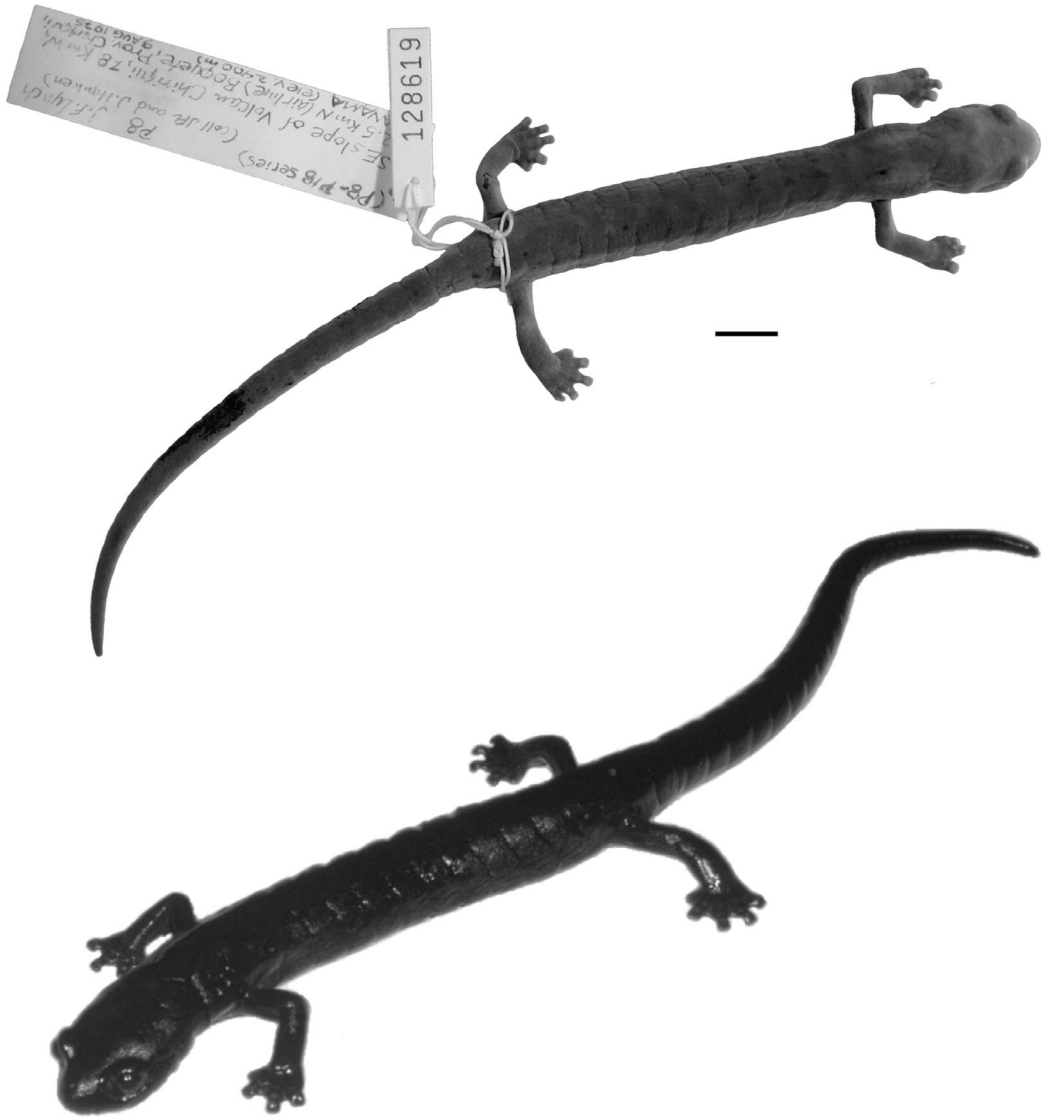


Fig. 2. Above: holotype of *Bolitoglossa magnifica* (MVZ 128619); scale bar, 1 cm. Below: live *B. magnifica* from the type locality (specimen number unavailable).

in females (6.9; 6.1–7.2). Snout broadly rounded to somewhat truncated. Nostrils small; nasolabial protuberances inconspicuous in females, poorly developed in males. Eyes relatively small, do not extend laterally beyond jaw margins in dorsal view. Skin on dorsum of head rugose. Premaxillary teeth 2.3 (2–3) in males, 3.5 (2–5) in females; in males, teeth protrude anteriorly through upper lip but are small. Maxillary teeth 29.0 (25–35) in males, 45.7 (25–58) in females. Vomerine teeth 19.3 (17–21) in males, 28.5 (26–32) in females. Limbs long, especially in males; limb interval 1.8 (1.5–2.5) in males and 3.1 (2.5–3.5) in females. Hands and

feet large, well developed, with stout, bluntly pointed digital tips. Fingers, in order of decreasing length, 3–2–4–1; toes 3–4–2–5–1. Two or more phalanges of longest digits free of webbing in adults; webbing more extensive in juveniles. Subterminal pads strongly developed on all digits. Tail short, never exceeds SL; standard length/tail length ratio 1.17 in both sexes (range 1.09–1.32 males, 1.02–1.34 females). Mental gland in adult males inconspicuous, oval, broader than long. Gland lightly pigmented, only residual dermal melanophores scattered around individual pores. Postiliac gland visible as large pale spot.

TABLE 1. DIAGNOSTIC FEATURES OF SEVEN SPECIES OF LARGE BLACK *Bolitoglossa* FROM TALAMANCA-BARÚ: ADULT MALES.

	<i>B. anthracina</i> ¹	<i>B. copia</i> ²	<i>B. magnifica</i>	<i>B. nigrescens</i>	<i>B. obscura</i>	<i>B. robusta</i>	<i>B. sombra</i>
Sample size	1	1	3	—	—	10	7
Tail ring	no	no	no	—	—	yes	no
Standard length (SL), in mm	46.0	81.5	50.9–69.6	—	—	44.6–113.9	44.1–61.5
mean	46.0	81.5	58.6	—	—	83.4	52.7
Maxillary teeth per side of jaw	31–35	40–39	12–18	—	—	15–51	10–28
mean (both sides)	66	79	29.0	—	—	65.5	34.3
Vomerine teeth per side	12–12	19–18	7–11	—	—	9–20	11–23
mean (both sides)	24	37	19.3	—	—	28.9	32.9
Limb interval	1.5	2.5	1.5–2.5	—	—	1.5–4.0	0.5–2.0
mean	1.5	2.5	1.8	—	—	3.0	1.5
SL/Head width	6.3	6.2	6.1–6.3	—	—	5.7–6.7	5.5–6.4
mean	6.3	6.2	6.2	—	—	6.2	5.9
SL/Shoulder width	—	11.5	8.7–8.9	—	—	7.0–8.6	8.4–10.2
mean	—	11.5	8.8	—	—	8.0	9.1
SL/Tail length	0.79	0.98	1.09–1.32	—	—	0.90–1.50	1.11–1.46
mean	0.79	0.98	1.17	—	—	1.09	1.27

¹ Brame et al. (2001).² Wake et al. (2004).

In preservative, overall coloration black. Widely scattered, obscure, pale patches near tail base and on tail. Few pale flecks scattered on flanks and belly. Iris blackish-brown.

Measurements of the holotype (in millimeters).—Head width 13.8; snout to gular fold (head length) 20.8; head depth at posterior angle of jaw 8.4; eyelid width 3.0; eyelid length 5.1; anterior rim of orbit to tip of snout 5.3; horizontal orbit diameter 3.6; interorbital distance between angle of eyes 7.5; interorbital distance be-

tween eyelids 5.0; length of groove extending posteriorly from eye 3.7; distance between nuchal groove and gular fold 7.3; snout to forelimb 25.3; distance separating external nares 5.4; snout projection beyond mandible 1.3; snout to posterior angle of vent (standard length) 99.9; snout to anterior angle of vent 91.9; axilla to groin 55.6; number of costal interspaces between appressed limbs 3; tail length 84.9; tail width at base 6.3; tail depth at base 7.4; forelimb length (to tip of longest finger) 19.7; hind limb length 23.1; hand width 7.4;

TABLE 2. DIAGNOSTIC FEATURES OF SEVEN SPECIES OF LARGE BLACK *Bolitoglossa* FROM TALAMANCA-BARÚ: ADULT FEMALES.

	<i>B. anthracina</i> ¹	<i>B. copia</i>	<i>B. magnifica</i>	<i>B. nigrescens</i>	<i>B. obscura</i>	<i>B. robusta</i>	<i>B. sombra</i>
Sample size	2	—	6	3	1	8	2
Tail ring	no	—	no	no	no	yes	no
Standard length (SL), in mm	57.5–70.8	—	61.5–104.0	58.1–94.1	87.7	64.9–133.5	69.9–82.7
mean	64.2	—	90.1	74.4	87.7	105.1	76.3
Maxillary teeth per side of jaw	39–46	—	12–31	18–37	17–18	29–52	27–39
mean (both sides)	85.0	—	45.7	53.7	35	84.6	68.0
Vomerine teeth per side	15–21	—	11–16	12–31	9–10	12–23	24–28
mean (both sides)	34.5	—	28.5	42.7	19	33.9	50.5
Limb interval	1–3	—	2.5–3.5	2.5–4.0	2.5	3.0–4.0	1.5–2.5
mean	1.5	—	3.1	3.2	2.5	3.3	2.0
SL/Head width	7.0	—	6.1–7.2	5.9–6.5	6.7	4.0–7.0	6.5–6.7
mean	7.0	—	6.9	6.2	6.7	6.1	6.6
SL/Shoulder width	8.7	—	8.9–10.6	7.1–8.6	8.4	7.2–10.5	8.0–8.3
mean	8.7	—	9.6	7.8	8.4	8.8	8.2
SL/Tail length	0.99	—	1.02–1.34	1.23–1.26	1.16	0.91–1.27	1.08–1.27
mean	0.99	—	1.17	1.25	1.16	1.01	1.17

¹ Brame et al. (2001).

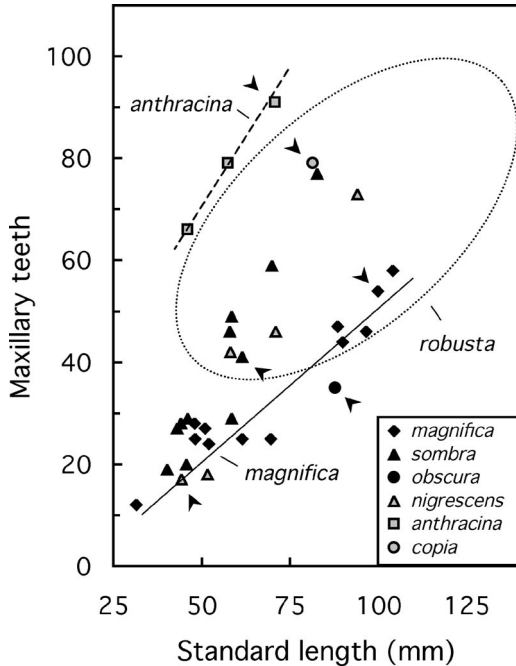


Fig. 3. Maxillary tooth counts for large black *Bolitoglossa*. Total number of teeth is plotted against standard length (SL) for individual specimens of six species (legend; arrowheads point to holotypes). Ellipse encloses all values for *B. robusta*, which are not plotted individually. Linear regression lines are depicted for *B. magnifica* (solid) and *B. anthracina* (dashed).

foot width 8.8; length of fifth toe 1.4; length of third toe 3.0; distance between vomerine teeth and posterior vomerine patch 1.1. Numbers of teeth: premaxillary 5, maxillary 27–27, vomerine 16–16.

Coloration of holotype (in alcohol).—Ground color uniformly black, dorsally and ventrally (Fig. 2A). Few obscure, pale patches ventrolaterally on trunk. Gular region and jaw margins slightly paler, and soles considerably paler, than ventral ground color.

Coloration in life.—Based on field notes of the type series by J. Hanken and J. F. Lynch (10 and 9 August 1975, respectively; Fig. 2B): Large individuals (up to 10 cm SL) virtually entirely black. Some with faint, diffuse pale markings on sides of tail. Smaller individuals (4–5 cm) black or charcoal gray with fine white speckling all over and some more conspicuous (but still faint) white or silver blotches on tail.

Osteology.—The following account is based on MVZ 128622 (Fig. 5). Skull well articulated. Premaxillary bone with broad dental process,

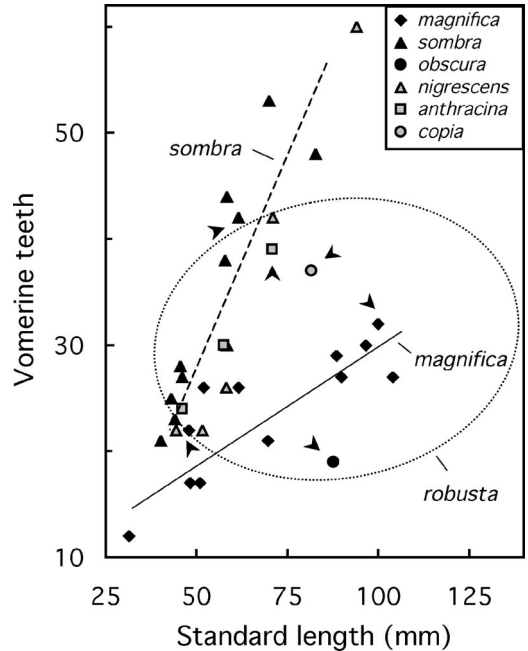


Fig. 4. Vomerine tooth counts for large black *Bolitoglossa*. Total number of teeth is plotted against standard length (SL) for individual specimens of six species (legend; arrowheads point to holotypes). Ellipse encloses all values for *B. robusta*, which are not plotted individually. Linear regression lines are depicted for *B. magnifica* (solid) and *B. sombra* (dashed).

which is firmly articulated to each maxillary bone. Slender frontal processes widely separated at origin on dental process and remain separated as they ascend posteriorly and embrace large internasal fontanelle. They terminate at anterior margin of orbit, where they expand slightly and form small sinuous processes that interlock with similar processes from anterior part of frontal bone. Large nasal bones very long and narrow; extend posteriorly beyond ends of frontal processes of premaxillary bones, nearly to level of orbitosphenoids. Posterior margin of each bone deeply incised. Extra processes from medial margin overlap frontal process of premaxilla near its midpoint. Laterally, each nasal overlapped slightly by anterior and dorsal ascending process of maxilla. Relatively weak maxillary bones extend caudad and end at level approximately three-fourths of distance through orbit; posterior 10–15% of each bone lacks teeth. In addition to its strong articulation with premaxilla and weak articulation with nasal, palatal portion of maxilla is well articulated with body of vomer. Ascending process of maxilla separated from frontal bone by very large distance. Right prefrontal is tiny spicule, about

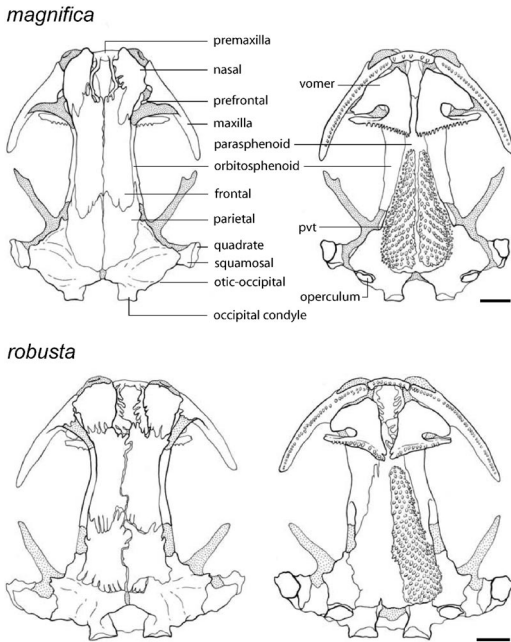


Fig. 5. Adult skulls of *Bolitoglossa magnifica* and *B. robusta* depicted in dorsal (left) and ventral views. Illustrations are drawn from cleared and stained whole mounts (*B. magnifica*, MVZ 128622; *B. robusta*, MVZ 183660); cartilage is stippled, bone is unshaded. The right posterior vomerine teeth (pvt) were removed earlier from the specimen of *B. robusta*. Scale bars, 2 mm.

half as long as diameter of external naris. It articulates with posterodorsal portion of ascending process of maxilla but fails to contact nasal and is widely separated from frontal bone. Left prefrontal bone and both septomaxillary bones absent. Premaxillary and maxillary teeth small, weak, and barely extend below ventral limit of each bone.

Dorsal surface of skull relatively smooth, lacks major ridges or crests. Frontoparietal fontanelle absent. Frontal bones stout and broad, extend anteriorly to midpoint of nasals. They are well articulated to one another, to frontal processes of premaxilla, to nasals, to underlying orbitosphenoids, and to posterior parietals. Parietal bones stout and well articulated to orbitosphenoids, otic-occipitals, and frontals; small lateral pad overlies ascending process of palatoquadrate cartilage. Posterolateral border of each parietal contributes to low ridge on otic-occipital, which overlies anterior semicircular canal. Ridge continues onto stout otic-occipital and curves in the direction of squamosal, which participates in lateral-most portion of this complex structure. Squamosal nearly vertical; articulates firmly with quadrate and has small additional

ossification that extends ventrally over surface of quadrate. Quadrate massive, lacks distinctive processes. Small region of ossification in quadrate-maxillary ligament on left side. Operculum simple, round disk; lacks stylus. Occipital condyles short and stout.

Paired vomers large and well developed, intervomer fontanelle narrow; bones closely approach one another both in front of and especially behind fontanelle. Extensive articulation between anterolateral borders of vomer body and broad palatal portion of maxilla, but no articulation with premaxilla. Preorbital process of vomer long and very stout, extends laterally beyond lateral margin of body of vomer and approaches maxilla. Posterior parts of vomer articulate broadly with anterior extension of parasphenoid on its ventral surface. More than 100 articulated teeth in each broad posterior vomerine patch.

Mandible stout; paired dentary bones tightly articulated anteriorly. Prearticular bone large and stout, but muscular process relatively low. Hyobranchial apparatus cartilaginous. Cornua long, more than one-third length of basibranchial. First ceratobranchial extremely slender; second ceratobranchial short and stout. Ceratohyal attached to posterior process of palatoquadrate cartilage by very short, stout ligament. Elongate epibranchials extend posterior to insertion of forelimbs, nearly to caudal end of third trunk vertebra. Urohyal and lingual cartilages absent.

Vertebral column with 1 atlas, 14 trunk, 1 sacral, 2 caudosacral, and 30 caudal vertebrae. Atlas fully ossified. Diapophyses and parapophyses well separated from each other on all vertebrae. Last trunk vertebra lacks ribs. Transverse processes present on all but last two caudal vertebrae; they arise near extreme anterior margin of each vertebra and extend anterolaterally. Those of first caudal vertebra extend well anterior to rest of vertebra; ends are broad and blunt. Well-developed keel on hemal arch of all but last vertebrae, and no keel on hemal arch of first vertebra.

Limbs well developed. Humerus short and stout. Carpal morphology typical of *Bolitoglossa*, with eight separate cartilages and very large distal carpal 4. Phalangeal formula (hand) 1-2-3-2. Terminal phalanges of digits 2-4 expanded and flat distally. Femur stout; no tibial spur. Eight cartilaginous tarsal elements; distal tarsals 4 and 5 form single, large element. Phalangeal formula (foot) 1-2-3-3-2. Terminal phalanges of digits 2-5 expanded, as in hand.

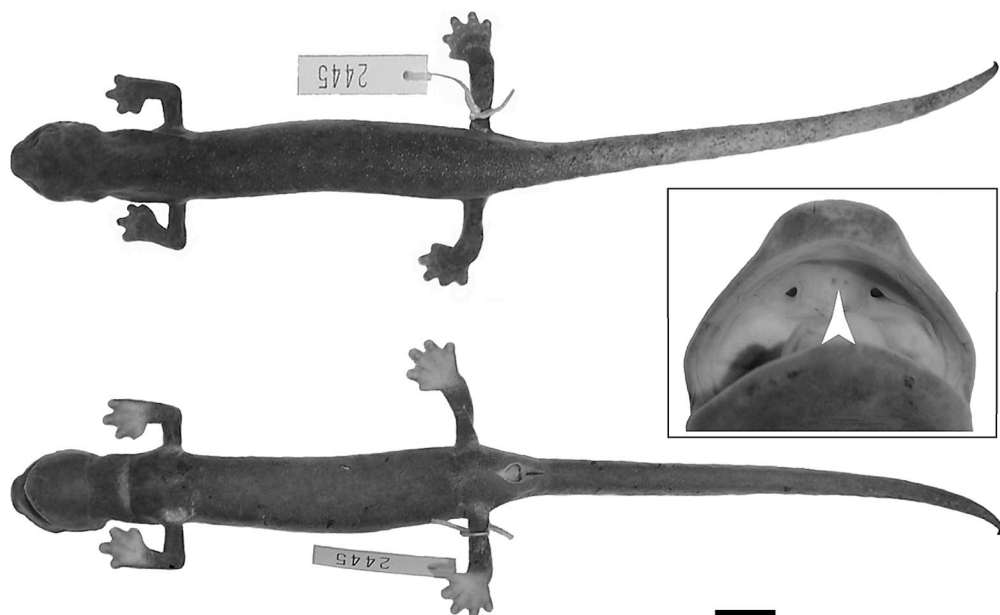


Fig. 6. Holotype of *Bolitoglossa obscura* (UCR 2445), an adult female from Parque Nacional Tapantí, Prov. Cartago, Costa Rica. Dorsal (above) and ventral views; scale bar, 1 cm. Inset: close-up of head in ventral view; arrowhead points to the location of glandular openings in the roof of the mouth.

Habitat and range.—The species is known from five localities on the Pacific slopes of the southern Cordillera de Talamanca-Barú Massif in southwestern Panamá, between Cerro Punta and Boquete, Prov. Chiriquí (Fig. 1). These localities lie within the Tropical Premontane Rainforest and Tropical Lower Montane Rainforest zones (Holdridge, 1967). Elevations range from 1250 to 2450 m. The entire type series was collected in oak forest with abundant moss and small bromeliads in the forest canopy. Salamanders were collected under logs and rough-hewn planks or inside rotting stumps. One was found under a small rock.

Remarks.—Pending additional data that provide insight into its phylogenetic relationships, we assign *B. magnifica* to the *B. (Eladinea) schizodactyla* species group, along with other big black *Bolitoglossa* from Costa Rica and Panamá (Parr-Olea et al., 2004).

Etymology.—The name derives from the Latin word *magnus*, or great, and in the adjectival form *magnifica*, or splendid, in recognition of the beauty and extraordinarily large adult body size of this species, relative to nearly all other neotropical salamanders.

***Bolitoglossa obscura*, new species**

Tapantí Giant Salamander

Figure 6

Holotype.—UCR 2445, adult female, Costa Rica, Prov. Cartago, 8 km S of Tapantí, Parque Nacional Tapantí, from Quebrada Valverde, 9°43'18"N, 83°46'48"W, 1555 m elevation, D. C. Robinson, 18 January 1969.

Paratypes.—None.

Diagnosis.—This species of *Bolitoglossa* is distinguished from most other salamanders in Talamanca Central America by its large adult size (87.7 mm SL) and uniformly dark coloration. It is distinguished from all other large black *Bolitoglossa* by having many fewer and smaller maxillary and vomerine teeth, and by the following additional traits (Table 2; Fig. 3): from *B. robusta* by lacking a distinctive cream-colored ring at the base of the tail; from adult *B. nigrescens* in being somewhat more slender and having slightly more elongate limbs; from *B. magnifica* by being somewhat more robust; from *B. anthracina* by having stouter limbs bearing shorter and more robust digits; and from *B. copia* in having less interdigital webbing and in lacking white coloration on the jaw region and throat.

Description.—Known only from holotype, an adult female. Body robust. Head short and moderately wide; SL 6.7 times head width. Snout broad, bluntly truncated. Nostrils small; nasolabial protuberances modestly developed. Eyes moderate in size, do not protrude beyond jaw margins in dorsal view. Discrete pair of glandular openings in roof of mouth between internal nares (Fig. 6). Relatively few, very small teeth; premaxillary and maxillary teeth barely protrude from the gums. Limbs short and stout; limb interval 2.5. Hands and feet large, well developed, with stout, bluntly pointed digital tips. Webbing relatively well developed; only distal-most 1–1/2 phalanges of longest digits free. Fingers, in order of decreasing length, 3–4–2–1; toes 3–4–2–5–1. Subterminal pads well developed on all digits. Tail short, less than SL; standard length/tail length ratio 1.16. Large pale postiliac gland.

Measurements of the holotype (in millimeters).—Head width 13.1; snout to gular fold (head length) 19.9; head depth at posterior angle of jaw 4.8; eyelid width 2.9; eyelid length 5.6; anterior rim of orbit to tip of snout 4.8; horizontal orbit diameter 3.8; interorbital distance between angle of eyes 6.3; interorbital distance between eyelids 3.6; distance between nuchal groove and gular fold 6.1; snout to forelimb 25.4; distance separating external nares 4.4; snout projection beyond mandible 0.8; snout to posterior angle of vent (standard length) 87.7; snout to anterior angle of vent 81.8; axilla to groin 47.8; number of costal interspaces between appressed limbs 2.5; tail length 75.6; tail width at base 5.1; tail depth at base 6.7; forelimb length (to tip of longest toe) 19.3; hind limb length 20.3; hand width 7.4; foot width 9.6; length of fifth toe 1.2; length of third toe 2.7; distance between vomerine teeth and posterior vomerine patch 0.9. Numbers of teeth: premaxillary 3, maxillary 17–18, vomerine 9–10.

Coloration of holotype (in alcohol).—Dorsal and ventral coloration nearly uniform dark-gray to black (Fig. 6). Irregular white patches on snout, around nostrils, and in front of eyes; small obscure, whitish markings on eyelids and in temporal region. Subocular groove with unpigmented line. Paler highlights on trunk near limb insertions and along gular fold; gular region paler than adjacent regions. Wrist, ankle, and knuckles paler dorsally; palms and soles unpigmented. Many tiny cream-yellow glands cover dorsum. Glands distended with secretion, which lightens otherwise dark ground color. Tail with creamy, yellow mucus dorsally.

Osteology.—The following account is based on a radiograph of the holotype. There is little of the extraneous bony growth of the skull that is seen in both *B. magnifica* and *B. robusta*. Prefrontal bones very distinct. Internasal fontanelle very large. Vomers separated anteriorly by very broad intervomer fontanelle but approach one another posteriorly. Maxillary lacks teeth along about 40% of its length. Vomerine teeth extend only to base of preorbital process of vomer. Premaxillary, maxillary, and vomerine teeth very small. Phalangeal formulae 1–2–3–2 (hand) and 1–2–3–3–2 (foot). Tip of each terminal phalange expanded to same width as base.

Habitat and range.—*Bolitoglossa obscura* is known only from the type locality, which is located inside the Parque Nacional Tapantí, Prov. Cartago, Costa Rica (Fig. 1). This area lies in the Tropical Premontane Rainforest zone (Holdridge, 1967).

Remarks.—At the time of collection, the holotype was depositing a clutch of 31 eggs. The specimen (and eggs) were preserved soon thereafter, which has left the vent widely spread. Each egg measures approximately 7 mm in diameter. (These eggs are assigned the same catalog number as the holotype). *Bolitoglossa obscura* occurs in sympatry with two tiny (SL < 35 mm) moss-mat-inhabiting species of plethodontid salamanders, *B. diminuta* and *Nototriton picadoi*. It also may be sympatric with *B. robusta*, *B. gracilis*, and *N. tapantí*, three other species known from slightly lower elevations in the Tapantí area (Wake, 1987; Good and Wake, 1993; see Discussion). Pending additional data that provide insight into its phylogenetic relationships, we assign *B. magnifica* to the *B. (Eladinea) schizodactyla* species group, along with other big black *Bolitoglossa* from Costa Rica and Panamá (Parra-Olea et al., 2004).

Etymology.—The species name is derived from the Latin adjective *obscura*, meaning dusky or unclear, in recognition of both the salamander's dark coloration and our initial confusion of it with other species of large black *Bolitoglossa*.

***Bolitoglossa sombra*, new species**
Shadowy Web-Footed Salamander
Figure 7

Bolitoglossa nigrescens. Lips (1993):107.

Holotype.—MVZ 225872, adult male, Costa Rica, Prov. Puntarenas, from aqueduct trail, along Río Cotón, below Las Tablas, 8°56.6'N,

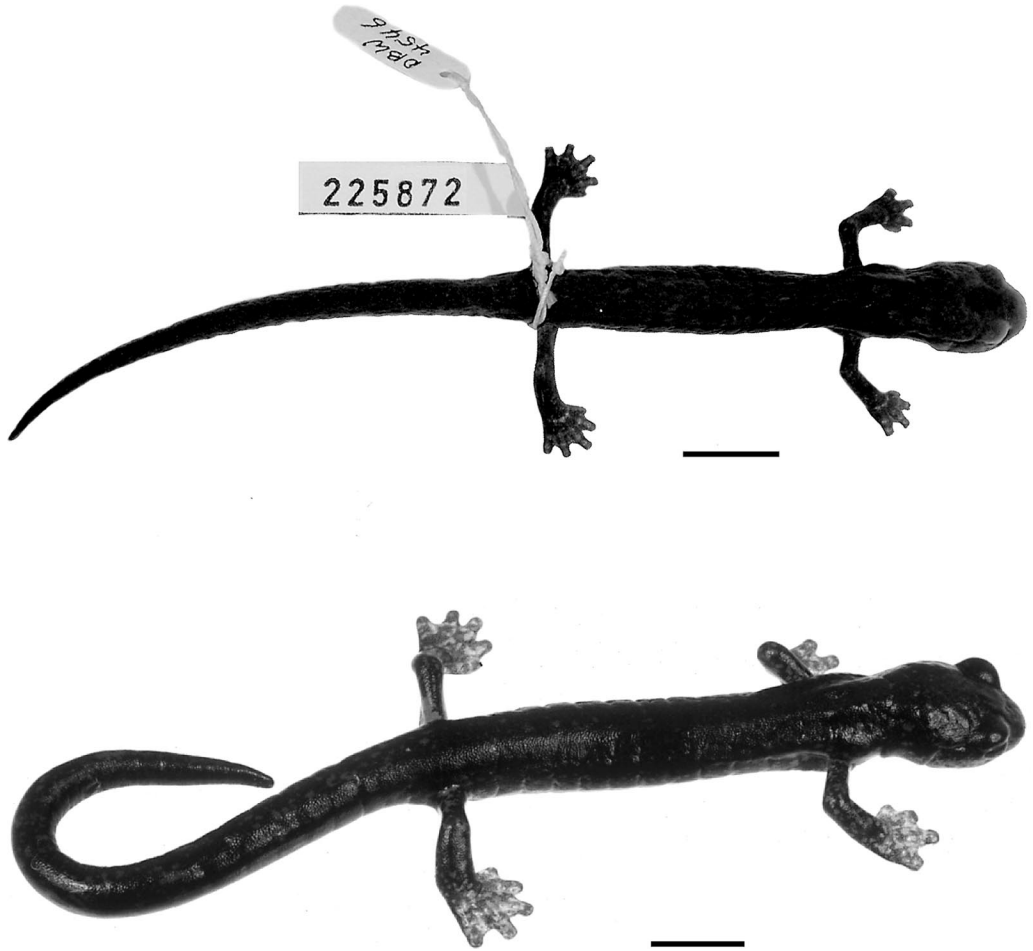


Fig. 7. Above: holotype of *Bolitoglossa sombra* (MVZ 225872), an adult male from Las Tablas, Prov. Puntarenas, Costa Rica. Below: holotype in life. Scale bars, 1 cm.

82°45.0'W, 1760 m elevation, M. García-París, E. Jockusch, E. Meyer, and D. Wake, 20 May 1994.

Paratypes.—All from Costa Rica: Prov. Puntarenas: MVZ 225871, 225873–78 (six specimens), same locality as the holotype; UCR 8030, Las Tablas, Coto Brus, 8°56.4'N, 82°45.1'W, ca. 1800 m elevation, D. C. Robinson, 13 September 1981; LACM 146321, between Agua Caliente and Valle de Silencio, just south of Cerro Frantzius, ca. 9°02.7'N, 82°55.7'W, 1800–2000 m elevation, C. Guyer and K. R. Lips, 15 July 1990; LACM 146322, Las Tablas, ca. 1800 m elevation, C. Hartmann and K. Lips, 18 October 1992.

Referred specimens.—Costa Rica: Prov. Puntarenas: UCR 8212, Las Tablas, ca. 1800 m elevation; UCR 10720–21 (two specimens), south slope of Cerro Frantzius, 9.5 km NNW of Agua Caliente, 2200–2300 m elevation; KU 100603,

Zeledón Place (= Las Tablas), 1900–2000 m elevation; LACM 148148, between Agua Caliente and Valle de Silencio, 1800–2000 m elevation. Panamá: Prov. Chiriquí: UMMZ 173547, Santa Clara, Finca Ojo de Agua, 1500 m elevation.

Diagnosis.—A moderately large, sexually dimorphic species with females larger than males. Basic coloration charcoal-gray with many small whitish flecks dorsally, but may lighten and darken in life. The species is distinguished from other large adult black *Bolitoglossa* by the following combinations of traits (Tables 1, 2; Fig. 3): from *B. robusta* by lacking a cream-colored ring about the base of the tail, by fewer maxillary teeth, and by many protein differences (data not shown); from *B. nigrescens* in having a more slender trunk (SL averages 8.2 times the width across the shoulders in *B. sombra*, vs. 7.8 in female *B. nigrescens*), relatively shorter limbs, and

on average fewer maxillary and vomerine teeth; from *B. magnifica* in having a smaller size and more maxillary and vomerine teeth; from *B. obscura* by having more maxillary and vomerine teeth; and from *B. copia* by having less interdigital webbing and lacking white pigment around the jaws and in the gular region and throat. *Bolitoglossa sombra* cannot be confused with the newly described *B. anthracina*, which has a narrower head and many more maxillary teeth.

Description.—Moderately large size; mean adult SL 52.7 mm (range 44.1–61.5) in seven males and 76.3 (69.9–82.7) in two females. Head broad in males—SL averages 5.9 times head width (5.5–6.4)—but somewhat narrower in females (6.6; 6.5–6.7). Snouts broadly truncated. Nostrils small; nasolabial protuberances small (females) to moderately well developed (males). Adult males with oval mental glands broader than long. Eyes moderate in size, do not protrude beyond jaw margins in dorsal view. Premaxillary teeth 3.0 (2–4) in each sex; teeth small and protrude anteriorly through upper lip in males. Maxillary teeth 34.3 (20–49) in males, 68.0 (59–77) in females. Vomerine teeth 32.9 (23–44) in males, 50.5 (48–53) in females. Limbs long, especially in males; limb interval 1.5 (0.5–2) in males and 2.0 (1.5–2.5) in females. Hands and feet large and well developed, with stout, bluntly pointed digital tips. Fingers, in order of decreasing length, 3–2–4–1; toes 3–4–2–5–1. Approximately two distal-most phalanges on longest digits free of webbing in adults; webbing more extensive in juveniles. Subterminal pads strongly developed on all digits. Tail short, never exceeds SL; standard length/tail length ratio 1.27 (1.11–1.46) in males and 1.17 (1.08–1.27) in females. Mental gland pigmented but paler than surrounding ground color. Postiliac gland visible as large pale spot.

In preservative, overall coloration black with obscure, whitish markings. Markings most prominent in vicinity of tail base and on tail. Few pale flecks scattered on flanks. Iris blackish-brown.

Measurements of the holotype (in millimeters).—Head width 10.6; snout to gular fold (head length) 14.2; head depth at posterior angle of jaw 5.4; eyelid width 2.4; eyelid length 3.6; anterior rim of orbit to tip of snout 3.8; horizontal orbit diameter 2.4; interorbital distance between angle of eyes 5.3; interorbital distance between eyelids 3.7; length of groove extending posteriorly from eye 3.7; distance between nuchal groove and gular fold 4.6; snout to forelimb 18.6; distance separating external nares

3.8; snout projection beyond mandible 1.3; snout to posterior angle of vent (standard length) 61.5; snout to anterior angle of vent 55.2; axilla to groin 33.5; number of costal interspaces between appressed limbs 0.5; tail length 55.4; tail width at base 3.9; tail depth at base 4.5; forelimb length (to tip of longest finger) 14.3; hind limb length 16.4; hand width 4.8; foot width 7.1; length of fifth toe 1.0; length of third toe 1.8; distance between vomerine teeth and posterior vomerine patch 0.6. Numbers of teeth: premaxillary 4; maxillary 18–23; vomerine 16–23 (in patches).

Coloration of holotype (in alcohol).—Body dark, black to gray-black (Fig. 7). Few obscure, light-gray to white patches dorsolaterally on first three caudal folds behind arm on left side only. Venter only slightly paler than dorsum, except for pale, pigmentless area anterior to gular fold. Melanic pigment less intense in vicinity of mental gland and near wrist and ankle joints. Nasolabial protuberances light gray.

Coloration in life.—David Wake recorded coloration for most of the type series from Las Tablas, Costa Rica on 20 May 1994. Holotype (MVZ 225872) mottled charcoal-gray, gray-black, and pale brown-black when first captured, but became black in captivity. Ground color of captive animal dark blackish brown. Dorsum with many small flecks, which ranged from gray, to light gray, to white; light-gray flecks most numerous and most obscure. White pigment widely scattered dorsally. Head with markedly rugose appearance. Venter lead-black with few widely scattered white flecks. Proximal portions of anterior limbs same color as dorsum, but posterior limbs obscure dark orange. Hands and feet somewhat paler than dorsum, with more gray. Iris dark brown.

Another adult male (MVZ 225871) was virtually identical to the holotype, although coloration was less vivid and included more obscure pale markings. Subadult animal (MVZ 225873) was solid, dark black in captivity, with two whitish patches on ventrolateral parts of tail base. In nature, at night, this animal was light gray. Another subadult (MVZ 225874) was black all over, including iris and throat region, but proximal portions of hind limbs were dark coppery-brown. Obscure but very white small patches along lateral and ventrolateral surfaces of body and tail, but most evident near the tail base. Three juveniles (MVZ 225875–76, 225878) were generally black but had some obscure whitish patches, which were most evident near the tail base. Smallest animal (MVZ 225878) had largest

patches of white, one on left lateral trunk and several on tail. All animals had very rough or rugose, glandular skin.

Karen R. Lips recorded coloration for LACM 146322, an additional paratype from Las Tablas: absolute black; no markings. She also recorded coloration for two specimens collected along the trail from Agua Caliente to Valle de Silencio. LACM 146321 (paratype): dorsal and ventral color black; silver punctations aggregated as diffuse spots on the neck, sides, and along the tail. LACM 148148 (referred specimen): dorsum uniform black; sides black with silver punctations; venter dark gray with silver punctations, some coalescing to form a few large spots; tail black with several large, diffuse silver spots.

Osteology.—The following account is based on radiographs of UCR 8030 and 8212. Skull moderately well developed. Small fontanelle between paired frontals and parietals. Premaxillary bone weakly developed; long, sinuous frontal processes separate for entire lengths. Prefrontal and septomaxillary bones absent. Each vomer with well developed, tooth-bearing pre-orbital process. Maxillary bones relatively short, extending posteriorly to level about two-thirds through orbit. Vertebral column with 1 atlas, 14 trunk, 1 sacral, 2 caudosacral, and 23 caudal vertebrae. Ribs on all but last trunk vertebrae. Transverse processes of first caudosacral vertebra perpendicular; those of second caudosacral vertebra directed sharply anterolaterally; and those of first caudal vertebra directed sharply anteriorly but do not overlap those of previous vertebra. Transverse processes present at anterior ends of first 10–12 caudal vertebrae. Phalangeal formulae 1–2–3–2 (hand) and 1–2–3–3–2 (foot). Terminal phalanges of longest toes expanded distally, T-shaped. Slightly more than two phalanges free of webbing on longest digits of hand and foot. No tibial spur.

Habitat and range.—*Bolitoglossa sombra* is known from several adjacent localities on the Pacific slopes of the Cordillera de Talamanca of Costa Rica and extreme western Panamá, from Cerro Frantzius to the vicinity of Las Tablas near the Panamanian border, and possibly near Santa Clara in nearby western Panamá (we are uncertain concerning the identity of the single specimen from this locality; Fig. 1). These localities lie within the Tropical Premontane Rainforest and Tropical Lower Montane Rainforest zones (Holdridge, 1967). Elevations range from 1500 to 2300 m.

At Las Tablas, the species was encountered at night along a trail in heavy forest. All specimens

(MVZ 225871–78) were found on moss-covered tree trunks, on stumps, or on a concrete structure providing access to an underground aqueduct. One was found walking rapidly up a tree trunk; another was found resting in a machete slice in a tree trunk. In general, the salamanders occurred at heights 0.6–1.5 m above ground. All were agile, active, and alert, and they freely used their prehensile tails as they moved. LACM 146322, from the same locality, was collected from between mossy buttresses of a tree on top of leaf litter at 0930 hr.

Two specimens were taken along the trail from Agua Caliente to Valle de Silencio. LACM 146321 was found beneath moss on a tree trunk ca. 2 m above ground between 1830 and 2000 hr, whereas LACM 148148 was taken from a leaf axil of a bromeliad during the day.

Remarks.—*Bolitoglossa sombra* occurs in sympatry with *B. compacta*, *B. marmorea*, and *Oedipina grandis* on the Pacific slopes of Cerro Pando at elevations between 1700 and 2100 m. The species is assigned to the *B. (Eladinea) schizodactyla* species group (*B. sp. 2*; Parra-Olea et al., 2004).

Etymology.—The species name is derived from the Spanish word *sombra*, or shadow, in recognition of the characteristically dark external coloration.

REDESCRIPTIONS

The original description of *Bolitoglossa nigrescens* (Taylor, 1949) was based on a single immature female collected by E. Taylor from along the highway between Millville (= Villa Mills) and San Isidro de El General, Costa Rica, in summer 1947. The species has remained rare and enigmatic and was long overlooked; we know of only four additional specimens in museums. Because the diagnosis was based on a subadult, which makes comparisons with similar species difficult, we present a new diagnosis and describe an adult individual.

Although *Bolitoglossa robusta* (Cope, 1894) is the most distinctive species of large black salamanders from Talamanca-Barú, some confusion has existed regarding whether specimens assigned to new taxa by Brame et al. (2001) and herein are merely variants of either that species or *B. nigrescens*. For this reason, and to facilitate comparisons among this complex of large black salamanders, we also provide a redescription of *B. robusta* based on all available material.

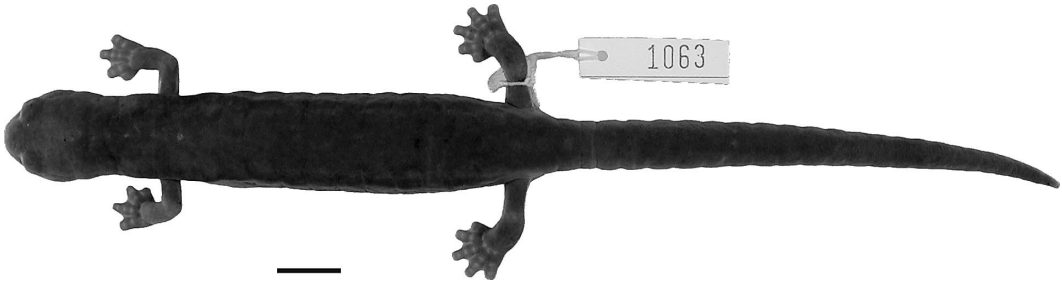


Fig. 8. Adult female *Bolitoglossa nigrescens* (UCR 1063) from 4 km S of Villa Mills, Prov. San José, Costa Rica, which is near the species' type locality. Scale bar, 1 cm.

***Bolitoglossa nigrescens* (Taylor, 1949)**

Black Web-Footed Salamander

Figure 8

Magnadigita nigrescens: Taylor (1949):282. Holotype: KU 23816: Costa Rica, Prov. San José, Boquete road camp (= Boquete), ca. 9°27.4'N, 83°41.1'W, 6000 ft (1829 m) elevation.

Bolitoglossa nigrescens: Wake and Brame (1963): 386.

Bolitoglossa nigrescens: Frost (1985):580.

Reference sample.—All from Costa Rica: Prov. San José: UCR 1063, 4 km S of Villa Mills, ca. 9°32.0'N, 83°42.5'W, 3000 m elevation; Prov. Cartago: UCR 2636, Casa Blanca de Tejar near Empalme, 9°48.3'N, 83°57.0'W, 1650 m elevation; MVZ 79628, near El Tablón, 4 km S by 11 km W of Cartago, ca. 9°49.4'N, 84°01.3'W, 1900 m elevation.

Referred specimen.—Costa Rica: Prov. San José: UCR 6543, Pico Blanco, ca. 9°52.4'N, 84°09'W, 2090 m elevation.

Diagnosis.—A large, robust, black species with moderately extensive webbing on hands and feet. It is distinguished from other large black *Bolitoglossa* by the following combinations of traits (Table 2; Fig. 3): from *B. magnifica* by having more maxillary and vomerine teeth and a relatively broader head; from *B. robusta* by lacking a lightly colored ring around the base of the tail, by its smaller adult size and somewhat smaller limbs, and by its more numerous vomerine teeth; from *B. obscura* by having shorter limbs and more maxillary and vomerine teeth; from *B. sombra* by having a broader head and shorter limbs; from *B. copia* by having less interdigital webbing and lacking white pigment around the jaws and in the gular and throat regions; and from *B. anthracina* by having a broader head, fewer maxillary teeth, and shorter, more robust digits. The species is distinguished from all sympatric associates, as well as other large black species, by the combination of coloration, adult size, degree of digital webbing, and numbers of teeth (Table 3).

Description.—Large size; mean SL in three adult females 74.4 mm (range 58.1–94.1). Head

TABLE 3. COMPARISON OF *Bolitoglossa nigrescens* WITH SYMPATRIC CONGENERS.

	<i>B. nigrescens</i>	<i>B. cerroensis</i> ¹	<i>B. pesrubra</i> ¹	<i>B. sooyorum</i> ²
Standard length (SL, in mm)				
adult males	—	54–72	26–57	58–65
adult females	58–94	49–76	38–67	35–71
SL/Head width				
adult males	—	7.1–7.7	5.9–7.1	5.8–7.1
adult females	5.9–6.5	6.7–7.7	5.9–7.1	5.8–7.1
Tail length/total length (%)	42–45	46–52	49–51	49–52
Limb interval	2.5–4.0	1.5–2.0	0–3.0	0–1.0
Maxillary teeth per side of jaw	18–37	19–45	45–65	43–79
Vomerine teeth per side	12–31	19–25	21–33	22–32
Elevational range (m)	1650–3000	2134–3000	2600–3500	2540–3000

¹ Data from Savage (2002).

² Data from Vial (1963).

broad; SL 6.2 times head width (5.9–6.5). Snout broadly truncated. Nostrils small; nasolabial protuberances modestly developed. Eyes small but relatively prominent, barely extend beyond jaw margins in dorsal view. Premaxillary teeth 2.7 (1–4). Maxillary teeth 53.7 (42–73) and very small. Vomerine teeth 42.7 (26–60), arranged in patches. Limbs short; limb interval 3.2 (2.5–4.0). Hands and feet large and well developed. Digits stout, bluntly pointed, and moderately webbed; 1–1/2 to 2 distal-most phalanges of longest digits free. Subterminal pads prominent and well developed on all digits. Fingers, in order of decreasing length, 3–2–4–1; toes 3–4–2–5–1. Tail short, does not exceed SL; standard length/tail length ratio 1.25 (1.23–1.26).

Measurements of an adult specimen from near the type locality (in millimeters).—UCR 1063, a female: head width 14.5; snout to gular fold (head length) 19.5; head depth at posterior angle of jaw 8.4; eyelid width 3.0; eyelid length 4.7; anterior rim of orbit to tip of snout 5.1; horizontal orbit diameter 2.7; interorbital distance between angle of eyes 7.1; interorbital distance between eyelids 5.1; groove behind eye extends posteriorly 5.5; nuchal groove in front of gular fold 7.3; snout to forelimb 24.5; distance separating external nares 4.4; snout projection beyond mandible 1.2; snout to posterior angle of vent (standard length) 94.1; snout to anterior angle of vent 86.7; axilla to groin 52.3; number of costal interspaces between appressed limbs 4; tail length 75.0; tail width at base 7.9; tail depth at base 8.3; forelimb length (to tip of longest finger) 17.8; hind limb length 18.3; foot width 9.9; length of fifth toe 2.1; length of third toe 2.6. Numbers of teeth: premaxillary 1; maxillary 36–37; vomerine 29–31.

Coloration in alcohol.—UCR 1063 uniformly dark black dorsally and ventrally, with slightly paler gular area and much paler soles of hands and feet. Jaw margins and nasolabial groove region paler than surrounding areas. Underside of posterior third of tail also somewhat paler than ground color.

Osteology.—The following description is based principally on UCR 1063 and supplemented by accounts of other specimens; all are derived from radiographs. Skull heavily ossified and very well articulated, with same kinds of extra bony processes seen in *B. robusta*, especially on nasal bone, on posterior part of each ascending (frontal) process of premaxillary bone, and on frontal bone. No frontoparietal fontanelle, but large internasal fontanelle between ascending

processes of premaxilla. Septomaxillary and prefrontal bones absent. Large vomers appear to articulate posteriorly and diverge anteriorly, although not nearly as much as in *B. robusta*. Long preorbital process appears to fall short of lateral margin of body of vomer.

Vertebral column with 1 atlas, 14 trunk, 1 sacral, 2 caudosacral, and 25 caudal vertebrae. Last trunk vertebra bears ribs (unlike *B. robusta* and *B. magnifica*). Transverse processes of first caudal vertebra arise on anterior margin of vertebra and extend sharply anterolaterally, terminating anterior to midpoint of second caudosacral vertebra. Right process sharply pointed; left one bluntly pointed. Transverse processes of second caudosacral vertebra arise from midpoint of vertebra, but because they sweep anteriorly and then sharply laterally they do not overlap those of first caudal vertebra. Phalangeal formulae 1–2–3–2 (hand) and 1–2–3–3–2 (foot). Terminal phalanges broadly expanded, more than in *B. robusta* but less than in *B. magnifica*.

Holotype (KU 23816), an immature female, has lightly articulated skull that is incompletely ossified. Premaxillary bone slender with elongate and well-separated frontal processes. Nasal bones large, but prefrontal and septomaxillary bones absent. Each vomer with tooth patch associated with preorbital process. Vertebral column with 14 trunk vertebra—all but the last bear rib—and 20 caudal vertebrae. Phalanges weakly ossified; phalangeal formulae 1–2–3–2 (hand) and 1–2–3–3–2 (foot). No tibial spur.

Third specimen (MVZ 79628) has 14 trunk and 26 caudal vertebrae. Last trunk vertebra lacks ribs. Digits less expanded than in UCR 1063. No septomaxillary or prefrontal bones.

Habitat and range.—*Bolitoglossa nigrescens* is known from five localities in the northern and central portions of the Cordillera de Talamanca of Costa Rica (Fig. 1), within the Tropical Lower Montane Rainforest and Tropical Montane Rainforest zones (Holdridge, 1967). Elevations range from 1650 to 3000 m.

Remarks.—*Bolitoglossa nigrescens* is an extremely rare, high altitude species. It was recognized as valid by Frost (1985:580), Savage (2002), and Parra-Olea et al. (2004), but not by Savage and Villa (1986). Specimens discussed as *B. nigrescens* by Hanken and Wake (1982) are herein referred to *B. magnifica*. Salamanders referred to *B. nigrescens* by Lips (1993) are placed in *B. sombra*. The species is assigned to the *B. (Eladinea) schizodactyla* species group (Parra-Olea et al., 2004).

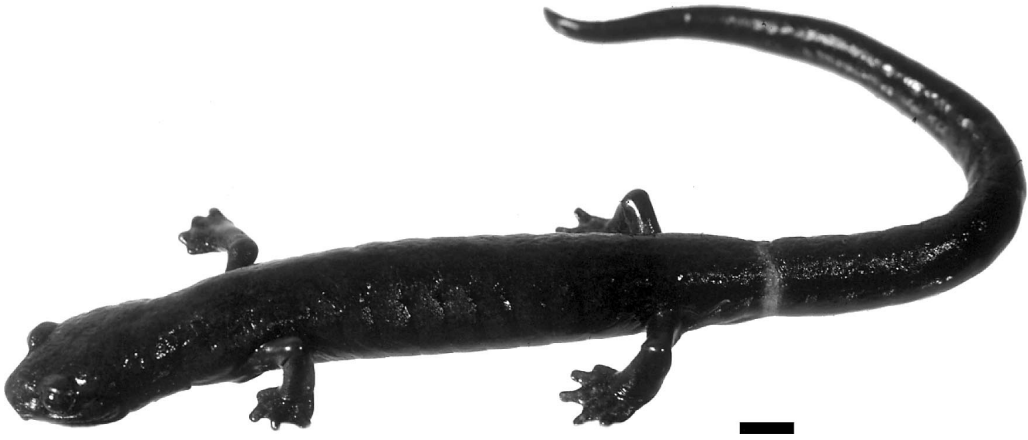


Fig. 9. Adult *Bolitoglossa robusta* from Salto El Angel, Prov. Alajuela, Costa Rica, 4 February 1984 (specimen number unavailable). Scale bar, 1 cm.

Bolitoglossa nigrescens occurs sympatrically with three other species of *Bolitoglossa* (Table 3; Wake, 1987; García-París et al., 2000). The largest of these, *B. cerroensis*, has relatively small hands and feet, few maxillary teeth, and a relatively narrow head. Occasionally, melanistic individuals are found that might be confused with *B. nigrescens*, but even the darkest *B. cerroensis* has a venter mottled with yellow, orange or cream markings on brownish-black ground color. At elevations around 2800 m on Cerro de la Muerte (in the vicinity of Ojo de Agua), Costa Rica, populations of *B. pesrubra* include a few solid black individuals, which might be misidentified as *B. nigrescens*. These animals, however, have narrower heads, longer tails, and a more gracile form than juvenile *B. nigrescens*, and adult *B. nigrescens* are much larger than *B. pesrubra*. *Bolitoglossa sooyorum*, the third sympatric species, has a mottled or speckled color pattern of tan to copper on a rich brown background. It has more maxillary teeth, longer limbs, and broader hands and feet than *B. nigrescens*.

Etymology.—The name of this species derives from the Latin adjective *niger*, or black, and suffix *-escens*, meaning incipiency, or state of beginning. The combination refers to the black color of the holotype and to its (likely) juvenile condition.

***Bolitoglossa robusta* (Cope, 1894)**

Ringtail Salamander

Figure 9

Oedipus robustus: Cope (1894):194. Holotype: AMNH 5464: Costa Rica, Prov. Cartago, "Faldas of Volcano Irazu," ca. 9°57'N, 83°52'W.

Spelerpes robustus: Günther (1902):301, pl. 76a.

Oedipus robustus: Dunn (1926):362.

Magnadigita robusta: Taylor (1944):218.

Magnadigita robusta: Taylor (1949):279.

Magnadigita robusta: Taylor (1952):727.

Bolitoglossa robusta: Wake and Brame (1963):386.

Bolitoglossa robusta: Savage and Villa (1986):44 (in part).

Reference sample.—Costa Rica: Prov. Alajuela: KU 35503–5 (three specimens), Isla Bonita, 1200 m elevation; KU 35740–45 (five specimens), Cinchona, 1360 m elevation; MVZ 207060, Peñas Blancas trail from Monteverde, 1540 m elevation. Prov. Cartago: KU 30489–91 (three specimens), Cervantes, 1441 m elevation; MVZ 183660 (cleared and stained), Colorado Swamp just outside Juan Viñas, 6.3 mi from Turrialba, 1200 m elevation. Prov. Puntarenas: KU 35739, "Zeledón"; MVZ 207058, Monteverde Reserve, Chomogo trail, 1630 m elevation; MVZ 207059, Monteverde Reserve, Río trail, 1510 m elevation; MVZ 207091, Monteverde, Cliff edge trail, 1460 m elevation. Panamá: Prov. Bocas del Toro: KU 116632–33 (two specimens), Río Changena, 830 m elevation; KU 116634–37 (four specimens), Río Claro, at Río Changena, 910 m elevation. Prov. Chiriquí: MVZ 210326, Fortuna, 1200 m elevation.

Referred specimens.—Costa Rica: Prov. Alajuela: USNM 210986, Río La Paz Grande, 4 km airline N of Varablanca junction, 1 km S of Varablanca, 1380 m elevation; KU 25071, 25074–75 (two specimens), 25209, Isla Bonita, 1200 m elevation; MVZ 111124, 4.9 km (rd.) N rd. to Volcán Poas (at Varablanca) on Hwy. 9; MVZ 190829–30 (two specimens), Salto el Angel (= Salto La

Paz Grande), 1360 m elevation; MVZ 207061, Volcán Cacao, first stream below Casa Mengo, 1075 m elevation; BMNH 1902.5–12,63–64 (two specimens), Cariblanco, 830 m elevation. Prov. Cartago: MCZ 6919–27 (nine specimens), Cedral de Navarro, 1400 m elevation; KU 25067–70 (four specimens), 25072, Turrialba, 646 m elevation; KU 25073, 41014, Cervantes, 1441 m elevation; LACM 148146, Juan Viñas, 1036 m elevation; LACM 148147, Tapantí, 1316 m elevation; LACM 148150, Capellades, 1590 m elevation; UCR 1695–96 (two specimens), Río Macho, near Orosi, 1114 m elevation; UCR 6021, Moravia de Chirripó, 1116 m elevation; UCR 7108, between Turrialba and Cartago. Prov. Heredia: UF 30711, Buena Vista, 2 km N of Barva, 1350 m elevation. Prov. Puntarenas: LACM 148149 and 148152, Monteverde, 1450 m elevation; LACM 148151 and 148153, Monteverde, 1372 m elevation; MVZ 210327, Monteverde, Campbell house, 1500 m elevation; UCR 1344, 8967, Monteverde, 1400 m elevation. Prov. San José: MVZ 181275, Cascajal region, ca. 2.3 km ENE of San Isidro de Coronado; UCR 2203–4 (two specimens), near Santa Ana (Cerros de Escazú), 1289 m elevation; MVZ 128275, UCR 4616, 8211, Bajo La Honduras, 1150 m elevation; UCR 9379, Bajo La Honduras, 1245 m elevation; UCR 6215, between Alto La Palma and La Honduras, 1300–1400 m elevation; UCR 7464, Cerro los Cuarteles (= Cerro Dragón), Fila Santa María (nr. Santa María de Dota, ca. 1700 m elevation); UCR 7612–13 (two specimens), Finca Lara de Coronado, 1580 m elevation; BMNH 1902.1–25,35–40 (six specimens), 95.7–13,40, 96.10–8,73–76 (four specimens), MCZ 5119, USNM 37773–74 (two specimens), La Palma, 1500 m elevation. Panamá: Prov. Chiriquí: MVUP 1227, Loma del Silencia, Fortuna area, 2000–2121 m elevation.

Diagnosis.—A very large, stout-bodied species. It differs from all other members of the genus in having a distinct, lightly colored (reddish or pinkish to cream) ring around the base of the tail. It is further distinguished from other large adult black *Bolitoglossa* by the following combinations of traits (Tables 1, 2; Fig. 3): from *B. anthracina* by its broader head, fewer maxillary and vomerine teeth, shorter legs and stouter digits, larger size, and more robust habitus; from *B. magnifica* by having more maxillary teeth and rhomboidal nasal bones; from *B. nigrescens* by its larger size and more slender habitus; from *B. obscura* by having more maxillary and vomerine teeth; and from *B. copia* by having less interdigital webbing and lacking white pigment around the jaws, throat and gular region.

Bolitoglossa sombra is somewhat smaller and has more vomerine teeth and longer limbs than *B. robusta*.

Description.—Adults very large; mean SL 83.4 mm (range 44.6–113.9) in ten males and 105.1 (64.9–133.5) in eight females. Head broad; SL 6.2 times head width in males (5.7–6.7), 6.1 (4.0–7.0) in females. Snout broadly rounded to subtruncate. Nostrils small; nasolabial protuberances poorly developed to absent in females, moderately developed in males. Adult males with conspicuous gray mental glands, slightly broader than long. Eyes moderate in size, protrude slightly beyond jaw margins in dorsal view, especially in males. Premaxillary teeth 6.1 (4–8) in males, 8.5 (5–12) in females. Teeth in males somewhat enlarged and protrude anteriorly through upper lip. Maxillary teeth 65.5 (31–100) in males, 84.6 (60–102) in females. Vomerine teeth 28.9 (18–40) in males, 33.9 (25–41) in females. In some individuals, vomerine teeth occur in patches, which are formed by extra tooth rows in the distal part of the preorbital process of the underlying bone. Limbs short; limb interval 3.0 (1.5–4.0) in males and 3.3 (3.0–4.0) in females. Hands and feet moderate in size but broad, with stout, truncated digit tips. Fingers, in order of decreasing length, 3–(2–4)–1; toes 3–4–2–5–1. Extensive webbing; only 1 to 1–1/2 distal-most phalanges of longest digits free. Subterminal pads well developed on all digits. Tail long, may exceed SL; standard length/tail length ratio 1.09 (0.90–1.50) in males and 1.01 (0.91–1.27) in females. Mental gland lightly pigmented. Postiliac gland visible as pale spot in many but not all individuals.

In preservative, overall coloration dark-gray to black. Rose or cream-colored to reddish-brown ring at tail base in nearly all individuals, but ring is suffused with darker pigment laterally and/or dorsally in a few specimens.

Coloration in alcohol.—MVZ 207058: Dorsum and venter dark gray-black. Few tiny, widely scattered white flecks near eyelids and jaws and also ventrally, mostly in gular region and on limbs and tail. Some additional, very obscure flecks dorsolaterally. Cream-yellow ring around base of tail, just anterior to the constriction where tail joins trunk. Ring less than one body segment wide and barely extends onto tail. Distinct pair of inguinal spots on either side of body. Second specimen (KU 116637) also dark gray-black dorsally and ventrally. However, a series of obscure, light-gray to gray-white markings appear at widely scattered places along flanks and become larger and more abundant behind hind limbs.

Few obscure pale flecks on hind limbs but not forelimbs. Few whitish flecks on anterior gular area, but otherwise no ventral markings anterior to tail. Tail ring faint gray-white. Distinct gray-white patches on lateral sides of tail; smaller markings dorsally and ventrally. Mental gland round and flesh colored.

Coloration in life.—One of us (D. Wake) recorded coloration for several specimens on 13 August 1987 and 21 November 1988. MVZ 207059–60 and 207091 (Monteverde, Costa Rica): All salamanders distinctly blackish overall with some brownish areas, particularly at elbows, knees, and tail tip. Tail ring cream, with rose to dark orange overtones. Venter obscurely mottled with grayish, salt and pepper pattern. Throat black, iris brownish black. Hands and feet of juveniles bright yellow to orange (appears pale in preservative). MVZ 210326 (Fortuna, Panamá): ground color dark shiny black, with prominent ring around tail base. Ring golden to peach dorsally, becoming cream-colored laterally and white ventrally. Some coppery or brassy pigment on dorsal surface of femur and more obscurely on dorsal surface of forelimb. Bold whitish, irregular spots prominent on tail, especially laterally and ventrally. Spots generally somewhat smaller than eye and number about 60. Few (three left, eight right) whitish spots along flanks of trunk, with another one middorsally and several more in shoulder region as well as near eye and on back of head. Dense suffusion of white speckles covers background of dorsal and lateral surfaces, with concentration laterally. Gaps in this suffusion on black belly. Speckles slightly larger and more uniformly distributed on gular region than other ventral surfaces. Iris dark-gray to black.

Osteology.—The following description is based on one cleared and stained specimen (MVZ 183660, a female, ca. 100 mm SL; Fig. 5), and two dried skulls (MCZ 6920, a female of moderate but unknown size, and MCZ 6924, a smaller male). Skull substantially broader than those in *B. magnifica* and *B. sombra* but nevertheless resembles them in several ways. These include the presence of extra bony projections in many areas, especially on the premaxilla, the ascending process of the maxilla, the nasal, and the frontal; and the same complicated, interlocking articulations among the frontal, the nasal, and the premaxilla, between the nasal and the maxilla, and between the paired frontals and parietals. There are no septomaxillary bones.

Bolitoglossa robusta also differs from *B. magnifica* and *B. sombra* in several respects. The male

has moderately long premaxillary teeth, which are substantially longer than the maxillary teeth and appear to be unicuspid. Maxillary bones are more robust and bear teeth almost to the posterior tip on one side and within about 5% of the tip on the other side. Prefrontal bones are absent in the largest specimen but clearly present in both of the smaller individuals. When present, the prefrontal is small to very small, and much smaller than the nasal. In MCZ 6920, the prefrontals have overlapping articulations with both the nasal and the frontal. Vomers closely approach one another posteriorly but diverge anteriorly; their anterior tips are widely separated by a distance approximating the length of the preorbital process. (This large intervomer fontanelle is one of the main osteological features that differentiates *B. robusta* from the other species.) Nasal bones are rhomboidal (vs. elongate in *B. magnifica*) The nasal foramen is very broad and partially covered posteriorly by fingerlike projections of the ascending processes of the premaxilla. Additional fingerlike projections extend from the posterior edge of the parietal bone. Otic-occipitals almost completely lack crests; there is only one small crest that extends from the anterolateral margin. There is a rudimentary columella attached to the operculum in the largest individual but it is absent in the others.

The vertebral column includes 1 atlas, 14 trunk, 1 sacral, 2 caudosacral, and 28 caudal vertebrae. The last trunk vertebra does not bear ribs. Transverse processes are present on all but the last four caudal vertebrae. Transverse processes of the first caudal vertebra arise at the extreme anterior end of the vertebra and extend almost laterally, with a slight anterior bias.

Limb bones are shorter than in *B. magnifica*. Digits also are smaller and less stout, and terminal portions of the digits are narrower and not as flat. Mesopodial patterns and phalangeal formulae are the same in the two species. There is no tibial spur.

Habitat and range.—This terrestrial salamander is found on the slopes of the cordilleras of Costa Rica, from Volcán Cacao near the Nicaraguan border, southeastward through the Cordillera Central and the Talamanca-Barú Massif, to the region of Prensa Fortuna, Prov. Chiriquí, Panamá (Fig. 1). It is found in Tropical Premontane Wet and Tropical Lower Montane Rainforest zones (Holdridge, 1967). Elevations range from 650 m to 2100 m, but the species is most common between 1000 and 1600 m. It is often found under fallen logs and in thick leaf litter, or under moss. It has been found walking on

the ground at night and has been taken in bamboo 40 cm above the ground.

Remarks.—Generally, *Bolitoglossa robusta* is found at lower elevations than both *B. magnifica* and *B. nigrescens*, but further field study may reveal some overlap among species. *Bolitoglossa anthracina* and *B. obscura* occur in virtual sympatry with *B. robusta* in the southern and northern portions of the Cordillera de Talamanca-Barú, respectively. E. R. Dunn's unpublished notes list a specimen of this species from Carrillo, Prov. San José, Costa Rica, elev. 500 m (Manuscript Notes on the Amphibia of Lower Central America, in possession of JMS). This animal was formerly in the Museo Nacional de Costa Rica but is now lost. It may have been collected at a higher elevation on the mountain slopes above Carrillo. This species is assigned to the *B. (Eladinea) schizodactyla* species group (Parra-Olea et al., 2004).

Etymology.—The name derives from the Latin adjective *robustus*, meaning hard and strong like an oak, probably in reference to the large size and robust physique of this species.

DISCUSSION

The Caribbean slope of the Cordillera de Talamanca-Barú region (700–2000 m) supports a rich montane salamander fauna (Wake, 1987, in press; García-París et al., 2000). Eight species in three genera occur on the transect from Tapaní National Park to the summit of the cordillera in Costa Rica, including one species of *Bolitoglossa* that is undescribed (sp. B; García-París et al., 2000). Among the species considered in this paper, *B. obscura*, *B. robusta*, and *B. nigrescens* all occur on this transect. A different combination of fifteen species in two genera, including several unnamed species, occurs along the cordilleran crest and Caribbean slopes near the Panamá-Costa Rica border (Wake, in press). The cordilleran crest and Pacific slopes in the same region support a fauna of seventeen species of *Bolitoglossa* and *Oedipina*. *Bolitoglossa anthracina* (Brame et al., 2001) and *B. robusta* occur on both Caribbean and Pacific slopes, whereas *B. magnifica* and *B. sombra* are restricted to the Pacific slopes.

Even against this background we were initially surprised at the diversity represented by our samples of large black *Bolitoglossa* from the mountains of Costa Rica and western Panamá. Nevertheless, available biochemical data support our conclusion that these salamanders constitute at least seven evolutionary species. Earli-

er, Hanken and Wake (1982) utilized tissue from *B. magnifica* (identified as *B. nigrescens*) in an electrophoretic analysis of genetic differentiation among species of *Bolitoglossa* found in Central and South America. While that study included none of the other large species recognized here, it established the distinctiveness of *B. magnifica* from several other lower Central American taxa, viz., *B. marmorea*, *B. pesrubra* (as *B. subpalmata*, samples 3–5), and *B. subpalmata* (sample 1). Similarly, DNA sequence data were reported recently for two mitochondrial genes, cytochrome b (cyt b) and 16S RNA (Parra-Olea et al., 2004; methods as in García-París and Wake, 2000). The amount of sequence divergence between species considered herein and other named species is relatively great. For example, K2p distances for the 16S gene for *B. sombra* (as *B. sp. 2*) are 0.062 to *B. marmorea* and 0.068 to *B. cerroensis*. (The comparable distance to *B. robusta* is 0.053; Parra-Olea et al., unpubl. data) These are large distances for this slowly evolving gene. Finally, a genetic comparison of four populations of *B. robusta* with type material of *B. magnifica* revealed fixed differences at 11 of 19 allozyme loci (Good and Wake, unpubl. data). Data are too limited to warrant further discussion, but all observations are consistent with our recognition of each of these forms as a distinct taxon.

Any attempt to deduce relationships among the seven species of large black *Bolitoglossa* is limited at this time to phenetic comparisons. Additional analysis will be required to determine if patterns of morphological similarity correlate with evolutionary relationship (e.g., Parra-Olea et al., 2004). The relatively short-limbed and broad-headed *B. nigrescens* and *B. robusta* may be sister taxa, as are *B. anthracina* and *B. copia*, based on their similar body measurements and tooth counts. *Bolitoglossa obscura* and *B. sombra* have relatively long limbs and similar head and body proportions. Overall, *B. magnifica* shows no strong affinity with any one of the above species. This is due, at least in part, to its pronounced sexual dimorphism, which complicates comparisons considerably.

Patterns of morphological similarity do, however, correlate to at least a moderate degree with geography. *Bolitoglossa nigrescens* is best regarded as a montane endemic; it generally occurs at higher elevations than the wider-ranging *B. robusta*. Similarly, *Bolitoglossa anthracina* and *B. copia* replace one another from east to west along the Panamanian cordilleran axis, whereas *B. obscura* may be the Caribbean slope counterpart to *B. sombra* from the Pacific versant. Within these species pairs, *B. nigrescens* differs from

B. robusta in lacking a tail ring, in its generally smaller adult size, and in having more vomerine teeth. *Bolitoglossa copia* differs from *B. anthracina* by its more extensive interdigital webbing and white coloration on the face and throat. Finally, *B. obscura* differs from *B. sombra* in having many fewer maxillary and vomerine teeth. The distribution of *B. magnifica* on Pacific slopes resembles that of *B. anthracina* on Caribbean slopes, but otherwise there are no obvious similarities between *B. magnifica* and any one of the other species.

Seven species of large black *Bolitoglossa* are distributed from extreme northwestern Costa Rica (Volcán Cacao) to central Panamá (Cerro Peña Blanca; Fig. 1). No two of these species have yet been taken in sympatry, but this simply may be an artifact of limited geographic sampling for most species. It seems likely, for example, that the widely distributed *B. robusta* co-occurs with *B. anthracina* on the Caribbean slope in northwestern Panamá (Brame et al., 2001). *Bolitoglossa anthracina* occurs at an elevation of 1450 m on Cerro Pando, whereas *B. robusta* occurs at 830–910 m on the Río Changeña, which lies only 7–8 km away. The ranges of these two species similarly approach one another in the Fortuna Dam area, in the Pacific drainage of southwestern Panamá (Prov. Chiriquí). *Bolitoglossa robusta* also may be sympatric with *B. nigrescens* on the northern (Caribbean) slope of the Cordillera de Talamanca in central Costa Rica. Their known ranges are separated by a distance of only 6 km in Cartago province, between the area of El Tablón (1900 m; *B. nigrescens*) and Estrella (1525 m; *B. robusta*). The two species are separated by an even shorter distance in San José province, between the slopes above Santa Ana (1289 m; *B. robusta*) and Pico Blanco (2090 m; *B. nigrescens*) higher up on the Cerros de Escazú. Finally, *B. robusta* may be sympatric with *B. obscura* in central Costa Rica (Prov. Cartago). The type locality of *B. obscura* (1550 m) is about 12 km southeast of the nearest record for *B. robusta* at Río Macho (1114 m).

Bolitoglossa magnifica and *B. sombra* also may have overlapping ranges. We have assigned to *B. sombra* a specimen from extreme western Panamá (Santa Clara, Prov. Chiriquí, 1500 m), but this specimen could be referred to *B. magnifica*. (Morphological data are equivocal with respect to the assignment of this specimen to either species, and there are no molecular data.) This specimen was collected only 12 km south-southeast of the type locality of *B. sombra* in adjacent Costa Rica (east of Las Tablas, Puntarenas Prov., 1760 m).

We continue to be surprised by the high di-

versity of salamander species found in the Talamanca-Barú range in the frontier region between Costa Rica and Panamá. As presently understood, this fauna comprises 16 species of *Bolitoglossa* (4 as yet undescribed) and 4 species of *Oedipina*. These genera likely have been in the region only since the Miocene, ca. 20 ma (Savage, 1983; Wake, 1987). The effects of uplift, volcanic eruptions, and lava flows, combined with the limited dispersal capabilities of these terrestrial amphibians, seem to have contributed to localized speciation in populations isolated by these orogenic influences. We anticipate the discovery of more new taxa in the virtually unsampled 100 km of montane habitat in Costa Rica between Cerro Chirripó Grande and Cerro Pando, and in a similar stretch of forested habitat (ca. 215 km) between the Fortuna dam region of western Panamá and El Copé to the east.

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