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# A REMARKABLE NEW SPECIES OF SALAMANDER ALLIED TO *BOLITOGLOSSA ALTAMAZONICA* (PLETHODONTIDAE) FROM SOUTHERN PERU

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*Bolitoglossa altamazonica* has the most extensive geographical distribution of any species of salamander, ranging from the vicinity of the mouth of the Amazon River in northeastern Brazil to the headwaters of the Amazon in Bolivia, Perú, and Colombia, and into the Magdalena River drainage in central Colombia (Brame and Wake, 1963; Wake and Brame, 1966). The species is very much a "morphospecies," in the sense that the widely spread populations are considered to be conspecific on the basis of general similarity in morphology and coloration. Brame and Wake (1963) suggested that the species was a composite, but in the intervening years, while the number of specimens available for study has greatly increased, no progress has been made in determining if subdivision occurs in this vast geographic range. This is the most southern salamander in the world in distribution, and it is also one of the most truly tropical, in that most of the specimens have been collected at elevations below 500 m. Where plethodontid salamanders occur elsewhere in the tropics, they have become moderately to highly diversified (Wake and Lynch, 1976), and this species is an enigma. Crump (1977) presented a detailed morphological study of one population (from near Belém, Brazil) of *B. altamazonica* and compared it with three other species thought to be close relatives. While she generally corroborated and extended the earlier work, she also clearly

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showed that there was "minimal morphological differentiation" accompanying speciation in this group. Unfortunately, living specimens are rarely available, and it seems likely that adequate samples for electrophoretic analysis will never be available. We are convinced that several, perhaps many, species now masquerade under the name *B. altamazonica,* and we here begin a more detailed series of systematic analyses of this complex.

In 1971 some small salamanders were collected in southern Perú by a field party from the Museum of Zoology of Louisiana State University (LSUMZ). While these animals obviously differed from other *B. altamazonica* we had seen, and especially from a large sample from near the mouth of the Amazon at Belém, Brazil, the differences seemed initially to be rather subtle. We could not exclude the possibility that geographic variation was involved. However, a series of salamanders from a different part of the upper Amazonian drainage system, but relatively nearby in southern Perú, has recently become available to us. This latter series is nearly indistinguishable from the Belém sample studied by Crump (1977). The differences between the LSUMZ series and other *B. altamazonica* remained. On closer study we observed some remarkable morphological specializations in the hands and feet of the new species, and accordingly we have decided that it should now be described.

## MATERIALS AND METHODS

In addition to the type series (for locality see below) we have made a detailed investigation of two samples of *Bolitoglossa altamazonica.* The first is a portion of the sample used by Crump (1977), plus some additional specimens (now in United States National Museum—USNM) collected at the same locality: near Belém, Pará, Brazil (for details concerning this locality see Crump, 1971; 1977). The second sample was collected by Catherine A. Toft along the Río Manú at the point of confluence with the Río Alto Madre de Dios, Madre de Dios, Perú, elevation about 200-300 m (now in Museum of Natural History, University of Kansas—KU 154971-984).

Details on measurements are in Brame and Wake (1963). Morphometric analysis follows Lynch and Wake (1975, 1978).

## DESCRIPTION OF NEW SPECIES

The new species has hands and feet that are greatly reduced in size relative to other species of *Bolitoglossa.* The hands and feet are padlike, but can hardly be described as fully webbed, for the digits are greatly reduced in length. In preservative all of the hands and feet are partially rolled; we suspect that the species is mainly if not exclusively terrestrial, and that it uses these partly rolled appendages in a form of digitigrade locomotion. The pads are doubtless incapable of generating suction, which is a characteristic of *Bolitoglossa* with large, fully webbed feet (Alberch, 1981). We suspect that these animals use the hands and feet as essentially extensions of the limbs, rather than independent elements. In reference to its unique appendages and presumed locomotion, we name it:

### *BOLITOGLOSSA DIGITIGRADA* new species

Figures 1 and 4

*Holotype.*—LSUMZ 25514, an adult female collected along the Río Santa Rosa a few kilometers upstream from the Río Apurímac between Pataccocha and San José (12°44′ S, 73°46′ W), Departamento de Ayacucho, Perú, at an elevation of 1000 m (3300 ft.) on 2 May 1971 by Richard Thomas.

*Paratypes.*—LSUMZ 25509-12, same locality and collector as holotype, 1 May 1971; LSUMZ 25516, MVZ 175848-49, same locality as holotype; LSUMZ 25517-18, same locality and collector as holotype, 20 May 1971.

*Diagnosis.*—A small species (10 adults, 32.5-46.1, mean 38.5 mm standard length) with low numbers of maxillary (mean 15.3) and vomerine (mean 18.1) teeth; distinguished from all members of the genus *Bolitoglossa* by its very narrow hands and feet with greatly reduced amounts of bone (most digits have but a single ossified phalanx and no individual has been found to have more than two in any single digit); further distinguished from *B. altamazonica* by its broader head, from *B. peruviana* by its larger size, and from *B. equatoriana* and *B. palmata* by its smaller size. These are all of the species of salamander known to occur in the Amazon Basin.

*Description of Holotype.*—Adult female, snout short and broad. Nostril small; labial protuberances of nasolabial grooves moderately developed. *Canthus rostralis* short and indistinct. Standard length 6.0 times head width, 4.4 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, slightly protuberant. Weakly defined postorbital groove extends posteriorly from eye as shallow depression for 1.8 mm, then proceeds sharply ventrad at level of posterior end of mandible and extends across gular area as an indistinct and poorly defined nuchal groove, parallel to and 3.8 mm anterior to the sharply defined gular fold. Vomerine teeth 17, arranged in a single row on each side, extend from distal edge of internal nares in gentle arch toward midline then posteriad toward parasphenoid tooth patch, from which separated by slight distance equivalent to about 2 tooth loci. Maxillary teeth 22, very small, peglike but bicuspid, extend posteriorly to point less than halfway through eye. Premaxillary teeth 3, do not protrude through lip, slightly larger than maxillary teeth. Tail relatively short, 0.74 times standard length, very stout and strongly tapered, nearly round in cross section, strongly constricted at base. Post-iliac gland large and well defined. Limbs moderately short, limb interval 3.5; standard length 4.8 times right forelimb, 4.6 times right hind limb, and 15.9 times right foot width. Hands and feet greatly reduced, extremely narrow with extremely short digits; digits fused together more than webbed; digits poorly defined, with only longest one projecting beyond pad margin (Fig. 4). No subterminal pads. 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 7.4; snout to gular fold (head length) 10.2; head depth at posterior angle of jaw 4.5; eyelid length 2.9; eyelid width 1.9; anterior rim of orbit to snout 2.8; horizontal orbital diameter 2.7; interorbital distance 2.9; distance between vomerine teeth and parasphenoid tooth patch 0.6; snout to forelimb 12.8; distance separating internal nares 1.8; distance separating external nares 2.2; snout projection beyond mandible 1.0; snout to posterior angle of vent (standard length) 44.5; snout to anterior angle of vent 39.6; axilla to groin 24.3; tail length 32.7; tail width at base 3.8; tail depth at base 4.2; forelimb length 9.3; hind limb length 9.6; width of right hand 2.2; width of right foot 2.2.

*Coloration in Alcohol.*—The dorsum of the head is grossly mottled with tan and dark brown, but the nasolabial protuberances are conspicuously bright cream. The body is basically blackish, most intense on the sides, with a broad, heavily mottled, tan stripe. Ventral surfaces of the head and body are rather light, with punctate melanophores over a cream-light yellow background. There is some darkening midventrally on the trunk, forming an irregular stripe. The tail is dark dorsally, mottled with several dark colors; there are occasional large black spots. Laterally and ventrally the tail is lighter, and the venter is mainly a yellowish cream color with dark mottling. There are some large, whitish, superficial patches ventrolaterally. The limbs, hands, and feet are dark, with two shades of dark mottling.

*Coloration in life.*—Generally lichenate; blue to blue-gray and buffy with wide middorsal zone of buff to pale putty color and longitudinal streaking; some reddish color, especially on neck and tail.

*Variation.*—The species is known from 10 individuals, two of which are males. The largest male is exceeded in size by three females, and while our sample is small, this is the expected pattern of sexual dimorphism in *Bolitoglossa*. The eight females average 39.2 mm standard length, and the two males are 38.8 and 32.5 mm. Standard length is 5.6-6.6 (mean 6.0) times head width in females, and 5.6 in males. Both males have poorly defined, roughly round mental glands. No other sexual dimorphism is evident. Other structural variation is considered in the osteology and morphometrics sections (see below).

Our sample does not vary greatly in coloration. Most individuals are rather like the holotype—generally dark but with a lighter middorsal area that is buffy and mottled. Some individuals are very dark dorsally and one is almost uniformly dark, but the majority have a defined broad band. Ventrally all individuals show the irregular dark midventral stripe. All individuals have bright whitish color on the nasolabial protuberances.

*Remarks.*—The adult female which was cleared and stained had enormously swollen oviducts but the ovarian ova were very tiny. This suggests that the individual had recently laid eggs. The eggs either were not guarded, or were overlooked by the collector.

*Morphometrics.*—We examined variation in *Bolitoglossa digitigrada* and compared it with samples of *B. altamazonica* from Manú, Perú, and Belém, Brazil, using discriminant function analysis (University of California, Berkeley, SPSS version 7.0; see Lynch and Wake, 1975, 1978, for general description of approach for salamanders). We entered the following variables: standard length, head width, hind limb length, tail length, foot width, total maxillary tooth count, total vomerine tooth count. Sample sizes varied from 10 for the *B. digitigrada* sample to 14 for the Manú and 34 for the Belém samples. There are but two discriminant axes for three samples, and these are displayed in Figure 2. The first axis accounts for 96.6% of the observed interspecific variation. By far the most important variables in the first discriminant function are head width and foot width (Table 2). Frequently the first discriminant function segregates by size, but in the present instance our samples are all roughly the same size (mean standard lengths for the new species, Manú, and Belém are 38.5, 40.2, and 36.0 mm, respectively). *B. digitigrada* has a much broader head and a much narrower foot (Fig. 3) than our samples of *B. altamazonica*. There is a highly significant correlation ($p < .001$)

between standard length and head width (r=.889), and foot width (r=.861), for the three samples combined.

The two samples of *B. altamazonica* cluster closely (Fig. 2) and there is no overlap with *B. digitigrada.* A classification matrix for this discriminant analysis discloses that 94.8% of the individuals studied can be correctly assigned to their proper samples on morphological grounds. All of the misclassifications involve *B. altamazonica.* One Belém animal is classified in the Manú sample, and two Manú individuals are classified with Belém.

In many tropical salamanders dentition is useful in species discrimination, but dentition is not of value in separating these species. Crump (1977) studied four species of closely related South American *Bolitoglossa* (including *B. altamazonica*) and found the dentition to be so variable as to be meaningless as a diagnostic character. She reported no significant correlation between vomerine teeth and standard length. For our three samples considered separately we find the same result, but for the samples combined there is a low correlation (r=.249, p=about .05). She found a significant correlation between standard length and maxillary tooth counts for *B. altamazonica;* we find no significant correlation in our samples of *B. digitigrada* and the Manú sample of *B. altamazonica,* but for both we have samples with but a small range of sizes. When the three samples are combined the correlation of numbers of maxillary teeth and standard length is r=.591 ($p < .001$).

We also performed discriminant analysis by eliminating dentitional characters, so that we were using only external shape descriptors. Here all *B. digitigrada* were again correctly classified, but three Manú specimens were classified with the Belém group, and two of the Belém specimens were classified with the Manú group. When snout-gular fold length was added as a descriptor, discrimination fell further, and while all *B. digitigrada* continued to be correctly classified, three Manú and three Belém were cross-classified. In these two analyses standardized discriminant function coefficients for head width and foot width were approximately 10 times those of the next most important variables.

*Osteology.*—Information concerning osteology is derived from one cleared and stained specimen (MVZ 175849) and radiographs of the entire series. The Manú and Belém series were also radiographed, and two cleared and stained specimens for comparison have been available from Belém. Radiographs of other populations assigned to *B. altamazonica* have also been available, as have cleared and stained specimens of *B. peruviana, B. chica,* and *B. sima.*

The skull is compact and well developed, with strong sutural contacts between adjacent bones. The premaxillary bones are stout, with long frontal processes that are markedly expanded distally, where they extensively overlap the frontal bones. The palatal process of the premaxilla is narrow but well defined. Frontal processes are rather strong, and they remain separated around the sides of a rather large internasal fontanelle; the processes extend beyond the anterior rim of the orbit to terminate at the posterior end of the nasals. The nasals are relatively large, but are non-protuberant. The facial portion of the skull is small, but it is dominated by the nasals. In the cleared and stained specimen the nasals are fused with the prefrontals, and the nasolacrimal foramen is incised in the lateral margin of the composite structure. In some of the radiographed specimens a very distinct, small prefrontal is present, so the bone has a variable condition in this species. The nasals, prefrontals, or composite bone broadly overlap the facial processes of the frontals.

The vomers are well developed, but the body is rather small. They are widely separated by the large intervomerine fontanelle for most of their length, and approach each other, but do not make contact, at their posterior tips. Preorbital processes are long and spinous, and they extend beyond the lateral margins of the vomerine bodies. The processes bear small teeth to about the midpoint, or lateral margin, of the internal nares. The teeth are in a single series medially, but form a small patch laterally.

The frontals are well developed. Considering that the entire facial part of the skull is small, the facial portions of the frontals are rather well developed. The bones are tightly ankylosed to each other, to the ventral orbitosphenoids laterally, and to the parietals posteriorly. The relatively broad frontals have distinct lateral lobes which overlap the parietals. The parietals have distinct medial lobes which overlap the frontals. The parietals are well developed and tightly ankylosed to each other. There is a distinct lateral spur. The otic capsules are of moderate size and bear no crests or projections, although the bulges formed by the semicircular canals are clearly evident. The large parasphenoid is narrow anteriorly, but the orbitosphenoids remain well separated. The tip of the parasphenoid is blunt. Posterior vomerine teeth are in large patches on the parasphenoid. These patches approach each other very closely but do not touch. In the single cleared and stained individual there are 60 (left) and 61 (right) teeth. These are bicuspid structures that exceed the size of the maxillary teeth. The operculum has no stilus. Quadrates are moderate, and are joined to the skull by the fairly well-developed squamosals and the cartilaginous suspensorium.

The hyobranchial apparatus is typical of that found in most members of the genus and no features are worthy of special note.

Vertebral structure is similar to that of other species of *Bolitoglossa*. In most individuals there are one cervical, fourteen trunk, one sacral, two caudosacral, and a varying number of caudal vertebrae. The holotype has an anomalous vertebral column in that the sacrum is asymmetrical. There are 13½ trunk vertebrae and only 1½ caudosacral vertebrae. While such an asymmetry is commonly found in North American species of such genera as *Batrachoseps* and *Plethodon,* all tropical genera except *Oedipina* have 14 trunk vertebrae, and this apparently is the first description of an asymmetry (some specimens with abnormal fusions of trunk vertebrae have been encountered, Wake and Brame, 1969). Caudal vertebrae vary from 23 to 27 (mean 24.6) in the nine individuals with apparently unregenerated tails. The second trunk vertebra is marginally the longest in the body, and the first caudal vertebra that is shorter than it is about the ninth. The first trunk vertebra is the shortest in the body and the first caudal vertebra shorter than it is the twelfth. This does not include the first caudal, which together with the second caudosacral forms a constricted area in the tail base region. Ribs typically are present on the first 13 trunk vertebrae. The tail is robust basally, but it is strongly tapered near the tip. The first ten to twelve caudal vertebrae have well-developed transverse processes near their anterior end, directed sharply anteriad. The processes of the first caudal are very long and sweep forward along the last caudosacral vertebra, whose processes are also directed anteriorly. The processes of these two vertebrae do not cross.

The hands and feet are the most distinctive in the entire genus (Fig. 4). The phalangeal formulae for the hands of the cleared and stained specimen are 0, 1, 1, 1, and 1, 1, 1, 1 for the left and right sides, respectively. The formulae for the feet are 1, 1, 1, 1, 0, and 1, 1, 1, 0, 1 for the left and right sides, respectively. The phalanges are so small and so little mineralized that whether one counts 0 or 1 for the first digit of the right hand (Fig. 4) is arbitrary. The whole hand or foot is very small, barely larger than the diameter of the arm or leg. The digits are indistinct. As a result of this weak mineralization the radiographs are of little value. In several individuals no phalanges are visible in either of two radiographs, although the metacarpals and metatarsals are well ossified. In only a single large specimen (LSUMZ 25517) is more than one phalanx per digit present, and here two are seen in the third digit of the left hand only. The metapodials are well ossified elements that have the shape of somewhat flattened cylinders. The phalanges are very erratically developed, and what mineralization is present is highly irregular in most cases. In some instances the terminal parts of the digit are bony, as is typical in all other salamanders, but in most instances the digital tip is cartilaginous. There are seven carpals and eight tarsals in the typical pattern or generalized *Bolitoglossa*. There is no tibial spur, and the tibial crest is very indistinct.

*Locality and habitat.*—All of the specimens were found in coffee groves, and all were found in terrestrial situations. Four animals were taken in relatively open coffee groves, where shade trees were scattered. Three were on moist but not wet soil; one was in dry leaf litter beneath a mat of cut vegetation. Two other animals were taken from under a rock and under a log in a shady coffee grove. Temperatures of the air near the ground where animals were collected were 35°-37° C. and the temperature of the air spaces beneath the litter was 29°. These are extremely high temperatures for any salamanders. While none of the animals were found while active, we suspect that the species is fundamentally terrestrial, although it may engage in some climbing of low vegetation and bases of trees.

The type-locality lies on the Río Santa Rosa, which flows northeast from the Andes and joins the Río Apurímac just upstream from Luisiana (Hacienda Luisiana). About 7 km from its confluence with the Apurímac, the Santa Rosa comprises two streams that are not separately named on the 1:1,000,000 map of Perú issued by the Instituto Geografico Militar (1973). In its progress to the type-locality of *B. digitigrada* the Louisiana State University Museum of Zoology field party took the mule trail from Capricho towards Tambo; the trail crosses the Santa Rosa to the south side and recrosses it (the southern branch) upstream from the confluence of the two branches. Above this second crossing at San José (where there is a bridge), the trail ascends the ridge between the two branches of the Santa Rosa and proceeds over the easternmost range to Tambo. The specimens of *B. digitigrada* were all collected in the coffee groves on the south side of the Santa Rosa below the bridge over a distance of less than one kilometer. A week was spent at San José, during which time the junior author searched extensively in terrestrial situations. The last two specimens were collected during a brief effort on the return trip from higher elevations to Luisiana. Bromeliads were also searched at the type-locality and higher elevations without result. Night collecting for frogs and *Anolis* also yielded no evidence of salamanders. The expedition spent slightly less than three weeks working the trail above San José from stations at 1650 m, 1969 m, and 2606 m; similar collecting techniques produced no further salamanders.

## DISCUSSION

Populations of salamanders assigned to *Bolitoglossa altamazonica* have an enormous range, and we have long thought that the taxon might be a composite (Brame and Wake, 1963). Our efforts to treat this assemblage have been hampered by several factors. Until the collection of the Manú series, the only collection of any size was that from the Belém area, so it has been impossible to assess interpopulational variation. The small, lowland species of *Bolitoglossa* from South America are so similar in morphology (Crump, 1977) that it is necessary to have reasonable samples before attempting morphometric analysis. Further, no sympatry of populations assigned to *B. altamazonica* with any other species of salamander is known to occur, and we thus are faced with the old problem of dealing with slightly differentiated allopatric populations. We have had no living specimens or frozen tissues in our laboratories, so it has been impossible to conduct the electrophoretic and immunological analyses that would provide clues on degree of genetic differentiation of the populations. Finally, the three syntypes of *Bolitoglossa altamazonica* (Cope, 1874) are either lost or destroyed; these were collected in the Departamento de Loreto, Perú, and we have seen some other specimens from that area (Brame and Wake, 1963; Wake and Brame, 1966) that resemble those from Belém, but we cannot be certain as to the true identity of the species. The issue is further complicated by the fact that there are two other available names for the Belém population. The holotype of *Oedipus paraensis* Unterstein is lost (probably destroyed during the Second World War), and the four cotypes of *Eladinea estheri* Miranda Ribeiro are hatchlings that are valueless for morphological analyses (Brame and Wake, 1963).

The series from Manú is remarkably similar to that from Belém in all features (Figs. 2 and 3). The Manú specimens have slightly broader heads and may have slightly fewer teeth, but our samples are inadequate to demonstrate any statistical differences. As we have shown above, when we eliminate the dentitional characters in our discriminant function analysis, many individuals of both populations are misclassified as the other. This multivariate analysis is extremely effective in separating groups, so we are impressed with the general level of similarity of these samples. This similarity is especially impressive in view of the fact that these two samples are separated by over 2,700 air-line kilometers! In addition to size and shape similarities, the two populations show no distinctive color differences, although both are somewhat variable. Both populations are known to be arboreal by night. Crump (1971, 1977) reports finding individuals of the Belém population active and exposed on leaf surfaces and a variety of other nonterrestrial habitats by night, and, during the wet season, by day. The collector of the Manú sample, Catherine A. Toft, found all 14 individuals on leaves at night, at a height of approximately 0.5 m above the ground. While she reports that the animals were curled on the surfaces of leaves and might have been sleeping, we find this unlikely, for salamanders do not normally remain exposed while at rest. In support of her view she cites the presence of large numbers of 1 to 3 mm ants in the stomachs of the salamanders, and she thinks that this suggests that the salamanders forage in the leaf litter during the day. These animals and those from Belém were collected in lowland wet to rainforest, and on ground that was subject to periodic floods or was even permanently flooded (some habitats at Belém). Thus in virtually every aspect of their known biology these populations are very similar.

*Bolitoglossa digitigrada* is known from a locality that is only a little over 300 km W of the Manú locality, but about 700 to 800 m higher in elevation. However, the two localities are in separate drainage systems. The Río Manú eventually flows into the Río Madeira, while the Río Santa Rosa flows into the Río Apurímac, which in turn joins the Río Ucayali. These two great drainages are separated by various ranges of the Cordillera Oriental of southern Perú, notably the Cordillera Vilcabamba.

The morphological differences distinguishing the Manú sample from *B. digitigrada* are numerous, but the most significant involve width of head and feet. The Manú specimens have broader heads than other *B. altamazonica* (standard length is 6.0-7.0, mean 6.6 times head width in females and 6.3-6.5, mean 6.4 in males), but not so broad as those of *B. digitigrada* (5.6-6.6, mean 6.0 in females; 5.6 in the two males) (Fig. 4). The feet of *B. digitigrada* are the narrowest we have ever seen in a *Bolitoglossa,* and this external character alone will discriminate most *B. altamazonica* and *B. digitigrada* (Figs. 3, 4, and 5). The ventral coloration of *B. digitigrada,* with its distinctive but irregular midventral dark stripe, is also a feature that distinguishes the species from all *B. altamazonica*.

The decisive morphological feature distinguishing *B. digitigrada* from *B. altamazonica* is the extreme reduction of the feet and concomitant loss of many phalanges. The digits of *B. altamazonica* are very small, relative to those of most *Bolitoglossa* (Fig. 5), and we have encountered some instances of reduction. In radiographs the phalangeal elements are extremely difficult to see, but we have seen the full expected complement (1, 2, 3, 2; 1, 2, 3, 3, 2) in individuals in both the Belém and Manú populations. Losses also appear to be present, but we have had only two cleared and stained specimens (both from Belém) and they both have only the single phalangeal loss illustrated in Fig. 5 (1, 2, 3, 2, 2 in each foot). Doubtless further reductions will be found, but not to the extreme seen in *B. digitigrada*. Other populations assigned to *B. altamazonica* from several areas in Colombia and northern Perú have been examined radiographically, and these have better developed phalanges than do the populations from Belém and Manú. In these populations the digits are relatively long and the full generalized formula is present.

The hands and feet of *B. digitigrada,* and to a much lesser extent, those of *B. altamazonica,* are paedomorphic relative to those of the more generalized, upland species of South American *Bolitoglossa* such as *B. vallecula* from Colombia. The general phenomenon as it affects hand and foot evolution was introduced by Wake and Brame (1969), in discussing the appendages of *B. rufescens* and *B. occidentalis.* In those diminutive species the hands and feet appear to be relatively undeveloped. Other parts of the animals also appear poorly developed. Alberch and Alberch (1981) have considered this problem in detail, and have argued that it represents a case of progenesis, in which the major evolutionary change appears to be achievement of sexual maturation at a relatively early stage of ontogeny. The situation in the *B. altamazonica* group is somewhat different. The species are all small, on the order of the size of the *B. rufescens* group, and perhaps progenesis was the mechanism whereby small size and associated delayed development was introduced into the lineage. This would account for the generally reduced size and pad-like appearance of the hands and feet in all members of the *altamazonica* group. There is, for example, a marked gradient of development in any given digit of adults (Figs. 4 and 5), and this is typical of young plethodontid salamanders. In *B. digitigrada* the skull is rather more fully developed than in *B. altamazonica;* bones are well articulated and such elements as the prefrontal are occasionally present, and even when not separate the prefrontal may be represented by a lobe of the nasal. Yet, the hands and feet of this species are less developed than any other member of the genus. Because we already have some evidence of paedomorphosis in *Bolitoglossa* we might pursue this line of reasoning further for an explanation of this phenomenon. One possibility is that a dissociation of hand and foot development has occurred relative to the rest of the body. If this is a correct interpretation the hands and feet demonstrate a slowdown in rate of development (technically neoteny, Alberch *et al.,* 1979).

No major osteological distinctions other than those noted above separate *B. digitigrada* and *B. altamazonica,* but we have the impression that *B. digitigrada* has a more extensively ossified skull, with firmer articulations. P. Alberch (pers. comm.) has failed to find prefrontals in a series of cleared *B. altamazonica.* We find prefrontals to be present on both sides in one of two cleared specimens available to us, but not in the other. *B. digitigrada* seems to have fewer caudal vertebrae than *B. altamazonica* (23-27, mean 24.7 in 9 individuals as compared with 24-39, mean 30.4 for 9 individuals from Manú, and 27-33, mean 29.1 for 9 individuals from Belém; all of these individuals are adults with unregenerated tails). Since tail length does not discriminate the three populations to any significant degree (Table 2), this difference may constitute a significant shape difference. *B. digitigrada* seems to have a more sharply tapered tail than do *B. altamazonica* from the two populations studied.

The only other salamanders described from east of the Andes Mountains in South America are *B. palmata, B. equatoriana,* and *B. peruviana. B. palmata* is very poorly known, but it is a somewhat larger species with distinctively shaped hands and feet that have well-defined digits. It also occurs at relatively high elevation (2,000 m, Brame and Wake, 1962). *B. equatoriana* occurs in the lowlands but it, too, is somewhat larger than *B. digitigrada.* While some phalangeal reduction occurs in this species, the hands and feet are relatively large and broad (Brame and Wake, 1972). *B. peruviana* is a smaller species than *B. digitigrada,* but its feet are relatively broader (Crump, 1977; Fugler and Walls, 1979). Crump reports that *B. peruviana* has a head of roughly the same width as that of *B. digitigrada. B. peruviana* occurs at slightly higher elevations than does *B. digitigrada.* The digits of *B. peruviana* are more distinct, and few or no phalangeal reductions occur. We examined 2 cleared and singly stained skeletons of *B. peruviana* from Ecuador and found no reductions, but P. Alberch (pers. comm.) has examined additional specimens from the same population and finds the fourth toe to consistently lack one phalanx. Radiographs of two specimens of *B. peruviana* from another population also show that the fourth toe is polymorphic in regard to reductions. In other respects the hand and foot skeleton is much more fully developed than in *B. digitigrada.* The prefrontals of *B. peruviana* are relatively poorly developed. A tiny fragment representing a probable prefrontal is present on one side in one of our two cleared specimens. P. Alberch (pers. comm.) finds a prefrontal on one side in five of ten cleared specimens, but the bones are otherwise absent or fused with the nasals. The snout region of the skull in *B. peruviana* is very small and somewhat reduced, lying below the level of the frontals. However, we believe that apart from *B. altamazonica, B. peruviana* is the likeliest prospect as a potential close relative of *B. digitigrada.*

The distinctive ventral coloration of *B. digitigrada* is somewhat reminiscent of that of *B. equatoriana,* but in that species the light pigment is more clearly arranged into spots, rather than being pigment gaps.

## NEW LOCALITY RECORDS FOR *ALTAMAZONICA* GROUP

We take this opportunity to record some recent collections of *Bolitoglossa* from the Amazonian Basin. All of these are members of the *B. altamazonica* group, but considerable variation is shown from one locality to the next and we suspect that more than a single species is represented. Detailed comments concerning these populations are deferred to a later time. The most important point to be made concerning these localities is the extent to which gaps in the maps presented by Brame and Wake (1963) and Wake and Lynch (1976) have been filled.

University of Texas at Arlington, Collection of Vertebrates 4012-4015, 5323, Timbo, Vaupés, Colombia; 4934-35, 4938, 5324-26, 2 km SW Yapima (69°28′ W, 1°03′ N), Vaupés, Colombia.

American Museum of Natural History 103535-42, 3 airline km SSW Mishana on Río Nanay, 150 m, Loreto, Perú (eggs, hatchlings, and juveniles from this locality are catalogued as 103543-48); 88066-67, Santa Rosa de Sucumbio, Río San Miguel, Putumayo, Colombia (eggs associated with 88067); 88084-87, Cuisuime, Río Cuisuime, 320 m (60 airline km SE Macas) (2°40′ S, 77°42′ W) Morona-Santiago, Ecuador (these specimens were reported, without numbers, as *B. peruviana* by Fugler and Walls, 1979); 88471-84, headwaters of Río Loreto-Yacu, Yagua Indian Village, Loreto, Perú; 94351-52, Ashuara Village on Río Macuma, 300 m, ca. 10 kms above Río Morona (ca. 83 km ESE Macas), Morona-Santiago, Ecuador.

Texas Cooperative Wildlife Collection, Texas A & M University 36664, 40490, Moropon, Río Nanay, Loreto, Perú; 41749, Centro Union, Loreto, Perú.

Museum of Natural History, University of Kansas 183008, Villa Tunari, 460 m, Cochabamba, Bolivia; 154970, Casa de Campa, south slope of Serrania de Sira, E Río Pachitea Valley, 690 m, Huánuco, Perú.

Museu de Zoologia, Universidade de São Paulo 50314, Boca do Pauini, Río Purus (7°47′ S, 67°5′ W), Amazonas, Brazil; 50500, Canutama, Río Purús (6°33′ S, 64°21′ W), Amazonas, Brazil; 51190, Barreira do Matupiri, Río Madeira (5°34′ S, 61°7′ W), Amazonas, Brazil; 51630 (not examined), Porto Walter, Río Jurná (8°16′ S, 72°44′ W), Acre, Brazil; 52837 (not examined), Uruá (Parque Nacional de Amazonia), Río Tapajós (4°37′ S, 56°15′ W), Pará, Brazil.

United States National Museum 201698-99, Boca do Pauini, Río Purus, Amazonas, Brazil; 201697, Barreira do Matupiri, Río Madeira, Brazil; field number 044506 (not examined), Parque Nacional do Río Tapajós, Pará, Brazil.

Museum of Natural History, Los Angeles County 85903, Pucallpa, Loreto, Perú.

Instituto Miguel Lillo, Tucumán (no number), Yungas del Palmár, 1,000 m, Chapare, Cochabamba, Bolivia.

Museum of Vertebrate Zoology, Berkeley 68119, El Palmár, 1,000 m, Chapare, Cochabamba, Bolivia.

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**Table 1. Measurements and Data for *Bolitoglossa digitigrada***

| | Sex | Snout-Vent Length | Axilla-Groin Length | Head Width | Hindlimb Length | Forelimb Length | Tail Length | Numbers of Maxillary Teeth | Numbers of Vomerine Teeth | Limb Interval | Foot Width |
|---|---|---|---|---|---|---|---|---|---|---|---|
| LSUMZ 25509 | ♀ | 46.1 | 25.6 | 7.0 | 9.1 | 9.3 | 28.0 | 10 | 10 | 4 | 3.1 |
| LSUMZ 25514 | ♀ | 44.5 | 24.3 | 7.4 | 9.6 | 9.3 | 32.7 | 22 | 17 | 3½ | 2.8 |
| MVZ 175848 | ♀ | 43.1 | 22.6 | 7.2 | 9.1 | 9.2 | 31.2 | 17 | 26 | 3 | 3.1 |
| LSUMZ 25517 | ♀ | 36.7 | 18.5 | 6.5 | 8.2 | 8.4 | 25.2 | 20 | 22 | 1½ | 2.4 |
| LSUMZ 25512 | ♀ | 36.1 | 19.6 | 6.1 | 7.5 | 7.2 | reg. | 16 | 10 | 3½ | 2.2 |
| LSUMZ 25511 | ♀ | 36.0 | 19.4 | 5.9 | 6.9 | 7.9 | 25.7 | 7 | 20 | 3 | 2.2 |
| LSUMZ 25510 | ♀ | 35.8 | 18.5 | 6.0 | 7.0 | 7.2 | 27.2 | 18 | 20 | 2½ | 2.1 |
| LSUMZ 25518 | ♀ | 35.6 | 18.7 | 6.2 | 7.2 | 7.5 | 26.7 | 9 | 21 | 2½ | 2.0 |
| MVZ 175849 | ♂ | 38.8 | 21.2 | 6.9 | 8.7 | 8.8 | 30.8 | 17 | 16 | 3 | 3.0 |
| LSUMZ 25516 | ♂ | 32.5 | 17.7 | 5.8 | 6.8 | 6.4 | 21.5 | 17 | 19 | 2½ | 2.2 |

**Table 2. Standardized coefficients for stepwise multiple discriminant function analysis of morphometric variation in three populations of *Bolitoglossa*. The first axis explains 94.5% of the observed inter-group variation.**

| | *Discriminant Function* | |
|---|---|---|
| **CHARACTER** | **FIRST AXIS** | **SECOND AXIS** |
| Standard Length | −0.216 | 0.100 |
| Head Width | −2.417 | −0.303 |
| Hind Limb Length | 0.235 | 0.236 |
| Tail Length | −0.055 | 0.006 |
| Maxillary Tooth Number | 0.441 | 0.922 |
| Vomerine Tooth Number | −0.389 | −0.210 |
| Foot Width | 2.135 | −1.227 |

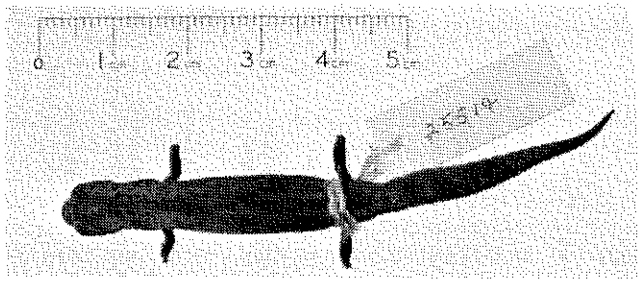

FIGURE 1. Holotype of *Bolitoglossa digitigrada,* LSUMZ 25514.

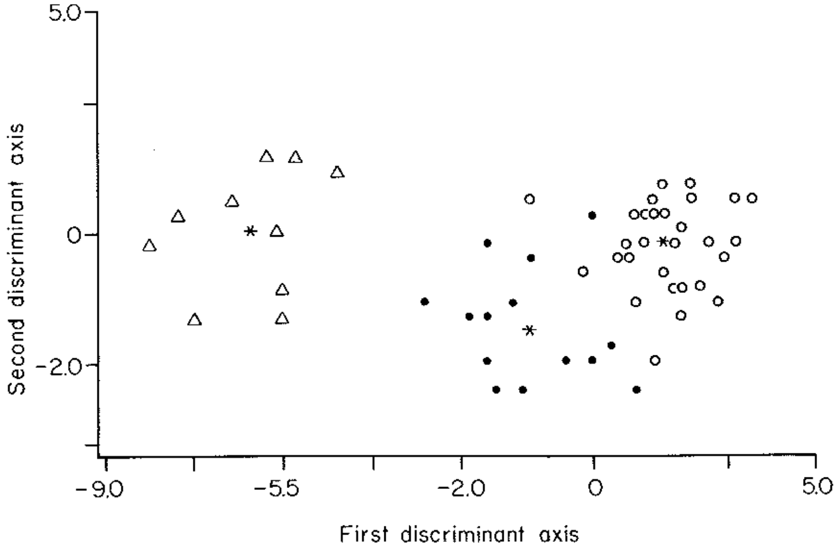

FIGURE 2. Plot of the two discriminant axes separating two populations of *Bolitoglossa altamazonica* (dot, Manú sample; open circle, Belém sample) and the single population of *B. digitigrada* (open triangle). Centroids are marked with an asterisk.

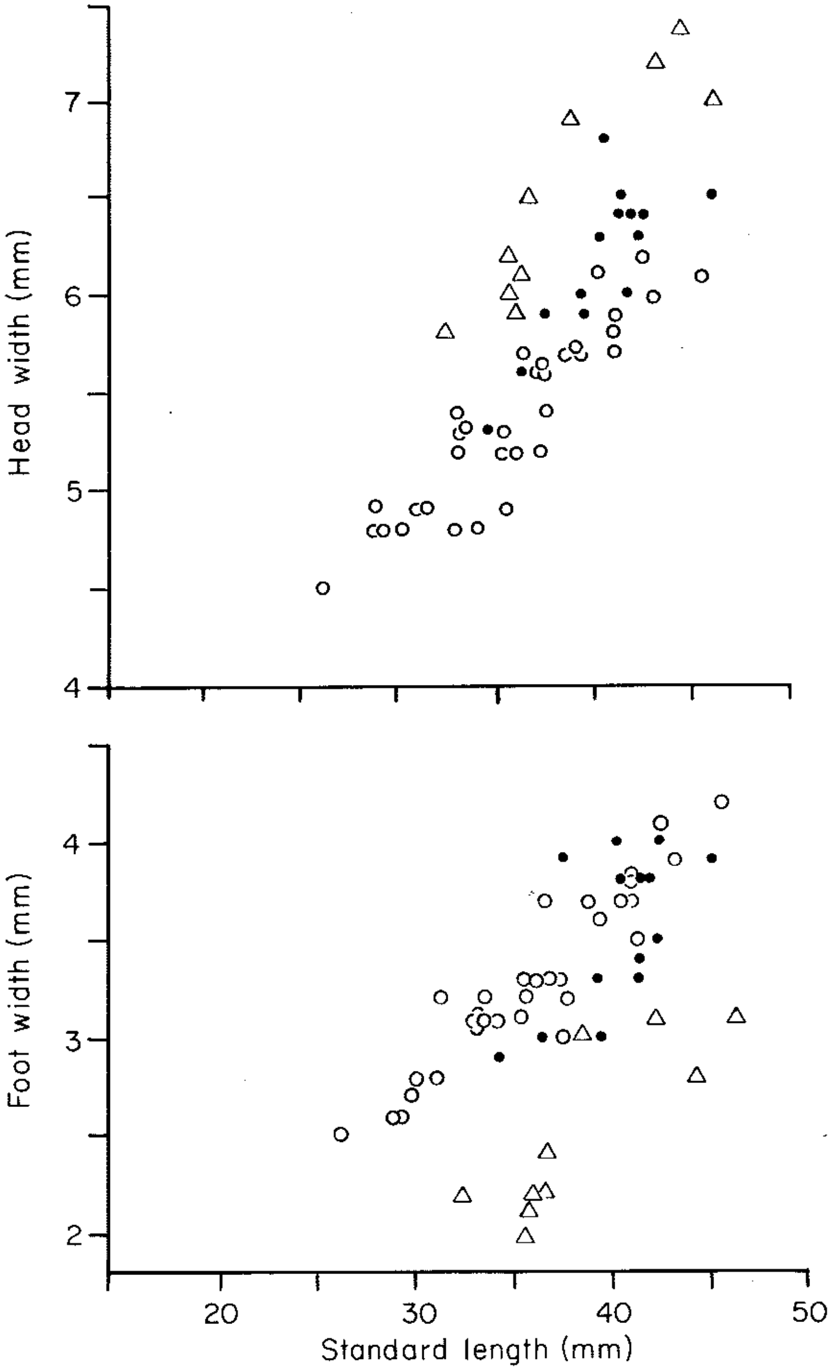

FIGURE 3. Relation of head width and foot width to snout-vent (standard) length for two populations of *Bolitoglossa altamazonica* (dot, Manú sample; open circle, Belém sample) and the single population of *B. digitigrada* (open triangle).

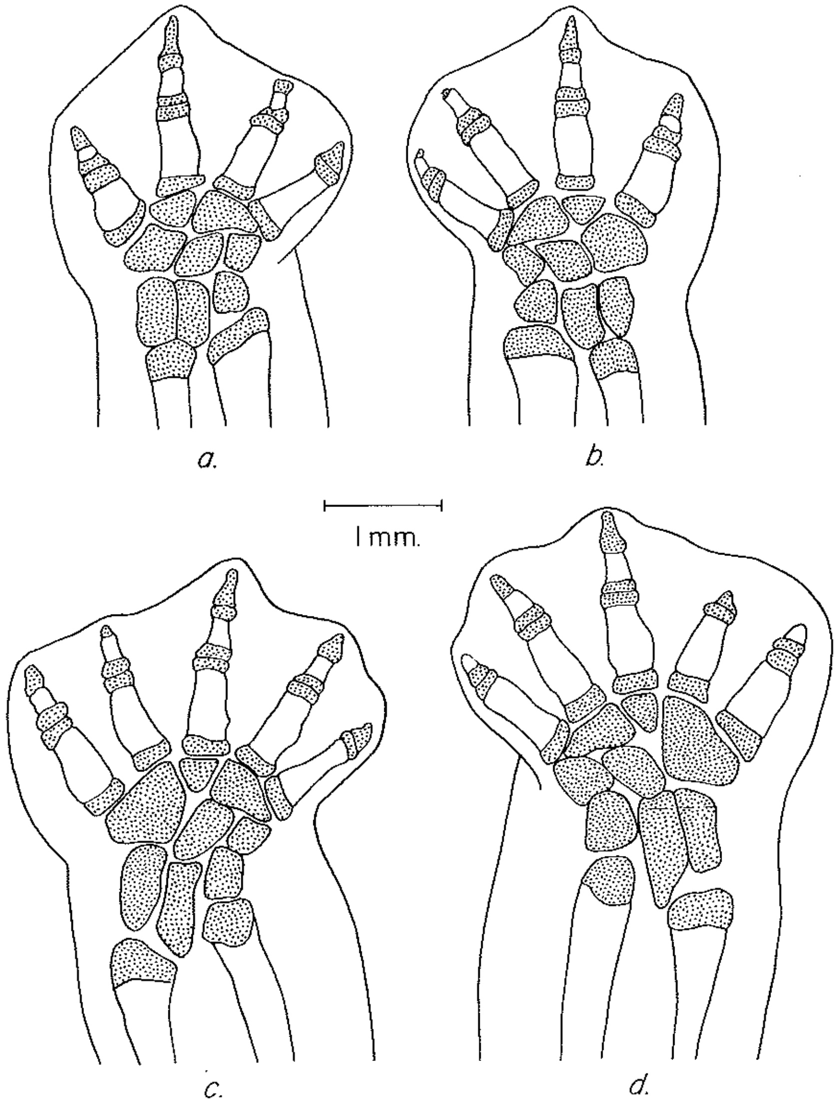

FIGURE 4. Drawing of the hands and feet of a cleared and stained specimen (MVZ 175849) of *Bolitoglossa digitigrada,* from projected image. Cartilage stippled. a. Left hand, b. right hand; c. left foot, d. right foot.

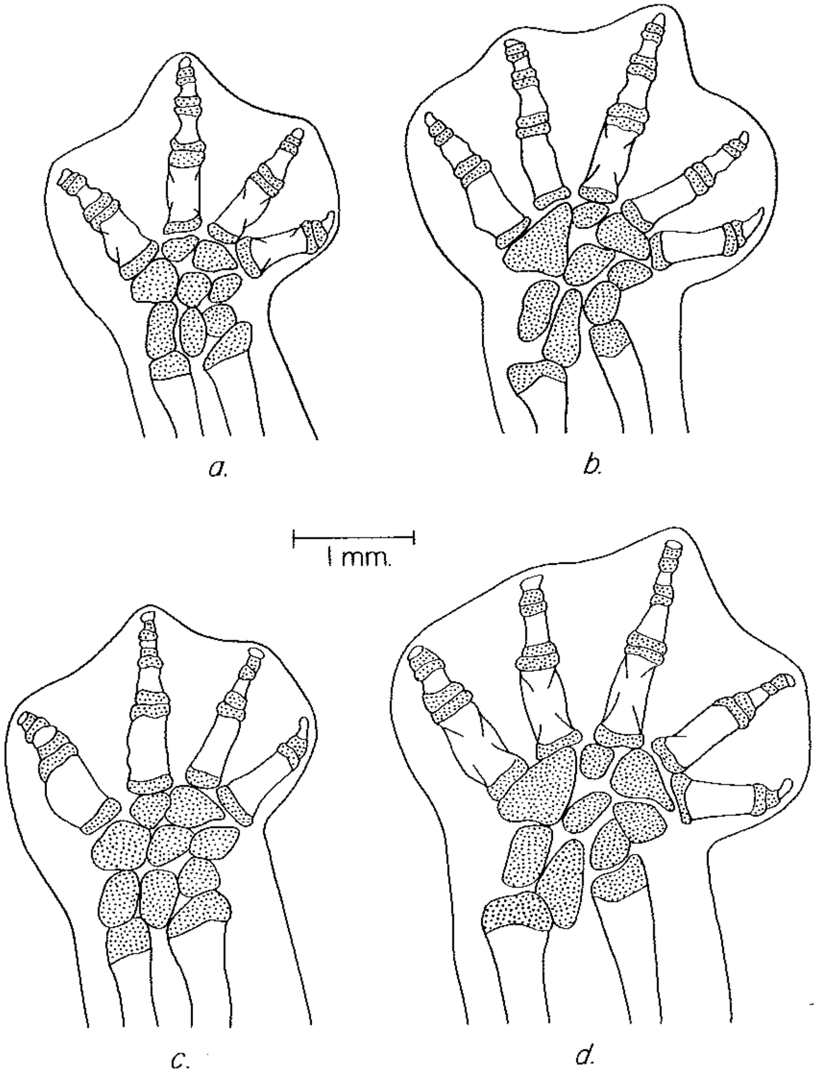

FIGURE 5. Drawing of the hands and feet of South American *Bolitoglossa,* from projected image. Cartilage stippled. a. Left hand, and b. left foot of *Bolitoglossa peruviana* from Puerto Libre, Napo, Ecuador; c. left hand, and d. left foot of *Bolitoglossa altamazonica* from near Belém, Pará, Brazil.

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