# SYSTEMATICS AND EVOLUTION OF NEOTROPICAL SALAMANDERS OF THE *BOLITOGLOSSA HELMRICHI* GROUP

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ABSTRACT: The *Bolitoglossa helmrichi* group includes *B. helmrichi* and *B. cuchumatana* of Guatemala, *B. flavimembris* of Guatemala and Mexico, and two new species, *B. hartwegi* from Chiapas, Mexico, and *B. stuarti* from near the Mexican-Guatemalan border. The group bridges the gap between the specialized lowland members of the *rufescens* group and the more generalized species of the uplands of Nuclear Central America, and provides support for an earlier decision to synonymize the genus *Magnadigita* with *Bolitoglossa*. In particular, hand and foot morphology of these species represents all stages of intermediacy between the slightly webbed, large digited structures of the upland species and the diminutive, fully webbed, small digited ones of the lowland species. As a result of the discovery of the new species, a nearly continuous morphocline is apparent which provides insights into the morphological events accompanying the evolution of a tropical lowland salamander fauna.

Lungless salamanders of the family Plethodontidae are notably successful in the New World Tropics, where more than forty per cent of salamander species occur. All are members of a single radiation, the supergenus *Bolitoglossa* (Wake, 1966). Salamanders are primarily a North Temperate group, and their entrance into the tropics came long after the major radiation of the order Caudata. The relative abundance of neotropical salamanders and the correlation of increased species diversity with tropical environments invite further scientific investigation. In earlier papers we have presented the results of our systematic studies on lower Central and South American salamanders of the genus *Bolitoglossa* (Wake and Brame, 1962, 1963a, 1963b, 1966a, 1966b; Brame and Wake, 1962a, 1962b, 1963a, 1963b). This paper is an analysis of five species of the *Bolitoglossa helmrichi* group from the highlands of Chiapas, Mexico, and Guatemala. These species provide data which elucidate evolutionary patterns associated with invasion of tropical lowlands, and enable formulation of hypotheses concerning morphological evolution during phylogeny. In future papers we plan to analyze the remaining species of the genus, with emphasis on patterns of evolution.

The *helmrichi* group can be defined as follows: salamanders of the genus *Bolitoglossa* having small to moderate size (adults average from 38 to 53 mm

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standard length (abbreviated SL throughout remainder of text), 60 mm in the single adult of *stuarti*); relatively broad heads (SL averages 5.5 to 6.3 times head width, 6.7 in the rather narrow-headed adult of *stuarti*); eyes moderate in size, not strongly protuberant; snout pronounced to moderate; moderate to high numbers of marginal teeth; limbs relatively long (limb interval averages 0.5 to 1.0); hands and feet with moderate to extensive webbing, moderate to extensive flattening, and digits of reduced size; tail shorter than body; light ventral pigmentation, especially on tail.

Content: *Bolitoglossa cuchumatana, B. flavimembris, B. hartwegi, B. helmrichi, B. stuarti.*

In the following sections brief redescriptions and diagnoses are presented for the Guatemalan species of the *helmrichi* group, *B. flavimembris, B. helmrichi,* and *B. cuchumatana,* and two new members of the group are described.

## **Bolitoglossa flavimembris** (Schmidt, 1936)

*Oedipus flavimembris* Schmidt, 1936: 158.
*Magnadigita flavimembris,* Taylor, 1944: 218.
*Bolitoglossa flavimembris,* Wake and Brame, 1963a: 386.

*Holotype*: FMNH 20381, an adult female from Volcán Tajumulco at 2195 m (7200 feet) on the trail above El Porvenir, San Marcos, Guatemala, **10**.[3]

*Material Examined*: FMNH 20322 (cleared and stained), 20333 (2), 100128, UMMZ 80935, all topoparatypes, **10**; UIMNH (field numbers) 2538, 2545, Mexico, Chiapas, Volcán Tacaná, El Chicuite, **9**, 2195 m (7200 feet); FMNH 142081, Guatemala, San Marcos, near Aldea la Fraternidad between San Rafael Pie de la Cuesta and Palo Gordo, **11**, 2400 m (7900 feet).

*Diagnosis*: A moderate-sized species of *Bolitoglossa* (1 adult male: 50.1 mm SL; 6 adult females: 40.5 - 64.5, mean 53.2 mm SL) with moderate numbers of maxillary (mean 49.1) and relatively low numbers of vomerine (mean 23.8) teeth in adults, distinguished from other members of the *helmrichi* group by its larger size, more robust habitus, broader head, relatively smaller and less completely webbed hands and feet (Fig. 15) and distinctive coloration (". . . back in life uniform Hair Brown, lighter on sides and venter, lightest on chin, limbs Colonial Buff, feet dark gray above and below, and an obscure dark line down middle of belly," Schmidt, 1936).

*Description*: *Bolitoglossa flavimembris* is a moderate to moderately large, robust species with a relatively short, broadly rounded snout. The one adult male is smaller than the mean size of the six adult females; females of *Bolitoglossa* are typically larger than males. The nostrils are small. Labial protuberances are poorly developed in males and females. A mental hedonic gland

[3]Bold face numerals here and below refer to plotted localities on map (Fig. 3).

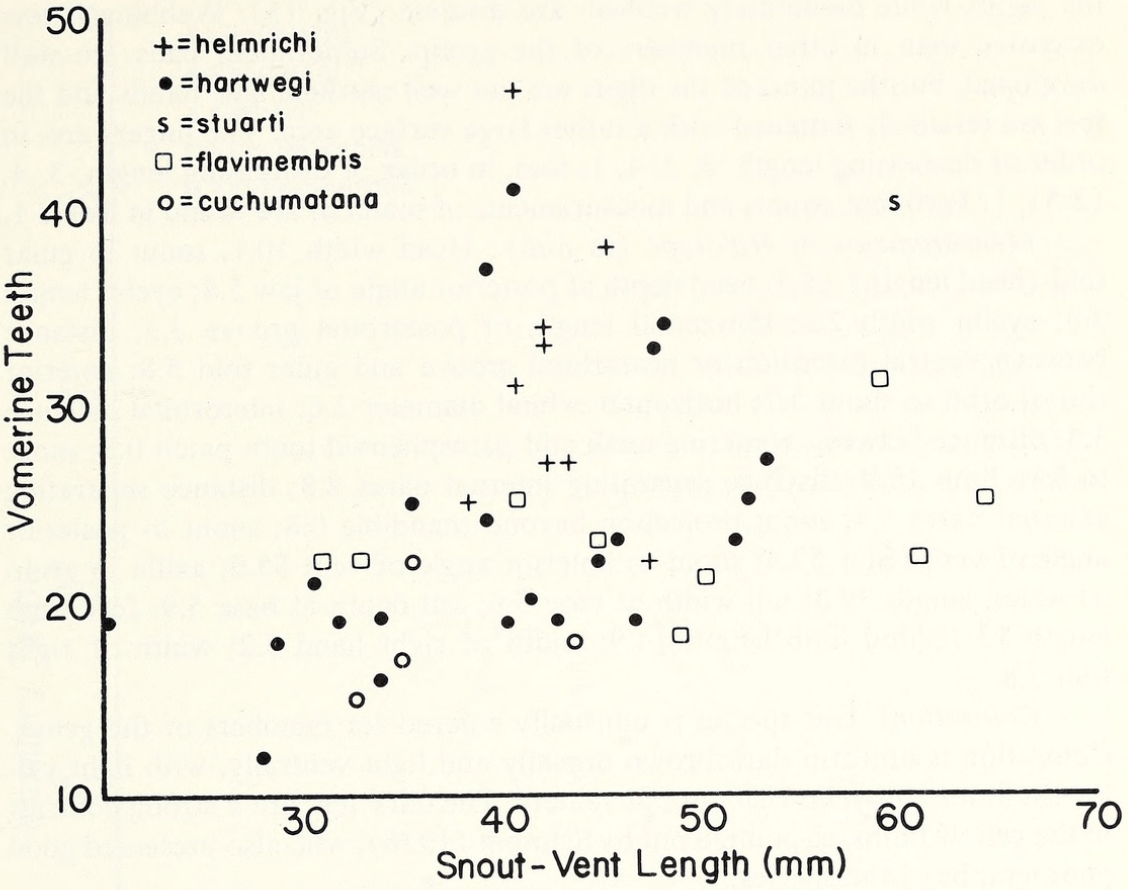


Figure 1. Variation in vomerine dentition in the *Bolitoglossa helmrichi* group.

is poorly developed in the male. The head is moderately broad, but rather variable (SL 5.4 - 6.5, mean 5.8 times head width in six females; 6.3 in male). A relatively deep groove extends below the eye, following its curvature, but does not communicate with the lip. The moderate-sized eyes are rather protuberant and are visible beyond the margin of the jaw when viewed from below. A shallow postorbital groove extends posteriorly from the eye as a shallow, irregular depression. At the posterior end of the mandible the groove proceeds sharply ventrally and extends across the throat, anterior to the gular fold, as a moderately defined depression. Vomerine teeth increase in number slowly with increasing size (Fig. 1). The teeth are typically in long, single series and extend beyond the medial border of the internal nares. Maxillary teeth extend beyond the center of the eye and increase in number slowly with increasing size (Fig. 2). Few premaxillary teeth (3-7) are present and they pierce the lip in the adult male. The trunk and tail are robust. The stout tail is nearly round in cross section and is rather strongly constricted at its base. Lightly pigmented postiliac glands are barely evident. Limbs are robust and of moderate length. Limb interval (costal folds between appressed limbs) varies from 1 to 2 (mean 1.5) in females and is 0.5 in the male. Hands and feet are moderate in size and

the digits, while moderately webbed, are discrete (Fig. 15). Webbing is less extensive than in other members of the group. Subterminal pads are well developed, but the joints of the digits are not well marked. The hands and the feet are relatively flattened with a rather large surface area. The fingers are, in order of decreasing length, 3, 2, 4, 1; toes, in order of decreasing length, 3, 4, (2-5), 1. Pertinent counts and measurements of material are found in Table 1.

*Measurements of Holotype* (in mm): Head width 10.1; snout to gular fold (head length) 14.2; head depth at posterior angle of jaw 5.8; eyelid length 3.8; eyelid width 2.2; horizontal length of postorbital groove 3.3; distance between ventral extension of postorbital groove and gular fold 5.8; anterior rim of orbit to snout 3.7; horizontal orbital diameter 2.6; interorbital distance 3.3; distance between vomerine teeth and parasphenoid tooth patch 0.8; snout to fore limb 18.9; distance separating internal nares 2.8; distance separating external nares 3.3; snout projection beyond mandible 0.8; snout to posterior angle of vent (SL) 59.4; snout to anterior angle of vent 55.6; axilla to groin 31.4; tail length 39.3; tail width at base 5.6; tail depth at base 5.9; fore limb length 13.7; hind limb length 14.9; width of right hand 5.2; width of right foot 5.8.

*Coloration*: This species is unusually colored for members of the genus. Coloration is uniform dark brown dorsally and light ventrally, with light yellowish limbs and yellowish tan tail venters. The dark feet are a strong contrast to the yellow limbs, as pointed out by Schmidt (1936), who also presented good photographs of the species.

*Range*: Known from the slopes of Volcán Tajumulco and Volcán Tacaná and from the mountains along the southwestern escarpment of the Guatemalan Plateau, at elevations between 7000 and 8000 feet, in San Marcos, Guatemala, and the border area of Chiapas, Mexico (Fig. 3). This report constitutes the first record of the species in Mexico.

### **Bolitoglossa cuchumatana** (Stuart, 1943)

*Oedipus cuchumatanus* Stuart, 1943: 14.
*Magnadigita cuchumatana,* Taylor, 1944: 218.
*Bolitoglossa cuchumatana,* Wake and Brame, 1963a: 386.

*Holotype*: UMMZ 89110, an adult male from an oak forest about 2 kilometers north of Nebaj, approx. 1900 m (6250 feet), El Quiché, Guatemala, **12**.

*Material Examined*: UMMZ 89111-13, topoparatypes, **12**.

*Diagnosis*: A small species (3 adult males: 35.2 - 43.5, mean 38.2 mm SL; 1 female 33.4 mm SL) with low numbers of teeth (maxillary: 26 - 38, mean 34.7; vomerine: 15 - 22, mean 18); distinguished from *B. flavimembris* by smaller size, more extensively webbed feet, and banded (or mottled) body

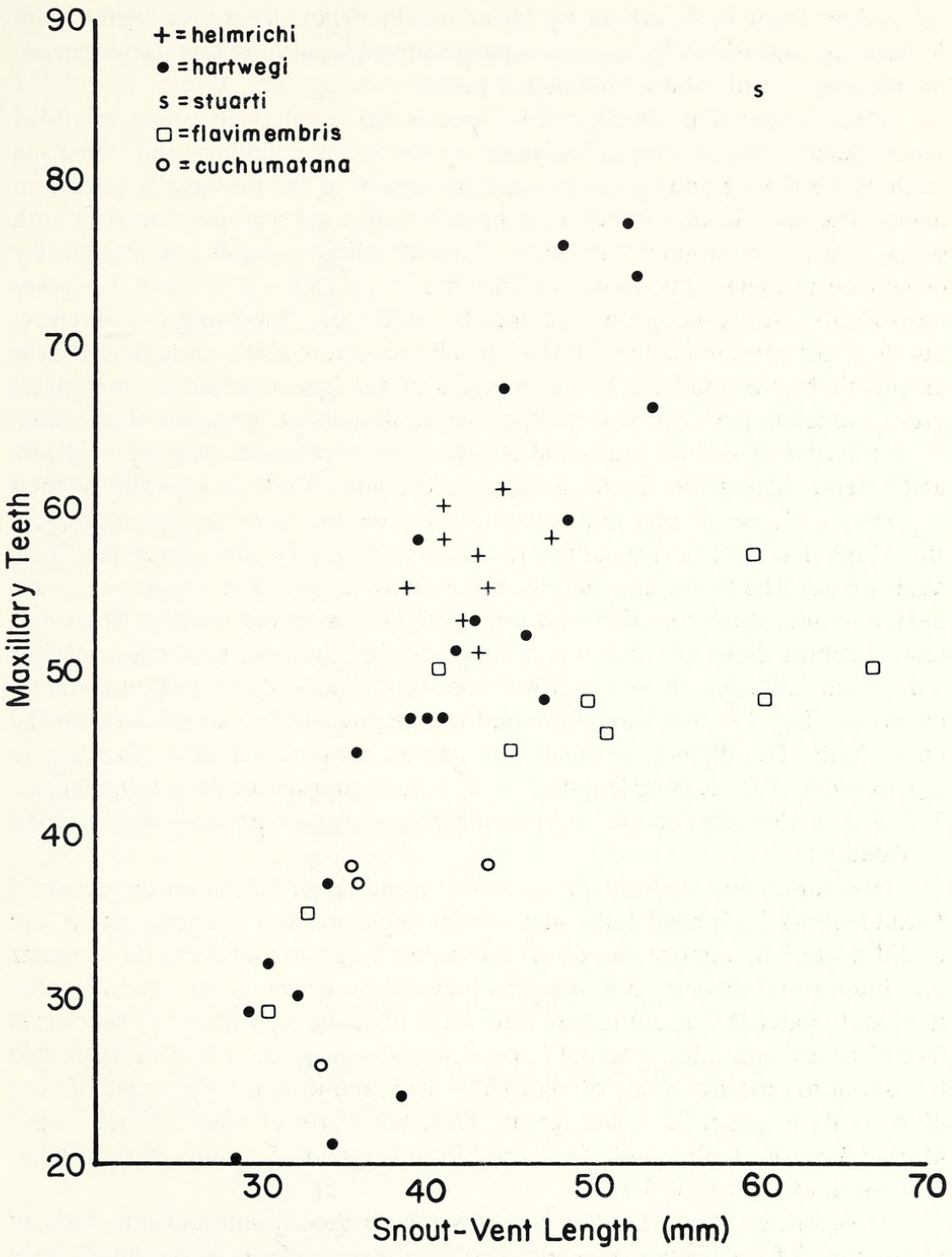


Figure 2. Variation in maxillary dentition in the *Bolitoglossa helmrichi* group.

coloration; from *B. helmrichi* by fewer maxillary and vomerine teeth; from *B. hartwegi* and *stuarti* by less extensively webbed hands and feet, larger terminal phalanges, and subterminal digital pads.

*Description*: This small, robust species has a relatively short, rounded snout. Sexual dimorphism is indicated by the fewer maxillary and vomerine teeth of the female and by the forward placement of the premaxillary teeth in males. The nostrils are small. Labial protuberances are well developed in both sexes, and are pronounced in males. Mental hedonic glands are moderately developed in males. The head is rather broad (SL 5.1 - 6.0, mean 5.5 times head width). A distinct groove extends below the eye, following its curvature, but does not communicate with the lip. The moderate-sized, protuberant eyes extend slightly beyond the lateral margins of the jaw. A shallow, postorbital groove extends posteriorly from the eye as a shallow, irregular depression. At the posterior end of the mandible the groove proceeds sharply ventrally and extends across the throat anterior to the gular fold, as a poorly defined depression. Vomerine and maxillary teeth increase in number with increasing size (Figs. 1 and 2). Premaxillary teeth are few (1 - 4), and pierce the lip in adult males. The trunk and tail are moderately robust. The swollen tails are nearly round in cross section and are strongly constricted basally. The moderately robust limbs are moderately long and limb interval varies from 0.5 to 2.0 (mean 1.0). Hands and feet are relatively large. Webbing is moderately extensive (Fig. 15) and leaves one-half to one phalanx free of the web on the inner digits. The digits bear small but discrete subterminal pads. The fingers are, in order of decreasing length, 3, 4, 2, 1; toes, in order of decreasing length, 3, 4, 5, 2, 1. Pertinent counts and measurements of the type series are included in Table 1.

*Measurements of Holotype* (in mm): Head width 7.3; snout to gular fold (head length) 12.2; head depth at posterior angle of jaw 3.2; eyelid length 2.9; eyelid width 1.8; anterior rim of orbit to snout 3.3; horizontal orbital diameter 3.2; interorbital distance 3.9; distance between vomerine teeth and parasphenoid tooth patch 0.6; snout to fore limb 14.2; distance separating internal nares 2.0; distance separating external nares 2.4; snout projection beyond mandible 0.9; snout to posterior angle of vent (SL) 43.5; snout to anterior angle of vent 40.4; axilla to groin 22.1; tail length 37.7; tail width at base 3.6; tail depth at base 3.6; fore limb length 11.7; hind limb length 11.8; width of right hand 4.5; width of right foot 5.5.

*Coloration*: Stuart (1943) has presented a description and an excellent photograph of the species. He described the dorsal surfaces of the head, body and tail as mottled with purplish brown and light reddish brown (pinkish in life), forming a broad middorsal stripe. Narrower, light reddish brown stripes extend from the eye to the base of the tail in three of the four specimens, with coloration of the back gradually fading into the ventral coloration in the fourth. Lateral surfaces are mottled with purple and reddish brown. Ventral surfaces

TABLE I

Measurements and Data for *Bolitoglossa cuchumatana*, *B. flavimembris*, and *B. helmrichi*

| | Sex | Snout-Vent Length | Axilla-Groin Length | Head Width | Hind Limb Length | Fore Limb Length | Tail Length | Numbers of Maxillary Teeth | Numbers of Vomerine Teeth | Limb Interval | Foot Width |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *B. cuchumatana* | | | | | | | | | | | |
| UMMZ 89110** | ♂ | 43.5 | 22.1 | 7.3 | 11.8 | 11.7 | 37.7 | 38 | 18 | 0.5 | 5.5 |
| UMMZ 89111 | ♂ | 35.9 | 18.8 | 6.5 | 8.9 | 8.2 | 28.2 | 37 | 22 | 2 | 3.7 |
| UMMZ 89113 | ♂ | 35.2 | — | 6.6 | 8.8 | — | 26.4 | 38 | 17 | 1 | — |
| UMMZ 89112 | ♀ | 33.4 | — | 6.5 | 8.2 | — | 23.0 | 26 | 15 | 1 | 3.7 |
| *B. flavimembris* | | | | | | | | | | | |
| FMNH 100128 | ♂ | 50.1 | 26.2 | 8.0 | 13.8 | 12.0 | 38.2 | 46 | 21 | 0.5 | 5.2 |
| FMNH 20333 | ♀ | 64.5 | 33.4 | 9.9 | 15.6 | 15.2 | 45.7 | 50 | 25 | 2 | 6.8 |
| FMNH 20381** | ♀ | 59.4 | 31.4 | 10.1 | 14.9 | 13.7 | 39.3 | 57 | 31 | 2 | 5.8 |
| FMNH 20322 | ♀ | 49.7 | 26.0 | 9.2 | 12.2 | 11.1 | 32.7 | 48 | 18 | 1.5 | 5.2 |
| UIMNH 2538 | ♀ | 44.9 | 23.0 | 7.9 | 11.2 | 10.7 | 31.1 | 45 | 23 | 1.5 | 4.2 |
| FMNH 142081 | ♀ | 40.4 | 19.2 | 7.2 | 10.3 | 8.7 | 36.2 | 50 | 25 | 2 | 4.3 |
| *B. helmrichi* | | | | | | | | | | | |
| UMMZ 89132 | ♂ | 47.6 | 24.5 | 7.8 | 12.2 | 11.0 | 31.8 | 58 | 22 | 1 | 5.2 |
| FMNH 20153** | ♂ | 38.4 | 19.9 | 6.8 | 11.2 | 9.9 | 35.8 | 55 | 25 | 0.5 | 4.3 |
| UMMZ 89133 | ♀ | 45.7 | 25.9 | 7.8 | 12.0 | 11.2 | 43.2 | 61 | 38 | 0.5 | 4.7 |
| UMMZ 89137 | ♀ | 42.6 | 21.2 | 7.2 | 10.5 | 9.3 | 38.6 | 51 | 27 | 1 | 4.1 |

** holotype

of the head and body are pale yellow, and the tail is light orange-yellow mottled with gray.

*Range*: Known only from the type locality in the Sierra de los Cuchumatanes, El Quiché, Guatemala (Fig. 3).

### **Bolitoglossa helmrichi** (Schmidt, 1936)

(?) *Spelerpes morio* (part) Brocchi, 1883: 113.

*Oedipus helmrichi* Schmidt, 1936: 152.

*Bolitoglossa helmrichi*, Taylor, 1944: 219.

*Magnadigita helmrichi*, Stuart, 1952: 5.

*Bolitoglossa helmrichi*, Wake and Brame, 1963a: 386.

*Holotype*: FMNH 21063, an adult male from mountains above Finca Samac, west of Cobán, Alta Verapaz, Guatemala, **13**, at 1300 m (4264 feet).

*Material Examined*: FMNH 20707 (8, 1 cleared and stained), topoparatypes; UMMZ S-1597 (cleared and stained); UMMZ 80929, 89136-7 (14), 89138, Guatemala, Alta Verapaz, Finca Samac, **13**, 1350-1500 m (4440-4920 feet); UMMZ 89132-34, 89135 (2), Guatemala, Alta Verapaz, Finca Chichén, **14**, 1700-1800 m (5600-5900 feet); UMMZ 89131, Guatemala, Alta Verapaz, Finca Volcán, **15**, 1410 m (4640 feet).

*Diagnosis*: A moderately small species of *Bolitoglossa* (5 adult males: 38.4 - 47.6, mean 43.1 mm SL; 5 adult females: 41.2 - 45.7, mean 42.8 mm SL) with moderately high numbers of maxillary teeth (mean 56.4) and moderate numbers of vomerine teeth (mean 30.9) in adults, distinguished from *B. flavimembris* by smaller size, higher numbers of maxillary and vomerine teeth, and coloration, from *B. cuchumatana* by higher numbers of maxillary and vomerine teeth, from *B. hartwegi* and *B. stuarti* by less extensively webbed feet, larger terminal phalanges, and discrete subterminal digital pads.

*Description*: *Bolitoglossa helmrichi* is a relatively small, rather stout species with a moderately large, truncate snout. Males and females are about the same size, but males apparently mature at a smaller size. The nostrils are small. Labial protuberances are moderate in females and only slightly better developed in males. Mental hedonic glands are moderately developed in males. The head is broad (SL 5.2 - 6.1, mean 5.7 times head width in 4 adult males; 5.4 - 6.1, mean 5.9 in 5 adult females). A relatively deep groove extends below the eye, following its curvature, but it does not communicate with the lip. The moderate-sized eyes are only slightly protuberant and are generally not visible beyond the margin of the jaw when viewed from below. A shallow postorbital groove extends posteriorly from the eye as a shallow, irregular depression. At the posterior end of the mandible the groove proceeds sharply ventrally and extends across the throat, anterior to the gular fold, as a moderately defined depression. Vomerine teeth increase in number with increasing size (Fig. 1). The teeth are typically in long, single series and extend beyond the medial border of the internal nares. Maxillary teeth extend beyond the center of the eye and increase in number with increasing size (Fig. 2). The few premaxillary teeth (2-3 in males, 3-7 in females) pierce the lip in adult males. The trunk and tail are of moderate dimensions, neither robust nor slender. The tail is nearly round in cross section and is strongly constricted at its base. The tail is always considerably shorter than standard length. Light-colored postiliac glands are barely evident. The slender limbs are moderately long. Limb interval varies from 0 to 1.0 (mean 0.5) in males and from 0.5 to 1.5 (mean 1.0) in females. Hands and feet are moderate in size and the digits are discrete (Fig. 15). Webbing is moderately extensive, but digital tips are free and bear well developed 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. Pertinent counts and measurements of four specimens are found in Table 1.

*Measurements of Holotype* (in mm): Head width 6.8; snout to gular fold

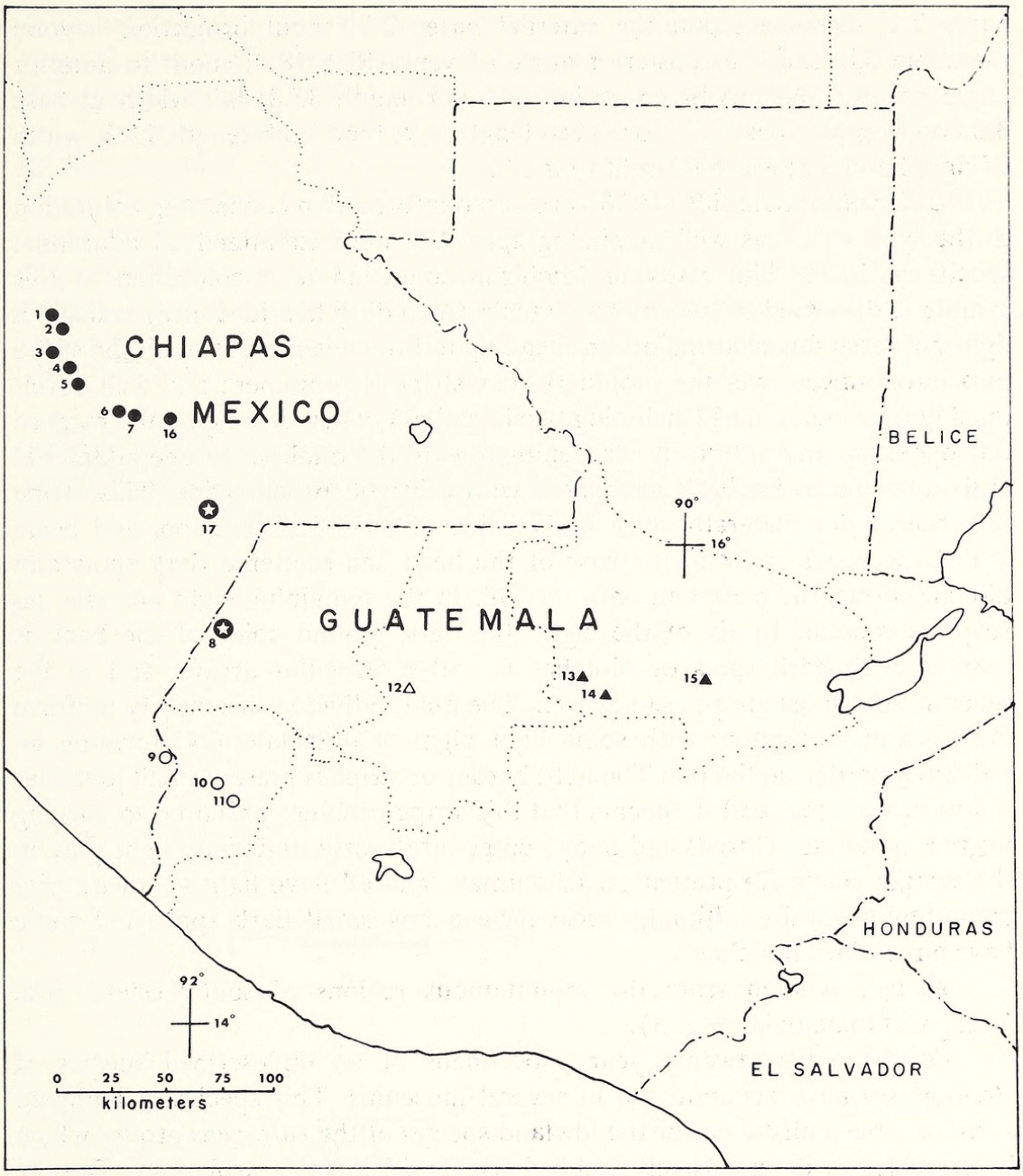


Figure 3. Distribution of the species of the *Bolitoglossa helmrichi* group in Chiapas, Mexico, and Guatemala. The map symbols indicate the collection localities for the different species: solid circle=*B. hartwegi*; open star in solid circle=*B. stuarti*; open circle=*B. flavimembris*; open triangle=*B. cuchumatana*; solid triangle=*B. helmrichi*. The numbers correspond to the locality data (indicated in bold face) in the holotype, paratype, and material examined sections of the text.

(head length) 10.2; head depth at posterior angle of jaw 3.1; eyelid length 3.0; eyelid width 1.7; anterior rim of orbit to snout 2.9; horizontal orbital diameter 2.2; interorbital distance 2.2; distance between vomerine teeth and parasphenoid tooth patch 0.8; snout to fore limb 12.1; distance separating internal

nares 2.1; distance separating external nares 2.9; snout projection beyond mandible 0.8; snout to posterior angle of vent (SL) 38.4; snout to anterior angle of vent 36.3; axilla to groin 19.9; tail length 35.8; tail width at base 3.3; tail depth at base 3.3; fore limb length 9.9; hind limb length 11.2; width of right hand 3.8; width of right foot 4.3.

*Coloration*: Schmidt (1936) presented information concerning coloration in the type series, as well as photographs. We have examined 23 additional specimens in the University of Michigan collections and coloration of this sample is discussed below. In 15 animals (including five juveniles) a distinct light-bordered dorsal stripe of tan blending to brown is present, with the stripe most pronounced over the shoulders. The stripe is prominent and well developed in four individuals (including two juveniles), where it is especially marked dorsolaterally and anteriorly, darkening toward the midline. In one additional individual the entire back is covered with a bright, broad stripe. This stripe is bordered dorsolaterally by a broken line of dark pigmentation, and bears a Y-shaped dark mark at the base of the head and scattered dark spots and blotches down the back and onto the tail. In the remaining eight animals, no stripe is present. In six of the eight, the dark ground color of the back is marked with dark spots or blotches in rather irregular arrays, and in the seventh light spots are present as well. The final individual has nearly uniform dark dorsal coloration, with some light pigment dorsolaterally, forming an indistinct border on the tail. The light border or stripe is present in all juveniles that we have seen, and it appears that this stripe becomes obscured to varying degrees in adults. Throats and body venters are nearly uniformly light gray in the sample. Tails are present on 17 animals, and all have light yellowish pigmentation ventrally, although most have a few small dark spots and some have larger dark blotches.

*Range*: Known from the mountainous regions of southwestern Alta Verapaz, Guatemala (Fig. 3).

Over the past twenty years, specimens of an undescribed species of *Bolitoglossa* have accumulated in several museums. This species, a highland form, has been mistaken for the lowland species of the *rufescens* group, which it resembles in its extensively webbed feet and general morphology. Despite these similarities, its relatives apparently are members of the *helmrichi* group. We name the species in memory of the late Professor Norman Hartweg of the University of Michigan, an able scientist who spent many years studying Chiapan amphibians and reptiles and who stimulated and guided many investigations of the biology of tropical organisms.

**Bolitoglossa hartwegi** new species

Figs. 4-13

*Holotype*: UMMZ 121557, an adult female from 4.5 miles W San

Cristóbal de Las Casas, **3**, Chiapas, Mexico, collected by Floyd L. Downs, June 30, 1960. The specimen was collected at about 2134 m (7000 feet) elevation under a log at the top of a slope covered with a pine-oak forest.

*Paratypes*: All from Chiapas, Mexico. MVZ 57098-57115 (18), 6 mi. SE San Cristóbal de Las Cases, **4**, 2226 meters (7300 feet); MVZ 57737-8, 32 mi. SE San Cristóbal de Las Casas, **6**, 2287 m (7500 feet); MVZ 66191, 35 mi. SE San Cristóbal de Las Casas, **7**, 2134 m (7000 feet); LACM 40603-7, JFC-65-130 (cleared and stained, to be deposited LACM), Municipio de San Cristóbal de Las Casas, SE slope near summit of Cerro Zontehuitz, **2**, 2865 m (9300 feet); LACM 40601, Municipio de San Cristóbal de Las Casas, SE

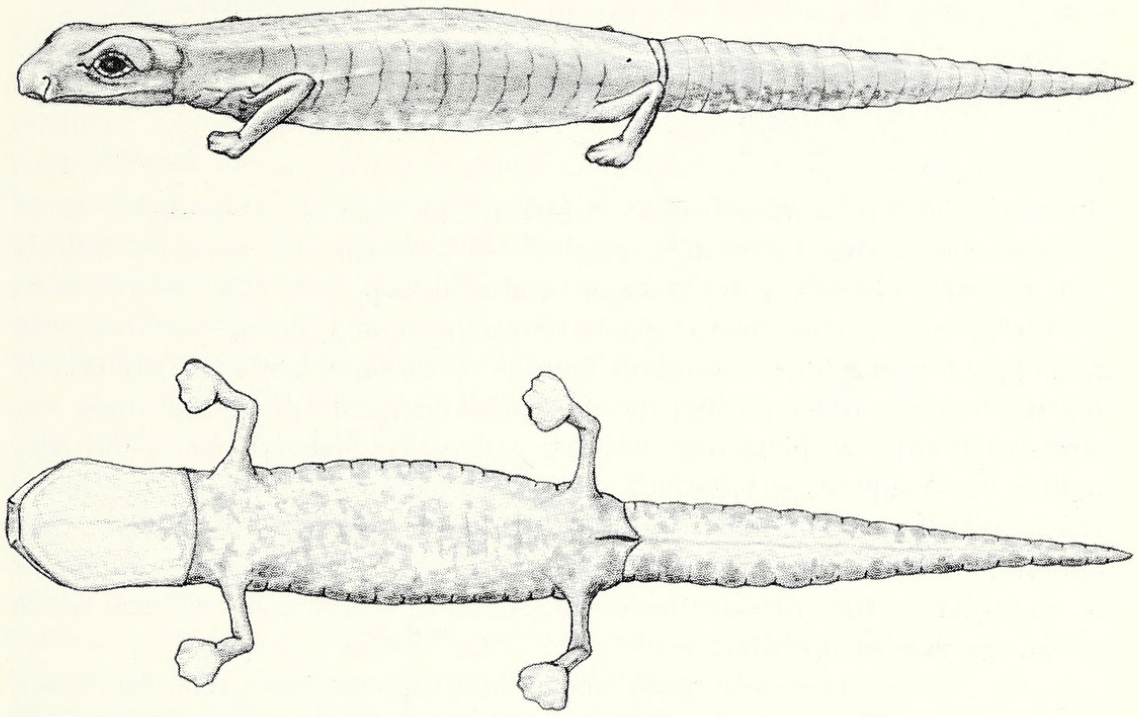

Figure 4. Holotype of *Bolitoglossa hartwegi* (UMMZ 121557). Dorsolateral (top) and ventral (bottom) views.

slope near summit of Cerro Zontehuitz, **2**, 2865 m (9400 feet); TCWC 21398-99, near summit of Cerro Zontehuitz, **2**, 2805 m (9200 feet); LACM 40602, Municipio de Chamula, San Cristóbal de Las Casas to Chenalhó Rd., 15.1 mi. N San Cristóbal de Las Casas, **1**, 2835 m (9300 feet); LACM 44209, 12 mi. E Teopisca, **16**, 2348 m (7700 feet); UAZ 20262, about 12 mi. SE San Cristóbal de Las Casas, **5**, 2043 m (6700 feet).

*Diagnosis*: A moderately small species (7 adult males: 34.0 - 46.9, mean 40.6 mm SL; 11 adult females: 34.2 - 53.6, mean 45.1 mm SL) with moderate to high numbers of maxillary teeth (female mean, 54.2; male mean, 50.0) and

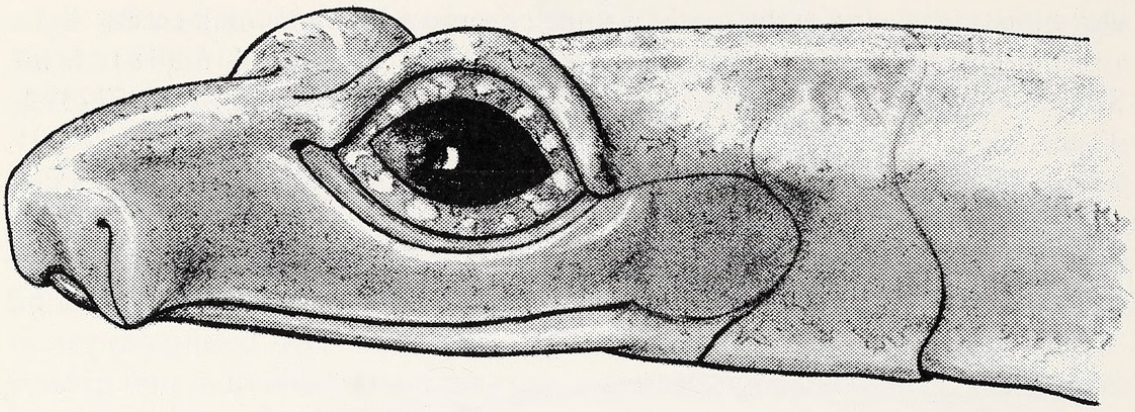

Figure 5. Head of holotype of *Bolitoglossa hartwegi* (UMMZ 121557).

moderate numbers of vomerine teeth (female mean, 27.7, male mean, 23.1) in adults; distinguished from *B. flavimembris* by smaller size, more extensively webbed hands and feet with phalangeal elements, especially the terminal ones, reduced in size and modified in shape (Figs. 9, 10, 15), no subterminal pads, and lack of uniform body coloration; from *B. cuchumatana* by more extensively webbed hands and feet, smaller terminal phalanges, no subterminal pads, and more teeth; from *B. helmrichi* by more extensively webbed hands and feet, smaller terminal phalanges, and no subterminal pads; from *B. stuarti* by smaller size, broader head, less extensively webbed hands and feet, relatively longer digits, and fewer maxillary teeth. Distinguished from members of the *rufescens* group by larger size, broader head, larger limbs, hands and feet, and much higher numbers of maxillary teeth.

*Description*: This moderately small, robust species has a relatively short, truncate snout. Females are larger than males (see *Diagnosis*). The nostrils are small. Labial protuberances are well developed in both sexes, and are pronounced in males. Mental hedonic glands are moderately developed in males. The head is broad (SL 5.6 to 5.9, mean 5.7 times head width in males; 5.5 to 6.8, mean 6.0 in females). A distinct groove extends below the eye, following its curvature, but does not communicate with the lip. The moderate-sized, protuberant eyes extend slightly beyond the lateral margins of the jaw. A shallow postorbital groove extends posteriorly from the eye as a shallow, irregular depression. At the posterior end of the mandible the groove proceeds sharply ventrally and extends across the throat, anterior to the gular fold, as a poorly defined depression. Vomerine teeth increase in number with increasing size (Fig. 1). The teeth are arranged in long or patchy series that extend well beyond the medial border of the internal nares. The small maxillary teeth extend beyond the center of the eye and increase in number with increasing

size (Fig. 2). The few premaxillary teeth (2-4 in males, 2-11 in females) pierce the lip in adult males. The trunk and tail are robust. The swollen tails are nearly round in cross section and are strongly constricted basally. Tail length is always less than body length. Postiliac glands are only faintly indicated. The slender limbs are moderately long; limb interval varies from 0 to 1.0 (mean 0.5) in males and from 0 to 2.0 (mean 1.0) in females. Hands and feet are relatively large. Webbing is extensive (Figs. 9, 10, 13, 15). The digits are discrete only distally and do not bear subterminal pads. The fingers are, in order of decreasing length, 3, 4, 2, 1; toes, in order of decreasing length, 3, 4, 2, 5, 1. Pertinent counts and measurements of the material studied are included in Table 2.

*Measurements of Holotype* (in mm): Head width 7.8; snout to gular fold (head length) 11.8; head depth at posterior angle of jaw 3.9; eyelid length 3.4; eyelid width 1.8; anterior rim of orbit to snout 3.2; horizontal orbital diameter 2.6; interorbital distance 2.9; distance between vomerine teeth and parasphenoid tooth patch 0.7; snout to fore limb 14.0; distance separating internal nares 2.1; distance separating external nares 2.3; snout projection beyond mandible 0.9; snout to posterior angle of vent (SL) 43.2; snout to anterior angle of vent 39.9; axilla to groin 22.3; tail length 31.0; tail width at base 4.2; tail depth at base 4.2; fore limb length 10.3; hind limb length 11.2; width of right hand 3.6; width of right foot 4.8.

*Coloration* (in alcohol): Coloration is highly variable in the species. The holotype (Figs. 4, 6, 7) is dark dorsally with some mottling and irregularity of pattern. Dorsal parts of the trunk and head are medium brown with some darker spots on the dorsolateral surfaces of the costal folds. A slight indication of a mid-dorsal band is present over the shoulders. The tail has a lighter ground color with a broken, irregular line of dark pigment on its lateral surfaces. Tips of the nasolabial protuberances are whitish. The trunk venter is basically light, probably yellowish or whitish in life, with a coarse reticulum of brown laterally. Midventrally the reticulum becomes dense and forms a rather large patch. The throat is only lightly marked with dark pigment. The tail venter is light with some coarse reticulations of dark pigment. The limbs are dark dorsally and light, coarsely marked with dark brown, ventrally.

The general dorsal color pattern of the holotype is also encountered in six paratypic adults. These differ from the holotype in having a very fine speckling of black dorsally. The tail is lighter than the back in four of the six.

One large paratype is almost uniformly gray-brown with no light coloration, even on the tail.

Dorsal bands are present in sixteen paratypes. In its highest state of development the band is a solid tannish-orange with a small, inverted, dark triangle behind the eyes and a few black spots in the midline (Fig. 8). Distinct bands are evident in eight individuals, but varying numbers of black specks, spots, and blotches have an obscuring effect in most. The band is obscure in

TABLE II

Measurements and Data for *Bolitoglossa hartwegi and B. stuarti*

| | Sex | Snout-Vent Length | Axilla-Groin Length | Head Width | Hind Limb Length | Fore Limb Length | Tail Length | Numbers of Maxillary Teeth | Numbers of Vomerine Teeth | Limb Interval | Foot Width |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *B. hartwegi* | | | | | | | | | | | |
| MVZ 57115 | ♂ | 46.9 | 25.3 | 7.9 | 12.0 | 11.8 | 34.2 | 48 | 19 | 0.5 | 5.1 |
| MVZ 57737 | ♂ | 45.4 | 22.8 | 8.1 | 11.7 | 11.7 | —* | 67 | 22 | 1 | 5.1 |
| MVZ 57098 | ♂ | 41.8 | 21.1 | 7.2 | 12.0 | 11.3 | —* | 51 | 20 | 0 | 5.7 |
| LACM 40601 | ♂ | 40.1 | 20.2 | 7.2 | 10.7 | 10.1 | —* | 47 | 20 | 1 | 4.3 |
| LACM 40606 | ♂ | 39.8 | 21.8 | 6.9 | 11.2 | 10.5 | 20.9 | 58 | 37 | 0 | 5.2 |
| LACM 40607 | ♂ | 35.9 | 17.2 | 6.4 | 9.2 | 8.7 | —* | 45 | 25 | 0 | 4.0 |
| TCWC 21399 | ♂ | 34.0 | 17.6 | 6.1 | 8.9 | 8.8 | 23.6 | 37 | 19 | 0.5 | 4.0 |
| MVZ 57099 | ♀ | 53.6 | 29.5 | 7.9 | 12.8 | 11.3 | 31.3 | 66 | 27 | 2 | 5.7 |
| UAZ 20262 | ♀ | 52.3 | 28.9 | 8.7 | 13.0 | 12.1 | —* | 74 | 25 | 1 | 5.3 |
| MVZ 57108 | ♀ | 52.0 | 28.2 | 8.6 | 13.2 | 12.6 | 37.2 | 77 | 23 | 0.5 | 6.4 |
| LACM 44209 | ♀ | 49.7 | 28.2 | 8.2 | 11.8 | 11.3 | 35.5 | 66 | 20 | 1.5 | 5.9 |
| LACM 40605 | ♀ | 48.5 | 26.5 | 7.6 | 12.0 | 11.7 | 33.0 | 69 | 34 | 1 | 5.3 |
| MVZ 57109 | ♀ | 48.0 | 26.6 | 7.3 | 12.2 | 11.9 | 33.2 | 76 | 33 | 1 | 5.9 |
| LACM 40602 | ♀ | 46.0 | 25.0 | 8.2 | 11.2 | 10.2 | —* | 52 | 23 | — | 4.9 |
| UMMZ 121557** | ♀ | 43.2 | 22.3 | 7.8 | 11.4 | 10.3 | 31.0 | 53 | 19 | 1 | 4.8 |
| JFC-65-130 | ♀ | 41.3 | 21.9 | 7.2 | 11.4 | 10.2 | 30.0 | 47 | 41 | 1 | 4.8 |
| MVZ 57112 | ♀ | 39.0 | 20.0 | 6.7 | 10.2 | 9.4 | 26.9 | 47 | 30 | 1 | 4.1 |
| MVZ 57738 | ♀ | 38.3 | 19.6 | 6.8 | 9.3 | 8.3 | —* | 24 | 24 | 1.5 | 4.0 |
| MVZ 57111 | ♀ | 34.2 | 16.6 | 5.7 | 8.3 | 8.1 | 22.6 | 21 | 16 | 1 | 4.0 |
| LACM 40604 | ♀ | 30.4 | 15.8 | 6.4 | 8.2 | 8.0 | 20.2 | 32 | 21 | 0 | 4.0 |
| *B. stuarti* | | | | | | | | | | | |
| UMMZ 123203** | ♀ | 60.0 | 32.1 | 8.9 | 15.5 | 15.6 | 37.2 | 85 | 40 | 0.5 | 6.2 |
| LACM 44210 | ♀ | 35.0 | 18.8 | 5.9 | 8.7 | 8.6 | 20.1 | 20 | 24 | 1.5 | 3.5 |

* regenerated tails
** holotype

the remainder, but is more evident than in the holotype. The tail is generally a little lighter than the trunk, except in individuals with well developed dorsal bands.

Most juveniles have indications of a light, dorsal band, and in these the tails are distinctly lighter than the body. In some juveniles, however, the dorsum of the trunk and tail is solid dark brown.

The entire sample is basically light colored ventrally. Seven adults have

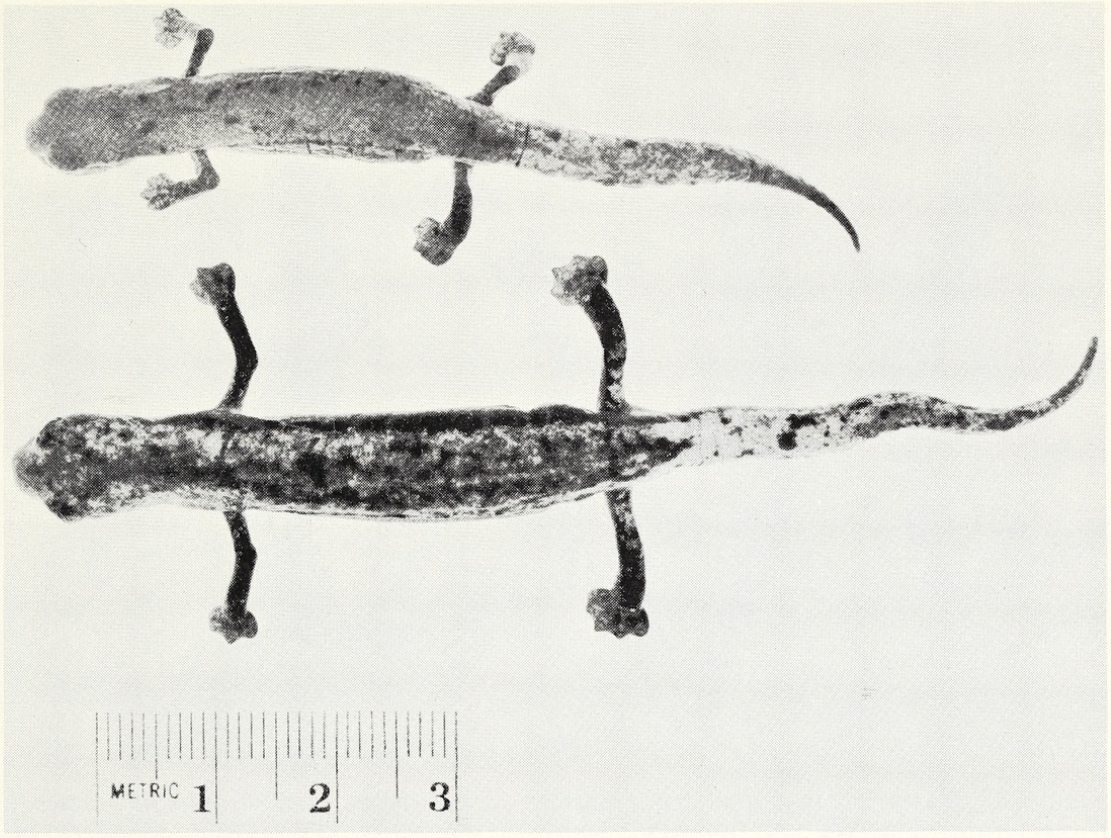


Figure 6. Holotypes of *Bolitoglossa hartwegi* (UMMZ 121557, top) and *Bolitoglossa stuarti* (UMMZ 123203, bottom), dorsal view.

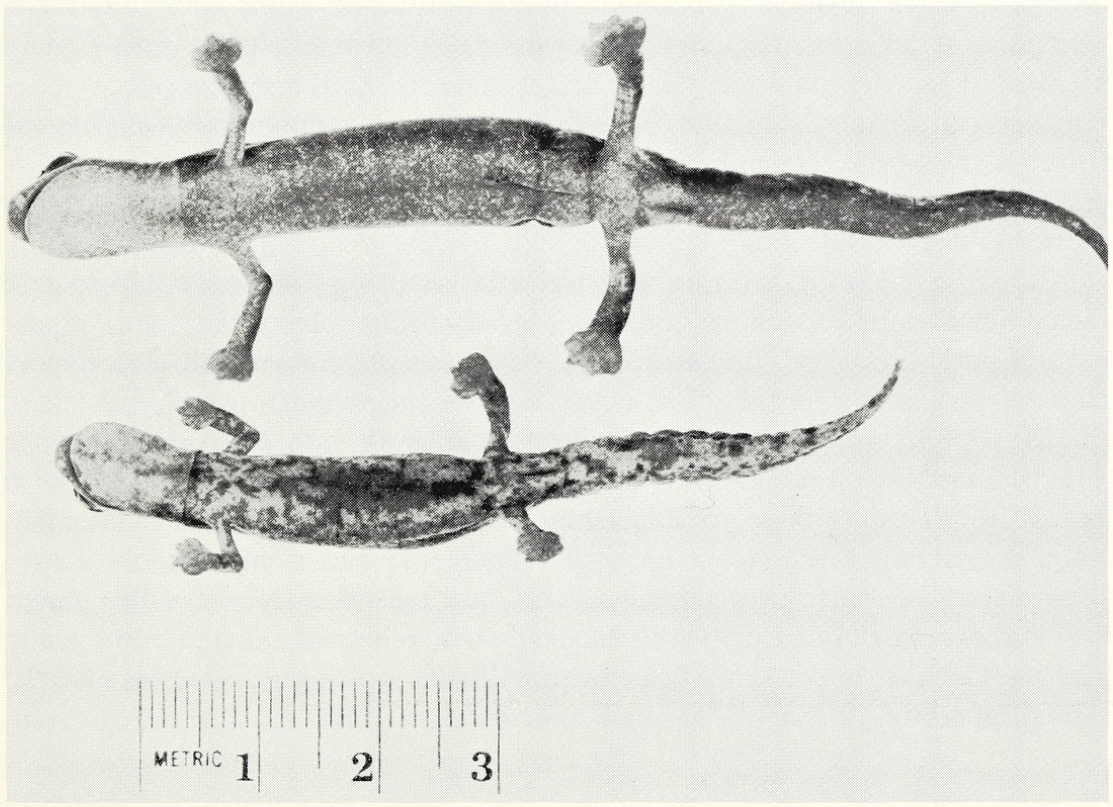


Figure 7. Holotypes of *Bolitoglossa stuarti* (UMMZ 123203, top) and *Bolitoglossa hartwegi* (UMMZ 121557, bottom), ventral view.


Figure 8. Variation in dorsal color pattern of paratypes of *Bolitoglossa hartwegi*. From left to right, MVZ 57109, MVZ 57108, MVZ 57737, MVZ 57099, MVZ 57738.

a coarse suffusion of darker pigment, generally in the form of punctate melanophores, which is most prominent midventrally. In other individuals the reticulum of dark pigment extends over most of the venter. In the most heavily pigmented individuals, some guanophores may overlie the melanophore punctations. Ventrolateral aggregations of guanophores are generally distributed throughout the sample.

Juveniles are mostly whitish ventrally, with some reticulations of darker pigment.

*Osteology*: Information concerning the osteology is derived from one cleared and stained specimen and from stereo radiographs of the holotype and several paratypes. For comparative purposes, we have examined cleared and stained specimens of eight *B. rufescens,* one *B. occidentalis,* two *B. helmrichi,* one *B. flavimembris,* four *B. morio,* four *B. rostrata,* two *B. engelhardti,* one *B. dunni* and one *B. franklini.* Radiographs of these species and of *B. stuarti* and *B. cuchumatana* have provided some information. Skeletons of many additional species of *Bolitoglossa* have been available and a comparative osteological analysis will be presented at a later date. For the purposes of this paper, comparisons of *B. hartwegi* will be limited to members of the *helmrichi* group and to other possibly related species, notably *B. morio* and members of the *rufescens* group.

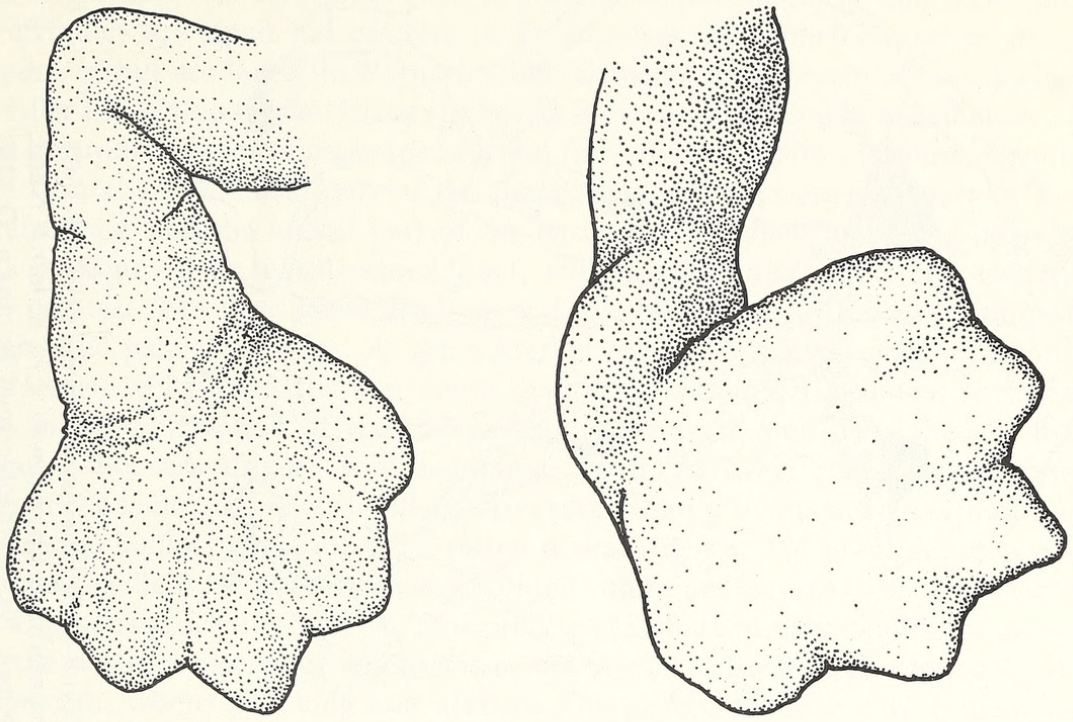

Figure 9. Left, dorsal view of right foot of holotype of *Bolitoglossa hartwegi* (UMMZ 121557); right, Figure 10, ventral view of right foot of holotype of *Bolitoglossa hartwegi* (UMMZ 121557).

*Bolitoglossa hartwegi* resembles the more generalized members of the genus in many features of its skeleton, especially in its well developed skull, but differs in other regards, especially hand and foot structure. The skull is solid and the bones are, in general, well articulated. In general morphology the skull is most similar to skulls of *B. helmrichi, B. flavimembris* and *B. morio,* and initial comparisons will be mainly among these four species. In all, the anterior cranial elements are well articulated. The nasals typically are moderately large and articulate with the facial lobe of the maxillaries and the facial expansion of the frontals. In *B. hartwegi* the nasal articulates with the frontal processes of the premaxillary and with the prefrontals, and this occurs in at least some of the other species as well. The nasals are generally protrusive, but to a lesser extent than in *B. rufescens* and *B. occidentalis.* In *B. morio,* nasals are sexually dimorphic, being large and protrusive in males, but quite small in females. Members of the *hartwegi* group may prove to be similarly dimorphic. Frontal processes of the premaxillary are usually somewhat dilated distally in the four species, and the tips are solidly articulated with the facial parts of the frontals. The processes are unique in *B. hartwegi* in being greatly

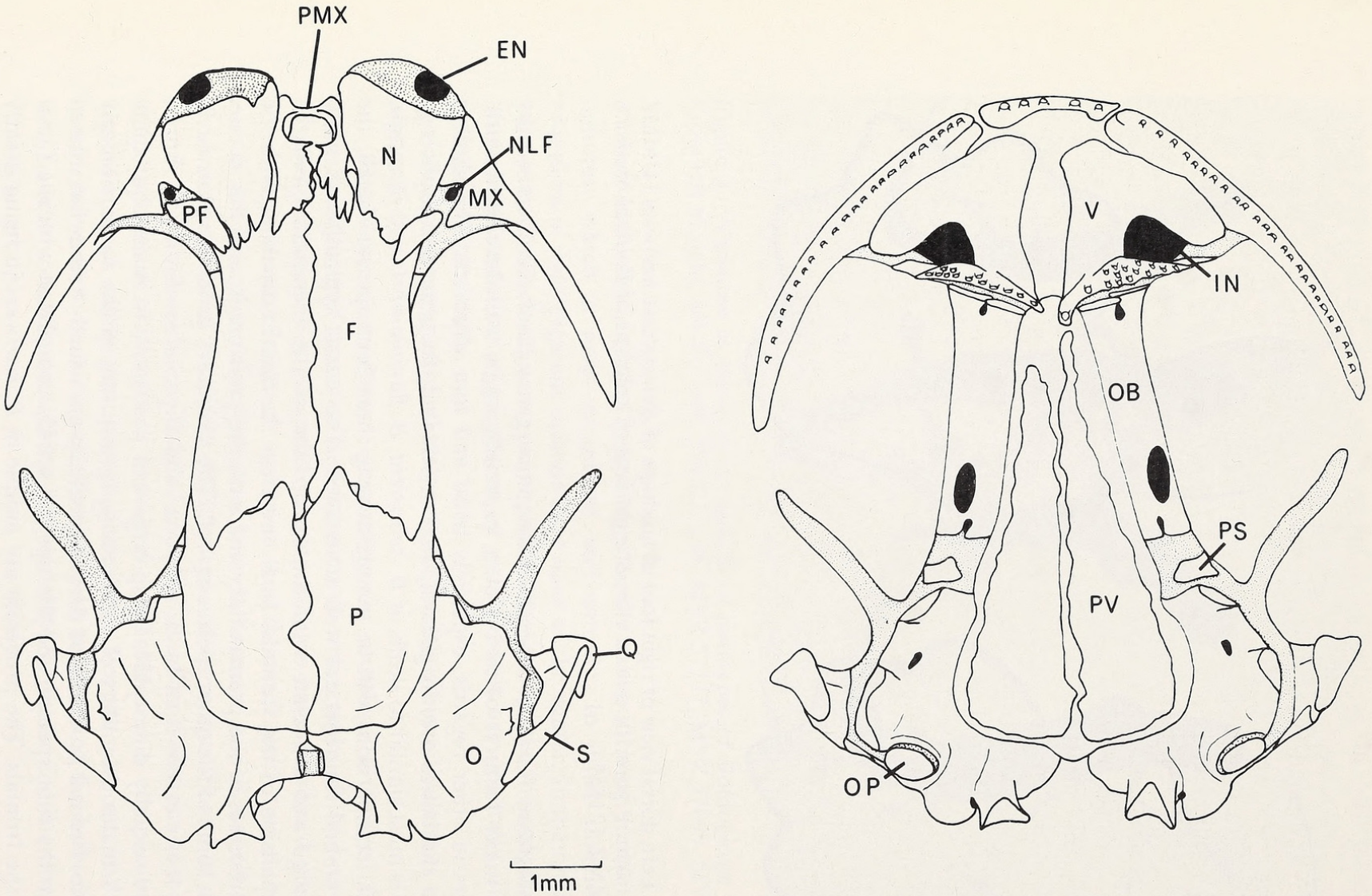


Figure 11. Dorsal (left) and ventral (right) views of skull of *Bolitoglossa hartwegi* (JFC-65-130). Cartilage stippled. Crowns of teeth and all posterior vomerine teeth removed. EN, External Naris; F. Frontal; IN, Internal Naris; MX, Maxillary; N, Nasal; NLF, Nasolacrimal Foramen; O. Otic Capsule; OB, Orbitosphenoid; OP, Operculum; P, Parietal; PF, Prefrontal; PMX, Premaxillary; PS, Lateral Spur of Parietal; PV, Outline of posterior patch of vomerine teeth, which lies below the parasphenoid; Q, Quadrate; S, Squamosal; V, Vomer.

expanded distally, with many erratic bony processes (Fig. 11). The processes are larger in *B. hartwegi* than in *B. helmrichi, B. flavimembris,* and *B. morio.* Prefrontals are small but discrete in *B. hartwegi, B. helmrichi* and *B. flavimembris,* but are larger in *B. morio.* The elements in *B. morio* are somewhat smaller than in such generalized species as *B. rostrata.* The main articulation of the prefrontals in all of these species, and the only articulation in some, is with the frontals. The dorsal part of the maxillaries, the anteromedial part of the prefrontals, and the lateral part of the nasals are notched in varying degrees for passage of the nasolacrimal duct, with the maxillary notching usually the greatest. The maxillaries are long and relatively stout with well developed facial and palatal portions. At the posterior end of the palatal portion, a lobe is formed which overlaps the lateral margin of the vomerine body, forming the major articulation of the two bones. Vomers are well developed in the species, but are usually well separated. In *B. hartwegi* the intervomerine fontanelle is broad, but is slightly narrowed anteriorly by inward growth of the vomerine bodies. Posteriorly the raised dental ridge of the preorbital process extends medially, beyond the margins of the vomerine body, for a short distance as a spinous process (Fig. 11). This process is a characteristic feature of many of the derived species of *Bolitoglossa* and is especially well developed in *B. helmrichi,* where it is long and arched. The processes are barely evident in *B. morio, B. flavimembris,* and in such generalized species as *B. dunni* and *B. rostrata.* Laterally the preorbital processes are long, and in *B. helmrichi* they extend beyond the vomerine body. The facial portions of the frontals are moderately well developed in these species, and the areas are especially large in *B. morio* and *B. flavimembris.* The frontals are closely articulated with one another at the anterior end of the interorbital region, but in most individuals the bones are not typically in contact posterior to that point. In *B. hartwegi,* however, the bones are articulated for their entire lengths. The frontals are usually articulated with the parietals by means of a lateral lobe of each frontal that overlaps each parietal. In *B. hartwegi* this articulation is particularly strong and is augmented by a medial lobe of the parietal which overlaps the frontal. All four species have a well developed, small, lateral parietal spur, which is characteristically present in the tribe Bolitoglossini (Wake, 1966). Small, laterally oriented crests are present on the otic capsule in the four species, but they are quite variable in four specimens of *B. morio* and are probably variable in the others also. In all four species the parasphenoid is a large bone with a moderately broad anterior tip. The orbitosphenoids are well separated at this point. Patches of posterior vomerine teeth borne on the parasphenoid approach the midline but are not in contact. The right patch bears 66 teeth, the left, 72, in the single *B. hartwegi.* In none of the species is a stilus present in even rudimentary form on the operculum. Squamosals and quadrates are small. The dentary is relatively weak and the prearticular is low and relatively small. The

hyobranchial apparatus (Fig. 12) has a form that is rather typical of generalized members of the genus.

The skulls of *B. occidentalis* and *B. rufescens* differ from that of *B. hartwegi* in being much weaker (see also Hansen and Tanner, 1958). The bones of the facial part of the skull are poorly articulated, if at all. The premaxillary is small with very slender, slightly dilated frontal processes. The maxillaries are very slender and are toothless in *B. rufescens* and bear a few small teeth in *B. occidentalis*. Palatal parts of the premaxillary are nearly absent and those of the maxillary are most prominantly represented by the lobe that forms the articulation with the vomer. The nasals are strongly protrusive, extending far anterior to the premaxillaries above the bulging nasal capsules. Prefrontals are usually absent, and the facial parts of the frontals are greatly reduced. The vomers are very greatly separated and are small, but the preorbital processes are long and sinuous, extending beyond the body of the vomer both laterally and medially. In some large *B. rufescens*, articulations between the nasals and frontals are established, but this is not typical. The frontals and parietals are separated medially and the only articulation between the two bones is laterally, by means of the prominant frontal lobes. The parasphenoid is reduced anteriorly and the orbitosphenoids are nearly in contact at this point. Otic crests and opercular stylar processes are absent. All skull elements are rather weakly developed.

The vertebrae of *B. hartwegi* are of the generalized *Bolitoglossa* type, with spool-shaped centra and unmineralized intervertebral cartilages. No basapophyses are present. The column is comprised of 1 cervical, 14 trunk or dorsal, 1 sacral, 2 caudosacral, and 26 caudal vertebrae. The holotype has only 12 trunk vertebrae; the sixth is abnormal and bears three pairs of ribs. Despite the anomalous vertebral reduction, the number of costal grooves is 13, as in all members of the genus. The holotype has 23 caudal vertebrae, MVZ 51099 has 24, MVZ 57109 has 27, and LACM 44029 has 23. Low numbers of caudal vertebrae are found in the *rufescens* group and in other members of the *helmrichi* group as well. Information for the various species follows: *B. occidentalis*, 23, 27, *B. helmrichi*, 26, 28, 32; *B. flavimembris*, 21, 22; *B. cuchumatana*, 24, 26; *B. rufescens*, 20 (1), 21 (4), 22 (2), 28 (1); *B. stuarti*, 20, 25. Related members of the *rostrata* group have numbers of tail vertebrae in the high portions of the ranges of these species, and often have more. Members of the predominantly lowland *platydactyla* group have as many as 40 caudal vertebrae.

Transverse processes are borne on the first 17 caudal vertebrae. The processes diminish in size in a nearly progressive pattern from the base toward the tip of the tail. The first and second caudal vertebrae lack hypophysial keels, and the third has a moderate-sized keel that is not free dorsoventrally as in some related species (*cf. B. morio*, Wake and Dresner, 1967, Fig. 4). Hypophysial keels are prominent on all but the last three vertebrae.

The first caudal vertebra of *B. hartwegi* has large and complex transverse

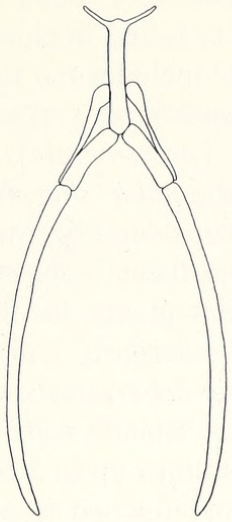

Figure 12. Hyobranchial apparatus of *Bolitoglossa hartwegi*.

processes that are bifurcated distally. The anterior prong is the dominant one and it extends sharply anterolaterally, well ahead of the anterior end of the centrum. The smaller and slenderer posterior prong extends almost directly lateral from the base. This pattern is broadly distributed in the *Bolitoglossa* of northern Middle America except in the *platydactyla* group and a few additional species (see below for discussion). Species with this condition also tend to have rudimentary to well developed tibial spurs, structures generally lacking in other species of the genus. In *B. hartwegi* the tibial spur is a well developed tibial crest, and the free distal portion is very short. Distinct tibial spurs are also present in all members of the *rufescens* and *helmrichi* groups that we have been able to examine directly, and they are visible in radiographs of *B. cuchumatana* and *B. stuarti*.

Hands and feet of *B. hartwegi* are large and are characterized by stout, flattened metacarpals and metatarsals, fusions of the third and fourth distal carpals and the third, fourth and fifth distal tarsals, and marked reduction in the more distal phalangeal elements (Fig. 13). These features, found also in members of the *rufescens* group, are discussed more fully below.

*Habitat*: Information concerning the habitat of *B. hartwegi* has been obtained from the field notes of Floyd L. Downs deposited at the University of Michigan Museum of Zoology, of William J. Riemer deposited at the Museum of Vertebrate Zoology, University of California, and of Dennis E. Breedlove, University of California, Berkeley, provided through the courtesy of Joseph F. Copp. The holotype was taken under a log in a pine-oak woodland. All specimens collected by Dr. Breedlove (LACM 40601-07) were taken on the ground, either in crevices of moss covered rocks, under moss on rocks, or

in fossiliferous shale. The animals were found in areas where many seepages were present, and all but one were found in cloud forest. The vegetation of the cloud forest on Cerro Zontehuitz includes the following as dominants, according to Dr. Breedlove: *Drimys granadensis* var. *mexicana, Oreopanax capitatus, O. xalapensis, Persea floccosa, Ternstroemia tepezapote, Quercus acatenangensis, Miconia glaberrima, Magnolia sharpii,* and *Podocarpus oleifolius.* LACM 40602, collected at a considerably lower elevation, was found in a fossiliferous shale outcrop on a northeast slope in an area with a cover of shrubs and bunch grasses. The dominant plants, identified by Dr. Breedlove, were: *Myrica cerifera, Muhlenbergia macroura, Garrya laurifolia, Coriaria thymifolia, Rondeletia* sp., and *Fuchsia arborescens.*

Specimens collected by W. J. Riemer were taken under and in rotten logs and under the bark of standing stumps up to 3 feet above the ground. One was taken from a bromeliad that was attached to a tree about 10 feet above the ground. Dr. Riemer noted that all of his specimens (MVZ numbers) were taken from cover that was found in relatively open, sunny places in the rather heavy forest.

*Range*: *Bolitoglossa hartwegi* occurs in the mountainous regions of east-central Chiapas (Fig. 3).

We take pleasure in naming the second undescribed species for Professor L. C. Stuart of the University of Michigan, the foremost student of Guatemalan amphibians and reptiles.

### **Bolitoglossa stuarti** new species

Figures 6, 7, 14, 15

*Holotype*: UMMZ 123203, an adult female from 7.8 mi (by road) SE of Ciudad Cuauhtémoc (El Ocotal), **8**, Chiapas, Mexico, in Huehuetenango, Guatemala, at about 950 m (3120 feet) elevation, collected by T. J. Cohn, September, 1961.

*Paratype*: LACM 44210, a young female from 1.4 mi (by road) S of La Trinitaria, **17**, Chiapas, Mexico, at 1615 m (5300 feet) elevation, collected by Dennis R. Paulson, July 14, 1965. The specimen was collected from an area of dry forest.

*Diagnosis*: A moderately large species (to 60.0 mm SL) with high numbers of teeth (to 85 maxillary and 40 vomerine); distinguished from *B. flavimembris, B. helmrichi* and *B. cuchumatana* by extensively, nearly completely webbed hands and feet, reduced phalangeal elements (especially terminals), and absence of subterminal pads; distinguished from *B. hartwegi* by larger adult size, narrower head, more extensively webbed hands and feet, shorter digits, and higher numbers of maxillary teeth in adults. Distinguished from species of the *rufescens* group by much larger size, proportionately longer limbs, larger hands and feet, and many more maxillary teeth.

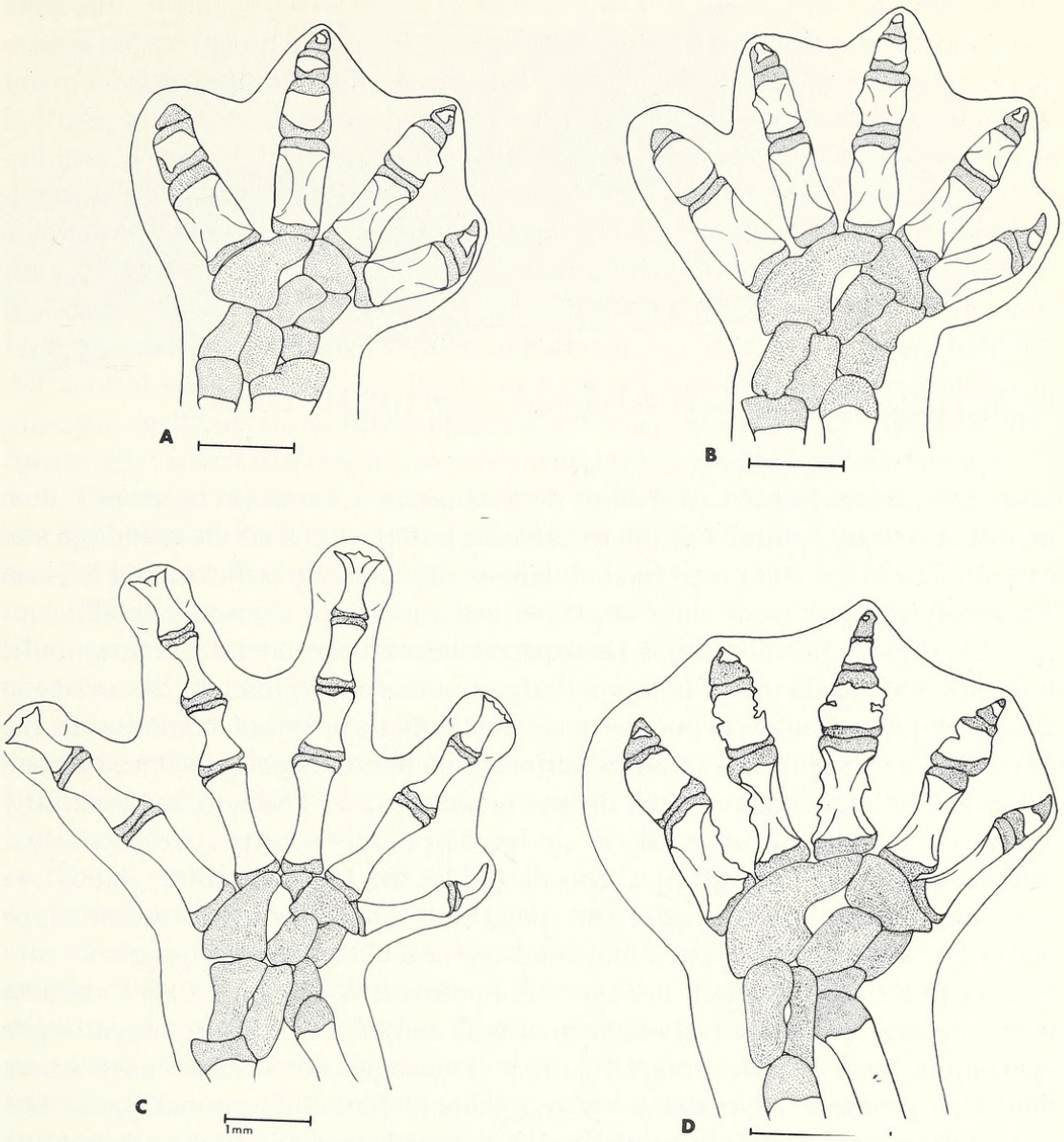


Figure 13. Hands and feet of *Bolitoglossa*. Cartilage stippled. Cutaneous outline indicated. Drawn through use of microprojector. A. Right hand of *B. hartwegi*; B. Right foot of *B. hartwegi*, C. Right foot of *B. rostrata*, D. Right foot of *B. rufescens*.

*Description*: This moderately large species is robust, relative to such forms as *B. helmrichi*, and has a rather short, moderately truncate snout. The nostrils are small. Labial protuberances of the nasolabial groove are small. The canthus rostralis is long and rounded. The head is relatively narrow (SL 6.7 times head width in adult holotype). A distinct groove extends below the eye, following its curvature, but does not communicate with the lip. The eyes are of moderate size and only slightly protuberant; they extend only slightly beyond the lateral margins of the head. A well defined postorbital groove extends

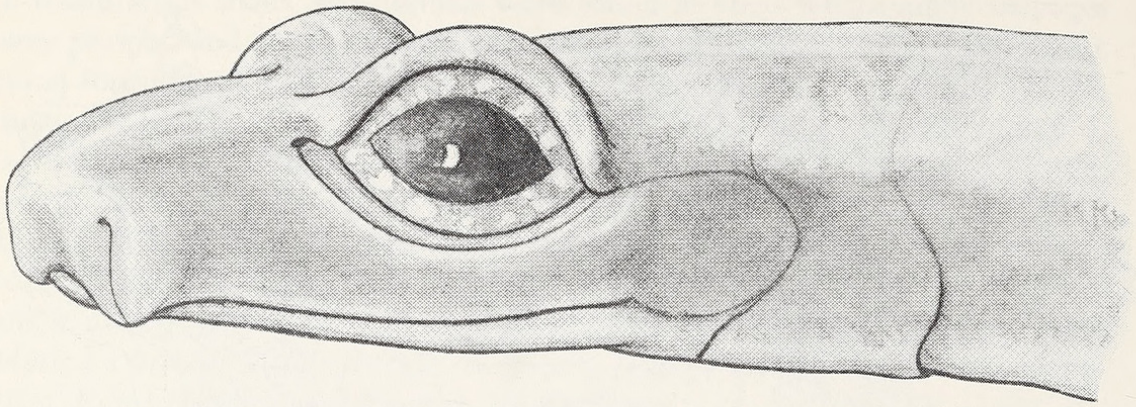

Figure 14. Head of holotype of *Bolitoglossa stuarti* (UMMZ 123203).

posteriorly from the eye as a shallow depression for 3.1 mm (in holotype), then proceeds sharply ventrally at the level of the posterior end of the mandible and extends across the gular area as an indefinite depression parallel to and 5.2 mm (in holotype) anterior to the sharply defined gular fold. Vomerine teeth occur in long, slightly patched series that extend beyond the lateral borders of the internal nares in the adult holotype; large numbers are present (24 and 40 in the paratype and holotype, respectively). Maxillary teeth are numerous in the holotype (85), and they extend posteriorly to a point about four-fifths through the eye. The premaxillary teeth do not pierce the lip. The tails are especially short (0.58 and 0.62 times SL in the paratype and holotype, respectively). Tails are rounded and strongly constricted at the base. Postiliac glands are conspicuous. Limbs are slender and long; limb interval is 0.5 in the holotype and 1.5 in the paratype. The hands and feet are characterized by great width relative to length. The digits are short and pointed. Webbing of hands and feet is so extensive as to be nearly complete, with only the tips of the longer digits protruding from the webbing (Fig. 15). The digits are discrete only where their tips protrude from the web, and there are no subterminal pads. The fingers are, in order of decreasing length, 3, 4, 2, 1; toes, in order of decreasing length, 3, 4, 2, 5, 1.

*Measurements of Holotype* (in mm): Head width 8.9; snout to gular fold (head length) 14.7; head depth at posterior angle of jaw 4.4; eyelid length 4.2; eyelid width 2.2; anterior rim of orbit to snout 5.0; horizontal orbital diameter 3.3; interorbital distance 3.1; distance between vomerine teeth and parasphenoid tooth patch 0.8; snout to fore limb 18.9; distance separating internal nares 2.8; distance separating external nares 3.2; snout projection beyond mandible 1.1; snout to posterior angle of vent (SL) 60.0; snout to anterior angle of vent 54.8; axilla to groin 32.1; tail length at 37.2; tail width at base 4.3; tail depth at base 4.4; fore limb length 15.6; hind limb length 15.5; width of right hand 4.4; width of right foot 6.2.

*Coloration* (in alcohol): The holotype is generally dark dorsally and light

ventrally. A broad dorsal band of light pigment extends from in front of the eyes nearly to the tip of the tail. The ground color of the band varies from a dull tan to a bright yellowish-tan. It is heavily mottled with dark brownish spots and blotches in the trunk region, but is bright and relatively unmarked above the tail base. Lines of dark pigment extend from behind the eyes and converge in the mid-dorsal area of the neck. The lateral surfaces of the trunk and tail are covered with an area of dark pigment that extends from the posterior margin of the eye almost to the tail tip. This pigment is lightest on the sides of the trunk and darkest along the tail. It is sharply demarcated from the dorsal band along both trunk and tail. Ventrolaterally on both trunk and tail the pigment lightens. All ventral surfaces are very light but have a more or less even suffusion of punctate melanophores. Melanophores are least numerous on the very light throat. All ventral surfaces are covered with large, scattered guanophores.

The tip of the snout is dark, but the tips of the nasolabial protuberances are light. Dorsal surfaces of the limbs are mottled with dark brown and light tannish pigment, but ventral surfaces are very light gray.

The juvenile paratype is lighter in general coloration than the holotype. The dorsal surfaces of the head and trunk are light reddish brown, becoming progressively lighter laterally and ventrally. Laterally the reddish element of the dorsal color disappears and the melanic reticulum is converted to isolated, punctate melanophores which are intermixed with small guanophores. This light "salt and pepper" effect is characteristic of the entire ventral surface, but, because the unpigmented flesh is exposed, the dominant coloration, especially on the tail venter, is a light yellow. Bright yellowish pigment lies above the base of the tail, and extends to near the tail tip, as in the holotype.

*Osteology*: Information has been derived from a series of stereo radiographs of the two known specimens. The skull has an unpaired premaxillary with broadly separated, slender frontal processes. The nasals are large and protrusive, and bear medially directed bony processes that in part overlap the frontal processes of the premaxillary. Moderate-sized, elongate-ovoid prefrontals are present. Vomers are widely separated medially, and small, medially directed processes carry the teeth medially, beyond the vomer body. The facial parts of the frontals are moderately well developed. Frontals and parietals are not sutured to their paired elements medially. The articulation between frontals and parietals is exclusively lateral. No stilus is present on the operculum. The vertebral column includes 1 cervical, 14 trunk, 1 sacral, 2 caudosacral and 20 (paratype) to 25 (holotype) caudal vertebrae. The last two trunk vertebrae lack ribs. Elsewhere in the *helmrichi* group, only the last trunk vertebra lacks ribs, except in three of six *B. hartwegi,* which are like *B. stuarti.* The arrangement of the vertebrae in the tail base region is unusual in the two specimens of *B. stuarti.* The last caudosacral and the first caudal vertebrae have extremely short centra, and the vertebrae in this region appear to be "crowded" together. The combined length of the centra of these two

vertebrae is just slightly longer than the length of the centrum of the second caudal vertebra. The transverse processes of the first caudal vertebrae are stocky but are distinctly bifurcated. The anterior prong of each process extends far forward, below the transverse process of the last caudosacral vertebra, and may extend as far as the posterior margin of the first caudosacral vertebra. This general pattern is typical of the *helmrichi* group, especially *B. hartwegi,* but the "crowding" is more extreme in *B. stuarti* than in the others. A distinct, stout tibial spur is present in the holotype, but it appears to be attached to the tibia for most of its length. Metacarpals and metatarsals are flat and broad (Fig. 15). Phalanges are highly variable in shape, but are greatly reduced in size distally. Proximal phalanges are usually stout, rectangular, flattened plates, but terminal phalanges are reduced to tiny dots of bone. The phalangeal formulas are 1-2-3-2 in the hand and 1-2-3-3-2 (1-2-3-2-2 on one side) in the foot of the holotype. The counts cannot be made for the feet of the paratype, but one hand has a formula of 1-2-3-2.

*Remarks*: *Bolitoglossa stuarti* is apparently a larger species than *B. hartwegi,* its close relative and close geographic neighbor. Although we have only two specimens, the holotype is larger than any *B. hartwegi* by over 6 mm, and the paratype is a juvenile at a size at which *B. hartwegi* is sexually mature.

*Range*: Known from the type locality and from the nearby La Trinitaria region along the Mexican-Guatemalan border at moderate elevations (950-1600 m) (Fig. 3).

## EVOLUTION OF THE *HELMRICHI* GROUP

*Relationships*: The five species of the *helmrichi* group may be further grouped into three assemblages: *B. flavimembris*; *B. helmrichi* and *B. cuchumatana*; *B. hartwegi* and *B. stuarti.*

The most primitive may be *B. flavimembris,* which is the largest of the species and has the least specialized hands and feet. Digits are well developed and discrete, and subterminal pads are well developed. The species has a broad head. These are features characteristic of other genera and we consider them primitive within the group.

Somewhat intermediate between the primitive *B. flavimembris* and the more derived *B. hartwegi* and *B. stuarti* are *B. cuchumatana* and *B. helmrichi.* They are smaller than *B. flavimembris* and *B. stuarti,* and do not get as large as the larger *B. hartwegi* in our sample. The two species have similarly shaped hands and feet, with more webbing than *B. flavimembris,* but with more discrete digits and less webbing than *B. hartwegi* and *B. stuarti.* Both species have subterminal pads. Many maxillary and vomerine teeth are present in *B. helmrichi,* fewer are present in *B. flavimembris,* and dentition is reduced even further in *B. cuchumatana,* which has less teeth than any other member of the group. Heads are broader in *B. flavimembris* than in *B. cuchumatana,* and *B. helmrichi* is somewhat intermediate.

The most derived species of the *helmrichi* group are *B. hartwegi* and *B. stuarti*. While *B. stuarti* has such possibly primitive features as large size and high numbers of maxillary teeth, the hands and feet are highly specialized with extensive webbing and the digits and phalanges are reduced in size. The smaller *B. hartwegi* also has many teeth, and its hands and feet are highly specialized in having extensive webbing, phalangeal reductions and mesopodial fusions. Subterminal pads are absent in both *B. stuarti* and *B. hartwegi*, and the tips of fingers and toes are characteristically pointed. *Bolitoglossa hartwegi* has longer digits, more phalangeal bone, and less webbing than *B. stuarti*. *Bolitoglossa hartwegi, B. stuarti, B. helmrichi,* and *B. cuchumatana* all have generally similar coloration, although there is much variation. All four commonly have a dorsal light band which tends to become obscured somewhat medially and posteriorly. As a result, a pair of dorsolateral light stripes, extending from behind the eyes over the shoulders and onto the back, are frequently present. All members of the *helmrichi* group have light ventral coloration, especially on the tail.

Relationships to species outside the group are somewhat difficult to assess, but it is likely that the *helmrichi* group is closely related to two other groups. The pattern of relationships is such that one is tempted to suggest that a "slice of time" has been preserved in the Guatemalan and Chiapan highlands. *Bolitoglossa flavimembris* is a nearly perfect link between the *helmrichi* group and the more primitive *rostrata* group, restricted to the highlands, and *B. hartwegi* is a nearly perfect link between the *helmrichi* group and the more derived *rufescens* group of the lowlands. Together the three groups form what we think is a natural assemblage with a common ancestor. All members of the three groups share a derived character not widely distributed elsewhere in the genus, a unique configuration of the transverse processes on the last caudosacral and first caudal vertebrae related to tail autotomy (Wake and Dresner, 1967). The processes on the last caudosacral vertebrae are usually nearly perpendicular to the body axis, or slightly bent posteriorly, and the processes on the first caudal vertebrae are sharply directed anteriorly and are distally bifurcated. This pattern is related to the sharply constricted region at the base of the tail, which is more marked in these groups than in other members of the genus. Correlated with this feature are several other characters, such as the tendency for members of the group to have tibial crests or free tibial spurs. We hope to present analyses of these features in future publications.

The *rostrata* group is, in our view, a large one, the members of which are large, with somewhat longer tails, less webbing of hands and feet, and longer digits than members of the *helmrichi* group. We include the following species: *B. rostrata, B. engelhardti, B. nigroflavescens, B. dunni, B. franklini, B. morio, B. macrinii, B. riletti, B. omniumsanctorum, B. lincolni, B. resplendens,* and *B. brevipes*. This group includes the genotype of *Magnadigita* Taylor (*nigroflavescens*). Stuart (1952) placed *B. dunni, B. engelhardti, B. cuchumatana,*

*B. helmrichi* and questionably *B. robusta, B. subpalmata* and *B. macrinii* in a *dunni* group, said to include bromeliad dwellers with large, protruding eyes, a single phalanx of the longest toe free of a web, flattened rostra, and streaks or stripes of red or brown coloration. His *franklini* group included *B. franklini, B. lincolni,* and *B. nigroflavescens,* robust species of moderate size with rounded snouts and moderate sized eyes. These species were said to have two phalanges of the longest toe free from the web and to be brightly colored with red and yellow, either in spots or stripes. They are bromeliad dwellers. Salamanders of his *morio* group, including *B. morio* and *B. omniumsanctorum,* are robust species of moderate size with rounded rostra. Eyes are smaller and less protruding than in the *dunni* group, and two phalanges were said to be free from the web. They are mottled brown and white, and flecked with white. Both species are ground dwellers. Though similar to the *dunni* group in most respects, *B. rostrata* was excluded because of its ground dwelling habits. The terrestrial *B. flavimembris* was assigned provisionally to the *franklini* group, but its different ecology and foot structure were noted. What we have done is to remove *B. flavimembris, B. helmrichi,* and *B. cuchumatana* to our *helmrichi* group, remove *B. robusta* and *B. subpalmata* to other groups, and place all other species discussed by Stuart in our *rostrata* group. In addition, we have added *B. riletti, B. brevipes,* and *B. resplendens,* species described since 1952, to the *rostrata* group. Certainly the *rostrata* group could be further subdivided, but we are unable to do so at the present time. It is apparent that *B. lincolni, B. resplendens* and *B. brevipes* are close relatives, *B. franklini* and *B. nigroflavescens* are close relatives, and *B. macrinii* and *B. riletti* appear to be close relatives; *B. riletti* is smaller than other members of the *rostrata* group. *Bolitoglossa engelhardti* is close to the *helmrichi* group, and it is also rather similar to *B. rostrata* in many features. With its very large head and long limbs, *B. dunni* is in a relatively isolated position. We are unsure of the relationships of the poorly known *B. omniumsanctorum.* We hope to discuss relationships in and of the *rostrata* group more thoroughly in future publications.

The *rufescens* group includes *B. rufescens, B. occidentalis,* and *B. bilineata* (which we consider to be a synonym of *B. occidentalis*). This is a group that includes species that are smaller than members of the *helmrichi* group, and have greatly reduced dentition, poorly developed skull bones, reduced phalangeal elements, mesopodial fusions, extensively webbed and flattened hands and feet with sharply pointed digital tips, and short tails.

*Bolitoglossa flavimembris* is the largest member of the *helmrichi* group and has the least webbing of hands and feet. In these features it resembles members of the *rostrata* group, yet its digits are more reduced and pointed and it has more webbing than any member of that group.

*Bolitoglossa hartwegi* resembles the *rufescens* group in having extensive hand and foot webbing, mesopodial fusions, and reduced phalangeal elements.

It differs sharply, however, in its larger size and its high numbers of marginal teeth.

Taylor (1941, 1944) and Hansen and Tanner (1958) recognized that *B. rufescens* and *B. occidentalis* differed considerably from the extensively webbed species of the *platydactyla* group, and suggested that two natural groups were represented. It is now apparent that the *rufescens* group is related not to the *platydactyla* group but to the *helmrichi* group. Our new knowledge of the *helmrichi* group demonstrates again the futility of separating species of *Bolitoglossa* into two groups on the basis of foot structure. This tendency has resulted in comparison of the *rufescens* group with the large *platydactyla* group rather than with its true relative, *B. helmrichi*, which had been placed in a different genus. Clear adaptive trends within groups of closely related species span the extremes of foot types in Costa Rica (Wake and Brame, 1963b) and South America (Brame and Wake 1963a) as well as in Nuclear Central America (see also Wake and Brame, 1963a).

Several years ago we suggested that the genus *Magnadigita* Taylor could no longer be recognized (Wake and Brame, 1963a). However, should it be found that the assemblage that includes the *rostrata*, *helmrichi*, and *rufescens* groups is a natural one that is sharply differentiated from other members of *Bolitoglossa* (genotype *mexicana*), the name *Magnadigita* is available for it. The genus *Bolitoglossa* as currently recognized includes over 50 species, and division of the genus into natural assemblages is desirable; we do not recommend such action, however, until the group as a whole becomes better known.

*Evolutionary Patterns and Trends*: In the view of Taylor (1944), species of *Magnadigita* had large, discrete digits and slight webbing, while species of *Bolitoglossa* had indistinct digits and extensive webbing (see also Wake and Brame, 1963a). A complete bridging of these two extremes is found in the *helmrichi* group, and hand and foot structure in this group is considered in detail in the following paragraphs.

In discussing degree of webbing we recognize five categories: a) unwebbed; b) slightly webbed (well over 2 phalanges of the longest toe free of web, and all toe tips free of web and bearing well defined subterminal pads); c) moderately webbed (about 2 phalanges or less of longest toe free of web, subterminal pads on the longest 2 to 3 toes); d) extensively webbed (no subterminal pads, toe tips pointed, marked indentations between tips of toes); e) completely webbed (little or no indentation between toe tips, only longest toe tip pointed and obvious). No members of *Bolitoglossa* are unwebbed. *Bolitoglossa rostrata* falls in category b, *B. flavimembris*, *B. cuchumatana* and *B. helmrichi* in category c, and *B. hartwegi* in category d (Fig. 15). *Bolitoglossa stuarti*, *B. rufescens*, and *B. occidentalis* fall in category d and category e, with some variation from individual to individual. The best examples of category e are individuals of the Ecuadorian species *B. sima* (Brame and Wake, 1963a,

Fig. 20 F) and the Panamanian species *B. schizodactyla* (Wake and Brame, 1966b, Fig. 2); the latter, however, lacks pointed digital tips.

Within the *helmrichi* group a clear trend in foot structure is evident, from the moderately webbed foot with large, discrete digits and well developed subterminal pads of *B. flavimembris,* through the increasingly flattened, more fully webbed feet of *B. cuchumatana* and *B. helmrichi,* to the extensively webbed feet with relatively indistinct digits found in *B. hartwegi* and in a more extreme form in *B. stuarti* (Fig. 15). Not much ecological information is available for the group. The known altitudinal range is from 950 m (*B. stuarti*) to over 2800 m (*B. hartwegi*), and *B. hartwegi* is known to range over 800 m altitudinally. We consider these elevations to be moderate to relatively high for *Bolitoglossa.* Apparently all occur in areas where bromeliads are common, and at least some individuals of all five species have been collected in bromeliads. The *B. flavimembris* taken by Schmidt (1936) were collected under stones and logs, but FMNH 142081 was collected from a bromelid in a wet, densely forested ravine. Wake and John E. Woods collected over 50 specimens of *B. flavimembris* in the vicinity of Finca La Lucha, above La Fraternidad, Guatemala, in March and April, 1969. Some were taken in bromeliads, but the majority were collected under ground cover and under the bark of logs. Stuart (1943) found three of the four *B. cuchumatana* in bromeliads, and considered *B. helmrichi* to be definitely a bromeliad inhabitant, stating (p. 16) "I have never seen it on the ground." Series of all five species with good ecological information are badly needed, and only speculations may be made concerning ecological correlations of morphological characters at this time. Members of this group have a distinct tendency in the direction of increased webbing of hands and feet, and this may be correlated to some degree with attainment of arboreality by at least some of the species and movement into areas of somewhat lower elevation. Yet, the extensively webbed *B. hartwegi* has been taken mainly in terrestrial situations at moderate to moderately high elevations, so the correlation is not high. Members of the *rostrata* group with much less webbing appear to be fully as arboreal as *B. hartwegi* (*e.g., B. franklini, B. nigroflavescens*).

In *Bolitoglossa,* highland species tend to be terrestrial and to have the least amount of webbing in the genus, while lowland species tend to be arboreal and to have the greatest amount of webbing. This is a generalization and there are some exceptions; a few species with extensive webbing inhabit bromeliads in the highlands (*e.g., B. hartwegi*). The slightly webbed *B. franklini* occurs in bromeliads. In addition, some species with relatively little webbing, such as *B. subpalmata,* are terrestrial in the highland portions of their range, but are found in bromeliads at lower elevations. All lowland species have extensive to complete webbing. Hands and feet are morphologically complex in *Bolitoglossa,* and to discuss them strictly in terms of degree of webbing can be quite misleading. They are functional complexes, modifications of which may involve

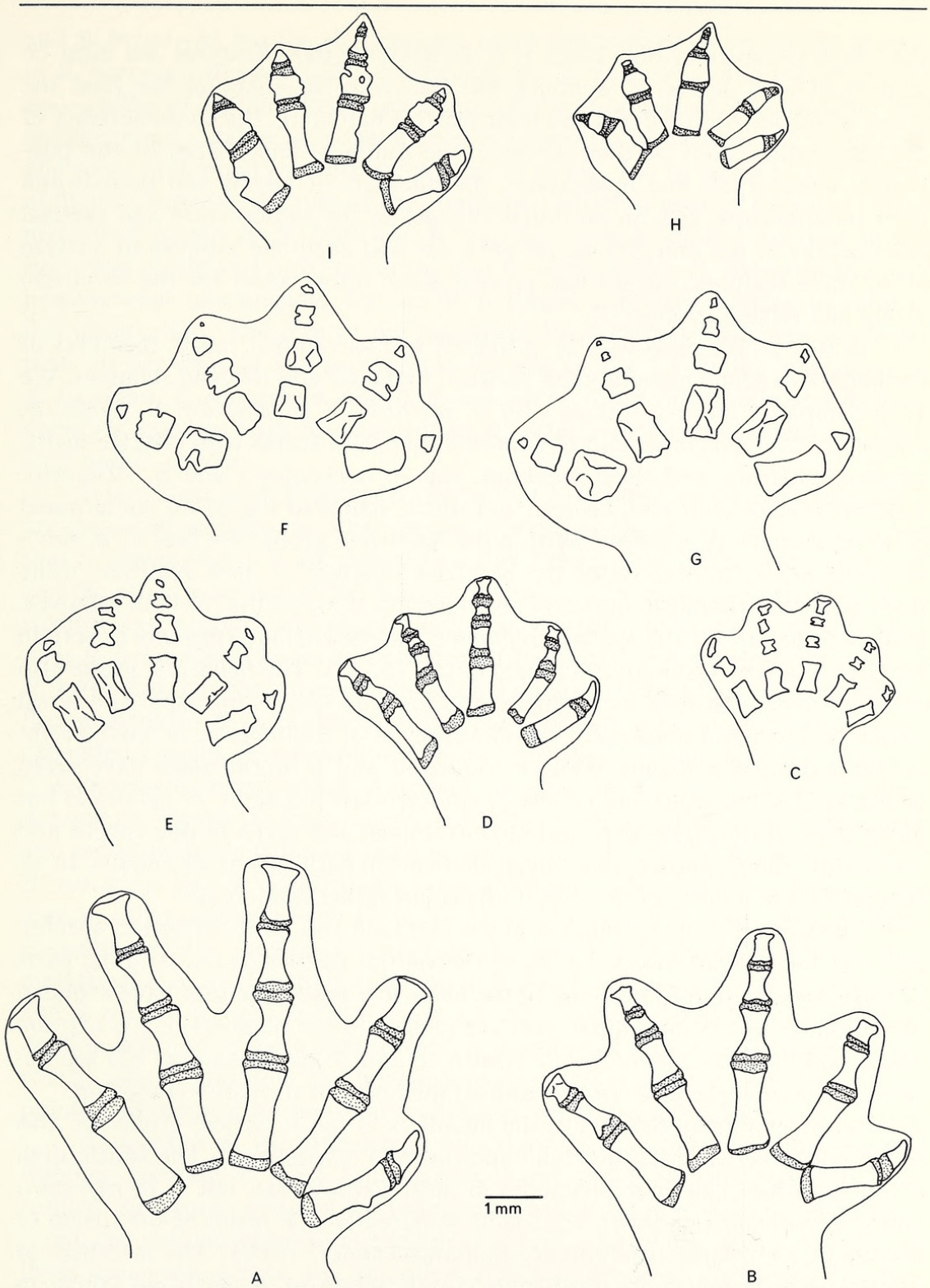


Figure 15. Outline of right feet of species of *Bolitoglossa*. Cutaneous outline, metatarsals and phalanges indicated. Cartilage stippled. All drawn to same scale. Drawn through the use of a microprojector from cleared and stained (C) or X-rayed (X) specimens. A. *B. rostrata* (C), B. *B. flavimembris* (C), C. *B. cuchumatana* (X), D. *B. helmrichi* (C), E. *B. hartwegi*, holotype (X), F. *B. hartwegi* (X), G. *B. stuarti*, holotype (X), H. *B. occidentalis* (C), I. *B. rufescens* (C).

the whole structure or only parts of it. In studying these features one must be concerned with degree of webbing, but also with the shape of the foot, the shape of the individual digits and their relative flattening, the characteristics of the subterminal pads or their absence, the numbers and shapes of the phalanges, metacarpals and metatarsals, the numbers of tarsals and carpals and their relationships, and proportional changes in the musculature and skeletal morphology of the unit. We as yet have not had adequate samples to analyze all of these features, but we can present some information for the *helmrichi* group and related species.

In foot structure as well as in habitat and elevational range, members of the *helmrichi* group generally fall between highland and lowland relatives. We have compared the five species with *B. rostrata, B. engelhardti, B. dunni, B. morio, B. nigroflavescens* and *B. franklini,* highland forms with discrete digits, subterminal pads, and slight webbing, and *B. occidentalis* and *B. rufescens,* lowland species with padlike feet, indistinct, flattened digits, no subterminal pads, and extensive webbing. Within the *helmrichi* group, the feet of *B. flavimembris* are nearest those of the highland relatives in most features, while those of *B. stuarti* and *B. hartwegi* are closest to those of the lowland relatives. Feet of *B. helmrichi* and *B. cuchumatana* are somewhat intermediate in certain features, but very distinctive in others (Figs. 15, 16). The *helmrichi* group also bridges the gap between the highland and lowland species in carpal and tarsal structure. Highland species are like most species of *Bolitoglossa* in having eight carpal and tarsal elements, while *B. rufescens* and *B. occidentalis* have seven elements in both carpus and tarsus. *B. flavimembris* has eight, *B. helmrichi* has eight in six of the eight carpi and tarsi examined and seven in one carpus and one tarsus, and *B. hartwegi* has seven elements in both carpus and tarsus. In all species the reductions are the result of fusions rather than losses.

Toe tips are bluntly rounded in the highland and more terrestrial species, and they bear well developed pads on the ventral surface of the terminal parts of the longest two to four digits. In the *helmrichi* group the toes have rounded or triangular tips. Subterminal pads are present in all members of the *rostrata* group and in *B. flavimembris, B. helmrichi,* and *B. cuchumatana,* but are absent in *B. hartwegi* and *B. stuarti,* and all members of the *rufescens* group.

In skeletal detail the feet of the members of the *helmrichi* group are also intermediate between the highland and lowland assemblages. The fourth digit of the hind foot has three phalanges in most *Bolitoglossa,* but in *B. rufescens* and *B. occidentalis* only two are found, apparently as a result of the fusion of two smaller elements (see also Hansen and Tanner, 1958). The members of the *helmrichi* group have three with the exception of *B. hartwegi* (three in three animals, three on one side and two on the other in another animal, and two on both sides in a fifth animal) and *B. stuarti* (three on one side and two on the other in the holotype). Terminal phalanges are large and distally expanded in generalized *Bolitoglossa,* including also *B. flavimembris, B. cuchumatana,*

and *B. helmrichi,* but the elements are small and pointed or erratically shaped in *B. hartwegi, B. stuarti, B. occidentalis* and *B. rufescens* (Fig. 15). Lengths and widths of all phalangeal elements in the osteological preparations and radiographs available to us have been enlarged by projection and measured, and some preliminary results are portrayed in Fig. 16. In terms of the lengths of digital elements, the sum of the phalangeal length is greater than that of the metatarsal length in *B. franklini, B. rostrata,* and *B. morio,* but less in the *helmrichi* group and in *B. rufescens* and *B. occidentalis. B. flavimembris* may be somewhat intermediate, but we do not have adequate samples to confirm this observation. The sum of the lengths of the terminal phalanges is greater than 50 per cent of the sum of the lengths of the remaining phalanges in *B. franklini, B. rostrata, B. morio, B. helmrichi, B. cuchumatana,* and *B. flavimembris,* but less than 50 per cent in *B. rufescens, B. occidentalis, B. hartwegi* and *B. stuarti.*

It is evident from Figures 15 and 16 that *B. helmrichi* and *B. cuchumatana* are quite distinct from the other species in terms of phalangeal proportions, and that *B. flavimembris* is the closest to a link between them, the *rostrata* group, and the other members of the *helmrichi* group. *B. cuchumatana* tends to have slightly less webbing and slightly better developed phalangeal elements than does *B. helmrichi.* The second phalanx of the fourth toe is extremely small in *B. helmrichi,* but the corresponding bone is longer than either the terminal or first phalanx in *B. cuchumatana.* In both species the terminal phalanges are expanded distally, thus resembling more generalized members of the genus.

*Bolitoglossa stuarti* and *B. hartwegi* are close to *B. rufescens* and *B. occidentalis* on Figure 16. In *B. stuarti* and *B. hartwegi* the phalanges, metacarpals and metatarsals are flattened and bear bony laminae, similar to those found in *B. rufescens* and *B. occidentalis.* Only slight indications of these laminae are seen in other species (Figs. 13, 15). An indication of the flattening of these elements and the growth of bone into the web is that the width of the fifth metatarsal is more than half its length in *B. hartwegi, B. stuarti, B. occidentalis* and *B. rufescens,* but less than half in the other species. Marked phalangeal reduction is found in these four species, with tendencies to lose a phalanx in the fourth toe. In addition, the terminal phalanges are greatly reduced and are pointed, in contrast to the situation in more generalized species.

As a result of the phalangeal reductions, carpal and tarsal fusions, and webbing increase in these four species, hand and foot pads result that are resilient structures, adapted for functioning as a unit. Independent digit action is reduced in favor of the total hand or foot action associated with movement of these organisms across wet, smooth surfaces in arboreal situations. The flattened pad and unitary functioning make locomotion by surface tension phenomena possible. Observations on the extensively webbed feet of living *B. yucatana, B. adspersa* and *B. rufescens* reveal that during locomotion the hands and feet are rolled flat onto the surface, proceeding from the ankle or wrist

distally in a rather slow and deliberate action of the entire pad, assuring that complete contact with the underlying surface is achieved.

Figure 15 illustrates a kind of morphocline in regard to foot structure in the *helmrichi* group and its relatives. While it is not likely that this represents a chronocline or a true phylogeny, it is quite possible that there are preserved in this series of species, morphological stages representative of ancestral conditions of some of the more derived types of foot structure. The discovery of *B. hartwegi* and *B. stuarti* fills an important gap in our knowledge of this genus and demonstrates both the pattern and manner in which extensively webbed forms are derived from more generalized types. In addition, it provides insights into factors associated with invasion and success in tropical lowland environments. We suggest that lowland invasions became possible with the evolution in the highlands of such species as *B. hartwegi,* forms adapted for life in both terrestrial and arboreal habitats and having the fully webbed feet associated with exclusively arboreal life in more specialized members of the genus. With the evolution of arboreality, movements into the heavily populated tropical lowlands became possible. All members of *Bolitoglossa* in the tropical lowland fauna are extensively to completely webbed, arboreal species, and it seems likely that terrestrial life in tropical lowlands for this genus is precluded. One reason may be competition with the numerous lowland species of lizards, frogs and snakes which overlap niche requirements of more generalized *Bolitoglossa.* In the case of *Bolitoglossa,* invasion of tropical lowlands has been accomplished several times in different geographic areas, always, to our knowledge, by specialized rather than generalized species. Specialization associated with arboreality has provided, for these salamanders, evolutionary access to the new ways of life associated with tropical lowlands.

Paedomorphosis also has been an important factor in the evolution of tropical salamanders, and it is possible that it may have been of significance in foot evolution. In *B. rufescens* and *B. occidentalis,* and to a lesser extent in *B. hartwegi* and *B. stuarti,* the feet have a rather embryonic appearance. In embryos of *B. subpalmata,* which has slightly webbed feet as an adult, pads are present, with protrusions where the digits will form. The form of the adult foot suggests that in such forms as *B. rufescens*, the digits have failed to grow out of the embryonic pad. The digits are very short and there is a distinct gradient of development from the proximal to the distal elements. The distal elements are highly irregular in shape and degree of ossification. The apparent extensive webbing in these forms is not so much the result of an increase in the integumentary web as the failure of the digits to grow out of the embryonic pad. The growth differentials between the digits and the carpal or tarsal regions of the hand or foot are quite different in, for example, *B. rostrata* and *B. rufescens,* and in the latter the growth of the digits relative to the growth of the tarsal portions is much reduced. Correlated with this developmental trend, which clearly is adaptive, is the trend to stiffen the entire pad and make it a more

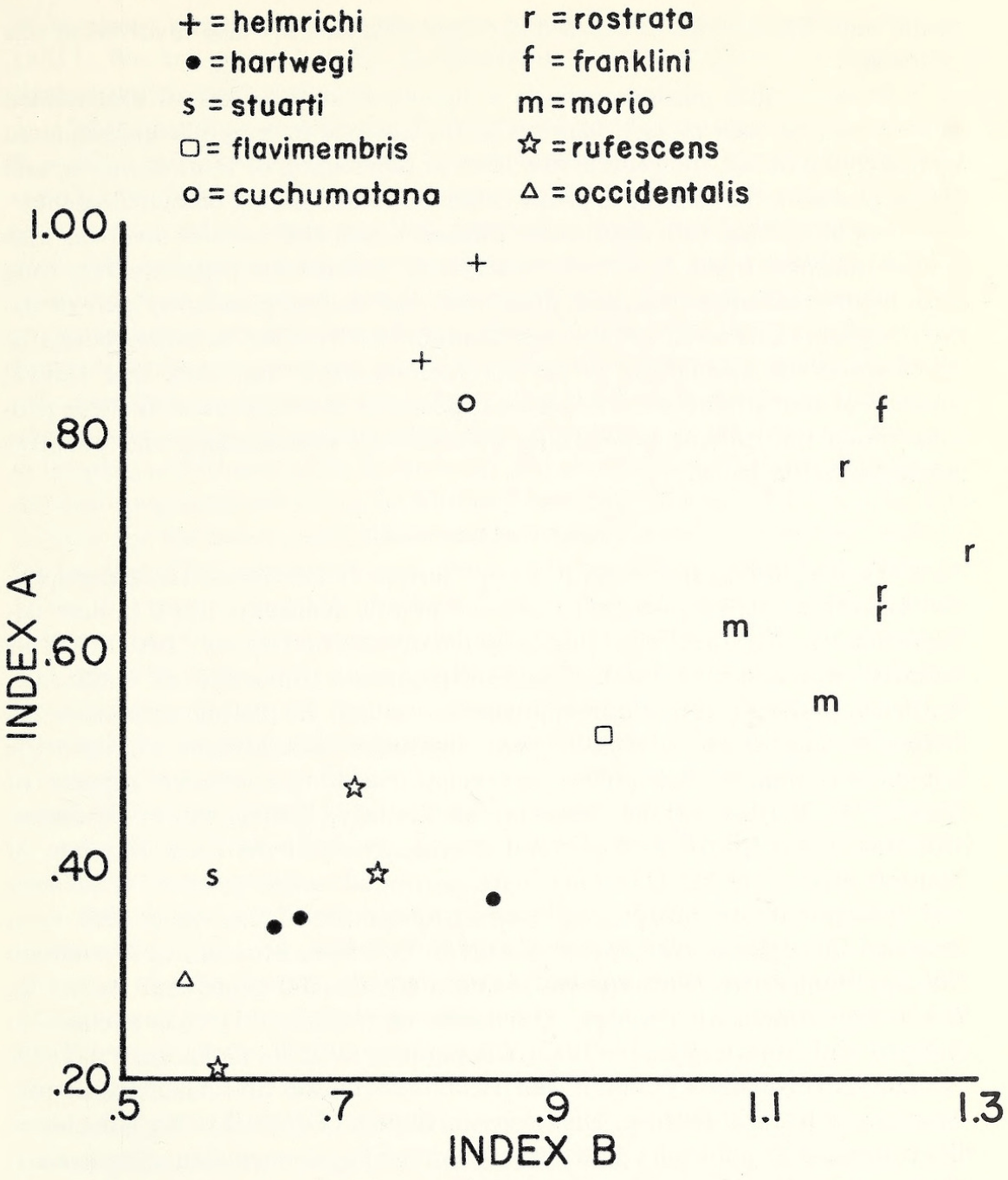


Figure 16. Proportional relations of phalangeal and metatarsal elements in *Bolitoglossa*. Index A. Total length of terminal phalangeal bone divided by total length of bone in phalanges other than the terminal ones; Index B. Total length of phalangeal bone divided by total length of metatarsal bone. Each point results from measurement of one foot of one individual.

effective climbing structure. For example, the flattening of the metacarpals and metatarsals and the digits, and the growth of lateral weblike extensions of bone into the integumentary pad add to the unification of the foot as a func-

tional unit. The fusions of tarsal and carpal elements are also involved in this process.

Evidence that paedomorphosis is operative in *B. rufescens* and related species may be seen in such features as the absence or irregular development of prefrontal bones, the general low level of ossification of skull elements, and the large size of the sensory capsules relative to surrounding cranial elements.

Not all species with extensively webbed hands and feet are involved with a paedomorphic trend. In *B. schizodactyla* of Panama the digits are very long with highly specialized terminal phalanges, and the integumentary part of the web is greatly increased (Wake and Brame, 1966b). Feet in other species of *Bolitoglossa* are specialized in yet different manners. We think that careful analysis of foot structure in the various species of *Bolitoglossa* is likely to provide much information concerning evolutionary relationships and adaptive processes in the genus.

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## ADDENDUM

Since submitting this paper, we have been able to examine two skeletons of

*Bolitoglossa veracrucis*, a species known only from the type series (Taylor, 1951). We are grateful to W. E. Duellman for allowing us to prepare two cleared and stained specimens.

In the original description, *B. veracrucis* was compared with *B. odonelli*, *B. mulleri* and *B. yucatana*, but it is now apparent that its closest relationships are with the *helmrichi* group. In its long, truncate, prominent snout, its large, extensively webbed hands and feet, generally similar head dimensions, rather short tail, and moderately high numbers of maxillary and vomerine teeth, it resembles both *B. hartwegi* and *B. stuarti*. Skeletal structure provides the most convincing evidence of relationship to the *helmrichi* and *rufescens* groups. The elongate transverse processes of the first caudal vertebra bear small, accessory processes that are similar to but smaller than those of *B. hartwegi*. Only seven carpals and tarsals are present, the result of fusions, and the digits are reduced in length and flattened as in *B. hartwegi* and its relatives. Phalangeal formulae for two specimens are 1-2-3-2 (Kansas University 26942) and 1-2-3-1 (KU 26953) for the hands, and 1-2-3-2-2 (1-2-3-1-2 for one foot of KU 26953) for the feet. The metacarpals and metatarsals are enlarged, flattened, platelike bones that occupy much of the base area of the web. The flattening is more extreme than in other species examined. Digits and phalanges are shortened and resemble those of *B. hartwegi*. Phalangeal bone has a total length that is less than 80 per cent of the total metatarsal length, and the total length of terminal phalangeal bone is less than 50 per cent of the total length of the non-terminal phalanges (*cf.* Fig. 16). Terminal phalanges are pointed and very small. Phalangeal formulae variation results from the failure of some terminals to ossify. In all of these features, *B. veracrucis* resembles *B. hartwegi*, *B. stuarti*, and the *rufescens* group.

*Bolitoglossa veracrucis* has a well-developed, solidly articulated skull that is more like those of *B. helmrichi* and *B. hartwegi* than those of the *rufescens* group or of other species that we have examined. The snout portion is particularly well developed, and the nasal bones are larger than in any member of the *helmrichi* group. They extend ventrally at the anterior end of the snout to partially envelop the medial border of the olfactory capsules. Premaxillary bones are less well developed than in *B. hartwegi*, with shorter and less dilated frontal processes. Prefrontals are small and round, with the greatest dimension being less than one-half that of the elongate prefrontal of comparably-sized *B. hartwegi*. Maxillary bones are longer than in either *B. hartwegi* or *B. helmrichi*, and they extend beyond the posterior limit of the eye. The intervomerine space is large; accordingly the spinous medial process, which bears the vomerine teeth, is longer than in *B. hartwegi* or *B. helmrichi*. The tibial spur is distinct and free in one tibia of one animal, and is distinct, but partly joined to the main shaft of the tibia at the tip of the spur, in the other three tibias examined. Many trunk vertebrae of both specimens bear well developed basa-

pophyses. All trunk vertebrae but the last bear well developed ribs in both individuals.

This combination of characters suggests close relationship of *B. veracrucis* to *B. hartwegi* and its relatives and indicates that the species should be considered a member of the *helmrichi* group. Its spotted color pattern (Taylor, 1951), consisting of a light mottling on a dark background, its prominent snout, and features of the skull and feet distinguish it from the members of the group discussed in this paper. The type locality of *B. veracrucis* (35 km SE Jesus Carranza, Veracruz, Mexico, 350 feet elevation) is considerably lower than the known range of any other member of the group. In this paper we have discussed the relationship of the upland *helmrichi* group to the lowland members of the *rufescens* group, and have pointed out morphological features that, in a sense, preadapt the group to life in lowland, arboreal habitats. Discovery that the lowland *B. veracrucis* is a member of the *helmrichi* group supports our theory. It is a close relative of montane species, yet it exemplifies an extreme in those trends that seem to be associated with arboreality and the ability to invade and succeed in tropical lowland habitats.

## SUMARIO

El genero *Bolitoglossa* incluye cerca de 60 especies de salamandras netamente neotropicales. En éste trabajo se definen las especies del grupo *helmrichi* de *Bolitoglossa* y sus relaciones evolucionarias són discutidas. Trés especies se reconocen ahora en éste grupo: *B. flavimembris* de la región de la costa montañosa del Pacífico en Guatemala y Chiapas, Mexico; *B. cuchumatana* de la Sierra de los Cuchumatanes, Guatemala, y *B. helmrichi* de las montañas de Alta Verapáz, Guatemala, más dós especies que aqui se describen: *B. hartwegi* de las tierras altas de Chiápas centrál, Mexico y *B. stuarti* de la región fronteriza de Chiapas, México y Huehuetenango, Guatemala. Miembros de éste grupo, presentan evidencia de relación general a especies de tierras altas que antes de incluían en *Magnadigita* y también un especies de *rufescens* del grupo de *Bolitoglossa* especializados a las tierras bajas. La posición intermedia de éstas especies es una demostración más de la tendencia en *Bolitoglossa* de presentar especies relacionadas que ocurren en una area geográfica restringida y para éstos grupos de mostrar una diversidad morfológica considerable, especialmente de las manos y patas. Las especies de tierras altas más generalizadas, tienden a tener membranas interdigitales más reducidas y a ser terrestres. Las especies de tierras bájas son arboreas y presentan las membranas más desarrolladas. Muchos estados intermediarios en estructura de las paras, se encuentran en el grupo de *helmrichi* y las modificaciones son aparentemente parte de la tendencia a la adaptabilidad arborea. Al menos dos aspectos de adaptación intervienen: una tendencia pedomórfica que produce un incremento inicial en las membranas asociado con retención del pié embriónico y una tendencia

adaptiva funcional con selección de estructuras locomotoras especializadas que operan en los apendices parcialmente modificados.

El descubrimiento de nuevos miembros del grupo *helmrichi* permite la demostración de un morphocline continuo en la estructura de las patas, el cual a su turno proveé aspectos en la adaptación morfologica de las salamandras neotropicales a las tierras bájas.

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