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NEW SPECIES OF SALAMANDERS, GENUS *BOLITOGLOSSA*, FROM PANAMA

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CONTRIBUTIONS IN SCIENCE

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NEW SPECIES OF SALAMANDERS, GENUS *BOLITOGLOSSA*, FROM PANAMA[1]

By DAVID B. WAKE,[2] ARDEN H. BRAME, JR.,[3] and WILLIAM E. DUELLMAN[4]

ABSTRACT: Three species of salamanders, *Bolitoglossa cuna, B. minutula,* and *B. compacta,* are described from Panamanian populations. *Bolitoglossa cuna,* from the Territorio de San Blas, is a lowland species with fully webbed hands and feet. It is a member of the *sima* group. *Bolitoglossa minutula* is the smallest member of the genus. It occurs at elevations between 1800 and 2000 m near the Costa Rican border, and has some similarity to the larger Costa Rican species, *B. epimela. Bolitoglossa compacta* is a large species with slightly webbed hands and feet which is sympatric with *B. minutula.* It is a relative of *B. cerroensis* of Costa Rica.

Gradually the notion that salamanders are rare and lack diversity in the tropics is being dispelled. The increased field work of recent years has disclosed that salamanders are widely distributed in tropical America, but densities are often low. As a result, most species are represented by rather small series in collections. As field work continues, the diversity of the group is becoming apparent. Often in a given restricted area several species live in broad sympatry and have varied structure and ecology. In the present paper we describe specimens of three new species collected principally by Charles W. Myers, William E. Duellman, and Linda Trueb since 1963. These species encompass much of the range of morphological diversity in Panamanian species of *Bolitoglossa* and add considerably to our knowledge of the Panamanian salamander fauna.

The first species occurs only in eastern Panama, along the Caribbean lowlands. It is named for the humans indigenous to the region.

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Bolitoglossa cuna, new species
Figures 1 and 2

Holotype: KU 116519, an adult female from Camp Sasardi, 12 m (39 ft) elevation, Territorio de San Blas, Panamá, obtained by Charles W. Myers on 6 February 1967.

Paratypes: USNM 150035-36, adult females from Armila, near sea level, Territorio de San Blas, Panamá, collected by C. O. Handley, Jr. and F. M. Greenwell on 26 February, 1963.

Diagnosis: A moderate-sized species (3 adult females: 46.6-55.7, mean 50.3 SL[5]) with high numbers of maxillary (mean 72) and vomerine (mean 35) teeth; distinguished from *B. silverstonei* by its more numerous teeth and narrower head, hands and feet; from *B. biseriata* by its more numerous teeth and narrower head; from *B. sima* by its shorter legs, more numerous teeth and narrower head. *B. cuna* is distinguished from all other members of the genus

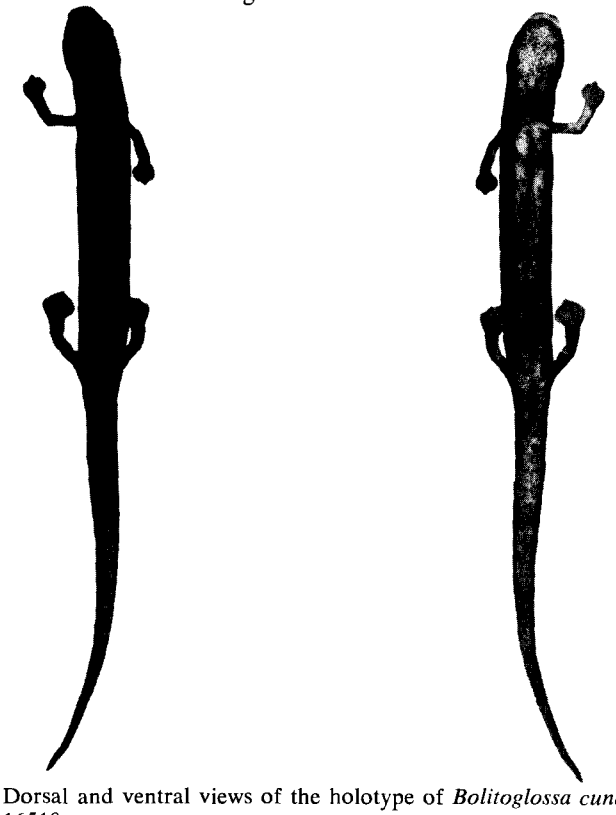

FIGURE 1. Dorsal and ventral views of the holotype of *Bolitoglossa cuna,* new species, KU 116519.

[5]Standard length, the distance in mm from the snout to the posterior end of the vent (all measurements are in millimeters).

by the combination of its nearly completely webbed hands and feet, its size and dentitional features, and its coloration (light golden tan mottled with some darker color dorsally; lighter venter with a peppering of small, dark spots).

Description of Holotype: Adult female, snout of moderate length. Nostril moderately small; labial protuberances of nasolabial grooves small and poorly developed. Canthus rostralis of moderate length, gently arched. Standard length 7.2 times head width; standard length 5.0 times snout-gular fold length. Deep groove below eye extends almost full length of opening, following curvature of eye, but does not communicate with lip. Eye moderately small, not protuberant. Well defined postorbital groove extends posteriorly from eye as shallow depression for 1.6 mm; proceeds sharply ventrad at level of posterior end of mandible and extends across gular area as nuchal groove parallel to and 3.3 mm anterior to sharply defined gular fold. Vomerine teeth 33, patched, extending to distal borders of the internal nares; patches extend from distal end in a straight line to near the center of the palate, where they are separated by 0.8 mm from the right and left parasphenoid tooth patches. Maxillary teeth 77, extend posteriorly to a point about three-fourths through eye. Five moderately small premaxillary teeth protrude through the lip. Tail relatively long, 0.9 times standard length; postiliac gland clearly evident. Limbs moderately short, limb interval 3.5; standard length 4.8 times right forelimb; 4.7 times right hind limb; 11.1 times right foot width; webbing of hands and feet so extensive as to be nearly complete, with only the longer digits protruding from webbing (Fig. 2). No subterminal pads. The fingers are in order of decreasing length: 3, 2, 4, 1; toes in order of decreasing length: 3, 4, 2, 5, 1.

Measurements (in mm): Head width 7.7; snout to gular fold (head length) 11.1; head depth at posterior angle of jaw 3.7; eyelid length 2.9; eyelid width 1.4; anterior rim of orbit to snout 3.8; horizontal orbital diameter 2.1; interorbital distance 3.8; distance between vomerine teeth and parasphenoid tooth patch 0.8; snout to forelimb 14.3; distance separating internal nares 2.3; distance separating external nares 3.1; snout projection beyond mandible 1.1; snout to posterior angle of vent (standard length) 55.7; snout to anterior angle of vent 52.5; axilla to groin 32.5; tail length 52.2; tail width at base 4.1; tail depth at base 4.1; forelimb length 11.5; hind limb length 11.9; width of right hand 3.8; width of right foot 5.0.

Coloration in Alcohol: The holotype is light reddish brown dorsally with dark brown lateral bands extending from the neck along the body and well onto the tail. The venter is cream with many small brown spots which leave some cream areas unmarked. There is a peppered effect on both dorsal and ventral surfaces consisting of tiny scattered dark brown melanophores.

The head is light reddish brown dorsally with the same general coloring as the dorsum of the trunk, although the lateral regions between the eyes and snout are distinctly paler. The ventral coloration of the gular area is like the trunk venter, mottled cream and dark brown with many tiny dark brown melanophores clearly discernible. The small eyes appear to have a gold ring

around the horizontally elliptical pupil. The dorsal surfaces of the limbs are mottled with dark brown, and are darker than the trunk dorsally. Ventrally the limbs are similar in color to the trunk venter. The ventral surfaces of the hands and feet are rather light grey brown.

Variation: The poorly preserved paratypes have more dorsal mottling than the holotype, with large blotches of light color which contrast with the dark brown ground color. There are no dark brown lateral bands. The dorsal coloration gradually becomes lighter along the lower lateral surfaces, finally fading to a uniform light grey ventrally. USNM 150036 has larger feet than the holotype or other paratype and USNM 150035 has a somewhat broader head (see Table I) but otherwise the external morphology of the three specimens is similar.

Osteology: All information has been derived from radiographs, and many details of the skull cannot be discerned. The skull is well developed with well articulated bones. The premaxilla is relatively slender and has processes of moderate length which are slightly dilated at their distal tips. The nasals are large and well developed, but are only slightly protuberant. They are closely articulated to the facial part of the maxillae. No prefrontals can be seen. The vomers are well separated for their entire length. The preorbital processes are long and extend well beyond the lateral margins of the internal nares. Teeth extend along these processes to about the level of the lateral margins of the nares. The moderately long maxillae extend to the posterior margin of the eyes. The operculum has no stilus. All but the last trunk vertebrae bear well developed ribs. There are one cervical, fourteen trunk, one sacral, two caudosacral and thirty-two caudal vertebrae in the single specimen (USNM 150036) which has a complete tail.[6] The holotype has a tail which is regenerated distal to the fifteenth caudal vertebra. The regenerated portion has twenty-one vertebrae. USNM 150035 lacks a tail.

The long, stout transverse processes on the first caudosacral vertebra are nearly perpendicular to the long axis of the body. The shorter and stouter processes of the second caudosacral vertebra are angled anteriorly, with blunt tips. The processes of the first caudal vertebra are very long and slant sharply in an anterior direction. They are much longer in the holotype than in the paratype, and extend nearly to the anterior end of the second caudosacral vertebra. The processes of adjacent vertebrae do not overlap. Processes on succeeding vertebrae are progressively shorter. They are present to about the twelfth vertebra in the holotype and to the nineteenth in the paratype. All lie at the anterior end of the vertebra and slant anteriorly.

In the holotype the second caudosacral and first caudal vertebrae are shorter than any trunk vertebrae and all of the unregenerated tail vertebrae. The mid-trunk vertebrae are the longest in the column, and all but the first trunk vertebrae are longer than any post-trunk vertebrae.

No tibial spurs are present, but a distinct ridge is visible in one paratype.

[6]See Wake (1966) for definitions of osteological characters.

TABLE I.
Measurements and data for specimens of new species of *Bolitoglossa*

	Sex	Snout–Vent Length	Axilla–Groin Length	Head Width	Hind Limb Length	Forelimb Length	Limb Interval	Snout–Gular Fold Length	Tail Length	Numbers of Maxillary Teeth	Numbers of Vomerine Teeth	Foot Width
B. cuna												
KU 116519*	♀	55.7	32.5	7.7	11.9	11.5	3.5	11.1	52.2	77	33	5.0
USNM 150035	♀	48.7	28.4	7.4	10.7	10.2	3.5	11.6	—	69	33	4.4
USNM 150036	♀	46.6	—	6.8	9.8	9.8	3.?	10.4	45.0*	66	38	4.6
B. minutula												
KU 116564	♀	36.5	20.0	5.4	8.2	7.8	3	7.8	33.0	36	15	3.3
KU 116575	♀	36.3	19.8	5.6	7.7	6.8	3	8.1	35.9	48	16	3.2
KU 116576	♀	36.0	20.0	5.3	7.8	7.8	3	8.2	36.1	43	18	3.2
KU 116577	♀	34.8	19.7	5.6	8.7	7.8	2.5	8.1	31.8	51	16	3.1
KU 116608	♀	34.2	18.9	5.2	7.8	7.2	4	7.5	—**	33	15	3.0
KU 116556	♀	34.1	18.2	5.6	8.1	7.7	2	8.1	34.2	42	16	3.3
KU 116595	♀	33.9	18.6	5.3	8.0	7.0	3	7.8	32.7	43	16	3.1
KU 116554*	♀	33.6	18.5	5.2	8.0	7.8	3	8.0	32.2	46	19	3.1
KU 116574	♀	33.2	18.7	5.3	7.8	7.2	3	7.2	34.3	47	19	3.2
KU 116607	♀	33.2	18.3	5.1	8.0	7.0	3	7.8	29.9	37	16	2.9
KU 116582	♀	31.9	17.6	4.9	7.3	6.3	3	7.2	27.8	34	12	2.9
KU 116611	♀	31.9	16.9	5.2	7.9	6.9	3	7.3	29.4	42	17	3.2
LACM 78731	♀	31.4	17.5	5.0	7.3	6.3	2.5	7.2	29.2	45	17	2.8
KU 116610	♀	30.1	16.7	4.9	6.8	6.3	3	7.2	25.8	37	23	3.0
KU 116555	♂	36.0	19.7	5.3	9.6	8.9	1	8.4	40.2	47	—	3.7
KU 116552	♂	35.7	19.3	5.7	9.8	8.9	1.5	8.0	38.2	46	22	3.7
KU 116579	♂	34.8	19.2	5.4	9.0	7.8	2	7.8	35.2	42	26	3.4
KU 116609	♂	34.7	19.2	5.6	9.2	9.0	2	8.2	—**	46	15	3.7
KU 116557	♂	34.5	19.2	5.6	8.9	8.6	1.5	8.0	—**	51	17	3.6
KU 116605	♂	34.1	18.2	5.1	8.3	7.8	2	7.9	33.9	48	22	3.1
KU 116578	♂	34.1	18.0	5.2	9.3	8.2	1	8.0	35.0	41	18	3.3
KU 116580	♂	33.9	17.4	5.2	8.5	7.8	1.5	7.8	37.0	45	15	3.2
KU 116606	♂	33.3	17.1	5.2	8.1	7.1	1.5	8.0	36.2	47	23	3.1
KU 116601	♂	33.1	17.1	5.4	8.1	6.9	1	7.8	33.6	46	20	3.0
KU 116604	♂	33.0	17.1	5.1	8.7	7.8	1.5	8.0	32.0	36	17	3.0
KU 116592	♂	32.7	17.1	5.4	8.4	8.0	1.5	8.2	32.2	55	40	3.0
KU 116553	♂	32.5	17.4	5.5	9.0	8.3	0.5	7.9	13.3**	43	16	3.2
LACM 78732	♂	32.5	16.2	5.0	8.3	7.8	1	8.1	35.1	39	17	2.9
KU 116597	♂	32.1	16.5	5.2	8.2	8.0	1	7.8	33.2	40	16	2.8
LACM 78729	♂	28.4	14.1	4.8	7.4	7.2	1	7.4	26.7	34	19	2.9
B. compacta												
KU 116662*	♀	74.2	40.0	10.3	17.7	16.2	2	14.9	68.8	36	20	7.4
GML	♀	73.1	39.4	10.0	16.2	15.0	2	13.9	65.0	44	22	7.4
KU 116659	♀	71.3	37.6	10.2	16.8	15.7	2.5	15.5	59.0	40	26	7.1
KU 116663	♀	70.6	39.6	10.4	16.8	15.8	2.5	15.1	70.1	50	19	7.2
KU 116664	♀	68.5	35.9	10.1	17.8	16.9	1.5	15.2	63.2	48	33	7.2
LACM 78728	♂	53.4	27.4	8.3	13.3	12.3	1.5	12.7	46.8	11	19	5.8
KU 116660	♂	44.9	24.5	7.3	12.4	11.8	1.5	10.9	36.0	20	22	4.9

* = holotype; ** = regenerated tail stubs.

Phalangeal formulae are 1, 2, 3, 2 and 1, 2, 3, 3, 2. This species has extensive webbing, and the hands and feet are very flattened. Accordingly, digits are indistinct, except at their tips. Metapodial elements are broad and flat (Fig. 2) and the phalanges become smaller in a markedly progressive way toward the tips. The basic dumbell shape of the elements is obscured by lateral bony webs. Terminal phalanges are small and irregular in shape, but tend to be pointed (Fig. 2).

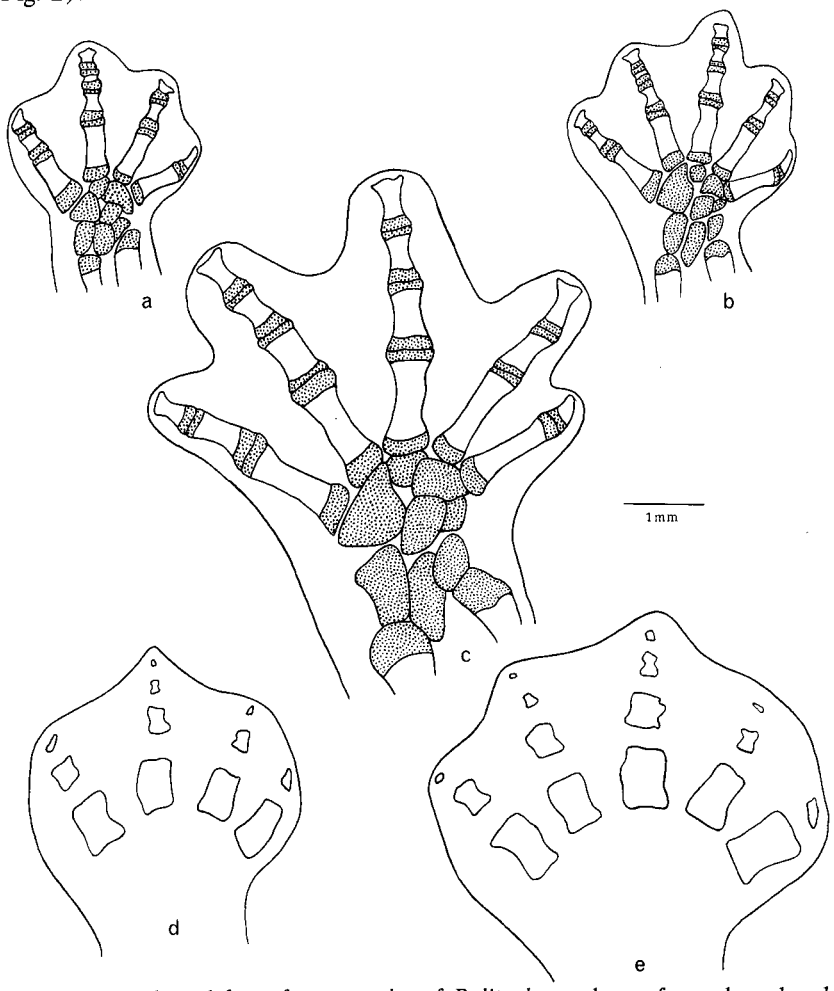

FIGURE 2. Hands and feet of new species of *Bolitoglossa*, drawn from cleared and stained, and x-rayed specimens, with aid of microprojector. Cartilage stippled. (a) Left hand of specimen of *B. minutula*. (b) Left foot of specimen of *B. minutula*. (c) Left foot of specimen of *B. compacta*. (d) Left hand of specimen of *B. cuna* (Holotype). (e) Left foot of specimen of *B. cuna* (Holotype).

Habitat: The holotype was on a leaf of an herb less than 1 m above ground at night in lowland rainforest composed of tall, buttressed trees with a lower story of palms and saplings. The herbaceous layer was poorly developed, and the ground had a deep layer of litter. At Camp Sasardi *B. biseriata* also was found in the same habitat.

Range: Known only from the narrow Caribbean lowland region of eastern Panamá.

A large series of a particularly small species of *Bolitoglossa* was collected on the slopes of Cerro Pando. As this is the smallest known species of the genus, we name it:

Bolitoglossa minutula, new species
Figures 2, 3, and 4

Holotype: KU 116554, an adult female, from the north slope of Cerro Pando, 1920 m (6298 ft) elevation, Provincia de Bocas del Toro, western Panamá, obtained by Charles W. Myers on 3 May 1966.

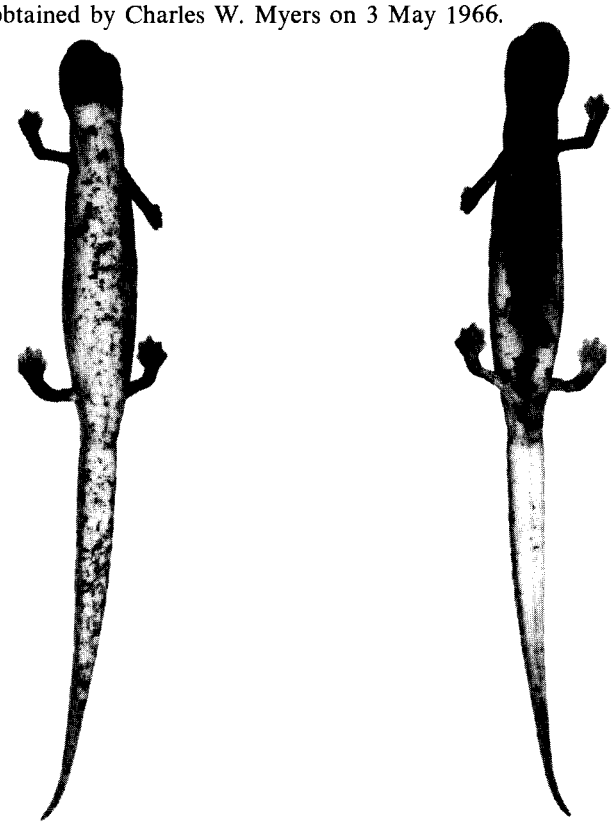

FIGURE 3. Dorsal and ventral views of the holotype of *Bolitoglossa minutula,* new species, KU 116554.

Paratypes: KU 104330 (cleared and stained), KU 116555-61, KU 116564-85, KU 116607-11, LACM 78729-35, all from type locality; KU 116562-63, 2000 m (6560 ft); KU 116593-605, 1920-1970 m (6298-6562 ft); KU 116606, 1810 m (5937 ft); all from north slopes of Cerro Pando, Provincia de Bocas del Toro, western Panamá collected by William E. Duellman, Charles W. Myers, and Linda Trueb on 3-10 May 1966.

Diagnosis: The smallest known species of *Bolitoglossa* (16 adult males: 28.4–36.0, mean 33.5 SL; 14 adult females: 30.1–36.5, mean 33.7 SL) with moderate numbers of maxillary (means; males, 44.1; females, 41.7) and moderately low numbers of vomerine (means; males, 20.2; females, 16.9) teeth; distinguished from *B. epimela* by its smaller size, relatively broader head, and its smaller, more extensively webbed hands and feet. *B. minutula* is distinguished from all other species of the genus by the combination of its small size, extensively webbed hands and feet which retain digital integrity, and dentitional features.

Description of Holotype: Adult female, snout moderately short. Nostril relatively small; labial protuberances of nasolabial groove moderately developed. Canthus rostralis moderately short, slightly arched. Standard length 6.5 times head width; standard length 4.2 times snout-gular fold length. Deep groove below eye extends almost full length of opening, following curvature of eye, but does not communicate with lip. Eye moderately large, originally slightly protuberant. Strongly defined postorbital groove extends posteriorly from eye as shallow depression for 1.7 mm, proceeds sharply ventrad at level of posterior end of mandible and extends across gular area as a moderately defined nuchal groove, parallel to and 2.4 mm anterior to sharply defined gular fold. Vomerine teeth 19, arranged in single row on each side, extend from distal edge of internal choanae in strongly arched pattern toward midline then posteriad towards parasphenoid tooth patch, from which separated by 0.8 mm. Maxillary teeth 46, extend posteriorly to a point about four-fifths through eye. Three premaxillary teeth protrude from behind the lip in the same general plan as maxillary teeth; same size as maxillary teeth. Tail moderately long, 0.96 times standard length, strong lateral compression, strongly constricted at base. Postiliac gland not evident. Limbs of medium length, limb interval 3; standard length 4.3 times right forelimb, 4.2 times right hind limb, and 10.8 times right foot width; webbing of hands and feet extensive, and nearly complete but tips of all digits protrude slightly from webbing (Fig. 2). Pattern one of zygodactyly and webbing combined. Subterminal pads weakly developed but present. The fingers in order of decreasing length: 3, 2, 4, 1; toes in order of decreasing length: 3, 2, 4, 5, 1.

Measurements (in mm): Head width 5.2; snout to gular fold (head length) 8.0; head depth at posterior angle of jaw 2.8; eyelid length 2.6; eyelid width 1.1; anterior rim of orbit to snout 2.2; horizontal orbital diameter 1.9; interorbital distance 1.8; distance between vomerine teeth and parasphenoid tooth patch 0.8; snout to forelimb 9.3; distance separating internal nares 1.2;

distance separating external nares 1.8; snout projection beyond mandible 0.4; snout to posterior angle of vent (standard length) 33.6; snout to anterior angle of vent 31.1; axilla to groin 18.5; tail length 32.3; tail width at base 2.6; tail depth at base 3.2; forelimb length 7.8; hind limb length 8.0; width of right hand 1.9; width of right foot 3.1.

Coloration in Alcohol: The dorsum of the head is black, except for the whitish nasolabial protuberances. The dorsal surfaces of the neck, trunk and tail have a pale yellow-white ground color. This area appears essentially unpigmented, with the exception of a fine punctation of black melanophores. Dorsal surfaces of the limbs are black, but the corresponding surfaces of the hands and feet are mottled with black and yellow-white. Lateral surfaces of the head and neck are black, but the same portions of the trunk and tail are colored like the dorsal surfaces. The gular region and anterior part of the trunk venter are black. The posterior part of the trunk venter is basically yellowish white, with a few large areas of black pigment located midventrally. Ventral surfaces of the tail base region are mottled black and pale yellow-white. The anterior half of the tail venter is a nearly immaculate yellow-white, but the posterior half, as well as the ventral surfaces of the limbs, are mottled black and white. Ventral surfaces of the hands and feet are a dirty gray-yellow.

Coloration in Life: Body and tail pale dull orange with dark gray flecks; head dark brown above and below; chest and belly heavily suffused with dark brown. Limbs brown, becoming orange on digits, minutely flecked with silver. Each cirrus paler brown than rest of head. Several silver flecks on upper lip below eye. Iris pale brown.

Variation: This species is sexually dimorphic, particularly in limb and foot differences. Males have longer limbs (19 males SL 3.5–4.1, mean 3.8, times hind limb lengths; 15 females SL 4.0–4.7, mean 4.3, times hind limb length). Males have 0.5–2 (mean 1.3) costal folds uncovered by appressed limbs (limb interval) versus 2–4 (mean 2.9) for females. Males also have larger feet (SL 9.4–11.5, mean 10.3, times right hind foot width compared to 10.0–12.5, mean 11.0, for females). Heads of males are somewhat broader (SL 5.7–6.8, mean 6.2, times head width, versus 6.1–6.8, mean 6.4, for females).

The species is highly variable in coloration, the holotype being at one extreme, mostly devoid of black pigment save head, limbs and front half of venter. Nine paratypes approach the holotype color but have more melanin present in varying degrees, but always to a greater extent than the holotype. Twenty paratypes are intermediate between the light (largely pigmentless) group (including the holotype) and the nearly all black group. This intermediate sample is characterized by being light to medium brown dorsally with indistinct, narrow stripes of darker black melanin midventrally and dorsolaterally. The venters are variously mottled dirty yellow and black; tail venters usually have more yellow than trunk venters. The final group of 29 paratypes is mostly very dark, but some (12) have much yellow mottling on ventral or

ventrolateral surfaces. Dorsally they are nearly totally uniform brown-black (see Fig. 3 and Table I for additional information).

Osteology: Information concerning osteology has been derived from two cleared and stained specimens (an adult male and female) and from radiographs of a number of additional specimens.

The skull is compact and well ossified. The premaxillary is small, with a narrow dental portion and virtually no palatal process. The bone is narrower and more anteriorly placed in the male than in the female. Frontal processes are very narrow and slender, but they remain separated for their entire length. They terminate at a point just a bit beyond the extreme anterior margin of the orbit, but fall short of the posterior edge of the nasals. Tips of the processes are undilated. There is only a very narrow internasal fontanelle, for the processes diverge only slightly. Contact with the frontals is very restricted. Nasals are large and protuberant. There is marked sexual dimorphism, with the male having inflated nasal capsules and enlarged nasal bones. The bones conform to the shape of the capsule to some extent, and are extended ventrally along the medial border of the capsule. Posteriorly the nasals extend to the orbit. They occupy most of the facial portion of the skull. On their posterolateral aspect the nasals are deeply evacuated by the foramen of the nasolacrimal duct. The evacuation is bordered posterolaterally by the small, triangular, facial process of the maxilla. Prefrontals are absent, and the nasal, and a small process of the frontal, occupy the space usually filled by the prefrontal. The maxillaries are slender bones with small processes. They fall short of the posterior margin of the eyeball.

The vomers are small bones which are widely separated from each other for their entire lengths. The intervomerine fontanelle is broad and has a spindlelike shape. Preorbital processes extend beyond the lateral margins of the vomerine bodies, and these processes bear small teeth which extend in series to about the mid-point of the internal nares.

Frontals are well developed, but have rather small facial portions. The two bones are in close proximity for their entire lengths, but direct contacts are rather restricted. A slight lateral lobe overlaps the parietal. Parietals are well developed and have the lateral spurs that are characteristic of the genus. They are in close proximity medially, and are rather well articulated to one another. The otic capsules are relatively large. They bear no crests or projections. The large parasphenoid is narrow anteriorly, but the orbitosphenoids are well separated from each other. The tip of the parasphenoid is blunt. Posterior vomerine teeth are in large patches on the parasphenoid. These patches approach each other closely, but do not touch. In the two cleared and stained individuals the patches bear 72 (left) and 70 (right), and 60 and 61 bicuspid, ankylosed teeth in the male and female, respectively. The operculum has no stilus. Quadrates are small, and are joined to the skull by the weak, narrow squamosals, and the cartilaginous suspensorium.

The hyobranchial apparatus is typical of other members of the genus

(Wake, 1966), and there are no features worthy of special note in the lower jaw.

Vertebral structure is similar to that of other species of the genus. There are one cervical, fourteen trunk, one sacral, two caudosacral and from 25 to 30 (mean of 10 adults is 27.2, mode 28) caudal vertebrae. In small individuals, such as those characteristic of this species, differentiation according to centrum length is difficult to discern in the types of preparation available. However, the first few caudal vertebrae nearly equal in length the longest trunk vertebrae. Ribs are present on all trunk vertebrae except the last one (8 specimens) or two (4 specimens). Transverse processes are present on all but the last four or five caudal vertebrae, which are very poorly developed. Transverse processes of the first caudosacral vertebra are long and directed almost perpendicularly to the body axis, or slightly in a posterior direction. Those of the second are much shorter and slenderer, and are directed strongly in an anterior direction. The long, slender and non-bifurcated processes of the first caudal vertebra arise at its anterior end. They are even more sharply oriented in an anterior direction than those of the preceding vertebra. They do not cross the immediately anterior pair of processes, but do extend to the origin of those processes at the midvertebral level of the second caudosacral vertebra. More posterior processes have a similar origin and orientation, but are much smaller and become increasing short as one moves down the column.

The distinctive hands and feet have rather well formed digits which are comprised of well developed phalangeal elements. The amount of skeletal material relative to webbing is high. The usual phalangeal formula in *Bolitoglossa* is 1, 2, 3, 2 for the hand and 1, 2, 3, 3, 2 for the foot. This pattern is seen in hands of all individuals studied (12) but one, which has a formula of 1, 2, 2, 2. The typical foot pattern is encountered in six of the twelve animals studied. In four of the specimens the formula is 1, 2, 3, 2, 2. One individual is assymetrical for the two formulas. A final individual has a formula of 1, 2, 2, 2, 2. Thus there is variation in a total of three digits, the longest (number 3) in the hand, and the longest (number 3) and next to longest (number 4) in the foot. Reductions do not occur in the terminal phalanges, but apparently in the penultimate phalanges in all instances. In no case is there a reduction of more than one phalanx per digit. The trend toward reduction is apparent even in those individuals which have the typical formula (Fig. 1). It is particularly evident in the very small amounts of bone in the penultimate phalanges of the third digits in both hands and feet. The terminal phalanges, in contrast, are not only well developed, but also display specialization. Most are distally expanded, with small lateral processes of bone. They probably are functionally significant in these climbing animals. The other phalanges are round in cross-section and unspecialized. The metapodial elements are only a little flattened, and are generally unspecialized. There are seven carpals and eight tarsals in the typical pattern of generalized *Bolitoglossa*. There is no tibial spur, and only a minute crest.

Habitat: With the exception of one individual found in a bromeliad on a log by day, all of these salamanders were obtained at night. One was on a boulder, and one was on a bare tree trunk; all others were on leaves of herbaceous vegetation. None was more than 1 m above the ground. The habitat is described further in the description of the following species.

Range: Known only from the vicinity of the type locality from 1810-2100 m (5937-6888 ft) elevation, north slope of Cerro Pando, Provincia de Bocas del Toro, Panamá.

A small series of rather stout-bodied, generalized species was obtained from the slopes of Cerro Pando. In allusion to its body form it is named:

Bolitoglossa compacta, new species
Figures 2 and 5

Holotype: KU 116662, an adult female from the north slope of Cerro

FIGURE 4. Dorsal views of male (left, KU 116555) and female (right, KU 116575) paratypes of *Bolitoglossa minutula*, new species.

Pando, 1920-1970 m (6298-6462 ft) elevation, Provincia de Bocas del Toro, western Panamá, obtained by Charles W. Myers on 9 May 1966.

Paratypes: KU 116663, same data as holotype; KU 116659-60, KU 104334 (cleared and stained), LACM 78728, 1920 m (6298 ft); KU 116664, 1810 m (6937 ft); all from north slope of Cerro Pando, Provincia de Bocas del Toro, Panamá, collected by William E. Duellman, Charles W. Myers, and Linda Trueb on 3-9 May 1966.

Referred Material: Gorgas Memorial Laboratory (no number), trail to Changena, 1829-2134 m (6000-7000 ft), presumably on the north slope of Cerro Pando, Provincia de Bocas del Toro, Panamá, obtained on 10 August, 1962, by Ratibor Hartmann.

Diagnosis: A moderately large, stout species (1 adult male: 53.4 standard length; 5 adult females 68.5–74.2, mean 71.5 standard length) with moderately low numbers of maxillary (male, 11; mean for females, 43.6) and moderate numbers of vomerine (mean 23) teeth; distinguished from *B. cerroensis* by its stouter body form, somewhat shorter legs, and much darker general coloration (very dark black, with some light orange and yellow blotches dorsolaterally which may fuse to form an indistinct pair of stripes or a poorly defined dorsal band); from *B. marmorea* and *B. sooyorum* by its smaller hands and feet and less numerous teeth; from *B. subpalmata* by its large size and less numerous maxillary teeth. *B. compacta* is distinguished from all other members of the genus by the combination of slightly webbed hands and feet, its coloration, its size and dentitional features, and its relatively simple vertebral pattern in the tail base (see Wake and Brame, 1969).

Description of Holotype: Adult female, snout moderately short. Nostril relatively small; labial protuberances of nasolabial grooves small and poorly developed. Canthus rostralis moderately short in length, gently arched. Standard length 7.2 times head width; standard length 5.0 times snout-gular fold length. Deep unpigmented groove below eye extends almost full length of open-

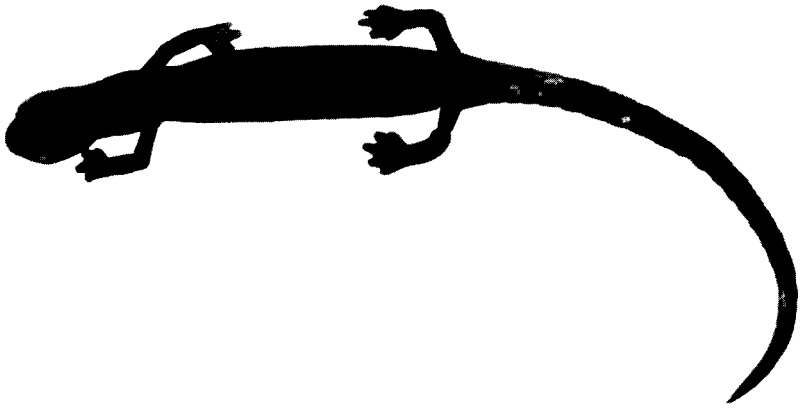

FIGURE 5. Dorsal view of holotype of *Bolitoglossa compacta,* new species, KU 116662.

ing, following curvature of eye, but does not communicate with lip. Eye moderately large, originally protuberant. Well defined postorbital groove extends posteriorly from eye as shallow depression for 2.2 mm, proceeds sharply ventrad at level of posterior end of mandible and extends across gular area as nuchal groove parallel to and 5.6 mm anterior to sharply defined gular fold. Vomerine teeth 20, arranged in a single row on each side, extending from distal edge of internal nares and curving gently toward the midline. Near the midline both rows angle sharply in the direction of the parasphenoid tooth patches, from which they are separated by 0.8 mm. Maxillary teeth 36, extend posteriorly to a point about half way through eye. Six moderately small premaxillary teeth protrude from well behind the lip. Tail strongly laterally compressed, of moderate length, 0.93 times standard length; postiliac gland clearly evident, pale and crescent-shaped. Limbs moderately long, limb interval 2; standard length 4.6 times right forelimb; 4.2 times right hind limb, 10.0 times right foot width. Webbing of hands and feet slight to moderate. Digits broad and truncate at tips. Subterminal pads present on all digits, very small on digit 1. The fingers in order of decreasing length: 3, 2, 4, 1; toes in order of decreasing length: 3, 4, 2, 5, 1.

Measurements (in mm): Head width 10.3; snout to gular fold (head length) 14.9; head depth at posterior angle of jaw 5.3; eyelid length 4.2; eyelid width 2.3; anterior rim of orbit to snout 4.2; horizontal orbital diameter 2.5; interorbital distance 4.0; distance between vomerine teeth and parasphenoid tooth patch 0.8; snout to forelimb 19.9; distance separating internal nares 2.7; distance separating external nares 3.6; snout projection beyond mandible 1.0; snout to posterior angle of vent (standard length) 74.2; snout to anterior angle of vent 67.2; axilla to groin 40.0; tail length 68.8; tail width at base 4.5; tail depth at base 5.3; forelimb length 16.2; hind limb length 17.7; width of right hand 5.4; width of right foot 7.4.

Coloration in Alcohol: The ground color of the holotype is deep black with irregular orange-yellow spots and blotches arranged in dorsolateral rows so as to form imperfect stripes. A few large orange patches occur about the base of the tail and there are some small spots on the top of the head behind the eyes and on the snout. Eyelids are mottled orange and black. A few small scattered yellow-orange spots are present middorsally on the trunk. Ventrolateral and ventral surfaces are uniformly black, almost as dark as the dorsum. No spots of lighter color are present ventrally. Limbs are uniformly black, but for one small light spot on the left hind limb just above the ankle. Palms of hands and soles of feet are greyish.

Coloration in Life: The dorsum varies from dark dull brown with conspicuous reddish brown blotches to deep brownish red. The venter is dull brown, and the iris is pale brown.

Variation: KU 116664 and KU 116660 are colored much as the holotype. Three other paratypes have more extensive orange patching. KU 116659 has extensive yellow-orange mottling on the dorsum of the head and numerous

yellow-orange spots middorsally on the trunk. KU 116663 is almost banded yellow-orange, the head being nearly completely tan-orange dorsally and the trunk dorsum mottled yellow-orange and black with a large bright orange patch at the base of the tail, and smaller streaks and spots on the rest of the tail dorsally. KU 116661 has a broad yellow-orange stripe (almost banded) but the head is mostly black except for orange-black mottled eyelids and snout. The first third of the tail is blotched with orange-yellow. Ventrolateral and ventral surfaces are uniformly black in all. The two male paratypes are much smaller than the five females (including holotype). In addition, the male paratypes have considerably broader heads (SL 6.2–6.4, mean 6.3, times head width; females 6.8–7.3, mean 7.0). Males have larger feet (SL 9.2 times right foot width as compared to 9.5–10.0, mean 9.8 for females) and males have longer hind limbs (SL 3.6–4.0, mean 3.8 times right hind limb length in contrast to 3.8–4.5, mean 4.2, for females). Appressed limbs leave 1.5 costal folds uncovered in males, but 1.5–2.5 (mean 2.1) in females. The males have considerably fewer maxillary teeth but they are also much smaller specimens than the females. See table I for additional data and measurement differences.

Osteology: Information concerning osteology has been derived from one cleared and stained specimen and from radiographs of KU 116664.

The skull is generalized for the genus *Bolitoglossa.* The premaxillary is the normal rather small structure with a moderately narrow dental process and a small palatal shelf. Frontal processes are slender and divergent. They are weak and have virtually no distal expansion. Contact with the expanded facial portions of the frontals is limited. The processes extend to about the level of the extreme anterior margin of the orbit, but do not reach the posterior margins of the nasal bones. The internasal fontanelle is very large and has a distinctive shape. The fontanelle is in the form of an inverted triangle, with two long sides extending anteriorly. The posterior border is straight, and is formed by the strongly divergent facial portions of the frontal bones. The nasals are moderately large but do not protrude from the general outline of the skull. Thus, the nasal capsules are small in a relative sense. Posteriorly the pointed margins of the nasals extend beyond the anterior-most extension of the orbit, but they do not reach the orbit, from which they are separated by the prefrontals. The prefrontal bones are well developed and regular in outline. They overlap the frontals and are in contact with the nasals. The prefrontals are about one-fourth to one-fifth the area of the nasals, and a little less than one-half the area of the facial processes of the maxillaries. The nasolacrimal duct enters the nasal capsule through a space bounded by the posterolateral margin of the nasal, the anterolateral margin of the prefrontal, and the dorsoanterior margin of the facial process of the maxilla. The maxillaries are moderately developed, and have a large facial process. Dentition is weak, and only a part of the bone is toothed. The maxillary extends about three-fourths of the distance through the eyeball.

The vomers are moderate-sized bones which are separated from each

other for their entire lengths. The intervomerine fontanelle is of moderate breadth, and is only a little broader at its midpoint than near either end. Preorbital processes are stout and bear a rather strong dentition which is patched in the cleared and stained individual. The processes extend well beyond the lateral margins of the vomerine bodies. Teeth extend to about the midpoint of the internal nares.

Frontal bones are well developed. Anteriorly the facial processes are restricted to lateral positions by the internasal fontanelle. The processes are long and narrow. The frontals are in close contact medially, but with rather slight articulation. The bones extend farther in a posterior direction laterally than medially. Parietals are separated by a slight gap from each other medially. They are extensively overlapped by the frontals. The parietal spurs typical of the genus are present. Otic capsules are of moderate size for the genus. There are no crests or projections. The blunt tip of the large parasphenoid is relatively broad, and the orbitosphenoids are well separated from each other medially. Posterior vomerine teeth are in large patches on the parasphenoid. These patches do not touch. In the single cleared and stained individual the patches contain 75 (left) and 76 (right) ankylosed, bicuspid teeth. These teeth are about the same size as the marginal teeth on the jaws. The operculum has no stilus. Quadrates are of moderate size and are joined to the skull by unspecialized, rectangular squamosals, and the cartilaginous suspensorium.

The jaws, both upper and lower, are quite weak and poorly developed for an animal of this size, relative to other species of this genus. The hyobranchial apparatus is typical of members of the genus.

Vertebrae have no special features. There are one cervical, fourteen trunk, one sacral, two caudosacral and 24 or 34 (two individuals) caudal vertebrae. The second trunk vertebra is the longest in the body, but caudal vertebrae 2 through 8 are as long as the mid trunk vertebrae. The first caudal vertebra shorter than the shortest trunk vertebra (the first) is the tenth. This does not include the first caudal vertebra which, together with the second caudosacral vertebra is much shortened in the constricted area at the base of the tail. Transverse processes are present on all but the last few vertebrae. The processes are long and nearly perpendicular to the body axis on the first caudosacral vertebra. On the second the somewhat shorter processes are directed first in an anterior and then in a lateral direction. The processes of the first caudal vertebra arise at the anterior end of the vertebra and proceed anteriorly and laterally, reaching a level somewhat short of the midpoint of the second caudosacral vertebra. They are not long relative to other members of the genus. They do not cross those of the more anterior vertebra. More posterior processes have a similar origin at the anterior end of the vertebra, and they become progressively shorter.

The hands and feet have a quite generalized structure. The phalangeal formulae are 1, 2, 3, 2 for the hands and 1, 2, 3, 3, 2 for the feet. The digits are discrete and comprised of well ossified, cylindrical phalangeal elements.

The terminal phalanges are well developed, with a generalized, moderately large expansion (Fig. 2). There are seven carpals and eight tarsals. There is no tibial spur.

Habitat: All specimens were found in undisturbed montane cloud forest (see Myers, 1969, for detailed description). The area, around 1920 m on the north slope of Cerro Pando, supports broad-leaved evergreen forest with a canopy height of about 20 m and an understory of palms and tree ferns. The area was extremely wet in May 1966; probably moisture is abundant continuously, as evidenced by thick growths of mosses on tree trunks and logs.

Four individuals were found on leaves of low herbs (< 1 m) at night; one was on a palm stem at night. At an elevation of 1810 m one individaul was found by day beneath the decomposing thatch of a former shelter.

Three species of *Bolitoglossa (compacta, marmorea,* and *minutula)* and *Oedipina grandis* occur in sympatry on the high northern slopes of Cerro Pando. All are active at night. The *Oedipina* is terrestrial, and *Bolitoglossa marmorea* is arboreal; individuals move about in the moss covering trunks and limbs of trees. *Bolitoglossa compacta* and *minutula* were found on leaves of low herbaceous plants; no ecological differences between the two species were noted.

On the lower Caribbean slopes (830-910 m) of the cordillera the four highland species are replaced by an assemblage of species having broad distributions in lower Central America: *Bolitoglossa biseriata, colonnea, robusta, schizodactyla,* and *Oedipina collaris.*

RELATIONSHIPS

The three species described in this paper are only remotely related, despite the fact that they are all members of the same genus. The genus is large and diverse, and new species are being discovered regularly. Any detailed consideration of relationships is premature, but at least some general comments can be presented.

The relationships of *Bolitoglossa cuna* are with members of the *sima* group (Brame and Wake, 1972), which occur mainly west of the continental divide in Panama, Colombia and northern Ecuador. The other members of the group include *B. sima, B. chica, B. biseriata,* and *B. silverstonei.* All are similar in size, extent of hand and foot webbing, general structure of the hands and feet, head proportions and general aspects of coloration. *B. cuna* has more teeth than any other members of this group and is larger than *B. chica.* It also has a narrower head than species of similar size. In general this group is so poorly known that further comments are inappropriate. Only skeletons of *B. sima* and *B. chica* have been available for study. There is no basis for postulation of relationship with any other species group.

Bolitoglossa minutula is a very distinctive species that does not fit in any currently recognized group. It is most similar to *Bolitoglossa epimela,* a species known from the Atlantic slope of Costa Rica at a considerably lower (915 m)

elevation (Wake and Brame, 1963). However, *B. epimela* has very large, somewhat less extensively webbed hands and feet and is a larger species, with a relatively narrower head. *B. epimela* has relatively few teeth for its size. The only other species that seems to be a possible close relative of *B. minutula* is a sympatric associate which appears to be undescribed. It is a somewhat larger species with less fully webbed hands and feet, but with similar numbers of teeth, and limbs of similar length. This species is somewhat intermediate between *B. epimela* and *B. subpalmata* in structural features (see Wake and Brame, 1963), having more teeth, a broader head and less hand and foot webbing than *B. epimela,* but being smaller and much slenderer than *B. subpalmata.* Thus, in a structural sense only, there is something of a morphological transition from *B. subpalmata* to *B. minutula.* In contrast, we do not see any indications of relationship of *B. minutula* to any of the fully webbed species of the neighboring lowlands (for example, *B. colonnea* or *B. biseriata*).

Bolitoglossa compacta falls in the *B. cerroensis-B. marmorea-B. sooyorum* section of the *B. subpalmata* group. There is a close similarity among these species in gross morphology, but structural distinctions can be recognized. Further, on both Cerro de la Muerte in Costa Rica *(B. sooyorum, B. cerroensis)* and on Cerro Pando *(B. marmorea, B. compacta)* two members of the section occur in sympatry. *B. sooyorum* and *B. marmorea* are apparent close relatives, as are *B. cerroensis* and *B. compacta.* Distinctions between members of the first pair are subtle, and they should probably be considered races. *B. cerroensis* and *B. compacta* are more distinct. *B. compacta* has shorter legs and a broader head, but the two species are similar in number of maxillary teeth, vomerine teeth and foot shape. The low numbers of maxillary teeth in this pair set them apart from other members of the *subpalmata* group. *B. compacta* is a darker *salamander,* but elements of the coloration, especially pattern, are similar. Light coloration tends to be yellow-orange to reddish brown in *B. compacta,* but lavender in *B. cerroensis.* Finally there are some osteological differences between the two species. It must be remembered that these are based on detailed study of only one *B. compacta* and two *B. cerroensis,* in addition to radiographs. However, *B. compacta* has prefrontal bones, which are fused with the nasals in *B. cerroensis.* In addition, the internasal fontanelle is much larger in *B. compacta,* and the premaxillary bones are less well developed. Structure of the phalangeal elements is nearly identical in the two species.

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RESUMEN

Tres especies de salamandras, *Bolitoglossa cuna, B. minutula, y B. compacta,* son descritas para poblaciones de Panamá.

Bolitoglossa cuna es una especie con manos y pies totalmente palmeados que habita a escasa altitud en el Territorio de San Blas. Es una especie miembro del grupo *sima.*

Bolitoglossa minutula es la especie más pequeña del género. Se le ubica a altitudes entre 1800 y 2000 m cerca de la frontera con Costa Rica. Tiene algunas similitudes con la especie costaricense de tamaño más grande, *B. epimela.*

Bolitoglossa compacta es una especie de gran tamaño con manos y pies escasamente palmeados y simpátrica con *B. minutula.* Está emparentada con *B. cerroensis* de Costa Rica.

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