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THE SALAMANDERS OF SOUTH AMERICA

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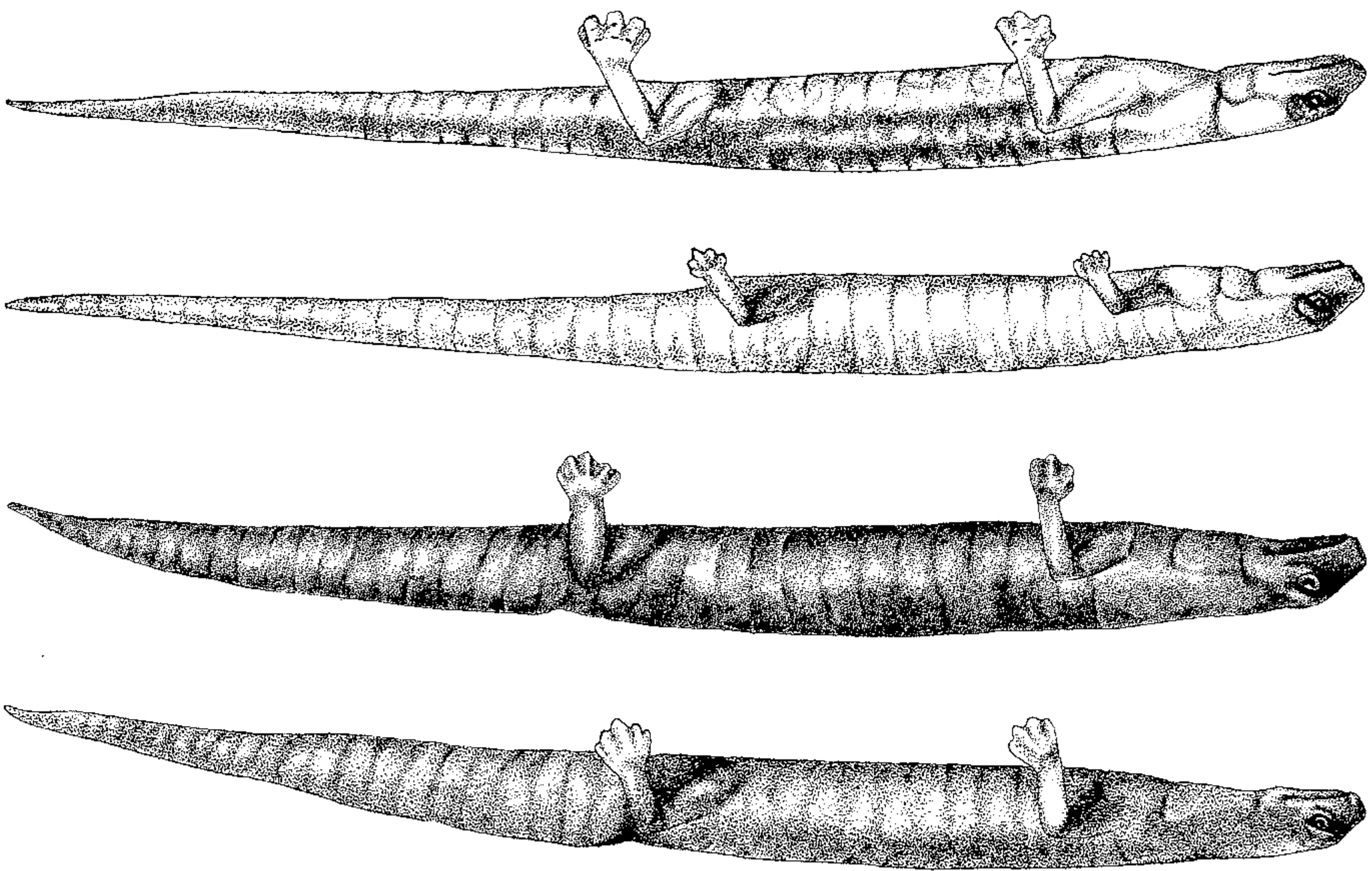


Fig. 26. Left to right, *Bolitoglossa vellutcula* MJA 8a, Yurumal, Colombia, female, holotype, 54.1 mm standard length; *Bolitoglossa chica* JAP 4366, Santo Domingo, Ecuador, female holotype, 48.7 mm standard length; *Bolitoglossa capitata* MJA 8a, La Gomela La Victoria, Colombia, female, holotype, 87.5 mm standard length; *Bolitoglossa macfari* MJA 8a, La Gomela, Colombia, female, holotype, 46.8 mm standard length.

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KEY TO THE SALAMANDERS OF SOUTH AMERICA

- 1a. Costal grooves 17 to 22; body elongate; sublingual fold present
 *Oedipina* ... 2
- 2a. Snout blunt and short; maxillary teeth extending posteriorly past level of internal choanae; eye large *O. complex*
- 2b. Snout long and pointed; maxillary teeth not extending posteriorly past level of internal choanae; eye small *O. parvipes*
- 1b. Costal grooves always 13; body short and robust; sublingual fold absent ..
 *Bolitoglossa* ... 3
- 3a. Limbs very long in females with only 2 costal folds separating appressed limbs; hands and feet nearly webless *B. hypacra*
- 3b. Limbs of females relatively short with from 2½ to 5 costal folds separating appressed limbs; hands and feet with moderate to complete webbing 4
- 4a. Snout noticeably shortened 5
- 5a. Vomerine teeth few (7 to 15); many tiny guanophores ventrally; size small (less than 46.9) *B. orestes*
- 5b. Vomerine teeth moderate (14 to 23); no guanophores ventrally; size moderate (to 53.3) *B. palmata*
- 4b. Snout moderate to long 6
- 6a. Head very broad (standard length 5.4 times head width); feet with only outer digits completely involved in web, with middle digit relatively free *B. nicefori*
- 6b. Head moderately broad to narrow (standard length 5.7 to 8.0 times head width); feet never with only outer digits completely involved in web 7
- 7a. Large (to 85.5 standard length); body robust; color solid lead black ...
 *B. capitata*
- 7b. Medium to small (standard length not over 70); color rarely solid lead black 8
- 8a. Number of maxillary teeth very low (0 to 4 in two specimens)
 *B. chica*
- 8b. Number of maxillary teeth moderate to high (11 to 87) 9
- 9a. Head very narrow (standard length 7.4 to 8.0 times head width); dorsum with large white patches in shoulder region *B. phalarosoma*
- 9b. Head moderate to broad (standard length 5.7 to 7.6 times head width); dorsum without large white patches in shoulder region 10
- 10a. Biseriate color pattern with black lateral bands, buff dorsal band and whitish ventral band; hands and feet fully webbed *B. biseriala*
- 10b. Color pattern not strongly biseriate; hands and feet variously webbed 11
- 11a. Tails usually with sharply defined reddish, yellowish, or white ventral stripe, or stripe broken into patches; hands and feet moderately webbed; rounded semitruncate terminal phalanges, or terminal phalanges with

- small rounded nubbins at tips 12
- 12a. Hands and feet moderately webbed; terminal phalanges rounded, semitruncate *B. valleculla*
- 12b. Hands and feet nearly completely webbed; terminal phalanges tipped with small round nubbins *B. savagei*
- 11b. Tails uniform or spotted ventrally, never with sharply defined yellow ventral stripe; hands and feet moderately to fully webbed, never with nubbins tipped phalanges 13
- 13a. Dorsal color dark brown to black, with rusty-gold longitudinally oriented dashes, streaks, or spots; hands and feet moderately webbed *B. adspersa*
- 13b. Dorsal color patterns uniform black or brown, or with dorsal band of tan, or with mottled brown, never with rusty-gold longitudinally oriented dashes, streaks, or spots; hands and feet almost fully webbed 14
- 14a. Usually light buff dorsal band with black lateral bands and gray venter; adults with high numbers of maxillary teeth (37 to 71) ... *B. borburata*
- 14b. Dorsal band never present; color of dorsum either uniform black or brown or mottled brown; adults with small or moderate numbers of maxillary teeth (11 to 44) 15
- 15a. Adults with low numbers of maxillary teeth (11 to 26)
 *B. altamazonica*
- 15b. Adults with moderate numbers of maxillary teeth (28 to 44) ... 16
- 16a. Large cream spots ventrally on trunk and tail *B. pandi*
- 16b. Coloration either solid dark or light ventrally 17
- 17a. Large fully webbed feet (standard length 9.2 to 10.6 times foot width); dorsum mottled brown *B. sinu*
- 17b. Small nearly fully webbed feet (standard length 11.6 to 13.7 times foot width); dorsum of uniform coloration *B. peruviana*

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can and Chapadmalan, and Blancan is considered by various authorities to be latest Pliocene to earliest Pleistocene.

Despite some controversy concerning dating of closure of the Bolivar portal, marine and terrestrial paleontological and geological evidence indicates that the portal was drained sometime from late Miocene to Pliocene and a complete and passable land bridge was formed by the time of the Blancan and Chapadmalan faunas.

Weeks (1947) and Olsson (1932) discuss several periods of major orogenic activity during Tertiary in South America. The Andes apparently were raised and lowered several times during Tertiary, but there is no evidence that the Tertiary Andes were ever as high as they are presently. Weeks states that the Andes were raised to their present conformation in a final major uplift during Pleistocene, but according to Nygren (1950) the high peaks of the Cordillera Occidental were raised in middle Miocene, with only slight changes in elevation during Pleistocene. The uplifts initiated in Miocene evidently persisted through Pliocene and Pleistocene and continue to today. Weeks (1947) mentions indication of glaciation during Pleistocene in the higher mountains and in Patagonia.

Two genera of plethodontids, *Bolitoglossa* and *Oedipina*, occur today in South America. Both entered South America from lower Central America to the northwest, and it seems apparent that several invasions took place. The time of the first invasion is not clear, but it probably occurred following closure of the Bolivar portal in Plio-Pleistocene. This idea was apparently first clearly stated, but not elaborated, by Dunn (1931) who thought the portal closure occurred toward the end of Miocene. The first group may have entered by island hopping, however, before a continuous land bridge was established. Both genera demonstrate fair amounts of vagility as shown by their relatively extensive ranges and by the fact that both have been able to reach the ancient Isla Gorgona across a 25 mile marine barrier.

Forerunners of the *atlamazonica* group of *Bolitoglossa* may have been the first to arrive in South America. The group is now the most widely distributed in South America, and has penetrated much farther south than other groups. Today it is peripheral in distribution, and occurs south of other South American species (Fig. 23). These points indicate that the group has probably been in South America for a relatively long time. In addition the group is well adapted to lowland tropical forests and the first invaders would be expected to be lowland species, since there is no evidence that high mountains ever existed across the Bolivar portal area. An additional feature indicating the relative age of the group is that it is not clearly related to any Central American species, a reflection of long separation. Today paired-species are found on either side of the Andes, possibly indicating that restriction of genetic interchange across the mountains is relatively recent.

A second invasion may have been accomplished by ancestors of the *palmata* group of *Bolitoglossa*. We think the invasion of this group was relatively

early because the group is highly specialized, has no close Central American relatives, and now occupies a peripheral highland position. The *palmata* group ancestors probably entered South America by a discontinuous highland route, almost certainly following the isthmian connection. The *palmata* group is adapted to a cool highland environment. It may have entered South America during an early glacial period when a relatively small depression of the mean annual temperature would have shifted the subtropical and lower montane forests to lower elevations than today and provided a temporary continuous corridor of favorable environment. It should be remembered, however, that the group shows some relationships to the *adspersa* group and may have evolved from the latter in South America.

Multiple invasions probably occurred from late Pliocene through Pleistocene, with both highland and lowland species involved. Certain members of the *adspersa* group of *Bolitoglossa* (e.g., *hypacra*) are obviously closely related to Central American species. Despite the fact that *hypacra* is relatively primitive its entrance into South America appears to have been rather recent because it is closely related to Panamanian and Costa Rican highland species, it is located in the highland region closest to Panamá, and it is not known elsewhere in South America. Other members of the *adspersa* group may have originated in South America from an ancestor that entered from Central America by a discontinuous highland route. The ancestor of the series *valleculla-savagei-borburata* appears to have been close to that that gave rise to *hypacra*. This common ancestor has given rise to the relatively primitive, slightly webbed species occurring at moderately high elevations (*valleculla*), to a species with more webbing occurring at moderate elevations (*savagei*), and to a specialized, fully webbed species of relatively low elevations (*borburata*).

The entrance of the two species of *Oedipina* and of the *phalarosoma* group of *Bolitoglossa* appears to have been recent. Both species of *Oedipina* are known from Panamá, and *B. phalarosoma* has Central American rather than South American relatives and is located in a northern Colombian lowland situation. All probably entered recently by humid lowland routes.

Recent movements may have been both into and out of South America. Some species (e.g., *B. biserialata*) that evolved in South America may have moved northward. *B. biserialata* is related to highland species of the *adspersa* group and upon entering the lowlands it may have moved back north into Panamá. Movement may have been in either direction, however, depending on the source of the ancestral forms.

The presence of only *Oedipina* and *Bolitoglossa* in South America is not surprising. These are the only genera known from Panamá, and two additional genera known from Costa Rica (*Chiropoterion*, *Parvinighe*) are not known from tropical lowland localities and could have entered South America only during long cool periods which probably did not exist in this area. Of the seven neotropical plethodontid genera only *Bolitoglossa* and *Oedipina* have had notable success in tropical lowland forests.

Tertiary disjuncts in Mexico live with warm temperate to subtropical plants, and this relation is typical of the ancient Arcto-Tertiary-Neotropical-Tertiary "ecotone." The northern borders of the tropics began to shift toward the equator in early Tertiary as a result of a general cooling trend. At this same time the Madro-Tertiary Geoflora developed *in situ* in western and southwestern United States and northern Mexico, in response to a general Tertiary drying trend. This geoflora expanded steadily from late Eocene and Oligocene through Miocene and Pliocene, and resulted in the present-day semiarid woodland, chaparral, thorn forest, arid scrub, desert grassland, and desert vegetation of southwestern North America. Axelrod thinks the disjunctions of Arcto-Tertiary plants developed during Eocene, and predate development of the intervening dry zone. He finds no evidence of a humid temperate forest in the intervening area during Pleistocene.

Because of the findings concerning geofloral distributional patterns it has been necessary to reconsider the statements of Dunn (1926) and Martin and Harrell (1957) concerning plethodontid distribution. We suggest that plethodontids were primitively associated with elements of the Arcto-Tertiary Geoflora, and in early Tertiary, when the "ecotone" between the Arcto-Tertiary and Neotropical-Tertiary Geofloras was far north, may have entered the "ecotone" along with their Arcto-Tertiary associates, both plant and animal. It is possible that the entire neotropical group of plethodontids was derived from a common ancestral stock, and thus it is likely that only a single group of plethodontids adapted to the ecotonal situation, the majority remaining in the region occupied by Arcto-Tertiary Geofloral derivatives. As the tropical border shifted southward in Oligocene and Miocene in response to the cooling and drying trends, the "ecotone" and its associated salamander fauna also shifted southward, especially at higher elevations. In early Tertiary the Madro-Tertiary Geoflora was developing in the increasingly arid southwestern United States and northern Mexico from Upper Cretaceous and Paleocene subtropical floras and was rapidly expanding in those areas (Axelrod, 1960). Madro-Tertiary elements continued their development during Oligocene and Miocene and expanded in the area between the northern border of the tropics and the main Arcto-Tertiary Geofloral region which had also shifted somewhat to the south. The final result of long-range Tertiary climatic trends was that the plethodontids were effectively separated by the arid region into two major groups: the northern group which continued a close association with Arcto-Tertiary Geofloral elements (and formed portions of the Eastern American and Western American Complexes of the Old Northern Faunal Element of Savage, 1960), and the neotropical group which was associated with the ancient "ecotone," and located to the south below the arid region that was the site of the Madro-Tertiary Geofloral expansion. The neotropical plethodontids are an excellent example of the Central American Complex of the Old Northern Faunal Element of Savage (1960).

An extensive Tertiary radiation took place in the neotropical plethodontids

and a number of species were able to move out of the ecotonal situation and adapt to areas occupied by Neotropical-Tertiary Geofloral derivatives in subtropical and tropical regions. Once this important change took place the plethodontids were able to spread southward rapidly. There is evidence that this ecological shift has occurred more than once. Today seven recognized genera and over 100 species of plethodontids occur in the neotropical region in a variety of forest habitats, from lowlands to high páramo, and from the northern limits of humid forest in northeastern Mexico south to central Bolivia and east to the mouth of the Amazon.

In this paper we are primarily concerned with entrance of plethodontids into South America, and it is necessary to consider very briefly the problem of land connections between Central and South America. Olsson (1932, 1942, 1956) has reviewed the geological history of Tertiary northeastern South America. He indicates that folding and uplift of the Andes began at the close of Cretaceous, and, as a compensation to this uplift, downfolding to the west resulted in the formation of the Bolívar geosyncline in the region of the present-day Golfo de Urabá and Río Atrato Valley in northwestern Colombia. Although the region is not well-known geologically, marine Tertiary deposits are found in northwestern Colombia commencing with upper Eocene and extending through Oligocene, Miocene, and probably into Pliocene. This indicates that South America was effectively separated from lower Central America for most of Tertiary by a narrow marine barrier, the flooded geosyncline or Bolívar portal. Geosynclines in Panamá, Costa Rica and Nicaragua also served as marine barriers during portions of Tertiary, and an archipelago existed in southern Central America with the islands separated by relatively narrow marine passages.

Nygren (1950) and Durham and Allison (1960) think the Bolívar geosyncline was drained earlier than Pliocene, probably in late Miocene. Nygren, who has studied sedimentation in the Bolívar geosyncline area in Colombia, believes that the seaway was open from Upper Eocene to middle Miocene, and that cross geosynclinal highs were probably above sea level for transitory periods during this time. Nygren states that the portal was closed in late Miocene and should have been no obstacle for migration of land faunas since that time.

The data of Simpson (1940, 1950, 1953) are in conflict with those of the geologists and paleontologists cited above in respect to dating of the closure of the Bolívar portal. Simpson, on the basis of fossil and recent mammal distribution, thinks South America was isolated from early Paleocene to late Pliocene. A few North American mammals entered South America and some South American mammals entered North America in late Miocene, but according to Simpson (1953) these may have utilized an island chain in moving north and south because so few groups migrated. Many North American mammals appear in South America for the first time in Chapadmalan faunas, and many South American mammals appear in North America for the first time in Blauan faunas. The evidence is strong for approximate equivalence of Blau-

hands and feet than *adpersa*, *hypacra*, *savagei*, and *valleculla*. The hands and feet of *pandi* are shaped differently than those of *niceforti* and *borburata*, and it is much smaller than *capitana* and has far fewer teeth. All *adpersa* skeletons (7) examined by us lack prefrontal bones, but well-developed prefrontals are present in *pandi*.

The relationships of the large *capitana* are rather puzzling. In gross structure it resembles *robusta*, a large Central American species with uniform dark blackish coloration, many maxillary and vomerine teeth, and robust limbs of moderate length. Both lack basiphysal accessory processes on the trunk vertebrae. *B. robusta*, however, is considerably larger than *capitana*, has a proportionately broader head, and has as little webbing as any member of the genus. *B. capitana* has nearly fully webbed hands and feet. *B. capitana* resembles *schmidti* of Honduras in size, webbing, and habitus, but *schmidti* has a broader head, fewer maxillary teeth, and has a color pattern of mottled black on gray. *B. adpersa* and *capitana* may be related. Proportions are similar in the species, but *capitana* has more maxillary teeth than any other South American species, while *adpersa* has fewer than any other member of its group. The hands and feet of *adpersa* have less webbing than those of *capitana*. Although we do not know its closest relative, *capitana* may be close to the ancestral stock that gave rise to the *adpersa* group. The main argument against this idea is the extensive webbing of the hands and feet found in *capitana*. Support for the idea is found in the generalized characters of *capitana* (size, numbers of teeth, coloration) and its resemblance to *robusta*, a generalized species that may be close to the ancestral stock of the *adpersa* group.

To summarize, four species groups of *Bolitoglossa* occur in South America. The relatively primitive *adpersa* group contains the presumably primitive *hypacra*, near the ancestral stock, and a series of closely related species, *adpersa*, *borburata*, *savagei*, and *valleculla*. Three species, *capitana*, *niceforti*, and *pandi*, are related to this series, but the relationship is not clear. *B. biseriata* is located on the borders of this group. Only two, the relatively advanced *biseriata* and *borburata*, are lowland forms; the remainder occur at moderate to high elevations.

Four specialized lowland species, *allamazonica*, *chica*, *peruviana*, and *sima*, comprise the *allamazonica* group. This advanced group may be linked with the *adpersa* group through *biseriata*.

Two specialized highland species, *palnata* and *orestes*, represent the *palnata* group. The affinities of this group may be with either the *adpersa* or the *allamazonica* group, or with both.

Set apart from all other South American species is the slender Colombian form, *phidrosoma*, whose affinities are with Central American species.

Origin of the South American Salamander Fauna

Salamanders occur predominantly in the Northern Hemisphere, and in tropical regions they have been successful only in the Americas, where an extensive radiation has taken place in the family Plethodontidae. Fossil records

of salamanders are totally lacking in Central and South America, but it seems evident that plethodontids have had northern origins and are to be considered members of the Old Northern Herpetofaunal Element (Dunn, 1931; Savage, 1960). Savage (1960) has discussed the historical and present association of this element with the Arcto-Tertiary Geoflora (for general discussion of geoflora development see Axelrod, 1960). The family Plethodontidae in North America today is associated primarily with derivatives of the Arcto-Tertiary Geoflora. The specialized neotropical plethodontid genera are separated from the North American genera by the semi-arid to desert regions of northern Mexico and southwestern United States. While the neotropical genera are associated in part with relicts and disjuncts of the Arcto-Tertiary Geoflora, it is significant that many species of these genera are closely associated with derivatives of the Neotropical-Tertiary Geoflora. Since the neotropical salamander genera have obvious northern affinities it is of interest to attempt an estimation of the date at which entrance into the neotropical region occurred and at which the association with Neotropical-Tertiary Geofloral elements began.

Dunn (1926) believed migration of salamanders southward took place in late Miocene to Pliocene, but he did not elaborate on this statement. Martin and Harrell (1957), in an attempt to explain the disjunct occurrence of certain identical and/or paired-species of trees and shrubs in eastern United States and the Mexican highlands, concluded that disjunctions occurred in pre-Pliocene rather than Pleistocene times, and they cited plethodontid distribution as a portion of their indirect evidence. Martin and Harrell stated that a continuous forest corridor is necessary for plethodontid dispersal, and, since the genera of neotropical plethodontids are in their opinion morphologically diverse, they concluded that entrance into the neotropical region and separation from the northern representatives of the family antedated the Pleistocene and was probably pre-Pliocene.

Axelrod (1960) reviewed the development of the major Tertiary geofloral patterns. At the beginning of Tertiary the Neotropical-Tertiary Geoflora formed a world-wide broad tropical belt that extended as far north as southwest Alaska on the West Coast of North America, and possibly to Nova Scotia on the East. The Arcto-Tertiary Geoflora formed a broad belt of temperate coniferous and deciduous hardwood forests north of this region. In the region where the two major geofloras met there was a mixing of elements resulting in the formation of what Axelrod calls a broad "ecotone." This "ecotone" formed in Middle Cretaceous, and probably extended southward along low mountains into Mexico during Cretaceous and early Eocene. Axelrod explains that high mountains were not required for southward migration because climatic zonation was weaker than today. Because the high latitudes were climatically mild, the tropics were probably cooler than today (in order to maintain the normal heat budget of the earth), and this effect facilitated southward movement of warm temperate types along low mountains. The disjuncts discussed by Martin and Harrell (1957) could have moved south at this time. Today these Arcto-

are somewhat intermediate in amount of webbing between *savagei* and *vallecula*. The color pattern of *adspersa* is very different from that of the other three species of the series. *B. adspersa* may be an offshoot from the main line that gave rise to *vallecula*, *savagei*, and *borburata*.

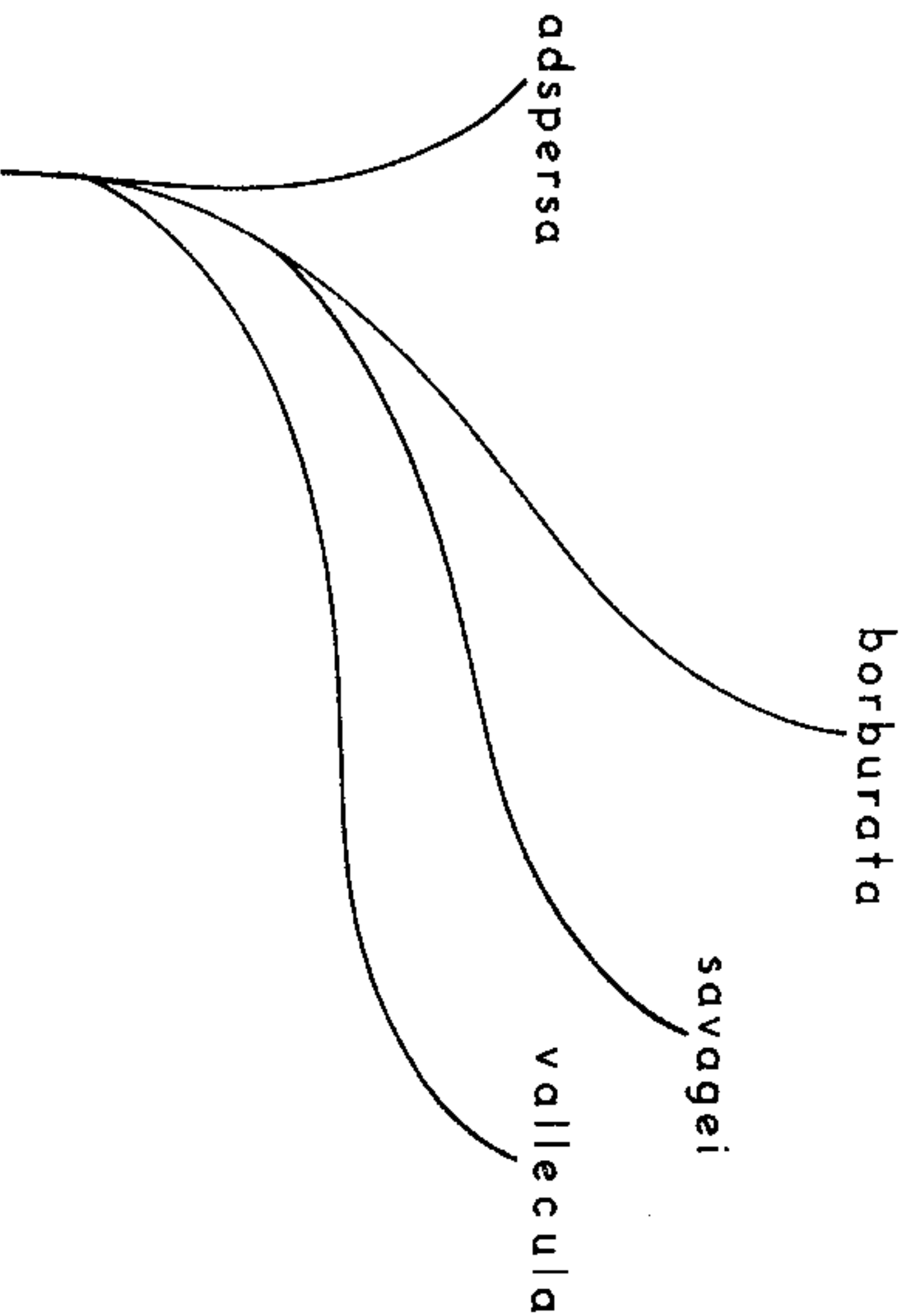


Fig. 25. Dendrogram illustrating relationships of four species of the *Bolitoglossa adspersa* group.

Within the series of four closely related species discussed above, the presumed gap, based on webbing, separating the old generic groupings (*Magnadigita* and *Bolitoglossa*) of Taylor (1944) has been bridged. According to the characters proposed by Taylor it would be necessary to place *vallecula* in *Magnadigita*, and *borburata* in *Bolitoglossa*. *B. adspersa* and *savagei* are intermediates, however, and the sequence of closely related forms, *vallecula* to *savagei* to *borburata*, very nicely joins the two webbing types.

We once stated that *borburata* was closely related to *lignicolor* of Panamá and Costa Rica (Brame and Wake, 1962 b). Although the two may be related we are no longer as convinced of close relationship as we were earlier. The two species resemble each other in a general way in regard to coloration. Both have prefrontal bones and extensively webbed hands and feet. There are, however, numerous differences. *B. lignicolor* is much larger and has far fewer maxillary teeth than *borburata*. The hands and feet of both are extensively webbed but are otherwise not similar. The digits of *lignicolor* are thick and heavy, and are joined by a thin web, but the entire foot of *borburata* is thin and flattened. Enlarged dermal glandules are present dorsally in *lignicolor*, but such glandules appear to be absent in *borburata*. Osteological differences also separate the two

species. The vomers of the two species are not similar. Well-developed basiphysal accessory processes are present on the trunk vertebrae of *lignicolor*, but are only faintly indicated in *borburata*. *B. lignicolor* appears to be more closely related to *aburadei*, *yucatanana*, and possibly *striatula* than to *borburata*.

The relationships of *biseriata* are not clearly defined. Tanner (1962) was handicapped by having only a single immature specimen with which to work. He thought the species was close to the *rufescens* group and compared it with *rufescens*, *occidentalis*, *colonnea*, *palustris*, *yucatanana*, and *striatula*. We have seen more material and suggest that the species is, instead, related to South American forms. It is a larger species than *rufescens* and *occidentalis* and has many more maxillary teeth than either of these species or than *colonnea*. It is possible that *biseriata* may be related to *striatula*. *B. striatula* resembles *biseriata* in having flattened, fully webbed hands and feet, moderate numbers of maxillary teeth, moderate numbers of vomerine teeth in series that are patched laterally, enlarged dorsal glandules, and extensive light pigmentation. *B. striatula* is a larger species, however, and differs greatly from *biseriata* in color pattern and details of coloration.

It is possible that *biseriata* is related to *vallecula*, *savagei*, and *borburata*. All have similar proportions, and *biseriata* is only a little smaller and has but slightly fewer maxillary teeth than the others. Trends toward light-colored wash-like dorsal bands, light pigmented ventral surfaces of trunk and tail, and increasing amounts of webbing of hands and feet have been noted earlier. It can be argued that all three trends reach a culmination in *biseriata*, but other characters dictate against such a relationship. The coloration of *biseriata* differs markedly from that of the other species, and the very flattened, fully webbed hands and feet bear no resemblance to those of *vallecula* and *savagei*.

In its tendency for reduced size, slightly reduced numbers of maxillary teeth, and its very flattened, fully webbed hands and feet, *biseriata* resembles the *altamazonica* group. It is possible that *biseriata* is on the borders of both the *adspersa* and *altamazonica* groups, forming a link between them.

The relationships of the three remaining members of the *adspersa* group, *capitana*, *nicefori*, and *pandi*, are enigmatic. *B. nicefori* is fairly close to *adspersa*, but differs in having a broader head, and more fully webbed and differently shaped hands and feet. The color pattern of the single *nicefori* differs from that of any seen in *adspersa*. Only a single aberrant specimen of *vallecula* (MLAS 5a) has hands and feet that resemble those of *nicefori*. *B. nicefori* has a much broader head than any other South American salamander, and again the only specimen that even approaches it in this character is the single *vallecula* mentioned above. We suggest that the relationships of *nicefori* lie with *adspersa*, and possibly with *vallecula*.

The relationships of *pandi* are with other members of the *adspersa* group, but we cannot name its closest relative. It resembles the group as a whole in size, general proportions, and numbers of teeth, but its coloration is different than that seen in any other member of the group, and it has more fully webbed

The relationships of the *palмата* group have been discussed previously (Brame and Wake, 1962 b). The combination of greatly shortened snout and very distinctive, nearly fully webbed hands and feet separate the two species (*palмата* and *orestes*) from all other *Bolitoglossa*. The relationships of the group may be either with the *adspersa* group, or with the *altamazonica* group. The hands and feet are more similar to fully webbed members of the *adspersa* group (e.g. *pandi*) than to any member of the *altamazonica* group, but do not resemble any other species closely. Both *orestes* and *adspersa* lack prefrontal bones, but we have so little information concerning presence or absence in other forms that it is difficult to relate species on that basis alone. All other South American species for which we have information (*borburata*, *pandi*, *savagei*, *sima*) have prefrontal bones. Size and general habitus of the *palмата* group may relate it to the *altamazonica* group. *B. palмата* and *orestes* are very closely related to each other, and are not obviously closely related to any other species.

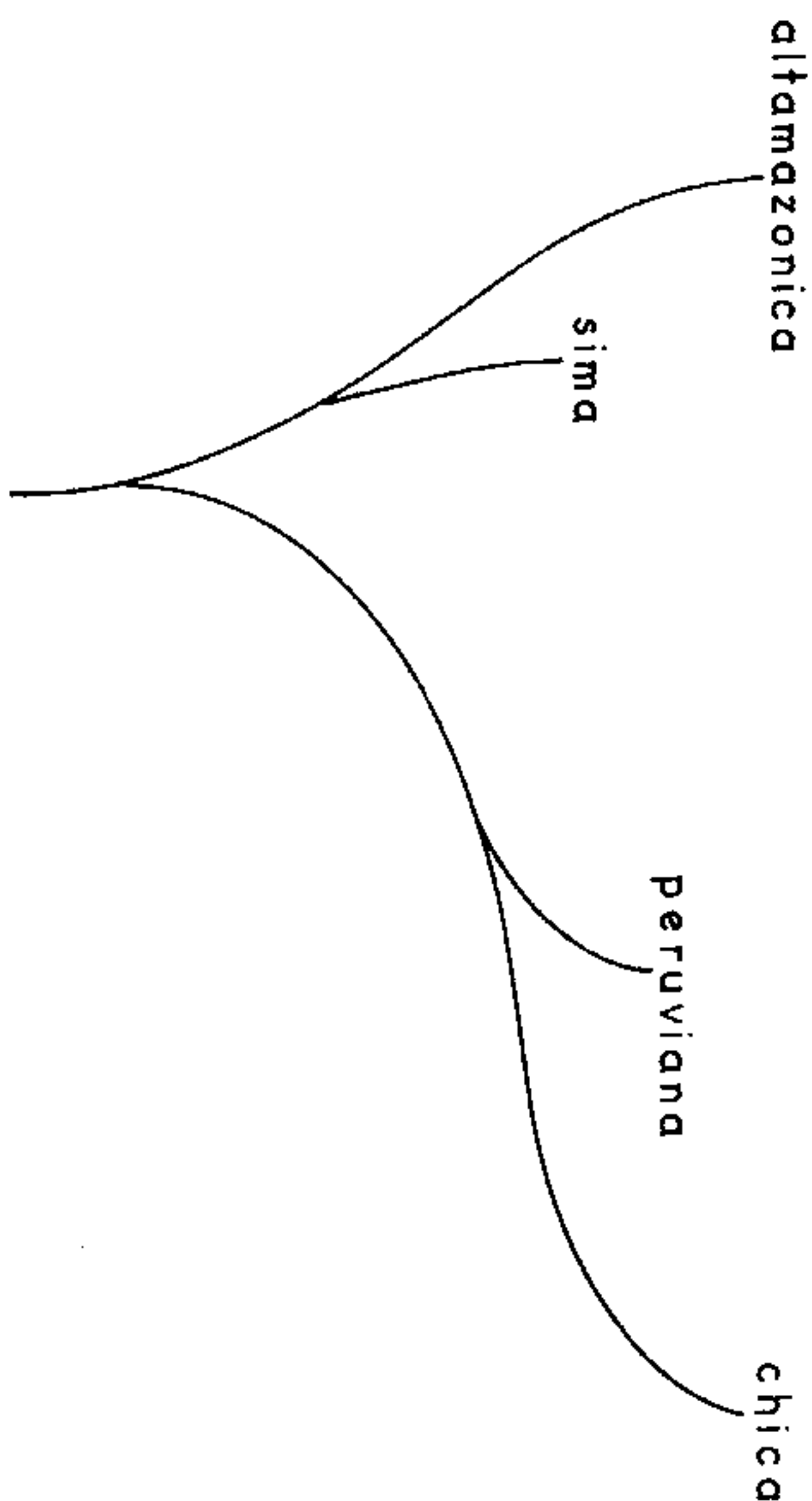


Fig. 24. Dendrogram illustrating relationships within the *Bolitoglossa altamazonica* group.

The *adspersa* group contains nine species: *adspersa*, *biseriata*, *borburata*, *capitata*, *hypacra*, *nicefori*, *pandi*, *savagei*, and *valleculea*. We cannot define the group at this time, but are convinced that all members are more closely related to other members of the group than to other South American salamanders. Certain species (*adspersa*, *borburata*, *savagei*, *valleculea*) are very closely related; the others are on the fringes of this core group.

One highland species, *hypacra*, is clearly related to southern Central American highland forms (*cerroensis*, *marmorea*, *subpalмата*). All have very little webbing, moderate numbers of teeth, and fairly similar proportions. We have previously discussed the relationship of *hypacra* to these Central American species (Brame and Wake, 1962 a). Apparently *hypacra* is the most gen-

eralized and primitive of the South American species. It has long limbs, relatively high numbers of teeth, and less webbing than any other South American species. It may be relatively close to *valleculea*, a somewhat smaller species with shorter limbs and only slightly more webbing of hands and feet.

A series of related species (*adspersa*, *borburata*, *savagei*, and *valleculea*) may have arisen from the same ancestral stock that gave rise to *hypacra* and its relatives. All are similar in size and proportions, including head width, and all have similar numbers of vomerine teeth that are similarly arranged. Several trends are evident in this series. Very little webbing is present in *valleculea*, but webbing increases in amount in *adspersa* and *savagei*, and reaches a maximum in the nearly fully webbed *borburata*. Maxillary teeth increase in number from the relatively low numbers of *adspersa* (mean 27) to the increasingly higher numbers of *valleculea* (44), *savagei* (48), and *borburata* (57). Limb length varies from relatively long in *valleculea* to moderate in *savagei* and *borburata* to relatively short in *adspersa*. A tendency for light dorsal banding is best developed in *borburata*, least developed in *adspersa*, and intermediate in development in *valleculea* and *savagei*. On the basis of relatively long limbs and very little webbing of hands and feet, we think *valleculea* is the most primitive of the series. The advanced end is not determined. *B. borburata* has specialized coloration and extensive webbing, but *adspersa* has reduced numbers of maxillary teeth (presumably advanced) and lacks prefrontal bones. *B. borburata* has high numbers of maxillary teeth (presumably primitive) and has well-developed prefrontal bones. Prefrontals are present in *savagei* as well, and appear to be present in two partially dissected *valleculea*. Our ideas concerning relationships of these four species may be clarified by the accompanying dendrogram (Fig. 25).

The relationship of *valleculea* to *savagei* is close. Both are very similar in size, proportions, and numbers of maxillary teeth, but limbs of *valleculea* appear to be slightly longer and its hands and feet are less fully webbed than those of *savagei*. There is a tendency for light ventral pigmentation in both, but the tendency is stronger in *valleculea* than in *savagei*.

B. savagei and *borburata* are also closely related. The two species resemble each other in most characters but differ in amount of webbing of hands and feet, and in coloration. *B. borburata* has almost fully webbed hands and feet, while those of *savagei* have less webbing. *B. borburata* has flattened digits with pointed tips, but *savagei* has more robust, rounded digits with rounded to more or less truncate tips.

B. borburata is much closer to *savagei* than to *valleculea*. *B. valleculea* is a little smaller, has slightly longer limbs, and has somewhat fewer maxillary teeth than *borburata*. Light ventral pigmentation, universally present in *valleculea*, is not found in *borburata*, and *borburata* has far more extensively webbed hands and feet.

As evidenced from the accompanying graph (Fig. 14), *adspersa* has fewer maxillary teeth than either *valleculea* or *savagei*. The hands and feet of *adspersa*

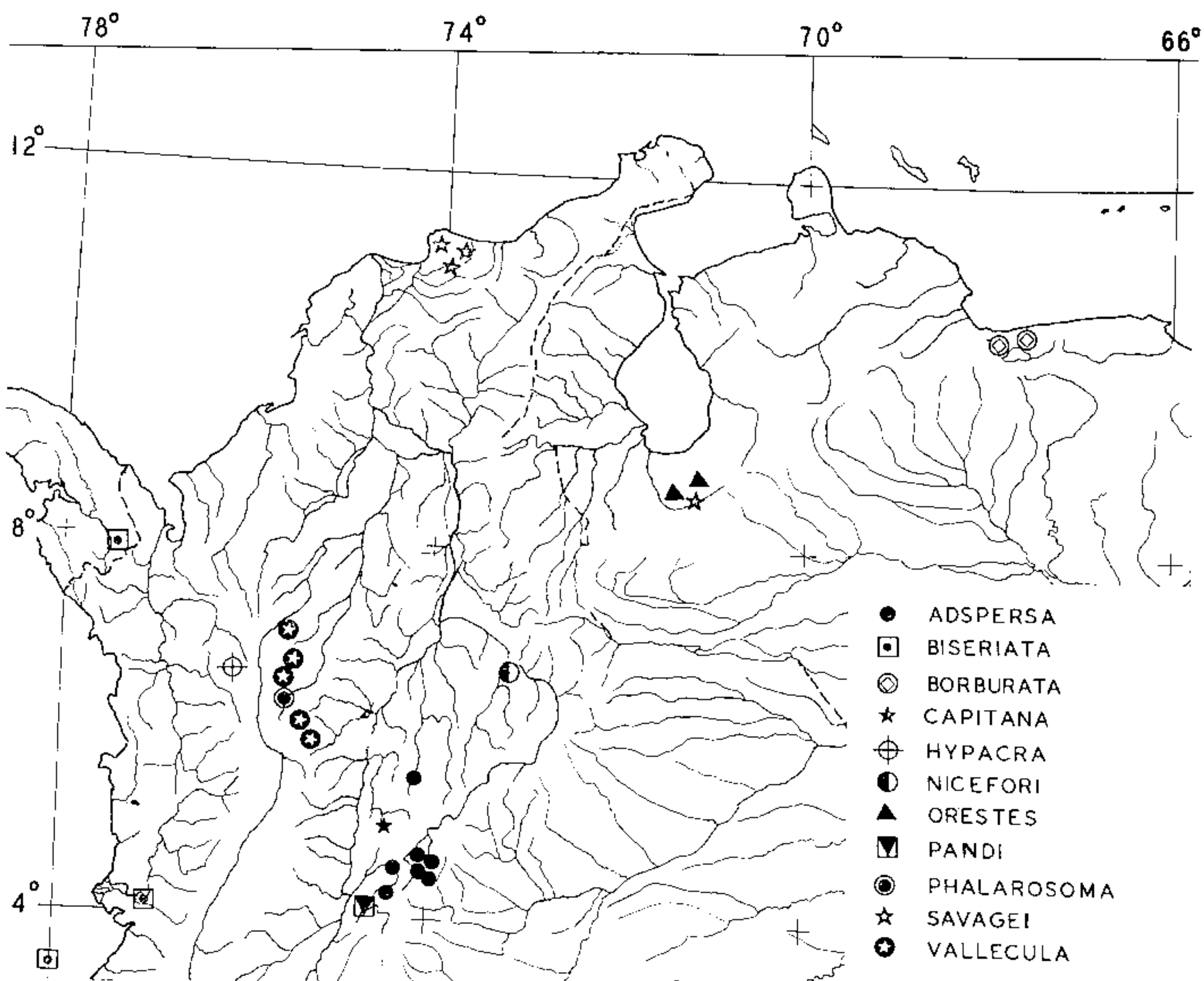


Fig. 23. Distribution of northern species of *Bolitoglossa* in South America.

The *altamazonica* group contains four species: *altamazonica*, *chica*, *peruviana*, and *sima*. The group may be related to *colomea* of Central America, to *biseriata* of Panamá and Colombia, or to the *palmata* group.

The highly specialized *colomea* resembles members of the *altamazonica* group in body proportions and in shape and extent of webbing of hands and feet, but differs in having a pronounced dermal interorbital ridge and a broader, shorter, and much more truncate snout. Few or no maxillary teeth are present in *colomea*, as in *chica*. Prefrontal bones are absent in *colomea*, but present

in *sima*; no information is available concerning the other species of the group.

Relationship of *biseriata* to the *altamazonica* group is indicated by similarity of hand and foot shape, extent of webbing, limb length, and size. The head of *biseriata* is slightly broader and it has more maxillary teeth than the *altamazonica* group. Coloration of *biseriata* is very different than that of any of the *altamazonica* group. *B. biseriata* appears to be closer to members of the *adspersa* group than to the *altamazonica* group.

The *palmata* group differs markedly from the *altamazonica* group in hand and foot shape, type of webbing, and in having a noticeably shorter snout. Snouts of the *altamazonica* group are shortened, but not as greatly as those of the *palmata* group. The *palmata* group also has shorter limbs and tends to have more maxillary teeth. Both groups are relatively small and have relatively narrow heads.

B. sima and *altamazonica* are closely related. They resemble each other in numbers and arrangement of vomerine teeth, ventral coloration, and shape of hands and feet. *B. sima* has more maxillary teeth, a slightly broader head, and relatively larger hands and feet (standard length 9.2-10.6 times right foot, mean 9.7; versus 11.1-13.3, mean 12.0 in *altamazonica*) than *altamazonica*.

The relationship of *chica* to *peruviana* is similar to that of *sima* to *altamazonica*. In both instances one is a Pacific species (*chica*, *sima*) and one is an Amazonian species (*peruviana*, *altamazonica*). *B. chica* and *peruviana* resemble each other in size, proportions, shape and webbing of hands and feet, and numbers and arrangement of vomerine teeth. *B. peruviana* has many more maxillary teeth, however, and has somewhat smaller hands and feet (standard length 11.6-13.7 times right foot; versus 10.1-11.4 in *chica*). Apparently *peruviana* is darker-colored than *chica*.

B. chica resembles *sima* and *altamazonica* in general proportions, but differs in having fewer maxillary teeth, less fully webbed hands and feet, and lighter coloration. Its hands and feet are smaller than those of *sima*, but larger than those of *altamazonica*.

B. peruviana and *sima* resemble each other in most body proportions and in numbers of maxillary teeth. The head of *peruviana* is somewhat broader, and its hands and feet are smaller and less fully webbed than those of *sima*. *B. peruviana* and *altamazonica* are similar in proportions, including head width and size of hands and feet, and apparently in coloration, but *peruviana* has more maxillary teeth and somewhat more fully webbed hands and feet.

In conclusion, the most generalized member of the *altamazonica* group may be *sima* which is the largest species and has the longest limbs, largest hands and feet, and the broadest head of the group. It also has relatively high numbers of maxillary teeth. The hands and feet of *sima* are more fully webbed than those of the other species, however, and the mottled color pattern may be specialized. The entire group is highly specialized, and is one of the more advanced groups of *Bolitoglossa*. A dendrogram illustrating the relationships within the *altamazonica* group is presented (Fig. 24).

more extensive light coloration of *alvaradoi* mentioned in our earlier paper, *alvaradoi* possesses well-developed basipophyseal accessory processes on the trunk vertebrae. These processes are absent in *phalarosoma*. The affinities of *alvaradoi* appear to be with *lignicolor* and its allies, but it also may be related to *phalarosoma*.

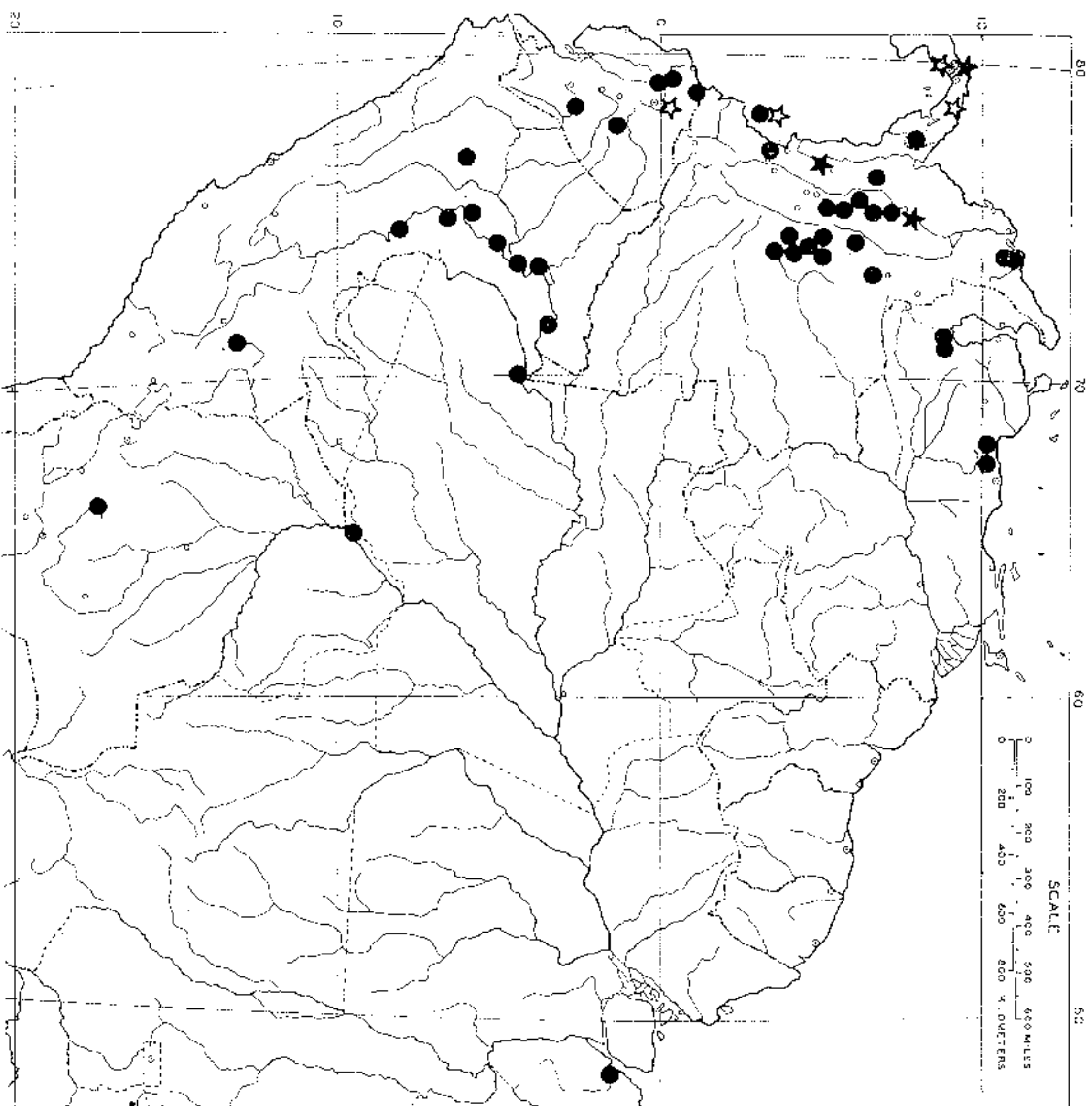


Fig. 21. Distribution of *Bolitoglossa* and *Oedipina* in South America. • *Bolitoglossa*; ★ *Oedipina* complex; ▲ *Oedipina parvipes*.

Several Central American species may be related to *phalarosoma*; these include *arboreoscandens*, *flaviventris*, and *platydactyla*. The unique holotype of *arboreoscandens* has a broader head, longer limbs, and more maxillary teeth than *phalarosoma*. The lighter belly and larger size of *flaviventris* separate it from *phalarosoma*. *B. platydactyla* is a much larger species with lighter coloration and slightly less webbing of hands and feet. Both *flaviventris* and *platydactyla* have basipophyseal accessory processes on their trunk vertebrae; no inter-

mation is available concerning *arboreoscandens*. *B. arboreoscandens* and *phalarosoma* resemble each other in slender habitus and webbing of hands and feet. The single *arboreoscandens* is solid dark-colored dorsally, but one specimen of *phalarosoma* is colored similarly. *B. flaviventris* and *platydactyla* are slender species with relatively narrow heads, and both have about the same numbers of maxillary teeth as *phalarosoma*. The color pattern of *flaviventris* is more similar to that of *phalarosoma* than is that of *platydactyla*. Hands and feet of *flaviventris* are extensively webbed, but are shaped a little differently than those of *phalarosoma*.

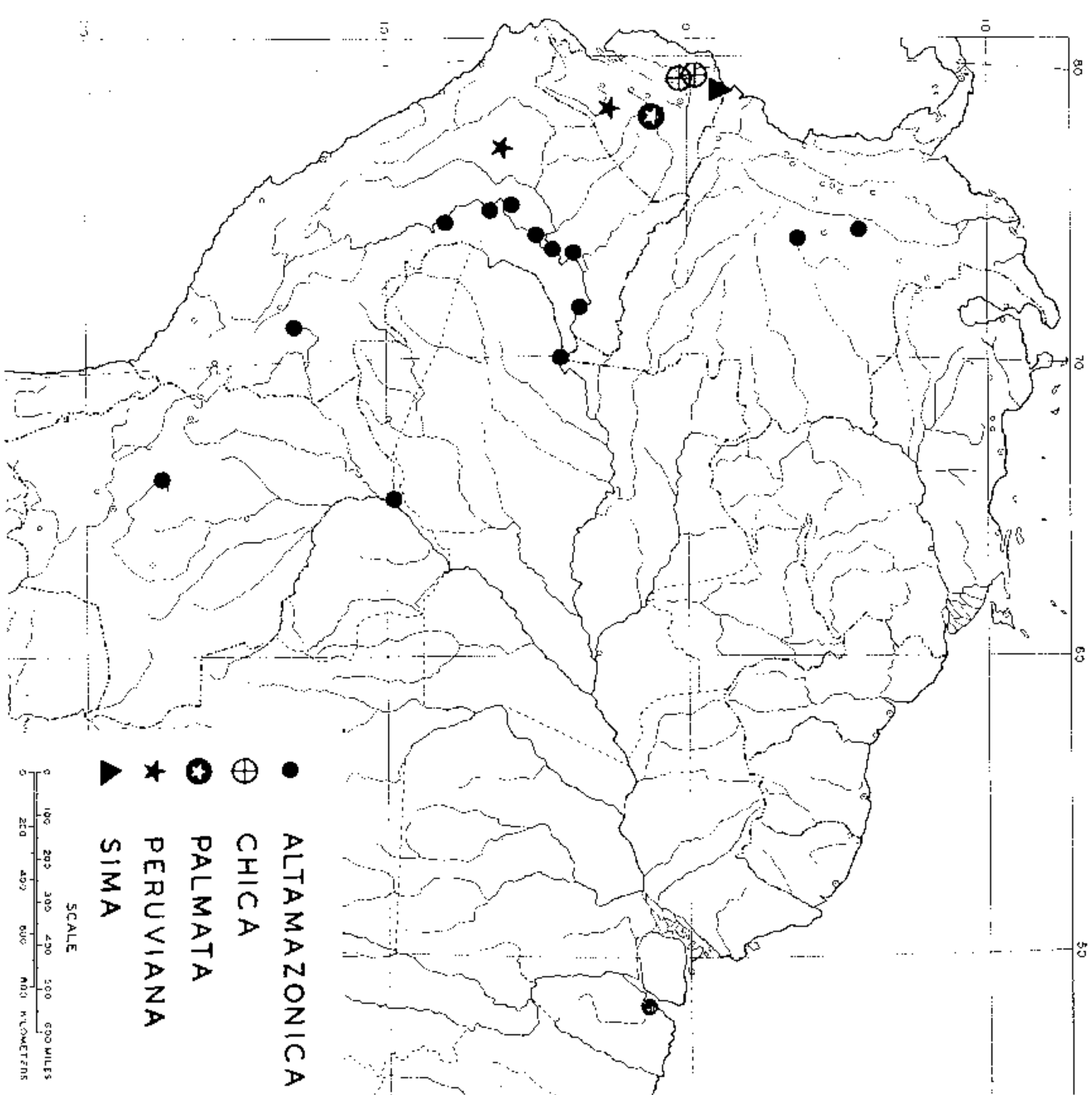


Fig. 22. Distribution of southern species of *Bolitoglossa* in South America.

We believe placement of *phalarosoma* in a separate species group is justifiable. Its relationships seem to be with Central American rather than South American salamanders, but we cannot name the closest relative.

lar with most acute angle posterior in position. Trunk vertebrae lack basipophyseal accessory processes. Trunk distended by presence of enlarged ova and greatly enlarged oviducts. Tail very short, regenerated. Post-iliac gland evident, grayish-white. Limb length moderate; limb interval about $2\frac{1}{2}$; standard length 4.9 times right fore limb; standard length 4.6 times right hind limb. Webbing of hands and feet extensive with terminal phalanx of longest finger and toe relatively free from webbing (Fig. 20C). Digit tips rounded with borders sloping proximally to meet sloping border of adjacent digit at point approximately corresponding with the articulation of the terminal and penultimate phalanges of digits involved. Web formed primarily by fusion of expanded lateral borders of digits, but since lateral borders start expanding near tip, webbing extends almost to tip of all toes. Digits moderately discrete, somewhat flattened. Subterminal pads small, poorly developed. Fingers in order of decreasing length: 3, 2, 4, 1; toes in order of decreasing length: 3, 4, 2, 5, 1.

Measurements: head width 7.8; snout to gular fold (head length) 10.3; head depth at posterior angle of jaw 4.5; eyelid length 3.3; eyelid width 1.8; anterior rim of orbit to snout 3.2; horizontal orbital diameter 2.3; interorbital distance 2.8; distance between vomerine teeth and parasphenoid tooth patch 0.4; snout to fore limb 14.9; distance separating internal nares 1.9; snout to posterior angle of vent (standard length) 50.4; snout to anterior angle of vent 46.9; axilla to groin 28.6; fore limb length 10.3; hind limb length 11.0; width of right hand 3.7; width of right foot 4.8.

Coloration in alcohol: ground color of eyelids, dorsum of trunk and tail, and dorsal and proximal portions of limbs a solid but somewhat muted reddish-gray with a slight bluish cast. Small and indistinct unpigmented area near base of tail only modification of dorsal ground color. Ground color lightens ventrolaterally and ventrally. Large irregularly shaped pigmented areas ventrally on trunk, limbs, and tail, and on the small piece of intact throat skin at lateral edge of gular fold. Cream-colored ventral pigment due to presence of numerous chromatophores (possibly guanophores) that are concentrated primarily in the ventrolateral regions but are present over most of the venter, often occurring as individual cells. Cream chromatophores virtually absent dorsally, present only in small concentration above insertion of left fore limb. Hands and feet with some irregular unpigmented areas dorsally, essentially unpigmented ventrally.

Remarks—The holotype is in a very poor state of preservation. We hesitate describing the species from this single individual and have done so only because of its readily discernible distinctiveness. The specimen has been in the Hamburg Museum since 1913 catalogued under the name "*Speleperes adpersus*." Because it was thought that the specimen was simply an example of that relatively common species, someone was allowed to dissect the head, probably to study the musculature. Surprisingly, color is remarkably well preserved.

The name *pandi* is derived from the name of the type locality. Fred Medem and J. R. Tansit have told us that the city of Pandi is in a relatively

dry region where one would ordinarily not expect to find *Bolitoglossa*. We were also told that it is hazardous to collect in the region due to unsettled political conditions, and our efforts to obtain additional material have failed.

Range—Cordillera Oriental, Central Colombia (Fig. 23).

DISCUSSION OF EVOLUTIONARY RELATIONSHIPS

Generic Relationships

Genus *Oedipina*

The genus *Oedipina* ranges from Guatemala to Ecuador and includes about 12 species.

Oedipina is represented in South America by two species, both known from Panamá, and it is likely that the genus is a relative newcomer to South America. The two species are found only in the lowlands of western Colombia and Ecuador. The genus as a whole has a much more limited South American distribution than *Bolitoglossa*. Both species, *complex* and *parvipes*, are members of the primitive section of the genus. They are fairly closely related to each other, and to the larger *elongatus* of Central America. The senior author is presently studying this genus and will discuss its relationships at a later date.

Genus *Bolitoglossa*

The genus *Bolitoglossa* ranges from southern Mexico to Brazil and Bolivia and includes about 50 species.

Bolitoglossa is represented in South America by 16 species, only one of which (*biseriata*) is known from Panamá. The genus is widely distributed in South America, and is known from very high elevations to sea level in both Atlantic and Pacific drainages.

The *Bolitoglossa* of South America fall into four groups. Three have been delimited earlier in this paper: the *phalarosoma*, *amazonica*, and *palmata* groups. The fourth is something of a catchall and is not easily delimited, but all of its members show evidence of relationship. Definition of the fourth group is not attempted at this time, but, for convenience, it is called the *adpersa* group in the following account.

The *phalarosoma* group contains a single very distinctive species, *phalarosoma*. The combination of very narrow head, slender habitus, distinctive coloration, and fully webbed hands and feet separate it from all other South American species. Its relationships are obscure. Wake and Brannan (1962) stated that it was probably related to *alvaradoi*, a Costa Rican species that resembles *phalarosoma* in coloration and in webbing of hands and feet. We have since examined additional examples of *alvaradoi* and, although small individuals resemble *phalarosoma* in coloration, habitus, and webbing of hands and feet, we are impressed by the many differences that separate the two species. In addition to the larger size, wider head, more maxillary teeth, and

Range—Cordillera Oriental, central Colombia (Fig. 23).

***Bolitoglossa pandi*, NEW SPECIES**

Figure 20C

Holotype—ZSZMH 2858; an adult female from Pandi, 1300 meters (4260 feet), Departamento de Cundinamarca, Colombia, collected by Wilhelm Fritzsche, September 19, 1913. The species is known only from the holotype.

Diagnosis—A medium-sized species (50.4 standard length) with moderate numbers of maxillary teeth (39) distinguished from *hypacra*, *savagei*, and *vallecula* by its extensively webbed hands and feet and distinctive coloration (solid dark reddish-gray dorsally with cream spots ventrally); from *adspersa* by extensive webbing of hands and feet and presence of prefrontal bones; from

TABLE 5. Data on *Bolitoglossa biseriata*, *B. pandi*, *B. nicefori*, *B. capitata*, and *B. borburata*

	Snout-Vent Length	Axilla-Groin	Head Width	Hind Limb Length	Snout-Gular Fold	Limb Interval	Tail Length	Maxillary Teeth	Vomerine Teeth
<i>Bolitoglossa biseriata</i>									
USNM 145657	♂ 36.7	21.9	6.0	8.4	8.8	4	29.2	33	24
USNM 145656	♀ 48.7	27.3	7.2	10.2	11.2	3	45.2	54	28
<i>Bolitoglossa pandi</i>									
ZSZMH 2858	♀ 50.4	28.6	7.8	11.0	10.3	2	—	39	20
<i>Bolitoglossa nicefori</i>									
MLAS 4	♀ 46.8	23.7	8.7	10.9	12.2	3	42.6	37	25
<i>Bolitoglossa capitata</i>									
MLAS 1b	♂ 64.4	35.7	9.6	13.4	13.9	3	53.2	57	28
CNHM 132986	♀ 85.5	49.1	11.5	18.3	17.3	3½	—	62	37
MLAS 1	♀ 84.4	47.2	12.5	18.4	16.8	4	70.8	87	34
MLAS 1a	♀ 82.3	45.5	12.3	17.0	16.2	3½	57.5	80	31
<i>Bolitoglossa borburata</i>									
UMMZ 113870	♂ 47.9	26.5	7.2	10.3	10.7	3	46.9	49	21
UMMZ 113870	♂ 47.6	26.4	7.9	11.2	11.3	3	42.4	57	22
UMMZ 113872	♂ 45.0	24.1	7.7	11.1	11.0	3	40.8	49	23
UMMZ 122386	♂ 41.4	23.1	7.6	10.4	9.9	—	—	37	18
UMMZ 113870	♂ 38.0	21.3	6.7	9.2	10.0	3	—	53	19
UMMZ 113872	♀ 62.9	35.2	9.8	13.7	14.0	3½	56.0	64	33
UMMZ 113870	♀ 58.0	32.4	9.2	13.8	13.2	3	49.0	61	22
UMMZ 113870	♀ 56.3	31.4	9.3	13.2	13.2	4	37.2	61	23
USNM 115509	♀ 56.2	29.8	8.4	11.7	13.1	—	—	71	23
UMMZ 113871	♀ 54.0	28.7	8.7	13.0	12.3	4	38.5	63	32
BM 1920.1.20.3726	♀ 50.5	27.7	8.2	10.7	11.5	4	43.8	50	20
UMMZ 113870	♀ 45.9	23.9	7.6	10.3	11.1	3	—	52	34
UMMZ 113870	♀ 33.2	17.5	5.6	7.9	8.2	3	—	41	18

biseriata by slightly less webbing and absence of a biseriata color pattern; from *capitata* by smaller size and reddish-gray rather than black ground color; from *nicefori* by narrower head and coloration.

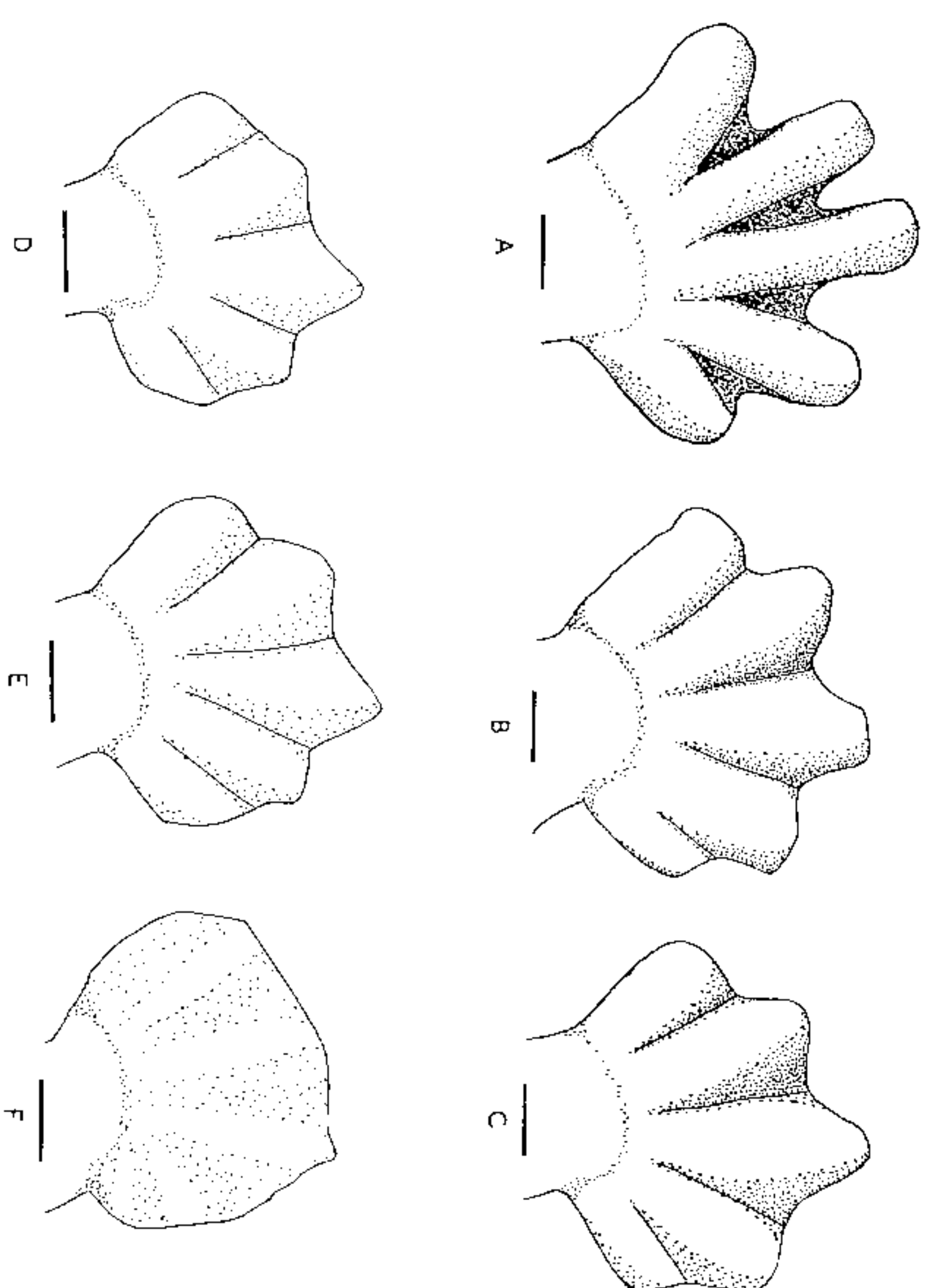


Fig. 20. Left Hind Feet. Outlines drawn through use of microprojector. Line equals 1 mm. A. *Bolitoglossa vallecula* MLAS 8c, Yatumal, Colombia. Male. B. *B. savagei* UMMZ 45618, Cerro San Lorenzo, Colombia. Male. C. *B. pandi* ZSZMH 2858, Pandi, Colombia. Female. Holotype. D. *B. dlumazonica* CNHM 78394, Cosñipata, Peru. Male. E. *B. chica* EPN 2411, lower Río Bolaniguas, Ecuador. Male. F. *B. sinuata* JAP 2994, Cachavi, Ecuador. Female.

Description of the holotype—Adult female, head badly mutilated, snout moderately long and somewhat truncate. Skin removed from entire head region, except eyelids. Groove below eye following curvature of eye. Eye and eyelid moderate in size. Standard length 6.5 times head width; standard length 4.9 times snout-gular fold length. Vomerine teeth 20, in curved series extending beyond lateral borders of internal nares. Maxillary teeth 39, extending slightly beyond center of eye. Two premaxillary teeth. Moderate-sized, well defined prefrontals present on either side of skull. Premaxillaries appressed to each other posteriorly, where anterior prevomerine tooth series meet; bones separate anteriorly to encircle internasal glandular region, fail to meet again anteriorly. Processes of prevomerine form posterior margin of internal nares and extend lateral to lateral border of nares; bear vomerine teeth. Premaxillae fused; frontal processes long, extending posterior to point slightly beyond orbital margin, processes slightly dilated posteriorly. Nares moderate for genus, triangular

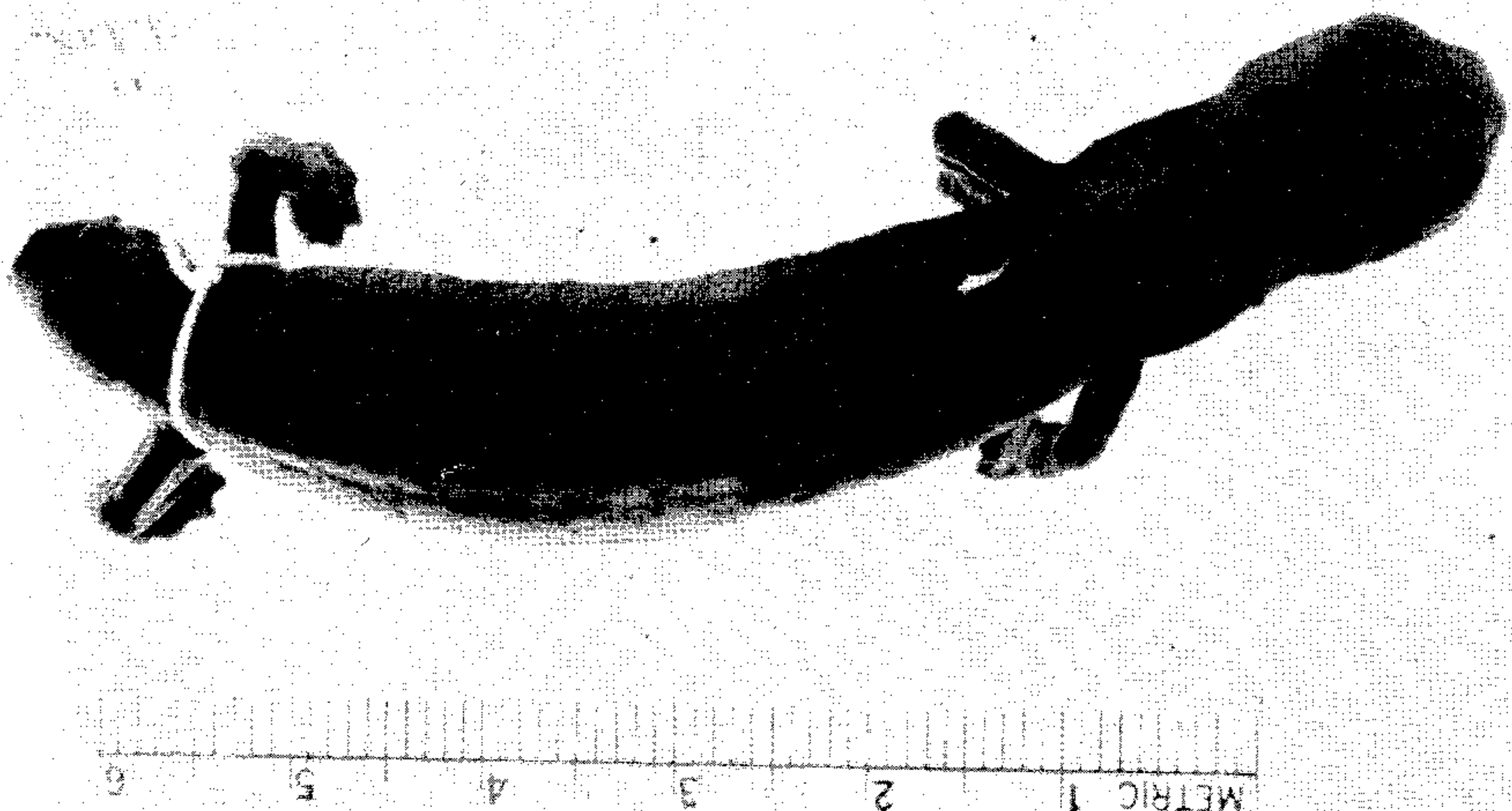


Fig. 19. *Bolitoglossa capitata* MLaS 1a, Hacienda La Victoria, Colombia. Female. Holotype.

posteriorly from eye as small depression for 4.4 mm., sharply proceeds ventrally at level of posterior end of mandible and extends across gular area parallel to and 5.8 mm. anterior to gular fold. Vomerine teeth 31, in series extending well beyond lateral border of internal nares. Maxillary teeth 80, extending posteriorly nearly to posterior border of eyeball. Premaxillary teeth 7, not piercing lip. Robust tail constricted at base, slightly compressed laterally. Post-iliac spot large and clearly discernible. Robust limbs of moderate length; limb interval 4; standard length 5.3 times right fore limb, 4.8 times right hind limb. Webbing of hands and feet extensive and thickened; virtually complete but web emarginate between all digits. Digits moderately flattened; not well defined except at tips. Tips of all digits rounded points that extend from webbing. Small, poorly defined subterminal pads. Fingers in order of decreasing length: 3, 2, 4, 1; toes in order of decreasing length: 3, 4, 2, 5, 1.

Measurements: head width 12.3; snout to gular fold (head length) 16.2; head depth at posterior angle of jaw 5.4; eyelid length 5.0; eyelid width 3.1; anterior rim of orbit to snout 4.8; horizontal orbital diameter 3.3; interorbital distance 3.3; distance between vomerine teeth and parasphenoid tooth patch 0.5; snout to fore limb 22.4; distance separating internal nares 3.0; distance separating external nares 4.2; snout projection beyond mandible 1.1; snout to posterior angle of vent (standard length) 82.3; snout to anterior angle of vent 76.4; axilla to groin 45.5; tail length 57.5; tail width at base 6.8; tail depth at base 7.2; fore limb length 15.5; hind limb length 17.0; width of right hand 5.7; width of right foot 7.2.

Coloration in alcohol: ground color of dorsal and lateral surfaces of head, trunk, and tail uniform lead black; venter gray-black, palms of hands and feet, lower edge of lower eyelids, and labial protuberances whitish. Limbs uniform lead black dorsally and ventrally. Post-iliac spots large, light, and well defined.

Variation—Pertinent counts and measurements of the type series are listed in Table 5. The single male is considerably smaller (64.4 standard length) than the three females (82.3-85.5 standard length). In *Bolitoglossa* females are normally larger than males. Heads are relatively narrow (standard length 6.7-7.4 times head width). Limbs of all are relatively short (limb interval 3-4). *B. capitata* has more maxillary teeth (mean 72) than other South American species and vomerine teeth are numerous (4; 28-33-37). Vomerine teeth are in long curved series that extend beyond the lateral edges of the internal nares. No significant variation in webbing of hands and feet or in coloration from that described for the holotype is discernible. All have virtually fully webbed hands and feet, and all are colored a uniformly dark black.

Remarks—Nieéforo María (1958) presented a photograph of MLaS 1a (then numbered MLaS 119). The foot of the holotype has been illustrated by Wake and Brune (1963).

The name *capitata* was derived from the Latin, *capitatus* (chief in size), and refers to the fact that the species is the largest known to occur in South America.

Coloration in alcohol: dorsal ground color of head, trunk, tail, and limbs lead black with suffused faded gray-white spots of irregular size concentrated between and behind the eyes on the head, just lateral to the midline on either side of the trunk, and in heavy concentrations on the tail and proximal limb surfaces. Ground color of ventral surfaces slightly lighter than that of dorsal surfaces, gray-black. Low concentration of faded moderate-sized guanophores on all ventral surfaces.

Remarks—The single example of *nicefori* was collected about 80 cm. above the ground in a bromeliad on a coffee plantation at moderate elevations. Its proportionately very broad head and its extensively, but not fully, webbed hands and feet distinguish it from *savagei*, which occurs to the north, and *adpersa*, which occurs to the south. It has been confused with *adpersa*, but apparently occurs at much lower elevations and in different habitats than *adpersa*. The foot of *nicefori* has been illustrated by Wake and Brame (1963).

We have named the species in honor of Hermano Nicéforo María, who, through efforts on our behalf, has made this study of South American salamanders possible.

Range—Cordillera Oriental, north central Colombia (Fig. 23).

***Bolitoglossa capitana*, NEW SPECIES**

Figures 19 and 26

Bolitoglossa andicola Nicéforo María, 1958. Bol. Inst. La Salle, 45(198): 11.

Holotype—MLaS 1a; an adult female from Hacienda La Victoria between Albán and Sasaima, 1780 meters (5840 feet), in the Cordillera Oriental about 50 km. NW. Bogotá, Departamento de Cundinamarca, Colombia, collected by Hermano Nicéforo María.

Paratypes—MLaS 1, MLaS 1b, same data as holotype; CNHM 132986, W. Albán, Departamento de Cundinamarca, Colombia, collected by Nicéforo María.

Diagnosis—A large species (4: 64.4-79.2-85.5) with large numbers of maxillary teeth (4: 57-72-87) distinguished from *adpersa*, *hypacra*, *savagei*, and *vellerula* by its large size, almost fully webbed hands and feet, and uniform lead black dorsolateral coloration; from *biseriata*, *borburata*, and *pandi* by its size and coloration; from *nicefori* by its size, relatively narrower head, and more maxillary and vomerine teeth.

Description of the holotype—Adult female, snout of moderate length, blunt tipped; nostrils moderately small, labial protuberances moderate; canthus rostralis arched, moderately well defined. Standard length 6.7 times head width; standard length 5.1 times snout-gular fold length. Well defined groove below eye follows curvature of eye, does not extend full length of eye opening, does not communicate with lip. Eye of moderate size, moderately protuberant. Upper eyelids very large. Moderately well defined postorbital groove extends



Fig. 18. *Bolitoglossa nicefori* MLaS 1, San Gil, Colombia. Female. Holotype.

Individuals from San Miguel are the most aberrant of the material examined. They are very large with especially large hands and feet and very high numbers of maxillary teeth. They also have much longer limbs than other *adspersa*. In other characters they closely resemble typical *adspersa*. The San Miguel material may represent a distinct species, but because of proximity of locality and similarity in most characters, we assign it to *adspersa*.

Dunn (1944) assigned the material from San Miguel, Aguadita, and Tegucigalpa Falls to *Oedipus andicola*. We have examined many *adspersa* and are unable to distinguish the material from these localities from "typical" *adspersa*. Dunn said the material differed from *adspersa* in being larger (males to 70 standard length, versus males to 53, females to 70 in *adspersa*), in being uniform above or with a broad light dorsal band, and in having limb intervals of 2 (versus 4 to 5 in *adspersa*). The size character will partially separate the material from *adspersa*, but examination of Table 4 shows that sharp breaks are seen only with males, and many Aguadita specimens are similar in size to *adspersa* from other areas. The other characters are of no value, and final determination of the systematic status of this material must await collection of additional specimens from the critical intermediate regions. We consider the material to be representative of a considerably variable species (*adspersa*).

The status of *Geotriton andicola* (= *adspersa*) has recently been discussed (Wake and Brane, 1962). We have since examined additional material and remain convinced that the description of Posada Arango (1909) fits that of *adspersa* more closely than any other Colombian salamander. Should the material from San Miguel prove to be representative of a species distinct from *adspersa*, the name *andicola* may be available for it.

According to Dunn (1944), Stebbins and Hendrickson (1959), and information accompanying some of the specimens, *adspersa* is a ground-dweller usually found at relatively high elevations in very moist situations. Stebbins and Hendrickson describe the habitat of their material in some detail.

The species is apparently oviparous (Nicolforo María, 1958; see also comments concerning habits of *Bolitoglossa savagei*) despite reports of viviparity and ovoviviparity by Peters (1863) and Posada Arango (1909).

Material of *adspersa* from certain localities near Bogotá mentioned by Dunn (1944) and Werner (1900) has been unavailable for study. All localities were in the Departamento de Cundinamarca. Nicolforo María informs us that some of the collection of the Instituto de La Salle was destroyed in rioting in 1948. Possibly some of the material mentioned by Dunn was lost at that time.

Range—Cordillera Oriental, central Colombia (Fig. 23).

***Bolitoglossa nicefori* NEW SPECIES**

Figures 18 and 26

Bolitoglossa adspersa (part) Nicolforo María, 1958. Bol. Inst. La Salle, 45(198): 12.

Holotype—MLaS 4; an adult male from 14 km. N. San Gil, 1500 meters (4900 feet), Departamento de Santander, Colombia, collected by Hermano Nicolforo María. The species is known only from the holotype.

Diagnosis—A medium-sized species (46.8 standard length) with moderate numbers of maxillary teeth (37) distinguished from all South American species by its exceptionally wide head (standard length 5.4 times head width); distinguished further from *adspersa*, *hypaetra*, *savagei*, and *vallecula* by its more fully webbed hands and feet and coloration (ground color lead black with some gray-white indistinct markings); from *capitana* by its smaller size; from *biseriata* and *pandi* by its extensive dark coloration.

Description of the holotype—Adult male, snout of moderate length, broad and truncate; nostril small, labial protuberances of nasolabial groove pronounced, white tipped; canthus rostralis indistinct. Mental hedonic gland faintly indicated. Head broad; standard length 5.4 times head width; standard length 3.8 times snout-gular fold length. Deep groove below eye extends full length of eye opening following curvature of eye, does not communicate with lip. Eye of moderate size, moderately protuberant. Well defined postorbital groove extends posteriorly from eye as shallow depression for 2.5 mm., sharply proceeds ventrally at level of posterior end of mandible and extends across gular area as poorly defined depression parallel to and 3.8 mm. anterior to gular fold. Vomerine teeth 29, in irregular slightly patched series extending to lateral borders of internal nares. Maxillary teeth 37, extending posteriorly to point about three-fourths diameter of eye. Three premaxillary teeth, piercing lip. Testes bilobed, unpigmented. Trunk moderately robust. Tail 0.91 times standard length; robust and almost round in cross-section, tapering rapidly to tip. Post-iliac gland pronounced, light gray. Moderately robust limbs of moderate length; limb interval 3; standard length 4.3 times right fore limb; standard length 4.3 times right hind limb. Hands and feet small; standard length 10.9 times right foot. Webbing of hands and feet extensive; slightly more than terminal phalanges of finger and toe 3 free from webbing; webbing of other digits virtually complete, but extreme tips protrude. Digits only moderately flattened, with rounded points at tips. Subterminal pads slightly developed. Fingers in order of decreasing length: 3, 2, 4, 1; toes in order of decreasing length: 3, 4, 2, 5, 1.

Measurements: head width 8.7; snout to gular fold (head length) 12.2; head depth at posterior angle of jaw 4.2; eyelid length 3.2; eyelid width 1.9; anterior rim of orbit to snout 4.0; horizontal orbital diameter 2.6; interorbital distance 2.9; distance between vomerine teeth and parasphenoid tooth patch 0.3; snout to fore limb 16.3; distance separating internal nares 2.2; distance separating external nares 2.6; snout projection beyond mandible 1.0; snout to posterior angle of vent (standard length) 46.8; snout to anterior angle of vent 43.7; axilla to groin 23.9; tail length 42.6; tail width at base 4.7; tail depth at base 4.7; fore limb length 10.9; hind limb length 10.9; width of right hand 3.4; width of right foot 1.3.

is seen; 20 males average 49.9 standard length with a limb interval of $1\frac{1}{2}$ to 4 (mean $2\frac{1}{2}$), and 22 females average 54.7 standard length with a limb interval of 2 to 5 (mean $3\frac{1}{2}$). Limbs of males are noticeably longer than those of females. Heads of males tend to be broader than those of females; standard length is 6.1 to 6.9 (mean 6.4) times head width in 20 adult males, 6.3 to 7.5 (mean 6.7) in 21 adult females. Most *adypersa* have low numbers of maxillary teeth as adults (6-32). Several populations have higher numbers; individuals from Páramo de Palacio have up to 43 teeth, from Aguadita up to 45, and from San Miguel up to 60. In general maxillary teeth increase in number with increasing size of individuals, but the correlation is not absolute (Fig. 14). Some large individuals have few teeth (ICNB, Monserrate-Arrayan, no number, 31 teeth at 68.0 standard length) while much smaller individuals from different regions have many more teeth (ANSP 24105, 44 teeth at 46.4 standard length). Considerable variation occurs in some local populations (e. g. Aguadita) and male individuals of similar size (46.4 and 45.2 standard length) from the same population may have markedly different numbers of teeth (44 and 21 respectively). Vomerine teeth are in curved series that extend to about the center of the internal nares. Numbers of vomerine teeth increase, in general, with increasing size of individuals. The range of vomerine teeth in adults over 45 standard length is 12 to 35 (mean 21).

Webbing of hands and feet is somewhat variable. This variation has been illustrated by Taylor (1944: 201, Fig. 2B; 224, Fig. 3) and Wake and Brame (1963: Fig. 1). More webbing is present than in *vallicula* and some individuals have as much webbing as certain *savagei*. In general digits are robust and well defined, with very pronounced subdigital pads. The digits are not flattened distally. The terminal phalanx of fingers 2 and 4 and of toes 2 and 5, the terminal and about one-half of the penultimate phalanx of finger 3 and toe 4, and the terminal and penultimate phalanges of toe 3 are free from webbing in most individuals. Specimens with slightly more or slightly less webbing are commonly encountered.

Coloration of 3 individuals of *adspersa* has been described in some detail from live material by Stebbins and Hendrickson (1959). Most individuals examined by us have a dark brown, blackish-brown, or black dorsal and lateral ground color, with a lighter grayish-brown ventral ground color. The dorsolateral surfaces of almost all *adspersa* are marked with many irregularly-shaped spots, flecks, streaks, and bars, all longitudinally oriented. In preservation these appear tan or yellowish to silverish, but in living salamanders they are metallic pale gold and rusty according to Stebbins and Hendrickson. A few guanophores are present ventrally, especially on the ventrolateral portions of the trunk and on the throat. The ventral melanophore network is a dense reticulum. The lower eyelid is whitish in most specimens. Only slight deviation from the above color description is encountered. Some individuals from Páramo de Palacio appear almost solid black dorsally, perhaps due to preservation. An individual from San Miguel (MLaS 2) has a poorly defined dorsal band that is a little lighter than the ground color.

TABLE 4. Data on *Bolitoglossa adspersa*

1963	SOUTH AMERICAN SALAMANDERS	43								
TABLE 4. Data on <i>Bolitoglossa adspersa</i>										
		Snout-Vent Length	Axilla-Groin	Head Width	Hind Limb Length	Snout-Gular Fold	Limb Interval	Tail Length	Maxillary Teeth	Vomerine Teeth
<i>Bolitoglossa adspersa</i>										
MLAS 2										
ICNB Tegundama	♂	69.1	36.3	10.6	17.2	14.5	2	55.2	60	24
ANSP 24101	♂	63.0	33.2	9.1	14.3	13.0	1½	—	35	28
ANSP 24102	♂	55.7	31.7	9.0	15.0	12.2	2	53.5	45	29
CNHM 81902	♂	53.4	29.0	8.2	13.8	11.7	2	50.1	42	35
ANSP 24106	♂	51.9	27.3	7.7	12.1	11.2	3	36.1	20	21
ICNB Palacio	♂	51.9	26.9	8.2	14.2	12.2	2½	45.2	38	21
MVZ 62991	♂	50.7	24.7	8.2	14.0	12.8	2	47.8	26	25
ANSP 24104	♂	50.5	28.3	7.8	11.3	11.5	3½	45.4	25	23
MVZ 62978	♂	48.1	26.2	7.6	11.0	10.7	3	40.6	23	14
ANSP 24110	♂	47.9	24.4	7.4	10.4	12.1	2½	34.8	32	26
MVZ 62954	♂	47.2	25.0	7.1	12.0	11.1	1½	—	17	19
ANSP 24105	♂	46.8	26.6	7.5	10.8	10.8	3	38.8	14	12
CNHM 81901	♂	46.4	24.7	7.6	11.2	10.9	2½	48.8	44	25
ANSP 24109	♂	46.4	24.6	7.1	11.0	10.0	2½	37.3	6	14
MVZ 62964	♂	45.2	24.7	7.0	10.8	10.2	2	38.8	21	21
ANSP 24107	♂	45.1	24.1	7.1	10.6	10.2	3	26.1	15	24
MVZ 62989	♂	44.9	24.9	7.1	10.2	10.2	3	30.9	17	15
ANSP 24108	♂	44.3	23.9	6.8	9.4	10.0	4	34.2	18	17
AMNH 20390	♂	43.7	23.9	6.8	10.2	9.8	2½	34.8	24	20
MLAS 2b	♂	43.1	23.7	6.8	10.8	10.0	3	27.2	19	14
ICNB Mons-Arroyan	♀	68.4	38.2	10.5	16.0	13.6	3½	56.2	49	17
MLAS 2a	♀	67.7	34.0	10.7	16.2	14.3	2	56.0	50	30
ICNB Palacio	♀	61.6	33.4	9.3	13.0	14.6	4	—	41	27
CNHM 81907	♀	61.0	36.7	8.9	13.2	12.2	4½	37.0	17	18
CNHM 81908	♀	57.0	31.7	8.2	12.6	11.3	4	49.0	22	21
AMNH 20392	♀	56.1	33.3	8.1	11.8	12.0	4	—	17	21
MVZ 62990	♀	55.9	31.0	8.0	12.1	12.1	4	—	26	13
ANSP 24111	♀	55.7	32.6	8.3	11.8	12.0	4	—	38	20
ICNB Palacio	♀	54.2	29.8	8.4	13.0	12.2	3½	45.8	41	23
ANSP 24103	♀	53.6	30.2	8.0	11.0	11.0	4	43.8	27	27
CNHM 81906	♀	52.8	29.0	8.1	12.3	10.8	3	41.0	18	22
MVZ 62977	♀	51.8	29.2	6.9	10.4	10.9	5	—	14	25
MVZ 62992	♀	50.7	27.6	7.4	10.4	11.7	4½	43.8	14	16
AMNH 7815	♀	50.4	29.7	—	10.3	10.8	3	—	22	17
AMNH 20398	♀	50.1	29.7	7.4	10.8	11.0	4	—	14	17
AMNH 20387	♀	50.0	28.4	7.8	11.0	11.3	4	—	24	17
ICNB Palacio	♀	50.0	28.0	7.7	11.2	11.2	3	44.2	31	20
MVZ 62993	♀	49.7	26.1	7.7	11.2	11.7	4	37.9	15	20
AMNH 20396	♀	47.6	25.7	7.5	10.4	11.2	4	—	15	20
AMNH 20388	♀	47.4	26.4	7.5	10.7	10.7	3½	34.0	29	18
AMNH 20383	♀	43.8	24.3	7.0	10.2	9.8	2½	—	20	18
AMNH 81903	♀	49.9	23.3	6.6	9.7	9.3	4	27.0	23	14

dark color laterally. The dorsum of the trunk and tail is strikingly pigmented with pink-beige to cream. Reddish-brown color is present on top of the head, and a few blackish markings are present on the dorsal portion of the trunk. A broad blackish stripe extends from the eyes and jaws posteriorly along the sides of the trunk and onto the tail where it narrows to a pin-stripe and becomes indefinite. The stripe is speckled with tiny punctate guanophores. Ventral surfaces of the head, trunk, and tail are cream-colored as a result of a dense guanophore reticulum. Scattered punctate melanophores are present ventrally, and they coalesce occasionally to form small, irregularly shaped dark brown spots. Limbs are dark blackish dorsally, cream ventrally. The tail is almost entirely cream-colored. The borders of the mouth are variegated with black, brown, and cream, with scattered tiny punctate guanophores. The iris is gray with numerous punctate melanophores.

The other Colombian specimen (USNM 145657) has the same general pattern as that described above but has less cream coloration and slightly more dark lateral and ventral coloration. The individual has a broad light dorsal band that is tan medially and yellowish-cream laterally. The head and limbs are light dorsally. The color pattern is strongly biseriata.

Extensive light coloration is present dorsally and ventrally in the holotype, with darker coloration laterally.

The holotype was collected in the leaf axils of a *Heliconia* (Tanner, 1962) and the Isla Gorgona specimen was found on a leaf of a broad-leaved shrub. No additional ecologic data are available. Apparently *biseriata* is a lowland, arboreal species.

Range—Central Panamá to southwestern coastal Colombia and Isla Gorgona (Fig. 23).

Bolitoglossa adspersa (Peters, 1863)

Figure 17

Spelepes (*Oedipus*) *adspersus* Peters, 1863. Monatsb. Königl. Preuss Akad. Wissens., Berlin, 1863: 468.

Geotriton andicola Posada Arango, 1909. Estudios Científicos: 125.

Magnadigitia adspersa Taylor, 1944. Univ. Kansas Sci. Bull., 30(1): 210.

Bolitoglossa adspersa Nicéforo María, 1958. Bol. Inst. La Salle, 45(198): 10.

Syntypes—ZMB 4916 (4 specimens); from Bogotá, 2500 meters (7150 feet), Departamento de Cundinamarca, Colombia.

Material Examined—COLOMBIA, DEPARTAMENTO DE CUNDINAMARCA: ZMB 4915 (4 specimens), ZMB 4932 (5 specimens), ZMB 4933 (3 specimens), ZMB 5141 (2 specimens), ZMB 8937 (3 specimens), all with same data as syntypes; CNHM 81901–2, Arrayan, 3100 meters (10000 feet); CNHM 81903–4, Cruz Verde, 3300 meters (10900 feet); CNHM 81905–8, Monserrate-Arrayan, collected by Nicéforo María; ZSZMH 1824, Bogotá, collected by Franz Werner; SM 29627, Bogotá, collected by Nicéforo María; NMB 3046–8, Bogotá, collected by Fuhrmann; MNHN 7815, Bogotá; ANSP

24101–11, Aguadita, 2550 meters (8400 feet); UMMZ 57485, 89424 (13 specimens), 78297 (5 specimens), 57486, Bogotá and vicinity, collected by Nicéforo María; AMNH 6829–35, 10324, 10326–45, 10247–9, 18355–438, Bogotá, collected by Nicéforo María and Apolinar María; MCZ 9083–152, Bogotá, collected by Nicéforo María; MCZ 7220–4, Bogotá; MCZ 20939, Fusagasuga, 1746 meters (5800 feet), collected by Bequaert; BM 1919.3.6.38–47, BM 65.6.12.19–20, Bogotá; MLAS 2, 2a, 2b, above San Miguel, 2800 meters (9200 feet), collected by Nicéforo María; MVZ 62953–93, E. Bogotá, 2650 meters (8700 feet), collected by Stebbins and Hendrickson; ICNB (no number), 2 specimens, Páramo de Palacio, 3 km. south Lagunas de Siecha, 3600–3650 meters (11900–12050 feet), collected by Jorge Hernández C.; ICNB (no number), 13 specimens, Cerro Monserrate, 3000 meters (9900 feet), collected by Jorge Hernández and Fred Medem; ICNB (no number), 9 specimens, Páramo Cruz Verde, 3100 meters (10200 feet), collected by Leopold Richter and E. R. Dunn; ICNB (no number), 1 specimen, below Salto Tequendama bordering Sabana de Bogotá, 2250 meters (7400 feet), collected by E. R. Dunn and Armando Dugand; ICNB (no number), 39 specimens, Cerro Monserrate-Arrayan, 2900 meters (9600 feet), collected by Her-nando Osorno Mesa and E. R. Dunn; LACM 1745-76, Cerro Monserrate, 3240 meters (10700 feet), collected by Fred Medem; and syntypes. DEPARTAMENTO DE SANTANDER: AMNH 20382–408, mountains near Muzo.

Diagnosis—A medium-sized species (20 males: 43.1–49.9–69.1; 22 females: 43.9–54.7–68.4) with moderate numbers of maxillary teeth (43: 6–27–60) distinguished from *biseriata*, *borburata*, *capitana*, *niceforti*, and *pandi* by less webbing of hands and feet and strongly demarcated digits, and distinctive coloration (pale gold spots, flecks, and bars dorsolaterally on a deep blackish-brown to black ground color); from *savagei* and *valleculea* by fewer maxillary teeth (Fig. 14) and coloration; from *hypacra* by more webbing of hands and feet and coloration.

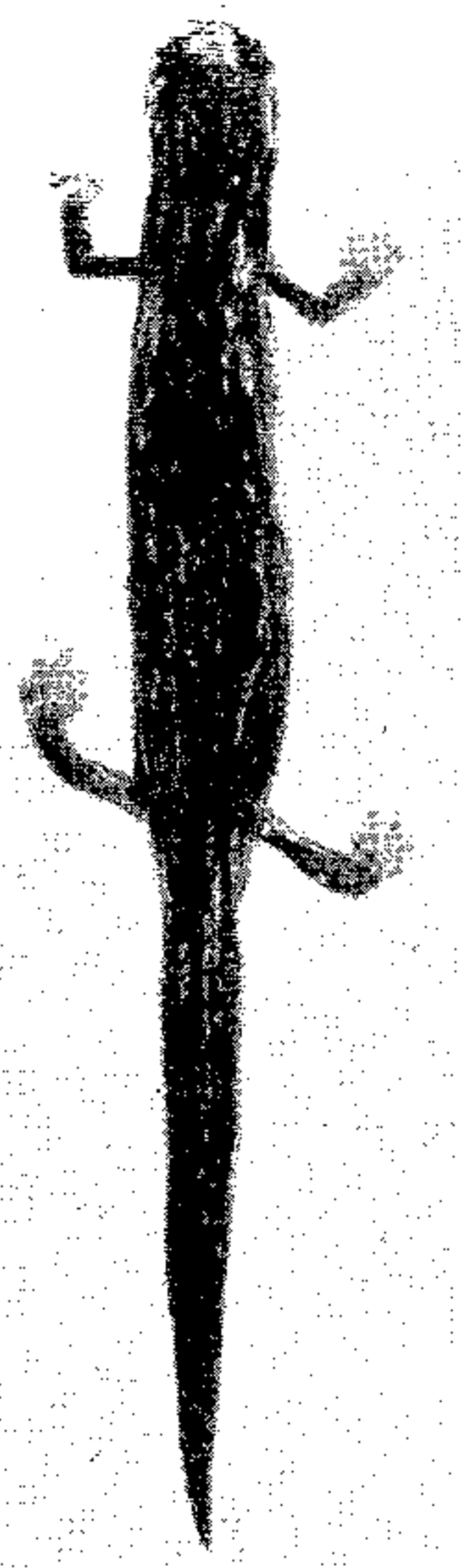


Fig. 17. *Bolitoglossa adspersa* LACM 1745, Cerro Monserrate, Colombia. Male. Line equals 1 cm.

Remarks—Pertinent counts and measurements of *adspersa* from various parts of its range are included in Table 4. *B. adspersa* is a moderately robust form with a moderate to relatively narrow head. Considerable variation is seen in regard to many characters of the species. Some evidence of sexual dimorphism

Webbing of hands and feet is virtually complete in *borburata*. The webbed pad is very extensive, but the tips of all digits extend from the pad. The digits are distally flattened and lack subterminal pads. Characters associated with webbing distinguish *savagei* from *borburata*. The digits of *savagei* are more discrete and cylindrical, less flattened, and less webbed than those of *borburata* and have well-developed subterminal pads. The digits of *savagei* are more robust than those of *borburata* and, when viewed ventrally, project from the pad as distinct, shortened, blunt-tipped nubbins. Viewed ventrally, the hands and feet of *borburata* have extensive pads from which the digits extend smoothly as broadly rounded to slightly pointed projections.

Coloration of *borburata* is similar in pattern to *savagei* but the two species are distinct in details. Seven of the 11 *borburata*, including the 5 largest individuals, are longitudinally streaked or banded with light coloration that overlies the dark ground color and is distinct from the darker lateral ground color. The holotype is also light dorsally. In the 4 remaining individuals the dorsal ground color is dark, with extensive mottling of irregular light patches that overlie the ground color. Ventral surfaces of the throat and trunk are gray-brown (lighter than the lateral surfaces in 9, darker in 2). Ventral melanophore networks are reticulate in 10, punctate in 1. Seven specimens have tails and the venters of all are darker than the trunk venters. One specimen (BM 1920.1.20.3726) has light yellowish spots (probably originally whitish) on the tail venter overlying the ground coloration. Tails of *savagei* and *vallecula* usually have light ventral ground color in contrast to the situation in *borburata*.

Range—Central highlands, northern Venezuela (Fig. 23).

Bolitoglossa biseriata Tanner, 1962

Figure 16

Bolitoglossa biseriata Tanner, 1962. Herpetologica 18: 18.

Holotype—UU 3847; from Río Tuira at mouth of Paya tributary, Provincia de Darién, Panamá, collected by P. Galindo.

Material Examined—USNM 145656, lower Río Calima, Departamento de Valle, Colombia, collected by I. Cabrera; USNM 145657, prison camp on Isla Gorgona, Departamento de Cauca, Colombia, collected by F. Medem; and holotype.

Diagnosis—A relatively small species (7: 33.0-41.1-48.7) with moderate numbers of maxillary teeth (7: 15-31-54) distinguished from all South American species by its characteristic color pattern (extensive light coloration dorsally and ventrally, very dark laterally); further distinguished from *adspersa*, *hyppara*, *savagei*, and *vallecula* by its completely webbed hands and feet with very flattened digits.

Remarks—Tanner (1962) described *biseriata* from a single Panamanian specimen collected near the Colombian border. Two recently collected Colombian

individuals are assignable to *biseriata*. Pertinent counts and measurements are listed in Table 5. In addition we have examined uncatalogued Panamanian material in CNHM.

The holotype is a juvenile and the low numbers of maxillary (15) and vomerine (11) teeth are not typical of adults. The feet are poorly preserved and the color is badly faded.

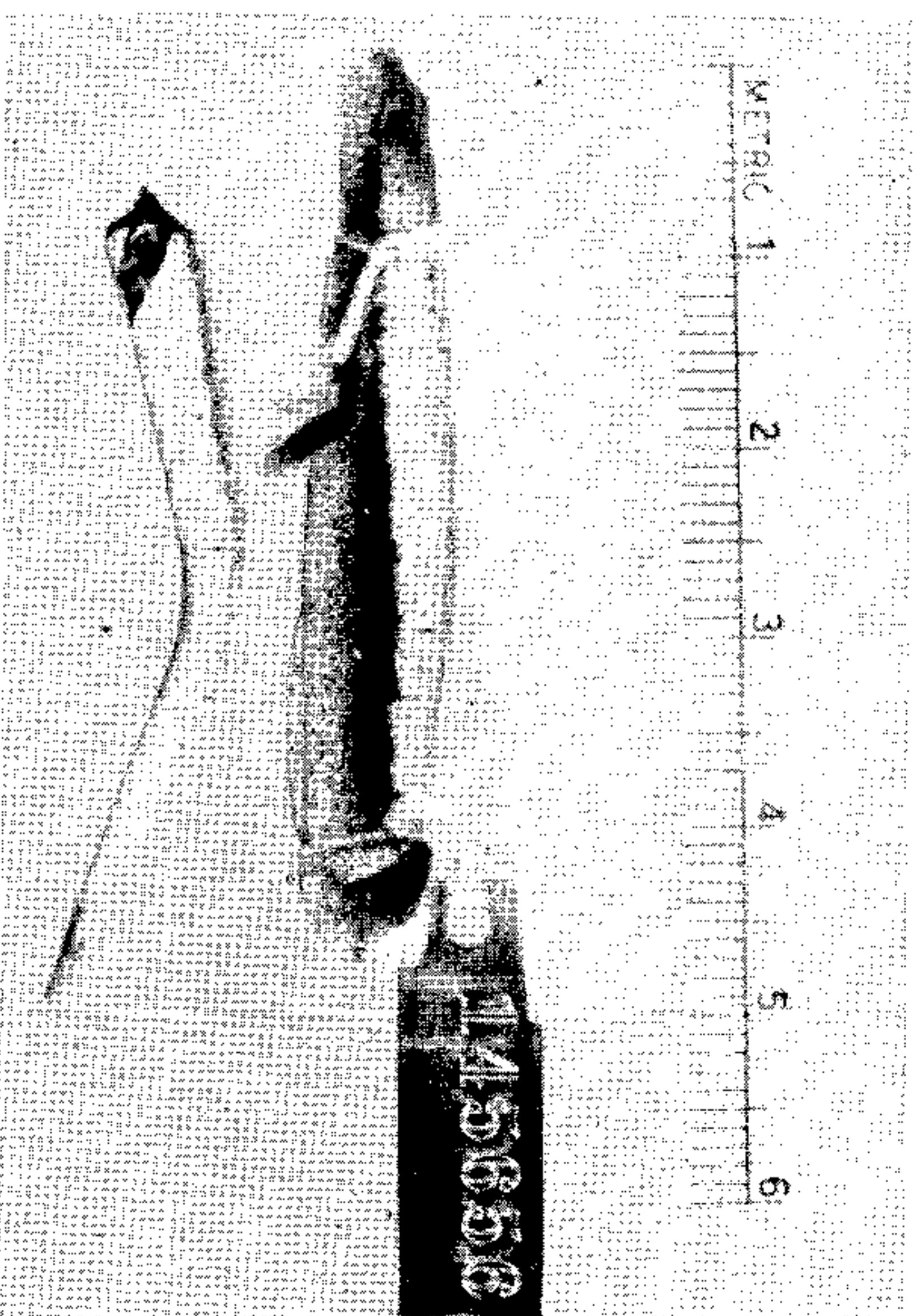


Fig. 16. *Bolitoglossa biseriata* USNM 145656, lower Río Calima, Colombia. Female.

B. biseriata is a relatively slender form with a relatively broad truncate snout and limbs of moderate length. Adults have moderate numbers of maxillary (maximum 54) and vomerine (maximum 28) teeth. Vomerine teeth are in series that are patched laterally and extend about to the center of the internal nares. Maxillary teeth extend to a point about three-fourths through the eye. Standard length is from 6.1 to 6.8 times head width. The moderate sized eyes are moderately protuberant. Dorsal surfaces of the head, trunk, and tail are sprinkled with many enlarged, evenly spaced, pigmented glandules.

Webbing of hands and feet is complete and the digits are very flattened and indistinct. The longest digits extend from the extensively webbed pad as small triangular points; other digits are indistinct. Hands and feet of the material examined are broader than those illustrated by Tanner (1962) and webbing is more extensive.

Coloration of the species is distinctive. Coloration of the largest specimen (USNM 145656) is well preserved, and is described in detail. A strongly biserial pattern is present with extensive light coloration dorsally and ventrally, and

tive tracts of a number of adult females and, although the oviducts of some were enlarged, we found no evidence of development proceeding in the oviducts. Very large ova were seen in the ovaries of some, but not in the oviducts. Peters (1863) reported finding developing ova 3 mm. in diameter in both oviducts of *Spelerpes adspersus* (\equiv *Bolitoglossa adspersa*) and stated that the species bears living young. Ruthven referred his material to *adspersa* and may have followed Peters in calling the species viviparous. Nicéforo María (1958) reported discovery of the eggs of *adspersa* at Dintel, Colombia (20 miles NW. of Bogotá), demonstrating that the species is oviparous. We have not seen the salamanders that were collected with the eggs and we have not examined *adspersa* from the Dintel area, but the locality is close to other *adspersa* localities in the Bogotá region and is at an elevation (2650 meters) similar to that at which *adspersa* is found. The only other species known from localities near Dintel is *Bolitoglossa capitana*, a species well-known to Nicéforo María (his *Bolitoglossa andicola*). Posada Arango (1909) reported that *Geonitron andicola* (\equiv *Bolitoglossa adspersa*) was an ovoviviparous form, but he offered no proof for his statement.

To the best of our knowledge ovoviviparity or viviparity in Central and South American plethodontid salamanders has never been proven. On the contrary, all species for which we have reliable information are oviparous. Literature references to ovoviviparity and viviparity in these salamanders apparently are based on the unproven statements of Peters (1863), Posada Arango (1909), and Ruthven (1922).

Jay M. Savage initiated a study of South American salamanders some years ago but abandoned the project. He called our attention to the presence of representatives of this species in various museums and pointed out the value of a systematic review of the South American salamanders. It is with pleasure that we name this species after him, in appreciation for his encouragement and invaluable advice.

Range—Sierra Nevada de Santa Marta, northern Colombia, and Cordillera de Mérida, western Venezuela (Fig. 23).

Bolitoglossa borburata Trapido, 1942

Figure 15

Bolitoglossa borburata Trapido, 1942. Bol. Soc. Venezolana Cien. Nat., 8, 297. *Oedipus altamazonicus* (part) Dunn, 1926. Salamanders of Family Plethodontidae, p. 440.

Holotype—USNM 115509; an adult female from Valle del Río Borburata, Estado de Carabobo, Venezuela, at 1200 meters (3900 feet) collected by P. Anduze.

Material Examined—VENEZUELA, ESTADO DE ARAGUÁ: UMMZ 113870 (7 specimens), UMMZ 5-1608 (cleared and stained), Rancho Grande, 1090 meters (3575 feet); UMMZ 113871, (Choroní Maricao Road;

UMMZ 113872 (2 specimens), mountain crest above Choroní. ESTADO DE CARABOBO: BM 1920.1.20.3726, Río San Esteban; and holotype.

Diagnosis—A medium-sized species (4 males: 38.0-44.6-47.9; 7 females: 45.9-54.8-62.9) with high numbers of maxillary teeth (11: 49-57-71) distinguished from *adspersa*, *hypaera*, *savagei*, and *vallecula* by its more fully, almost completely webbed hands and feet; from *nicefori* by its markedly narrower head; from *biservata* by absence of very light coloration ventrally; from *pauití* by more maxillary teeth in individuals of similar size, absence of cream-colored ventral spots, and gray-brown rather than reddish-gray ventral and lateral ground color; from *capitana* by smaller adult size and absence of uniform lead-black coloration; from *lignicolor* by smaller size and more maxillary teeth (21 *lignicolor*: 23-35-60).



Fig. 15. *Bolitoglossa borburata* UMMZ 113871, Rancho Grande, Venezuela. Female.

Remarks—Pertinent counts and measurements of the material examined are listed in Table 5. *B. borburata* is a moderately robust form with a relatively broad, sub-truncate snout and fairly short limbs (limb interval 3-4). It is very closely related to *savagei* which it resembles in numbers of maxillary and vomerine teeth, and in proportions. Apparently *borburata* is a larger species than *savagei*; 4 of the 7 females are larger than the largest *savagei* and only one *savagei* exceeds the female average. The eyes are slightly larger and more prominent than those of *savagei*. In addition *borburata* has more fully webbed feet and differs in details of coloration.

Sexual dimorphism is evident only in regard to size. The 4 males average 44.6 standard length; the 7 females average 54.8. Head width is slightly variable (standard length 5.9-6.7 times head width in individuals over 45.0 standard length). Vomerine teeth are in single long series in all individuals and teeth extend to the lateral borders of the intercalary or beyond.

ish and is a little lighter than the sides. Ventral melanophores are arranged in a dense, poorly defined reticulum. The venter is mottled with light markings of variable size and shape, and some moderate size guanophores are present. Tails are present in 47 individuals. In 21 the tail is almost uniform light yellowish ventrally, and in the remainder the tail is mottled with light yellow and dark brown. Only two or three approach uniform dark brown ventral coloration.

TABLE 3. Data on *Bolitoglossa savagei*

	Snout-Vent Length	Axilla-Groin	Head Width	Hind Limb Length	Snout Gular Fold	Limb Interval	Tail Length	Maxillary Teeth	Vomerine Teeth
<i>Bolitoglossa savagei</i>									
ZMB 25918	♂ 51.7	30.1	7.9	12.8	12.2	2	41.4	63	—
USNM 36696	♂ 50.6	28.0	7.7	11.0	11.3	3	—	50	23
UMMZ 45623	♂ 49.2	27.2	7.4	11.2	11.4	2½	—	65	20
UMMZ 45618	♂ 46.4	24.5	7.4	11.0	10.8	2	48.2	57	28
USNM 36694	♂ 46.2	24.9	6.9	10.6	9.6	3	49.3	41	16
UMMZ 63335	♂ 46.1	23.9	7.8	11.2	10.8	2	45.7	64	31
UMMZ 63335	♂ 46.0	23.4	7.4	11.2	10.8	2	44.8	61	27
UMMZ 45616	♂ 46.0	25.3	7.3	11.6	11.0	2½	44.7	49	22
UMMZ 45619	♂ 45.6	25.3	6.8	10.3	10.2	2	43.7	51	22
UMMZ 63335	♂ 44.9	23.9	7.6	11.2	11.0	2	40.0	51	31
USNM 33693	♂ 44.4	24.4	7.3	11.2	10.2	3	51.7	31	17
USNM 36698	♂ 44.1	23.8	7.3	10.6	10.5	2½	—	39	23
USNM 36695	♂ 43.4	24.5	6.6	10.2	9.8	3	50.9	52	21
MCZ 3894	♂ 42.0	23.4	6.7	10.0	9.9	2½	40.3	35	22
UMMZ 54593	♂ 40.9	21.3	7.1	10.8	9.3	2	42.2	40	21
UMMZ 63335	♂ 40.6	21.4	6.7	10.4	10.2	2	39.1	24	29
UMMZ 63335	♂ 40.0	21.9	6.5	9.0	9.9	2½	35.8	29	29
UMMZ 63335	♂ 39.3	26.0	6.6	9.2	9.8	2½	41.2	34	13
USNM 33697	♂ 38.4	21.7	6.2	9.2	8.9	3	41.6	23	16
UMMZ 45628	♂ 36.4	19.6	6.3	8.9	9.2	3	35.5	41	22
CNHM 1815	♀ 55.1	34.9	8.6	11.2	11.2	4	59.2	61	22
UMMZ 54595	♀ 54.5	33.3	8.9	12.2	12.3	3	53.0	79	33
UMMZ 48195	♀ 52.9	30.2	8.5	11.8	12.0	4	—	62	—
UMMZ 63335	♀ 51.8	28.9	8.0	11.2	11.8	3½	49.2	55	22
UMMZ 45617	♀ 50.9	29.6	7.2	10.8	10.2	4	—	50	24
MCZ 3895	♀ 50.7	28.6	7.9	11.5	11.2	3	47.2	43	19
UMMZ 45615	♀ 48.7	27.9	7.4	11.2	11.4	3	42.4	61	22
UMMZ 45620	♀ 47.3	25.7	7.1	11.0	10.8	3	49.0	42	25
UMMZ 45622	♀ 43.7	22.1	7.2	10.8	10.2	3	40.0	51	19
UMMZ 36699	♀ 43.2	23.9	6.4	9.7	9.5	3	44.0	31	15
UMMZ 45625	♀ 38.2	21.0	6.6	9.9	9.2	3	34.0	47	26
UMMZ 63335	♀ 36.7	19.6	6.1	8.3	8.7	2	30.2	24	21
USNM 36700	♀ 33.8	17.2	6.0	8.2	8.2	3	27.1	19	15
UMMZ 63335	33.4	17.6	6.1	8.2	8.6	2½	30.2	21	21
UMMZ 63335	30.6	16.6	5.7	7.6	7.8	2½	30.1	21	22
UMMZ 63335	21.4	10.7	4.2	5.0	5.2	1	17.1	0	7

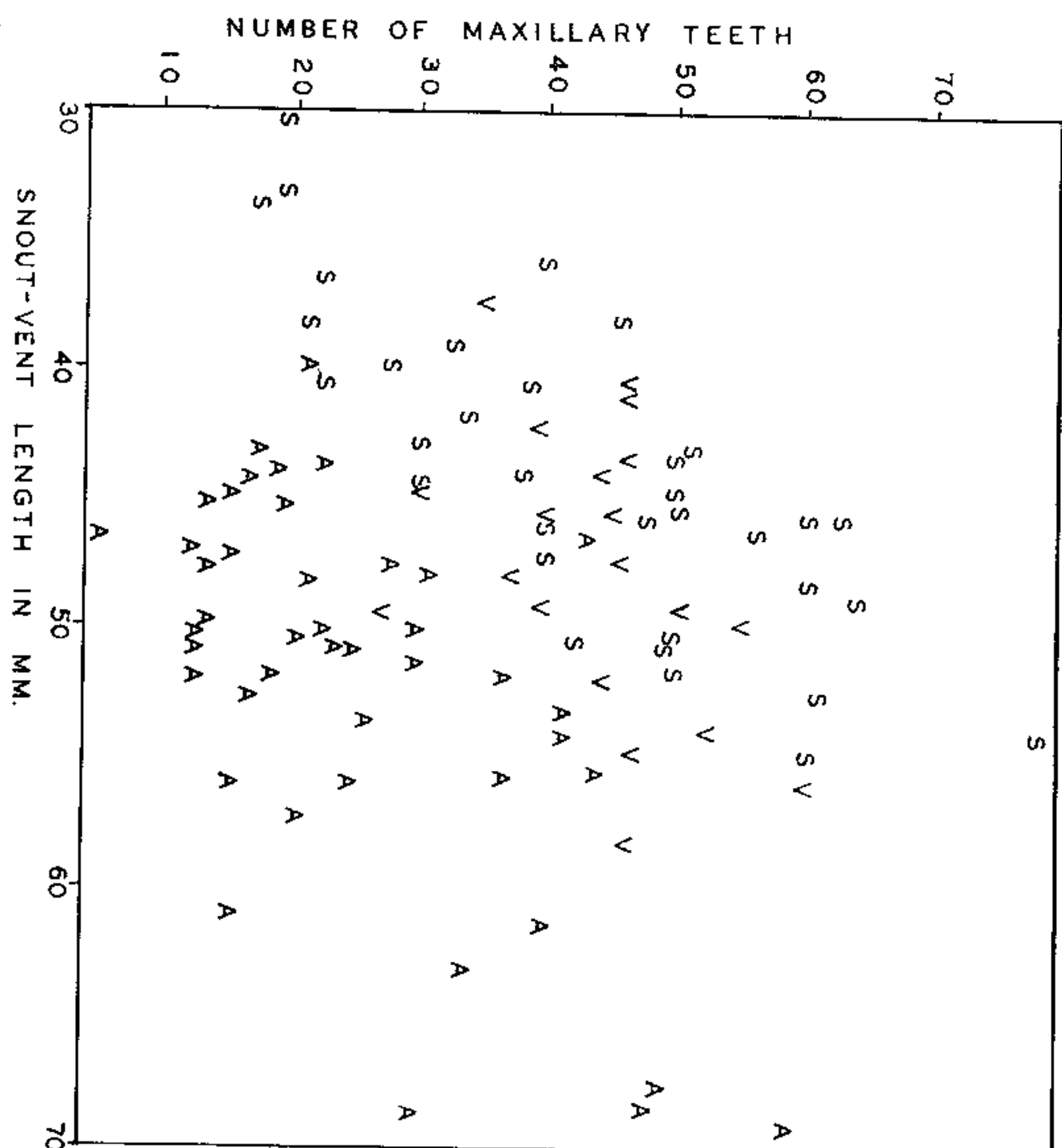


Fig. 14. Variation in maxillary teeth. A, *Bolitoglossa adspersa*; S, *B. savagei*; V, *B. vellecula*.

Remarks—A single specimen (ZMB 25918) from Mérida, Venezuela, agrees with the type series of *savagei* in all basic characters. The webbing of the hands and feet, similarity in habitus, and high maxillary tooth counts indicate the specimen is assignable to *savagei* or is a member of a population closely related to *savagei*. The individual is dark brown mottled with various shades of dark color. Pertinent counts and measurements for the specimen are included in Table 3.

Information concerning the habitat of *savagei* has been published by Ruthven (1922). The species apparently is limited to heavily forested regions and is, according to Ruthven, a "bromeliadicolous" form. He restricts the term bromeliadicolous to forms which breed in bromeliads or occur principally in bromeliads. Although principally found in bromeliads in trees and on the ground, specimens were occasionally found in decaying logs and stumps or under decaying leaves.

Ruthven (1922) states "this is a viviparous species," but comments no further and offers no evidence for the statement. We have examined reproductive

and more maxillary teeth (Fig. 14); from *vallecula* by more fully webbed hands and feet and less light pigmentation ventrally; from *hypacra* by more fully webbed hands and feet, shorter limbs, and coloration.

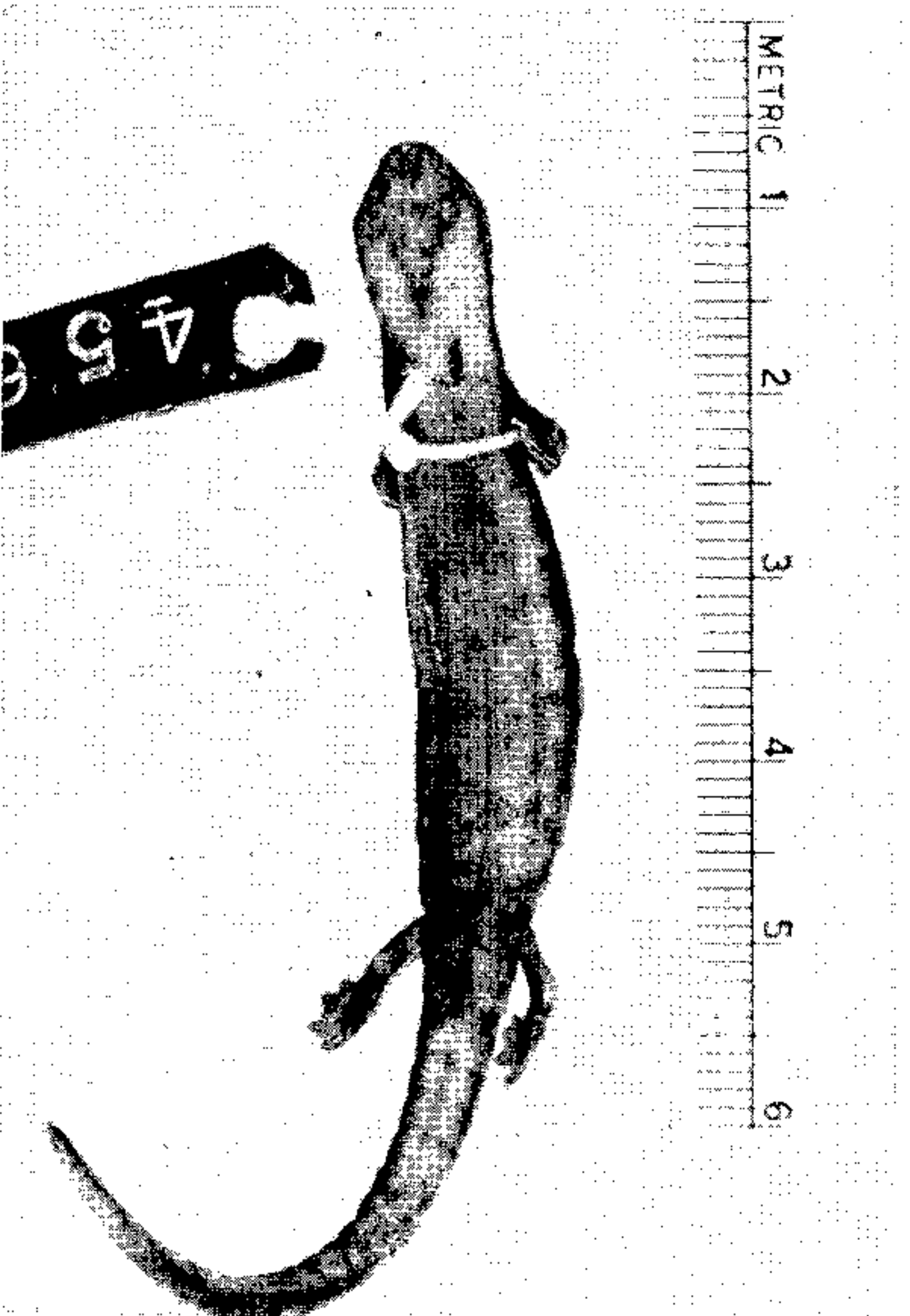


Fig. 13. *Bolitoglossa savagei* UMMZ 45615, Cerro San Lorenzo, Colombia. Female.

Description of the holotype.—Adult female, snout of moderate length, broadly rounded; nostril small, labial protuberances of nasolabial groove small; canthus rostralis of moderate length, rounded. Standard length 6.1 times head width; standard length 4.4 times snout-gular fold length. Shallow groove below eye extends almost full length of eye opening following curvature of eye, does not communicate with lip. Eye of moderate size, only slightly protuberant. Poorly defined postorbital groove extends posteriorly from eye as shallow depression for 2.4 mm., proceeds sharply ventrally at level of posterior end of mandible and extends across gular area as indefinite depression parallel to and 3.4 mm. anterior to gular fold. Vomerine teeth 33, in long curved series that extend beyond lateral borders of internal nares. Maxillary teeth 79, extending posteriorly to point about three-fourths through eye. Three maxillary teeth, none piercing lip. Tail of moderate size, 0.97 times snout-vent length; virtually round in cross section with little lateral compression; moderately constricted at base. Post-iliac gland not evident. Limbs of moderate length; limb interval 3; standard length 4.5 times right fore limb; standard length 4.5 times right hind limb. Webbing of hands and feet not complete; tips of digits knob-like, free from web; terminal phalanx of finger 3 and toes 3 and 4 free from web; web forms pad-like surface from which project the small rounded knobs of the digit tips.

Subterminal pads pronounced. Fingers in order of decreasing length: 3, 2, 4, 1; toes in order of decreasing length: 3, 4, 5, 2, 1.

Measurements: head width 8.9; snout to gular fold (head length) 12.3; head depth at posterior angle of jaw 4.5; eyelid length 3.7; eyelid width 2.2; anterior rim of orbit to snout 3.6; horizontal orbital diameter 2.8; interorbital distance 2.5; distance between vomerine teeth and parasphenoid tooth patch 0.8; snout to fore limb 15.2; distance separating internal nares 2.0; distance separating external nares 2.4; snout projection beyond mandible 0.7; snout to posterior angle of vent (standard length) 54.5; snout to anterior angle of vent 51.4; axilla to groin 33.3; tail length 53.0; tail width at base 4.6; tail depth at base 4.7; fore limb length 12.0; hind limb length 12.2; width of right hand 4.9; width of right foot 6.0.

Coloration: dorsum and venter of head and trunk light brown with markings of medium dark brown. Dorsal ground color almost uniform light brown with a few irregularly placed darker markings; ground color of lateral and ventral surfaces of trunk darker. Tail mottled light and dark brown dorsally and laterally; light yellowish ventrally. Limbs mottled light and dark brown. Throat uniform brown with some light spots.

Variation.—Pertinent counts and measurements of the type series are listed in Table 3. Sexual dimorphism is noted in regard to size and limb length. The 19 males average 43.7 standard length with a limb interval of from 2 to 3; 11 females average 48.8 standard length with a limb interval of from 3 to 4. Maxillary teeth are numerous and increase in number with increasing size (Fig. 14). *B. vallecula* and *savagei* have similar numbers of maxillary teeth, and both have more than *adspersa*. Vomerine teeth are numerous and range from 13 to 33 in adults. Vomerine teeth are in long curved series; slight lateral patching is present only in a few individuals. Head width is variable and some sexual dimorphism is indicated. Males over 42 standard length have slightly broader heads on the average (standard length 6.0-6.7 times head width, mean 6.3) than do females (standard length 6.1-7.1 times head width, mean 6.5).

Webbing of hands and feet is slightly variable in the series. The webbing in the holotype is less well-developed than in the majority of the series. Two phalanges of the longest digits are free from webbing in the least webbed individuals, but most are more fully webbed. The typical foot, viewed ventrally, is a large rounded pad from which project rounded knob-like digital tips containing but one phalanx. The most frequently encountered foot type is illustrated (Fig. 20B).

Coloration is rather variable. Of 55 specimens 28 have a definite longitudinal band dorsally with the light color usually sharply set off from the darker lateral color. Of the 28, some are striated with light and dark, others are predominantly dark streaked with light, and still others are predominantly light streaked with dark. A few are almost uniformly light dorsally. Nine of the remaining 17 specimens have light mottling on a dark background dorsally, and 8 are almost uniformly dark brownish gray. The venter of the trunk is brown-

truncate snout than other *vallecula*. This specimen is the most aberrant of the type series in webbing and coloration as well.

TABLE 2. Data on *Bolitoglossa vallecula*

	Snout-Vent Length	Axilla-Groin	Head Width	Hind Limb Length	Snout-Gular Fold	Limb Interval	Tail Length	Maxillary Teeth	Vomerine Teeth
<i>Bolitoglossa vallecula</i>									
MLaS 8e	♂ 51.9	28.0	7.4	12.2	11.3	2½	51.5	45	18
MLaS 10	♂ 49.7	26.6	7.9	11.8	11.0	2	56.4	54	24
MLaS 8g	♂ 49.2	24.5	7.6	12.6	11.2	1	61.0	40	21
MLaS 8b	♂ 47.9	24.4	7.2	11.8	11.0	1½	52.0	38	14
MLaS 8f	♂ 45.7	24.6	7.3	11.0	11.1	2	44.2	41	24
MLaS 10a	♂ 45.0	23.9	7.2	11.2	9.7	2	51.2	45	17
AMNH 39447	♂ 44.2	23.8	6.5	11.8	10.0	2	46.6	45	18
MLaS 5b	♂ 43.6	23.9	7.7	10.8	10.9	2	40.1	47	22
MCZ 8163	♂ 42.3	22.6	6.7	12.0	10.2	1½	—	40	19
MLaS 5	♂ 41.3	21.7	6.7	10.2	10.2	2	41.7	47	17
MLaS 5a	♂ 40.7	20.1	6.3	9.8	10.7	2	43.7	47	17
AMNH 39445	♂ 37.6	20.7	6.4	9.5	9.2	2	—	36	16
MLaS 8c	♀ 58.7	32.1	8.1	12.2	11.2	3	61.2	47	22
AMNH 14027	♀ 56.1	32.1	8.2	11.8	11.3	4	—	61	20
MLaS 9	♀ 55.8	31.1	8.1	12.0	11.8	2½	57.3	47	18
MLaS 8a	♀ 54.1	28.8	7.9	10.9	11.8	2½	50.0	53	20
MLaS 8h	♀ 49.3	26.8	7.1	11.0	10.7	3	47.5	28	14
MLaS 10b	♀ 49.2	27.3	7.7	11.0	10.9	2½	47.7	50	26
AMNH 39446	♀ 47.5	27.2	6.7	11.1	11.3	2½	—	46	19
MLaS 8d	♀ 44.6	24.2	6.8	11.0	10.0	2½	43.1	31	17

Although most paratypes resemble the holotype in general color pattern, some variation is evident. Fifteen individuals are lighter middorsally than laterally. Four exceptions, MLaS 5b, MLaS 8c, MLaS 10, and MLaS 10a, have dense melanophore networks dorsally and laterally and appear almost solid black when viewed from above. Dark lateral sides are present in all of the specimens. In those with light color dorsally the aspect is of a light striated wash. One (MLaS 8b) has extensive amounts of light, bright yellowish dorsally. The venter of the trunk of all individuals has at least some yellowish white coloration. The entire venter of some is light, most have light as the dominant color, but some are relatively dark with light areas that are sharply demarcated from the dark background. According to the collector, Nicéforo María, the light ventral surfaces of specimens from San Pedro and Retiro (MLaS 9, 10a, 10b) were red in life. In preservative MLaS 10b is salmon pink and the others are light pink. It seems likely that the other *vallecula* also had reddish ventral coloration that has faded in preservation. Light ventral color appears to be due to the absence of melanophores and presence of reddish and yellowish chromato-

phores. The throat is usually rather light, with many small lightly pigmented areas. Several are very dark ventrally (MCZ 8163, MLaS 8d, MLaS 5b). The venter of the tail is light-colored in contrast to the darker lateral portion in all 17 individuals that have tails. Light ventral tail coloration is dominant in 15 of the 17. In some the venter of the tail is almost entirely light colored.

Remarks—The salamanders from San Pedro and Retiro were collected in bromeliads at some distance from the ground. The salamanders from Yarumal were on the ground under stones and heaps of decaying vegetation.

There is some doubt concerning the locality data accompanying AMNH 14027. The catalogue lists the locality as "Andes, Colombia" but a note for this number states "label says 'Yarumal'." It is probable that Andes refers to the mountains in a very general way and not to the Colombian city of the same name. The type locality of *vallecula* is Yarumal, and it is likely that this specimen was collected there also.

The name *vallecula* is an allusion to the habitat of the species on the lower slopes and valleys of the Cordillera Central, northwestern Colombia.

Range—Cordillera Central, northwestern Colombia (Fig. 23).

***Bolitoglossa savagei*, NEW SPECIES** Figures 13 and 20B

Oedipus adspersus (part) Ruthven, 1922. Univ. Michigan Mus. Zool. Misc. Publ., 8: 49.

Oedipus adspersus (part) Dunn, 1926. Salamanders of Family Plethodontidae, p. 393.

Holotype—UMMZ 54595; an adult female from Cerro San Lorenzo, 1400-2100 meters (4500-7000 feet), Sierra Nevada de Santa Marta, Departamento de Magdalena, Colombia, collected in 1913.

Paratypes—COLOMBIA DEPARTAMENTO DE MAGDALENA, Sierra Nevada de Santa Marta: UMMZ 48213; UMMZ 48195, San Miguel, 1800-2100 meters (4500-7000 feet); UMMZ 45615-20, 45622-26, 45628-30, Cerro San Lorenzo, 1400-2100 meters (4500-7000 feet); UMMZ 63334, La Cumbre, 2140 meters (7000 feet); UMMZ 63335 (22 specimens) La Popa, 1525 meters (5000 feet) on Cerro San Lorenzo; UMMZ 54592-93, Quebrada Viernes Santo, east slope Cerro San Lorenzo, 1500-1800 meters (5000-6000 feet); CNHM 1815; USNM 36693-7000, Río Frío, 1000 meters (3280 feet); ANSP 19723-4, San Lorenzo Trail, Hacienda Cincinnati, 1830 meters (6000 feet); MCZ 3894-95, Cerro San Lorenzo.

Referred Material—ZMB 25918, Mérida, Estado de Mérida, Venezuela.

Diagnosis—A medium-sized species (20 males: 36.4-44.1-51.7; 11 females: 38.2-48.8-55.1) with high numbers of maxillary teeth (31: 23-48-79) distinguished from *biseriata*, *barbata*, *capitana*, *nicefori*, and *pandi* by incomplete webbed hands and feet; from *adspersa* by more fully webbed hands and feet

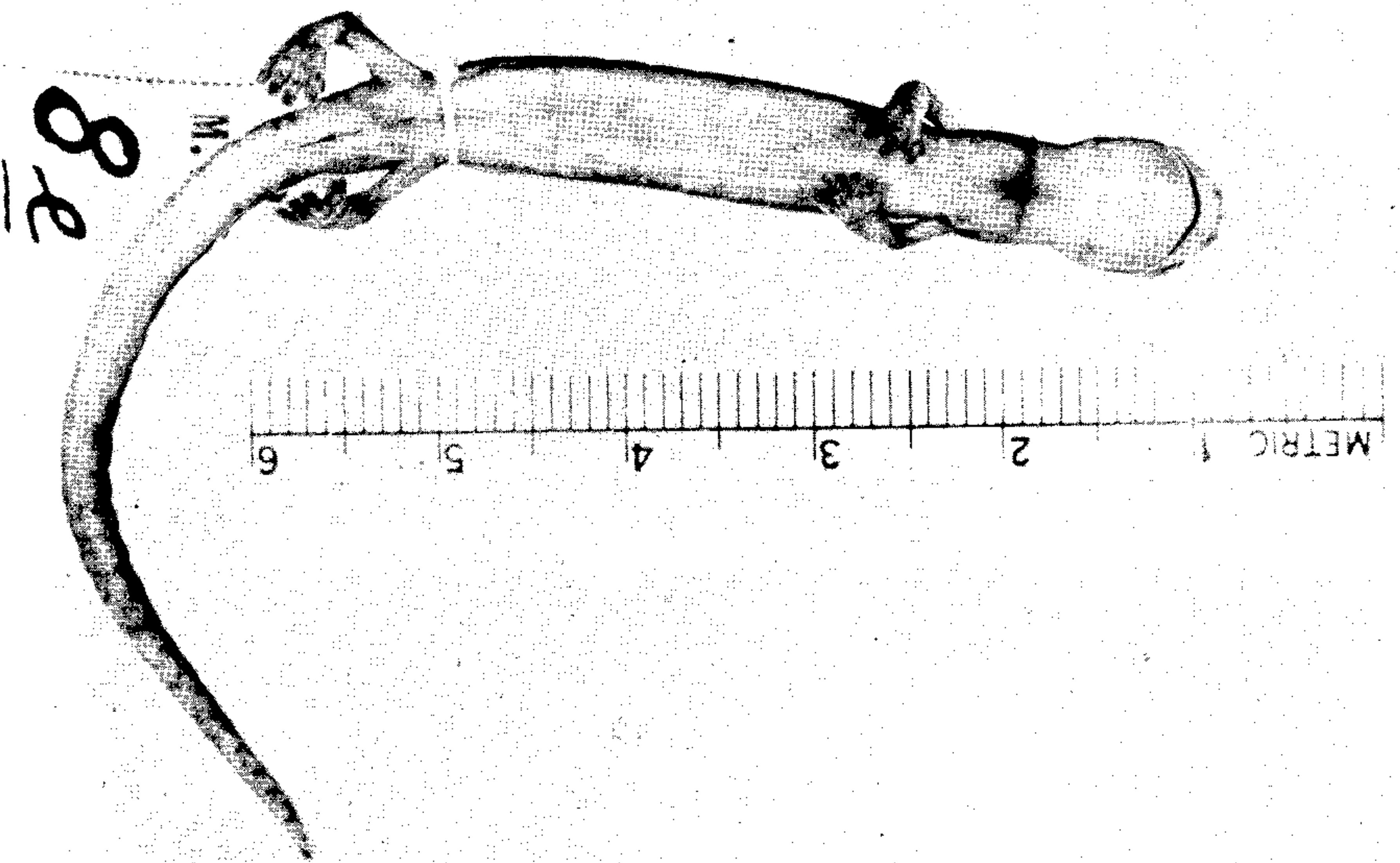


Fig. 13. *Bolitoglossa valleculea* MLaS 8c, Yacumal, Colombia. Male.

times right hind limb. Webbing of hand and foot not complete; tips of digits broadly rounded, free from web; 2 phalanges of toes 2, 3, and 4, $1\frac{1}{2}$ phalanges of finger 3, and terminal phalanx of fingers 2 and 4 and toe 5 free from web. Pronounced subterminal pads present on fingers and toes. Fingers in order of decreasing length: 3, 2, 4, 1; toes in order of decreasing length: 3, 4, 2, 5, 1.

Measurements: head width 7.9; snout to gular fold (head length) 11.8; head depth at posterior angle of jaw 4.7; eyelid length 3.8; eyelid width 1.9; anterior rim of orbit to snout 3.3; horizontal orbital diameter 2.5; interorbital distance 2.7; distance between vomerine teeth and parasphenoid tooth patch 0.7; snout to fore limb 15.6; distance separating internal nares 2.0; distance separating external nares 2.4; snout projection beyond mandible 1.0; snout to posterior angle of vent (standard length) 54.1; snout to anterior angle of vent 49.7; axilla to groin 28.8; tail length 50.0; tail width at base 3.2; tail depth at base 3.9; fore limb length 10.3; hind limb length 10.9; width of right hand 4.8; width of right foot 5.6.

Coloration: dorsal ground color of entire organism mottled dark brown as a result of varying concentrations of melanophores scattered on a light background. Center of back with many small and indistinct yellowish areas showing through melanophore network. Two distinct but discontinuous black lines extend on either side of the body from area over shoulders posteriorly along dorso-lateral portion of trunk and onto lateral portions of tail. A less distinct dark line extends from the canthus rostralis to behind eye and along lateral borders of trunk to insertion of hind limbs. Ground color of ventral surfaces yellowish with scattered grayish-brown suffusions that are comprised of punctate and reticulate melanophore patterns; much of ventral surface unmarked by melanophores and appears clear yellowish.

Variation—Pertinent counts and measurements of the type series are listed in Table 2. Sexual dimorphism is noted in regard to size and limb length. The 12 males average 44.9 standard length with a limb interval of from 1 to $2\frac{1}{2}$ (mean 2); 8 females average 51.9 standard length with a limb interval of from $2\frac{1}{2}$ to 4 (mean 3). Maxillary teeth increase in number with increasing size (Fig. 14).

Webbing of the hands and feet of the series is similar to that of the type, but some variation is seen. MLaS 5b has much more webbing than other *valleculea* but the webbing of all fingers and toes is obviously incomplete. Other individuals may have slightly more or less webbing than the type. Subterminal pads are evident in well-preserved individuals. The hands and feet of *adspersa* and *valleculea* are similar, but those of *valleculea* are less fully webbed with a few exceptions. In general, the amount of webbing is intermediate between the amounts in *hypaetra* and *savagei*, and resembles that in *adspersa*.

Considerable variation is seen in head width with some evidence of sexual dimorphism. Males have broader heads (standard length 5.7-7.0 times head width, mean 6.4) than females (standard length 6.4-7.3 times head width, mean 6.9). MLaS 5b, a male, has a noticeably broader head and a broader and more

Range—Cordillera de Guacamayo, central Ecuador (Amazonian drainage) (Fig. 22).

Bolitoglossa hypacra (Brame and Wake, 1962)
Figure 11

Magnadigia hypacra Brame and Wake, 1962. Proc. Biol. Soc. Washington, 75: 71.

Holotype—USNM 131481; an adult female from Páramo Frontino, 3610 meters (11850 feet), Departamento de Antioquia, Colombia, collected by M. A. Carriker, Jr.

Material Examined—*Holotype*. The species is known only from the holotype.

Diagnosis—A medium-sized species (62.8 standard length) with high numbers of maxillary teeth (48) distinguished from *biseriata*, *borburata*, *capitana*, *niceforti*, *savagei*, and *vallecula* by less webbing and distinctive coloration (coarse dorsal speckling of yellow-buff on dark brown ground color, and large yellow spots scattered sparsely on lateral and ventral brown ground color); from *subpalmata* by larger size, fewer maxillary and vomerine teeth, and coloration; from *cervoensis* by more maxillary and vomerine teeth; from *marmorata* by fewer vomerine teeth, smaller head, hands, and feet, shorter limbs, and coloration.

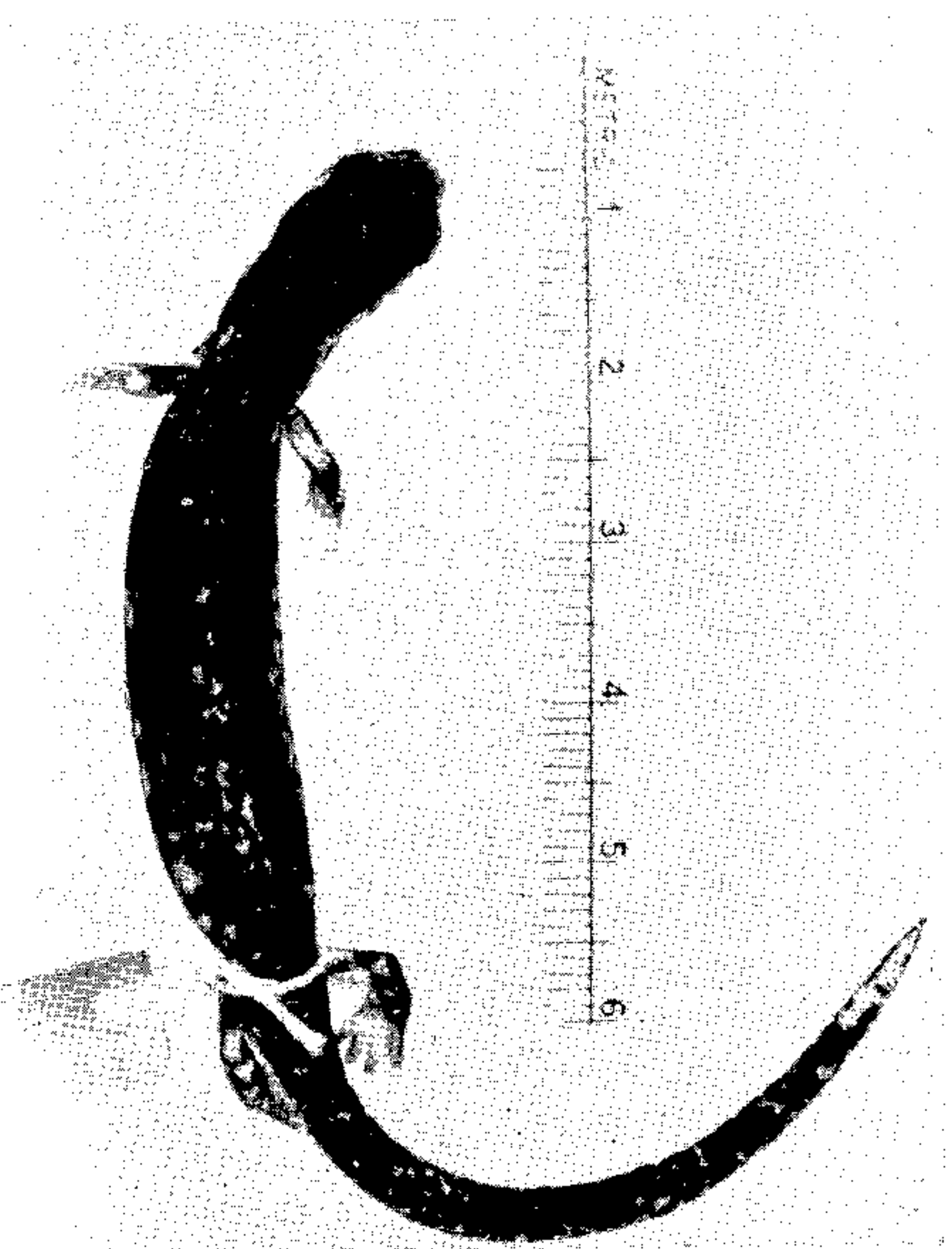


Fig. 11. *Bolitoglossa hypacra* USNM 131481. Páramo Frontino, Colombia. Female. *Holotype*.

Remarks—Detailed information concerning this species is to be found in the original description (Brame and Wake, 1962a).

Range—Cordillera Occidental, northwestern Colombia (Fig. 23).

***Bolitoglossa vallecula*, NEW SPECIES**
Figures 12, 20A, and 26

Oedipus adspersus (part) Dunn, 1926. Salamanders of Family Plethodontidae, p. 396.

Holotype—MLaS 8a; an adult female from Yarumal, 2300 meters (7550 feet), Departamento de Antioquia, Colombia, collected in January, 1962, by Hermano Nicéforo María.

Paratypes—COLOMBIA, DEPARTAMENTO DE ANTIOQUIA: MLaS 8b-8h (7 specimens), same data as holotype; MLaS 5, 5a, 5b, La Ceja, 2217 meters (7270 feet); MLaS 9, San Pedro, 2700 meters (8850 feet); MLaS 10, 10a, 10b, 6 km. toward Rionegro from Retiro, 2300 meters (7540 feet); AMNH 39445-7, Santa Rosa de Osos, 2640 meters (8660 feet); AMNH 14027, "Andes"; MCZ 8163, "Quindío" (probably from Sonson region, 2545 meters (8350 feet)). Apparently all were collected by Hermano Nicéforo María, and information supplemental to that accompanying the AMNH and MCZ specimens was provided by him.

Diagnosis—A medium-sized species (12 males: 37.6-44.9-51.9; 8 females: 44.6-51.9-58.7) with high numbers of maxillary teeth (16: 28-44-61) distinguished from *biseriata*, *borburata*, *capitana*, *niceforti*, *pandi*, and *savagei* by less fully webbed hands and feet (Fig. 20); from *adspersa* by more maxillary teeth relative to size (Fig. 14) and presence of red or yellow pigmentation on the ventral surfaces of trunk and tail; from *hypacra* by its smaller size and ventral coloration.

Description of the holotype—Adult female, snout of moderate length and width, truncate; nostril small, labial protuberances of nasolabial groove moderate; canthus rostralis of moderate length, angular, marked by dark pigment. Standard length 6.8 times head width; standard length 4.6 times snout-gular fold length. Distinct groove below eye extends almost full length of eye opening following curvature of eye, does not communicate with lip. Eye of moderate size, moderately protuberant. Well defined postorbital groove extends posteriorly from eye as shallow depression for 2.8 mm., proceeds sharply ventrally at level of posterior end of mandible and extends across gular area as well defined groove parallel to and 2.8 mm. anterior to gular fold. Vomerine teeth 20, in curved series that extend about to lateral borders of internal nares. Maxillary teeth 53, extending posteriorly to point about two-thirds through eye. Four premaxillary teeth, none piercing lip. Dentary teeth 72. Tail slender, 0.92 times standard length; moderately compressed laterally; moderately constricted at base. Post iliac gland not evident. Limbs relatively robust, of moderate length; limb interval 2.4; standard length 5.3 times right fore limb; standard length 5.0

Bolitoglossa orestes Brame and Wake, 1962

Figure 9

Oedipus adspersus (part) Dunn, 1926. Salamanders of Family Plethodontidae, p. 440.

Bolitoglossa orestes Brame and Wake, 1962. Copeia, 1962: 171.

Holotype—BM 1905.5.31.103; an adult female from Culata, 3000 meters (9810 feet), Cordillera de Mérida, Estado de Mérida, Venezuela, presented by W. F. H. Rosenberg.

Material Examined—VENEZUELA, ESTADO DE MÉRIDA: BM 1905.5.31.95-102, same data as holotype; LM 4506, NMB 2671, and AMNH 10557-60, Culata, collected by Rosenberg; MCZ 2605, Culata, collected by Briceño; CM 10086, Mérida, collected by Rosenberg; BM 1904.6.30.18, Mérida; AMNH 10555-56, Chama, 2000 meters (6540 feet), collected by Rosenberg; BM 1905.5.31.105-107, 108 (2 specimens), Fugueros, 3500 meters (11450 feet), (Estado de Mérida ?); NMW 9179: 1-4 and 9181: 1-4 (total 8 specimens), Culata and Chama, collected by Rosenberg; and holotype. Material examined is the type series.

Diagnosis—A small (9 males: 31.4-37.7-39.7; 13 females: 30.3-42.2-46.9) member of the *palmaria* group with low numbers of maxillary teeth (25: 7-20-30) distinguished from *palmaria* by its smaller adult size, small numbers of vomerine teeth (7-15), and great abundance of tiny guanophores ventrally.

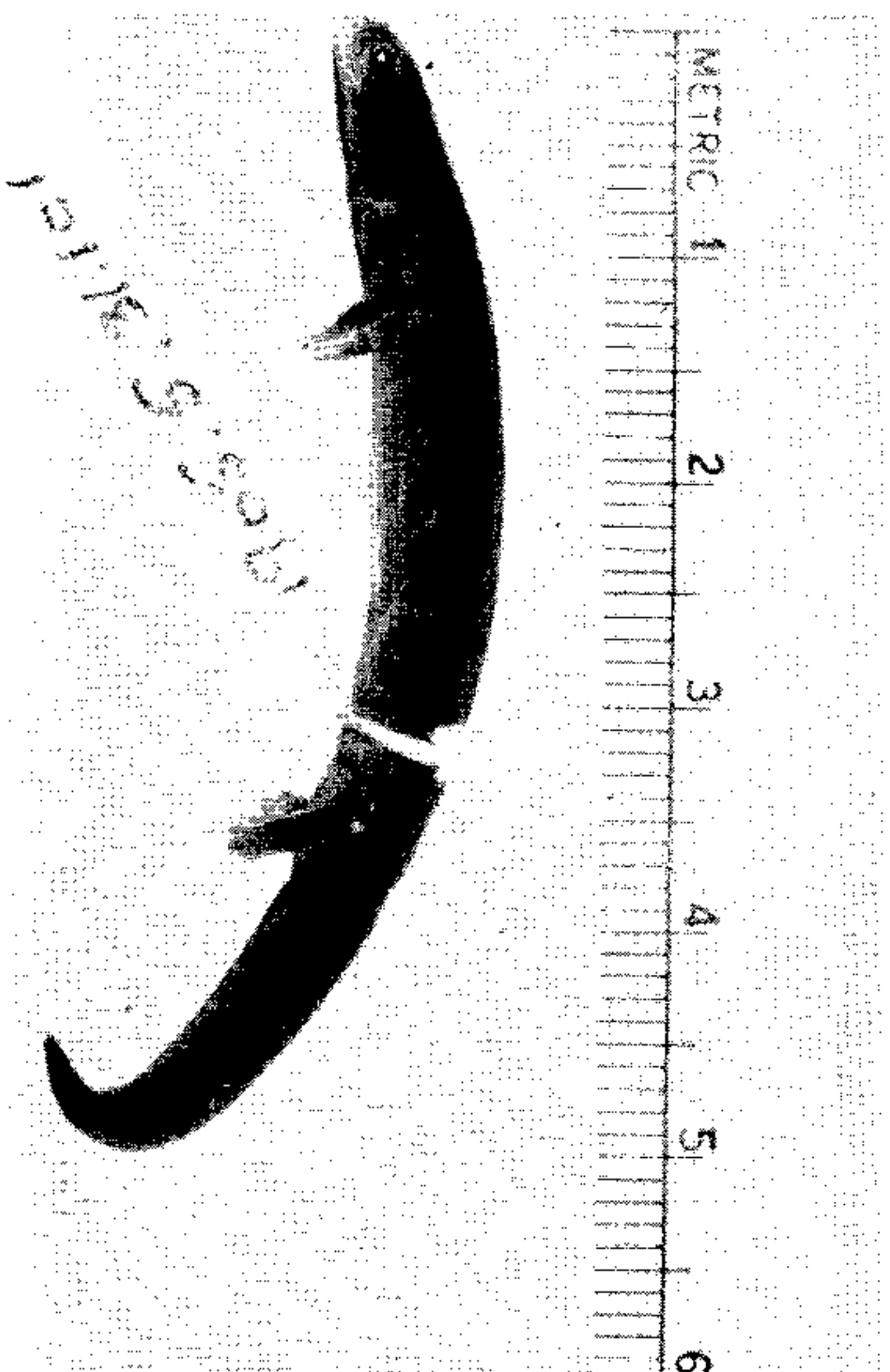


Fig. 9. *Bolitoglossa orestes* BM 1905.5.31.101, Culata, Venezuela, female.

Remarks—Detailed information concerning this species is to be found in the original description (Brame and Wake, 1962 b).

Range—Cordillera de Mérida, western Venezuela (Fig. 23).

Bolitoglossa palmata (Werner, 1897)

Figure 10

Speleperes palmatus Werner, 1897. Zool. Anz. 20: 266.

Oedipus altamazonicus (part) Dunn, 1926. Salamanders of Family Plethodontidae, p. 396.

Bolitoglossa palmata Brame and Wake, 1962. Copeia, 1962: 173.

Lectotype—ZIUW q43; a juvenile from "Cordillera," Ecuador, collected by M. Wagler.

Material Examined—CM 13118, between Baeza and Archidona, 2000 meters (6540 feet), Cordillera de Guacamayo, Provincia de Napo-Pastaza, Ecuador, collected by Philip W. Hershkovitz; UMMZ 84735 (3 specimens), same date as above; and lectotype.

Diagnosis—A medium-sized (1 male: 35.6; 3 females: 49.4-50.8-53.3) member of the *palmaria* group with moderate numbers of maxillary teeth (4: 24-39-47) distinguished from *orestes* by its larger adult size, larger numbers of vomerine teeth (14-23) and distinctive coloration (uniform light brown dorsally and laterally with a sharply demarcated dark brown venter).

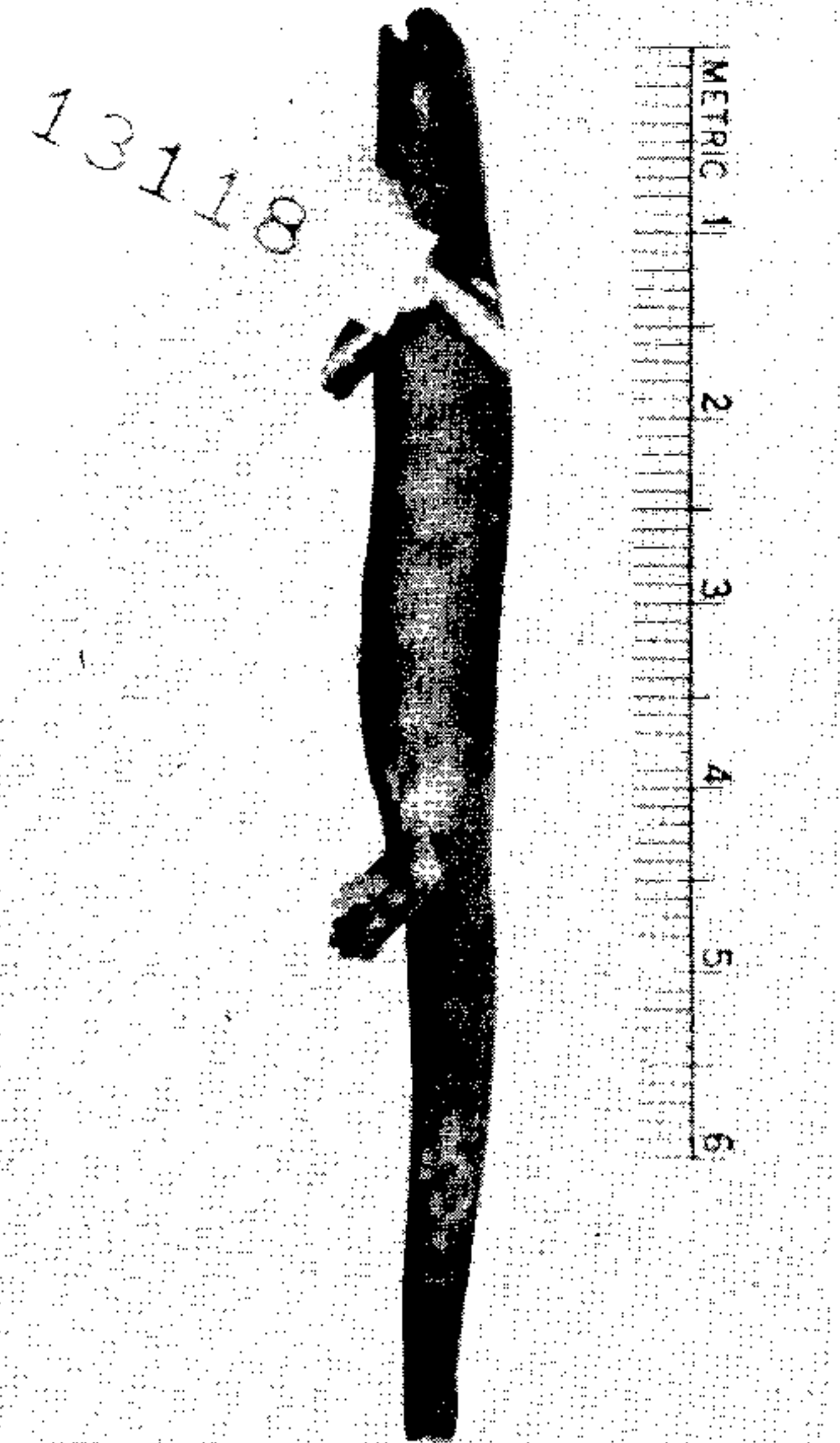


Fig. 10. *Bolitoglossa palmata* CM 13118, between Baeza and Archidona, Ecuador, female.

Remarks—The authors have recently redescribed this species and detailed information is found in our publication (Brame and Wake, 1962 b).

the hands and feet is very extensive. The specimen is now faded but it appears that the ground color was originally light, with mottling of darker color dorsally.

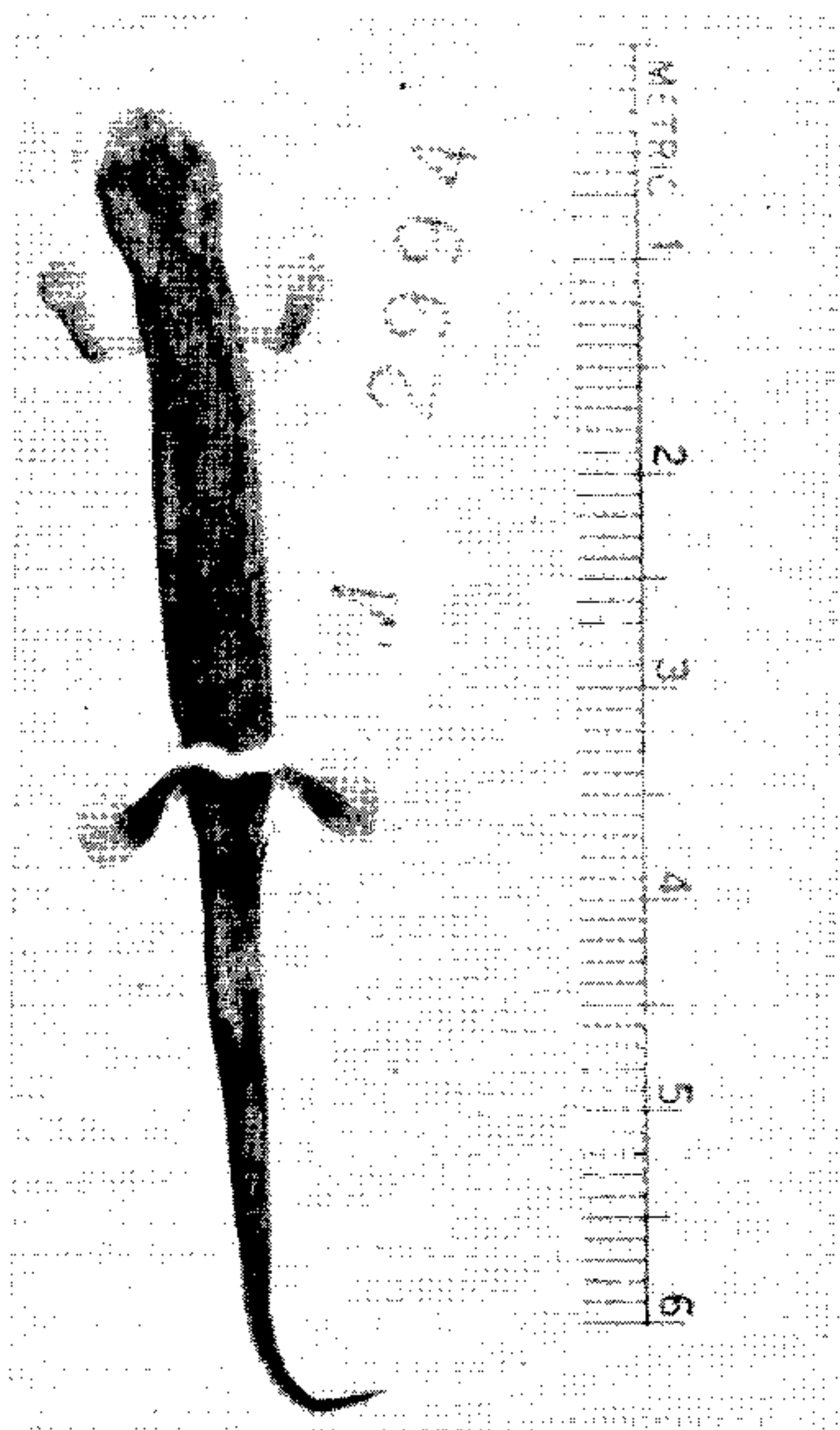


Fig. 8. *Bolitoglossa sima* JAP 2994, Cachavi, Ecuador. Male.

B. sima is a moderately robust species with a head of moderate width (standard length 6.2-6.6 times head width) and fairly short limbs (limb interval 3-4). The snout is of moderate length and width, and is flattened and truncate anteriorly. The eyes are of moderate size. Maxillary teeth increase steadily with size (Fig. 7), the largest specimen (45.9 standard length) having the highest numbers of teeth (44). Maxillary teeth extend posteriorly to a point between the front and center of the eye. Vomerine teeth are in a single series in three individuals, and are slightly patched laterally in two (USNM 20591, JAP 2993). The vomerine series extend to the medial border of the choanae in most. The tail is virtually round in cross-section with little lateral compression. Webbing of the hands and feet is complete and is more extensive than in any other South American *Bolitoglossa*. The digits are very flattened and indistinct. Tips of the longest digits project as small obtuse angles from the pad-like webbing (Fig. 20F). Size of hands and feet is greater in *sima* than in other members of the *altamazonica* group. All six specimens are similar in coloration, and are generally brownish, lighter ventrally than dorsally. The dorsal surfaces are mottled with several shades of from very light to very dark brown with no determinable pattern. Enlarged brown dorsal glandules are evident on the head and body. The top of the head is dark brown. All ventral surfaces are uniformly covered with tiny punctate melanophores.

Some information is available concerning the habitat of *sima*. The following information was provided by James A. Peters. Three salamanders col-

lected by him were found in the nesting bases of the stems of giant elephant ear plants, which catch and hold water. All were taken in plants that were shaded either by trees or by other elephant ear plants. The plants grow in large clumps, 10-15 feet in diameter, and the salamanders were in the innermost plants, well down toward the base of the stem. The general area was dense wet forest, but the actual collection locality was a grassy field, cleared for cattle grazing, with scattered trees left for shade. Elephant ear plants grow in the shade. No salamanders were found in the same plants growing in the forest proper.

Dunn (1926: 398) indicated on his map that USNM 20591 was from southern Ecuador in the Amazonian drainage. Information accompanying the specimen states that it is from Plaza de Oro, a locality in northwestern Ecuador in the Pacific drainage. The newly collected material is from the Pacific drainage, also in northwestern Ecuador not far from Plaza de Oro. Unfortunately specific information is not available concerning collection of the type.

Range.—Northwestern Ecuador near the Colombian border, and perhaps into Colombia (Fig. 22).

TABLE 1. Data on *Bolitoglossa altamazonica* group

	Snout-Vent Length	Axilla-Groin	Head Width	Hind Limb Length	Snout-Gular Fold	Limb Interval	Tail Length	Maxillary Teeth	Vomerine Teeth
<i>Bolitoglossa altamazonica</i>									
MCZ 24921	♂ 42.0	23.3	6.3	9.1	9.3	4	39.9	21	20
CNHM 78394	♂ 41.6	22.7	6.2	9.9	9.6	4	36.7	16	13
ZSMH 3090	♂ 30.6	15.5	4.9	6.4	7.1	2	31.0	—	15
MLAS 3	♀ 48.0	27.5	6.7	9.2	10.2	4½	28.2	26	21
BM 1913.7.28.29	♀ 42.5	24.8	5.8	8.9	8.9	4	43.0	19	9
AMNH 3746	♀ 43.6	24.3	6.8	10.2	10.2	2	—	—	16
AMNH 43569	♀ 41.3	21.9	5.7	9.8	9.7	3	—	20	17
MCZ 5124	♀ 39.8	22.5	5.7	9.0	8.7	4	44.5	14	13
BM 1913.7.28.30	♀ 37.9	20.9	5.6	7.8	7.9	5	37.8	14	12
CAS 65003	♀ 35.6	20.4	5.7	8.2	8.0	3½	34.0	11	14
USNM 85119	♀ 26.7	13.2	4.8	6.3	6.8	4	23.3	9	14
<i>Bolitoglossa sima</i>									
JAP 2994	♂ 36.7	19.6	5.9	8.8	8.8	3	32.6	31	10
USNM 20591	♀ 45.9	24.3	7.0	10.2	11.2	3	37.3	44	18
MNHN 3302	♀ 45.7	26.0	6.9	9.8	10.9	3½	49.0	32	20
JAP 2993	♀ 43.7	24.9	6.8	9.8	9.8	4	41.6	28	22
JAP 2995	28.2	14.3	5.0	6.1	7.0	—	22.4	18	9
<i>Bolitoglossa peruviana</i>									
BM RK 1946.9.6.17	♀ 42.3	24.0	5.9	6.7	9.6	3½	36.9	37	30
JAP 6773	♀ 37.0	22.1	5.8	8.4	8.0	4	34.2	36	13
<i>Bolitoglossa chima</i>									
TPN 9411	♂ 40.3	21.9	6.3	8.7	9.2	3½	41.8	4	31
JAP 4466	♀ 48.7	21.1	5.9	7.7	9.0	3	32.0	0	16

angular spot, base forward on the crown; lower surfaces and hind limbs brown, with slight lighter variegations." The color as described by Boulenger does not seem to differ greatly from that of some *altamazonica*.

The recently collected Ecuadorian specimen is tentatively assigned to *peruviana* on the basis of similarity of proportions, similarity of hands and feet, and high numbers of maxillary teeth (36). Several differences exist between this specimen and the type of *peruviana*, and we have some reservations about assignment of the specimen. Only 13 vomerine teeth are found and they extend to the medial edge of the choanae. The snout is proportionately somewhat shorter than that of the type. Ground color of the entire organism is solid dark blackish with blackish-brown dorsolateral streaks on either side from the back of the head, over the shoulders, and onto the trunk. The ventral surfaces are sprinkled with small white guanophores. White pigment is present on the snout, and a large white spot lies between the eyes. The only other member of the *altamazonica* group that approaches *peruviana* in numbers of maxillary teeth is *sima* from which the specimen differs markedly in its dark coloration, its ventral guanophores, its noticeably smaller and less fully webbed hands and feet, and its shorter snout. The individual was collected under a banana log in a plantation. Both it and the type of *peruviana* are from the Amazonian drainage.

Petracca (1904) mentions a specimen from Ecuador which he assigned to *peruviana*. The specimen, in the Torino Museum, is unavailable for study. Since no definite locality information or description is given, its taxonomic assignment must remain in doubt.

Range—North-central Peru to southeastern Ecuador (Fig. 22).

Bolitoglossa sima (Vaillant, 1911)
Figures 8 and 20F

Speleptes sinus Vaillant, 1911. Miss. Geogr. Amer. Sud., 9(2): 58.

Oedipus altamazonicus (part) Dunn, 1926. Salamanders of Family Plethodontidae, p. 396.

Holotype—MHNP 06-284; an adult female from "Equateur" collected by Dr. Rivet.

Material Examined—USNM 20591, Plaza de Oro, Provincia de Esmeraldas, Ecuador; USNM 22453, Ecuador or Colombia; JAP 2993-5, 1 km. N. Ca-chavi, 20 meters (66 feet), Provincia de Esmeraldas, Ecuador, collected by James A. Peters, Dec. 3, 1958; and holotype.

Diagnosis—A medium-sized (4: 36.7-43.0-45.9) member of the *altamazonica* group with moderate numbers of maxillary teeth (4: 28-34-44) distinguished from other members of the group by its extensively webbed hands and feet (Fig. 20F) and distinctive coloration (light dorsal ground color mottled with several shades of brown); distinguished further from *altamazonica* and *chica* by higher numbers of maxillary teeth; from *altamazonica* and *peruviana* by larger hands and feet (standard length 9.2-10.6 times foot width, versus 11.0-13.3 in *altamazonica* and 11.6-13.7 in *peruviana*).

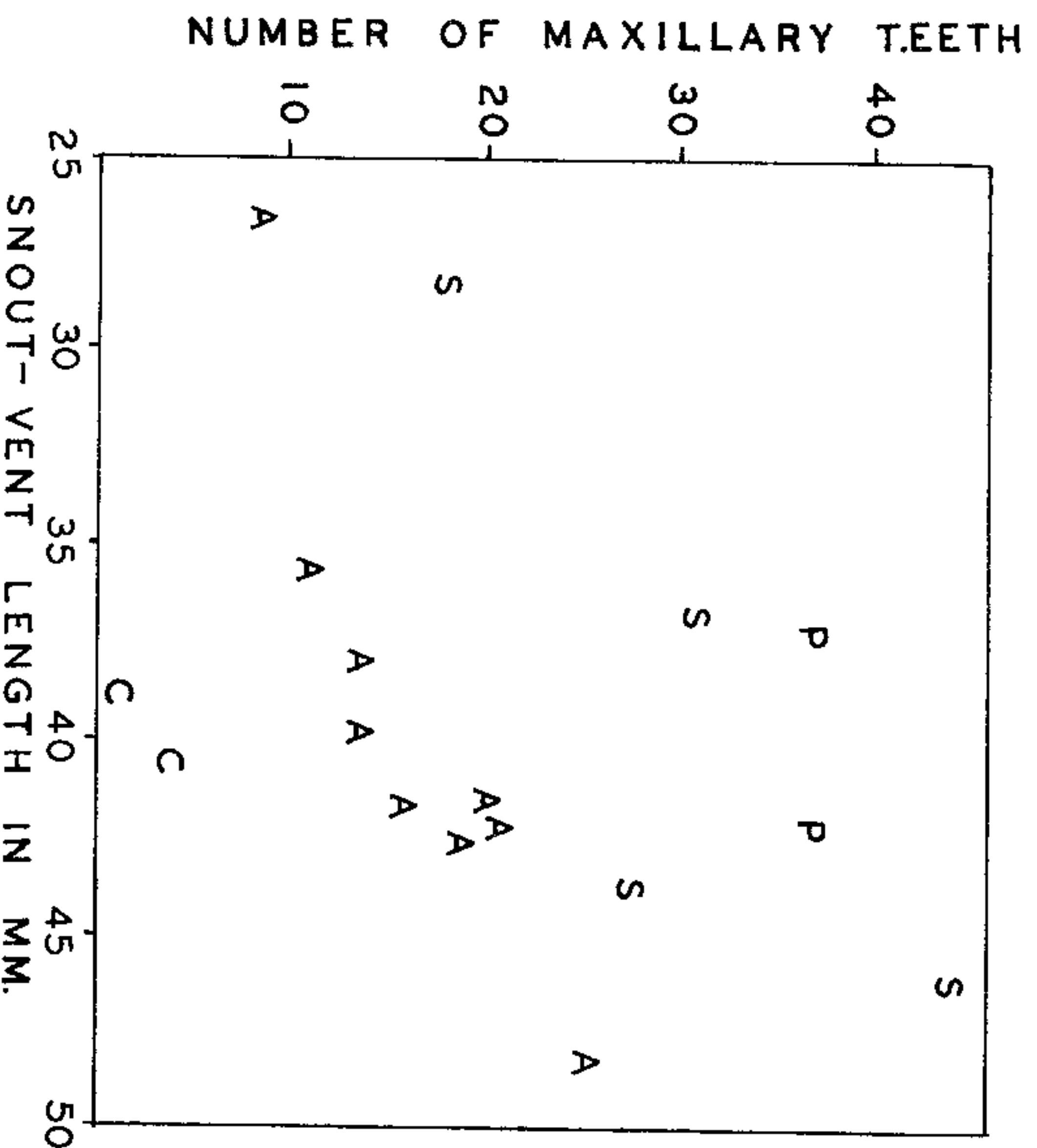


Fig. 7. *Bolitoglossa altamazonica* Group. Variation in maxillary teeth. A, *altamazonica*; C, *chica*; P, *peruviana*; S, *sima*.

Remarks—Vaillant (1911) described *sima* from a single Ecuadorian specimen. His description was obviously inadequate and Dunn (1926) placed the name in the synonymy of *altamazonica* without examining the type, stating that the description was poor and that the figure resembled *altamazonica*. We have examined the type and additional recently collected material and find that they are representatives of a distinct species. Pertinent counts and measurements of examined material are found in Table 1. USNM 22453 is in very poor condition and accurate measurements and tooth counts are not possible.

Some of the information given by Vaillant (1911) is in error and the description is inadequate in other ways. The following account is based on our examination of the holotype. Counts and measurements: 1 premaxillary tooth; maxillary teeth 24 (plus several that have been knocked out), vomerine teeth 20 (in single rows), costal grooves 13, limb interval $3\frac{1}{2}$, standard length 45.7, axilla-groin length 26.0, head width 6.9, snout-gular fold length 10.9, tail length 49.0, hind limb length 9.8. Maxillary teeth extend to the front of the eye on the left side and to the center of the eye on the right. The vomerine series extend to the lateral edge of the internal nares on both sides. Webbing of

Coloration in alcohol: light gray-brown dorsally, light gray laterally and ventrally. Light ground color of entire organism covered with even punctation of small melanophores that form some isolated reticula. Eyelid edges dark black. Sparsely scattered large guanophores on ventral surfaces of head, trunk, tail, and limbs. Uniformly cream-colored in life.

Variation—Pertinent counts and measurements of the only paratype are found in Table 1. The paratype is an adult male, and is a little larger than the holotype. It has a slightly narrower but more truncate snout. It is slightly less robust than the holotype and has a proportionately longer tail. The paratype has some small maxillary teeth (4) and has more vomerine teeth (31) than the holotype. The vomerine teeth are in series that extend to the lateral borders of the internal nares or beyond, and the series become patched laterally.

Coloration of the paratype has been altered both by preservation and by rather extensive growths of what appears to be a fungus. The skin of the dorsal and lateral surfaces is partially disintegrated in spots, and these spots are lighter in coloration than surrounding areas. Hair-like hyphae protrude from the infested areas. Dorsal and lateral surfaces appear dark brown, ventral surfaces light brown. Melanophores are in reticula over most of the organism, but are punctate in some scattered areas. Large guanophores are sparsely scattered over ventral surfaces, as in the holotype.

Remarks—The species is known from but two individuals. The greatly reduced numbers of maxillary teeth appear to be highly significant. *Bolitoglossa colonea* of southern Central America also has greatly reduced numbers of maxillary teeth, but differs markedly from *chica* in having a large interorbital dermal ridge and a shorter, more truncate snout.

The holotype was captured on a broad-leaved fern at night during a moderately heavy rain.

The name *chica* is derived from the Spanish word *chica* (small).

Range—Northeastern Ecuador (Fig. 22).

Bolitoglossa peruviana (Boulenger, 1883)

Figure 6

Speiarpes peruviana Boulenger, 1883. Ann. Mag. Nat. Hist., Ser. 5, 12: 165.

Oedipus altamazonicus (part) Dunn, 1926. Salamanders of Family Plethodontidae, p. 396.

Oedipus peruvianus Parker, 1939. Mem. Mus. Roy. d'Hist. Nat. Belgique, Ser. 12, 2: 87-89.

Bolitoglossa peruviana Taylor, 1944. Univ. Kansas Sci. Bull., 30(1): 219.

Holotype—BM 1946.9.6.17; an adult female from Moyobamba, 854 meters (2800 feet), Departamento de San Martín, Peru, collected by A. H. Roff in 1874.

Material Examined—JAP 6773, slightly above Río Paute 2 km. NN1; Mendez, circa 2000 meters (6560 feet), Provincia de Santiago—Morona, Ecuador, collected by Peter D. Spoecker on August 9, 1962; and holotype.

Diagnosis—A small (2 individuals: 37.0, 42.3 standard length) member of the *altamazonica* group with moderate numbers of maxillary teeth (36, 37, respectively) distinguished from *altamazonica* and *chica* by many more maxillary teeth; from *sima* by small hands and feet (standard length 11.6-13.7 times foot width, versus 9.2-10.6 in *sima*) that are less completely webbed.

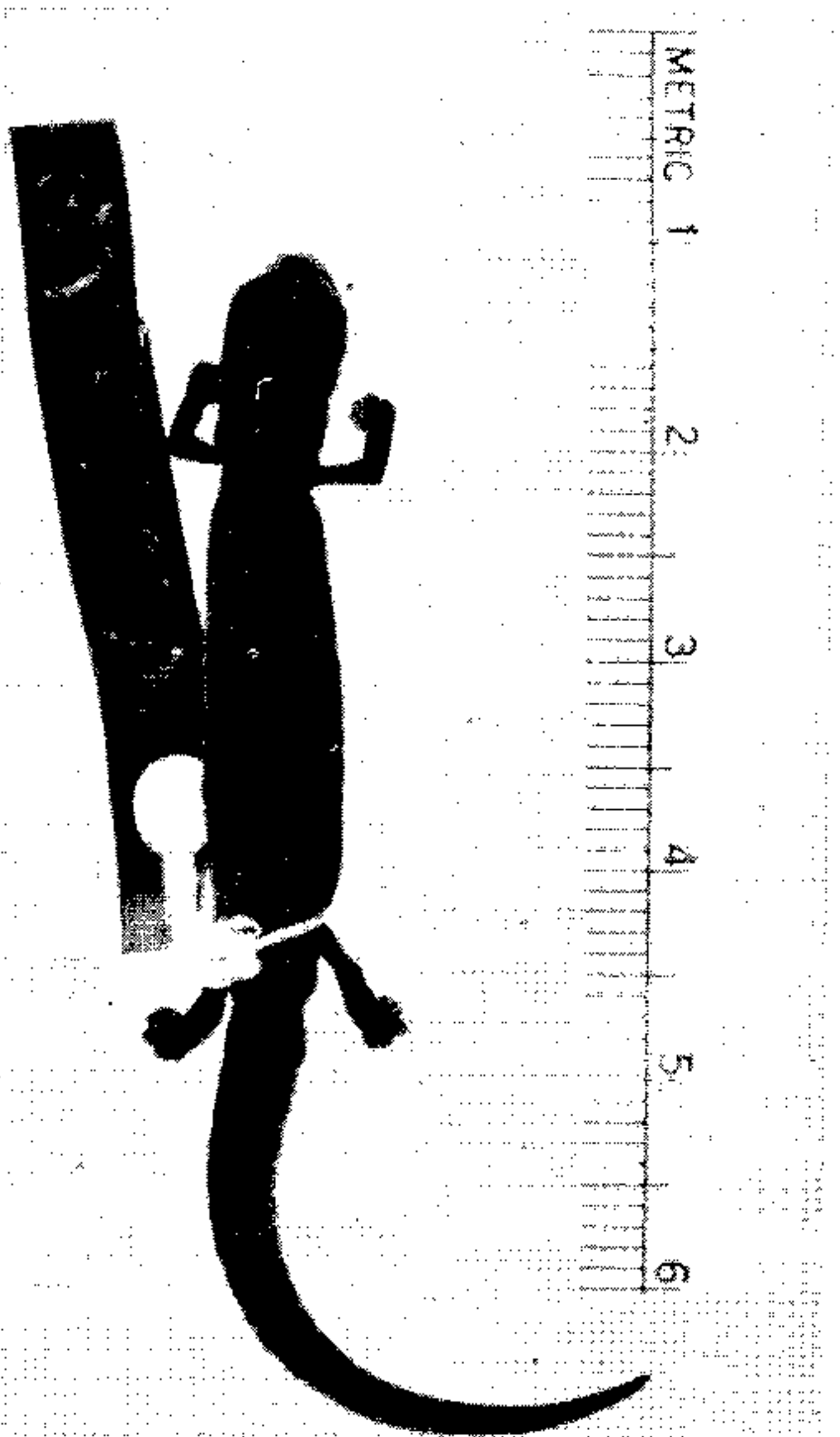


Fig. 6. *Bolitoglossa peruviana* JAP 6773, Mendez, Ecuador. Female.

Remarks—Pertinent counts and measurements of the material examined are found in Table 1. Parker (1939) examined the holotype of *peruviana* and compared it with *altamazonica*. He concluded that it was a member of a distinct species that differed from *altamazonica* in having more vomerine and maxillary teeth, vomerine teeth that extended past the lateral edges of the choanae and were only narrowly separated from the parasphenoid tooth patch, a divided parasphenoid tooth patch, and in unspecified details of coloration. Brane recently reexamined the type of *peruviana* and we concur with the conclusions of Parker. The type has 37 maxillary teeth while an individual of *altamazonica* of the same size and sex has but 19, and the maximum in *altamazonica* is 26. The type has 30 vomerine teeth while the individual of *altamazonica* of the same size and sex has but 9, and the maximum for *altamazonica* is 21. The vomerine teeth of certain *altamazonica* (MLAS 3) extend beyond the lateral borders of the choanae and that character does not separate the two species. Distance between parasphenoid and vomerine teeth, and separation or non-separation of the parasphenoid tooth patch are characters that are rather variable in *Bolitoglossa*, and are not of taxonomic significance. The holotype is now very light in coloration and is obviously faded. Boulenger (1883) described the color as "light brownish above, with ill defined brown longitudinal lines; a tri-

***Bolitoglossa chica*, NEW SPECIES**

Figures 5, 20E, and 26

Holotype—JAP 4366; an adult female from the grounds of the Hotel Zaracay, 2 km. E. of Santo Domingo, 670 meters (2200 feet), Provincia de Pichincha, Ecuador, collected on June 15, 1962, by Robert K. Mullen and Peter D. Specker.

Paratype—EPN 2411, an adult male from the lower part of the Río Bolaniguas, a southern affluent of Río Guallabamba in the Río Esmeraldas system, at about 0° 15' N. Latitude and 79° 06' W. Longitude (250-400 meters), Provincia de Pichincha, Ecuador, collected in August, 1956, by Manuel Olalla.

Diagnosis—A small (2 individuals: 38.7, 40.3 standard length) member of the *altamazonica* group distinguished from all other members of the group by very few or no maxillary teeth (0, 4, respectively); from *colomera* by absence of an interorbital dermal ridge.

Description of the holotype—Adult female, snout of moderate length, broad and truncate, slightly rounded at tip; nostril small, labial protuberances of nasolabial groove moderate; canthus rostralis indistinct, gently rounded. Standard length 6.6 times head width; standard length 4.3 times snout-gular fold length. Relatively deep, distinct groove below eye extends full length of eye opening, does not communicate with lip. Eye relatively small, only slightly protuberant. Poorly defined postorbital groove extends posteriorly from eye as irregular, indistinct depression for 1.8 mm., proceeds sharply ventrally at level of posterior end of mandible and extends across gular area as indistinct depression parallel to and 3.2 mm. anterior to gular fold. Vomerine teeth 16, in slightly curved series that extend to medial border of internal nares. No maxillary teeth. No premaxillary teeth. Relatively robust tail 0.84 times standard length; round with no lateral compression; marked basal constriction. Post-iliac gland not evident. Limbs short and slender; limb interval 3; standard length 5.4 times right fore limb; standard length 5.0 times right hind limb. Webbing of hands and feet nearly complete; digits fairly broad and well defined; triangular and broadly rounded tips of digits free of web, but total webbed area very extensive (Fig. 20E). Longest finger and longest toe more pointed than others. 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: head width 5.9; snout to gular fold (head length) 9.0; head depth at posterior angle of jaw 2.9; eyelid length 2.2; eyelid width 1.2; anterior rim of orbit to snout 2.9; horizontal orbital diameter 1.7; interorbital distance 2.7; distance between vomerine teeth and parasphenoid tooth patch 0.4; snout to fore limb 10.8; distance separating internal nares 1.9; distance separating external nares 2.3; snout projection beyond mandible 0.5; snout to posterior angle of vent (standard length) 38.7; snout to anterior angle of vent 35.4; axilla to groin 21.1; tail length 32.0; tail width at base 3.5; tail depth at base 3.6; fore limb length 7.2; hind limb length 7.7; width of right hand 2.9; width of right foot 3.4.

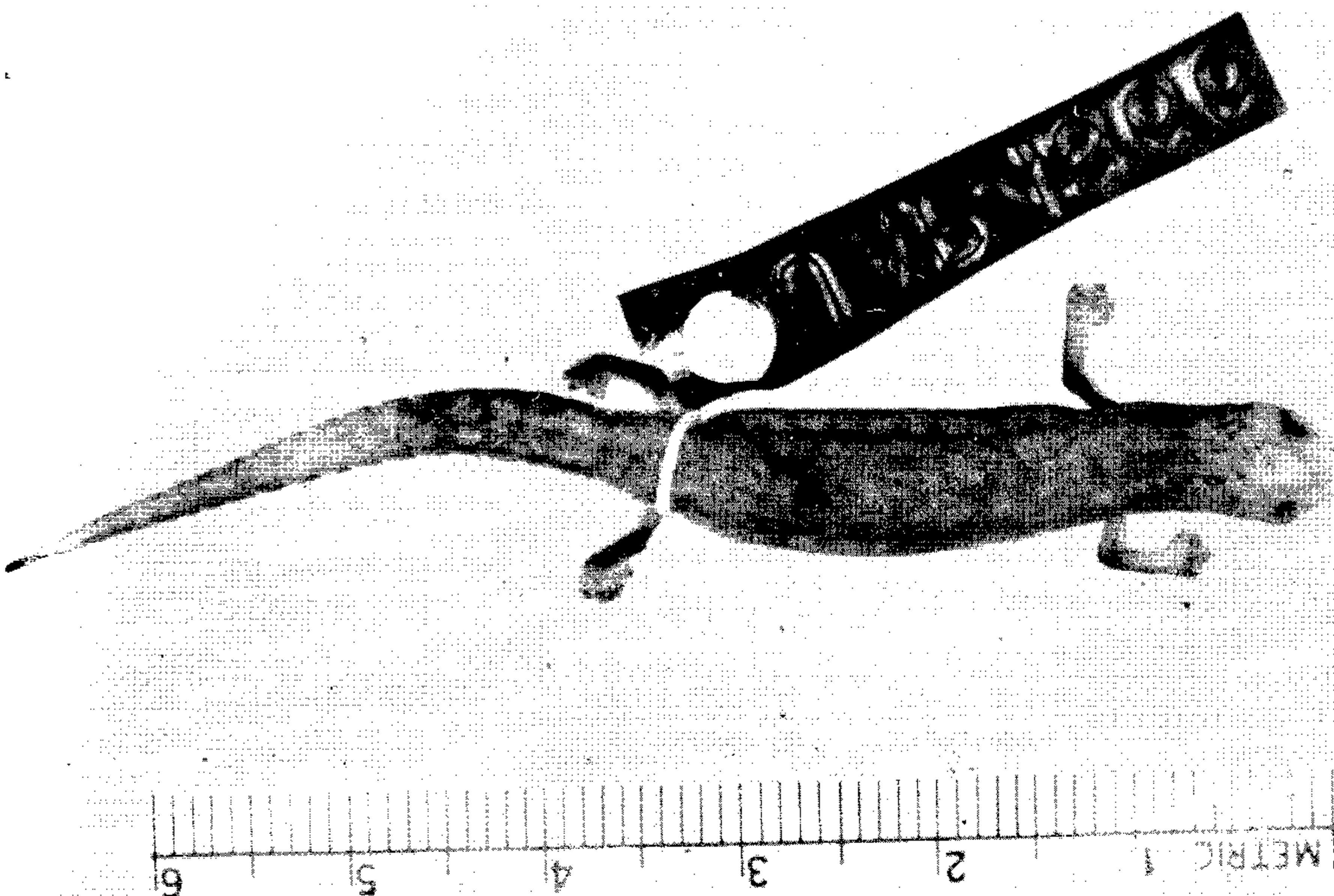


Fig. 5. *Bolitoglossa chica*, JAP 4366, Santo Domingo, Ecuador, Female, Holotype.

Material Examined—PERU, DEPARTAMENTO DE LORETO: USNM 85119, Iquitos, 117 meters (386 feet); MCZ 5124, Río Pacaya or Río Ucayali; BM 1913.7.28.29-30 (2 specimens), Río Pacaya; ZSMH 3090, between Iquitos and Leticia; AMNH 43569, Royaboya, 150 meters (495 feet), collected by H. Bassler. DEPARTAMENTO DE CUZCO: CNHM 78394, Cosñipata, 830 meters (2600 feet), collected by Kalinowski. BRAZIL, ESTADO DO PARÁ: CAS 65003, Belém, collected by the Hopkins-Branner Expedition. BOLIVIA, DEPARTAMENTO DE COCHABAMBA: AMNH 3746, "Cochabamba," collected by Miller and Boyle. COLOMBIA, DEPARTAMENTO DE META: MLaS 3, Acacias, 700 meters (2300 feet), collected by Nicéforo María. DEPARTAMENTO DE BOYACA: MCZ 24921, Muzo, 1240 meters (3980 feet), collected by Nicéforo María.

Diagnosis—A small (10: 30.6-40.3-48.0) member of the *altamazonica* group with low numbers of maxillary teeth (10: 11-15-26) distinguished from *chica* by more maxillary teeth; from *sina* by a narrower head, fewer maxillary teeth (Fig. 7), and emarginated, less fully webbed and smaller hands and feet; from *peruviana* by fewer maxillary teeth.

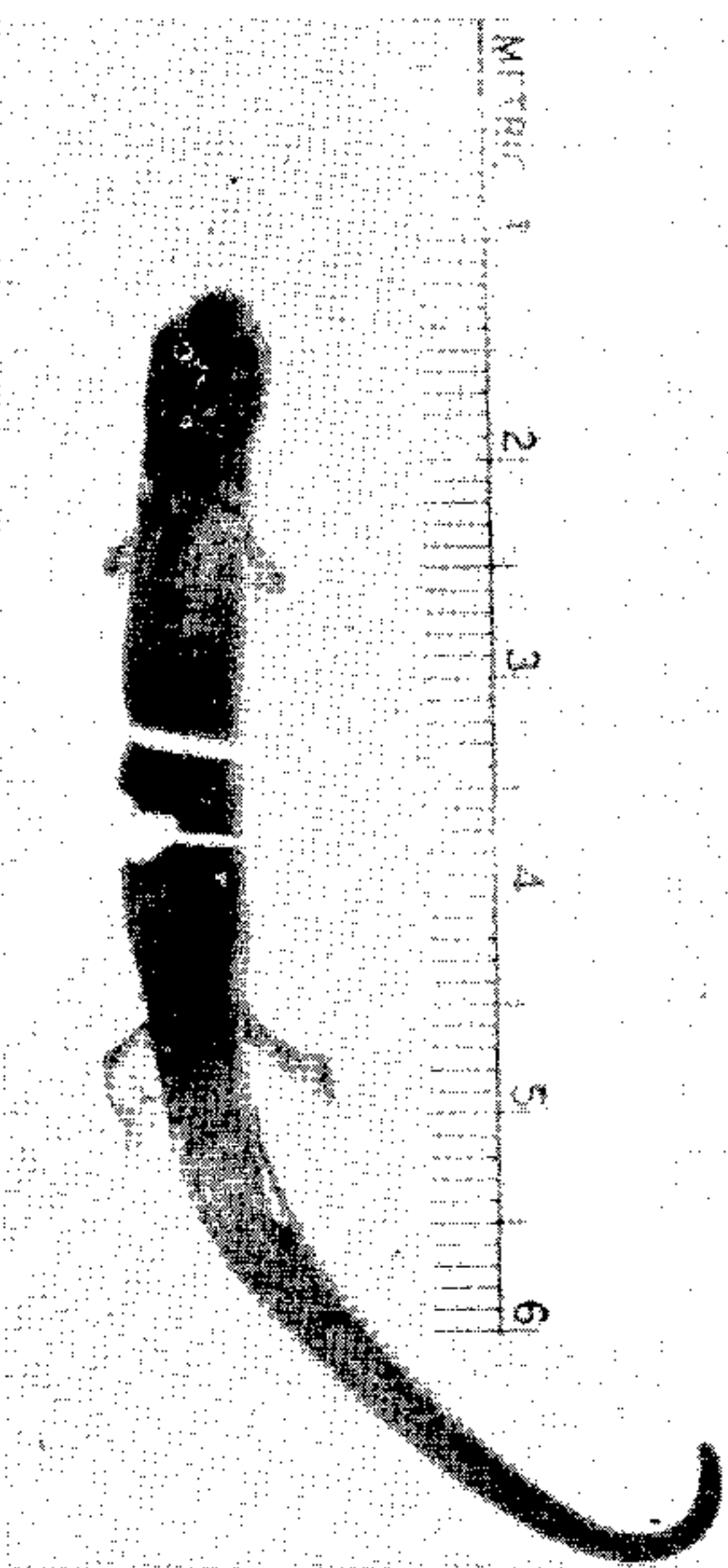


Fig. 4. *Bolitoglossa altamazonica* BM 1913.7.28.30, Río Pacaya, Peru. Female.

Remarks—Pertinent counts and measurements of the examined material are presented in Table 1. In addition to the material examined three specimens (MNRI) are known from Benjamin Constant, 110 meters (363 feet), on the Río Javary near the Peruvian border. Estado do Amazonas, Brazil (Myers and Carvalho, 1945), four newly hatched specimens (cotypes of *Eladinea estheri*, in MNRI and MP) are known from Utinga, near Belém, Estado do Pará, Brazil (Miranda Ribeiro, 1937), and a single individual (holotype of *Oedipus paraensis*, deposited in ZMB but now lost or destroyed) was collected at Santa Isabel, near Belém, Estado do Pará, Brazil (Unterstein, 1930). Darlington (1957) states that Dunn wrote him informing him of a salamander (number

tified) collected at about 200 meters in northern Bolivia. Parker (1939) mentions a single individual, that he calls *altamazonica*, collected in the Utinga forest, near Belém, Estado do Pará, Brazil. We have been unsuccessful in attempts to locate the last two specimens in museums.

The series examined by us is rather variable in coloration. Most individuals are darker dorsally and laterally than ventrally, but some have light dorsal streaking and mottling. Others are uniformly dark-colored dorsally. Patches or spots of light color are absent with the exception of light-colored areas around the nasolabial grooves, and, in one specimen (USNM 85110), on the snout. Ventral melanophore networks are reticulate, punctate, or intermediate. One specimen (MLaS 3) has some small guanophores scattered sparsely on its ventral surfaces. Most specimens are in poor conditions due to poor initial preservation or long term preservation and many are badly faded. Two specimens (BM 1913.7.28.29-30) are greenish due to preservation in a copper container. The ground color of the most recently collected individual (MLaS 3) is a dark blackish-brown.

The question of the validity of *Eladinea estheri* has been discussed by Parker (1939) and Myers and Carvalho (1945). The types are hatchlings and do not differ noticeably from hatchlings of other *Bolitoglossa*. Oviparity of the species led Miranda Ribeiro (1937) to establish the new genus on the false premise that all Central and South American salamanders were ovoviparous. All *Bolitoglossa* for which we have information are, on the contrary, oviparous. There are no other characters and there is no recourse but to place the name in the synonymy of *altamazonica*.

Unterstein (1930) described *Oedipus paraensis* from a single specimen collected near Belém, Brazil. The holotype is now lost. We have examined a specimen from Belém and find it to be identical with Peruvian material, and Parker (1939), who had Peruvian *altamazonica* for comparison, examined a salamander from Belém and called it *altamazonica*. Because the holotype is lost, because no information is contained in the original description that would distinguish *paraensis* from *altamazonica*, because *altamazonica* is known from the vicinity of Belém, and since all extant museum specimens from the area are assignable to a single species we refer the name to the synonymy of *altamazonica*.

Considerable variation is seen in the series of *altamazonica* examined by us (Table 1), and we are not certain that all are members of the same species. We have reservations, in particular, about assignment of the Colombian and Bolivian specimens. A Colombian specimen (MCZ 24921) is the only member of the species known to have been collected above 1000 meters in elevation. It is also from the Magdalena drainage, while all others are from the Amazonian drainage. Our *altamazonica* may be composite, but final solution of the problem must await the collection of additional material.

Range—North central Colombia through eastern Peru to central Bolivia; through Amazonian Brazil to Belém (Fig. 22).

GENUS *BOLITOGLOSSA*

Representatives of 16 species of *Bolitoglossa* have been found in South America (Figs. 22, 23, 24). These species appear to form four species groups, three of which are characterized below. The fourth contains nine apparently rather closely related species, but the group is diverse and it is impossible to define its limits at the present time. The definable species groups are:

The *phalarosoma* Group

One species: *Bolitoglossa phalarosoma*.

Moderate size (3 individuals: 46.8, 55.8, 58.2 standard length); head very narrow in relation to standard length (standard length 7.4, 7.6, 8.0 times head width, respectively); eyes moderate; snout moderate, not shortened; moderate numbers of maxillary teeth (30, 51, 43); limbs short (limb interval 4-4½); hands and feet flattened, completely webbed; ground color solid black with a few large white spots in two dorsolateral series over shoulders.

The *altamazonica* Group

Four species: *Bolitoglossa altamazonica*, *Bolitoglossa chica*, *Bolitoglossa peruviana*, *Bolitoglossa sima*.

Small size (adult means: 40.3, 39.5, 39.7, 43.0 standard length, respectively); head of moderately narrow width in relation to standard length (standard length 6.2-7.3 times head width); eyes moderate; snout not greatly shortened; low to moderate numbers of maxillary teeth but considerable interspecific variation (adult means: 15, 2, 37, 34, respectively); limbs short (limb interval 2-5); hands and feet flattened, completely or almost completely webbed; variable coloration with solid or mottled dorsal color, usually no banding or spotting dorsally.

The *palmata* Group

Two species: *Bolitoglossa orestes*, *Bolitoglossa palmata*.

Small to moderate size (adult means: 40.0, 47.2 standard length, respectively); head of moderate to moderately narrow width (standard length 6.0-7.1 times head width); eyes very large; snout very noticeably shortened; relatively low to moderate numbers of maxillary teeth (adult means: 20 and 39 respectively); limbs short (limb interval 3-5½); hands and feet characteristic with sharply demarcated, moderately robust digits that are flattened but thickened and rounded at tips, and are joined by thin web extending almost to tips.

The nine remaining species (*adpersa*, *biseriata*, *horburata*, *capitana*, *hypara*, *niceforti*, *pandi*, *savagei*, and *valleculea*) are, for convenience, included in the *adpersa* group.

Bolitoglossa phalarosoma Wake and Brame, 1962

Figure 3

Oedipus platydactylus (part) Dunn, 1926. Salamanders of Family Plethodontidae, p. 440.

Bolitoglossa phalarosoma Wake and Brame, 1962. Contrib. Sci. Los Angeles Co. Mus., 49: 1.

Holotype—BM 97.11.12.22; an adult female from Medellín, 1538 meters (5048 feet), Departamento de Antioquia, Colombia.

Material Examined—BM 97.11.12.21, same data as holotype (paratype); MLaS 6, "Antioquia," Colombia, and holotype.

Diagnosis—A medium-sized species (3 individuals: 46.8, 55.8, 58.2 standard length) with moderate numbers of maxillary teeth (30, 51, 43, respectively) distinguished from all other South American species by its very narrow head (standard length 7.4-8.0 times head width), flattened and completely webbed hands and feet, and distinctive coloration (ground color solid black with a few large white patches in two dorsolateral series along the sides of the head and over the shoulders).

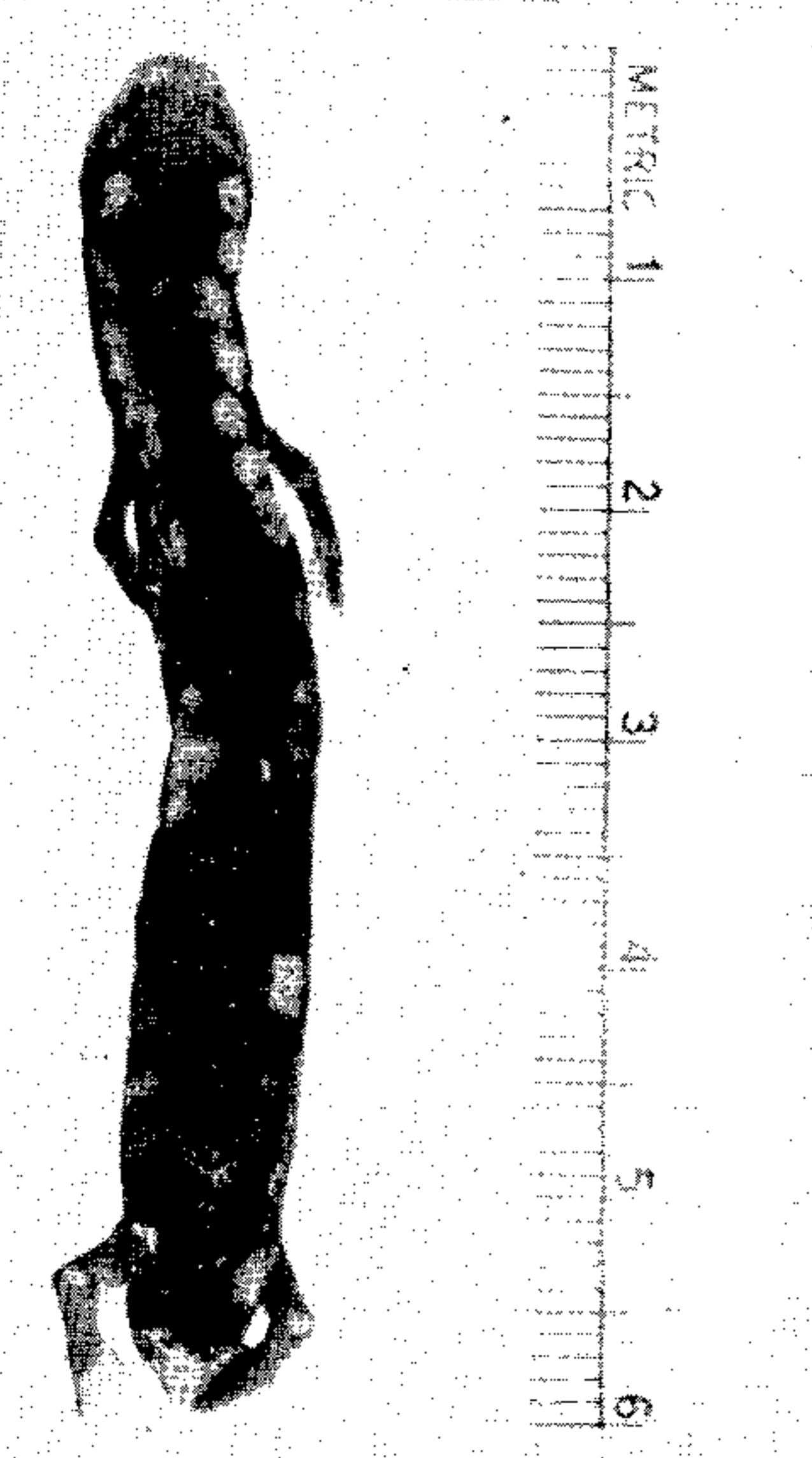


Fig. 3. *Bolitoglossa phalarosoma* BM 97.11.12.22, Medellín, Colombia. Female. Holotype.

Remarks—Detailed information concerning this species is to be found in the original description (Wake and Brame, 1962).

Range—Known only from Departamento de Antioquia, Colombia (Fig. 23).

Bolitoglossa altamazonica (Cope, 1874)

Figures 4 and 20D

Oedipus altamazonicus Cope, 1874. Proc. Acad. Nat. Sci. Philadelphia, 1874: 120.

Oedipus parvius Unterstein, 1930. Zool. Anz., 87: 270.

Plachina estheri Miranda Ribeiro, 1937. O Campo, 8(87): 42-46.

Bolitoglossa altamazonica Taylor, 1944. Univ. Kansas Sci. Bull., 30(1): 219.

Synatypes—ANSP or USNM (3 specimens); now lost or destroyed, from Nauta, Departamento de Tarma, Peru.

Important counts and measurements of the other Colombian specimen (a male) are: premaxillary teeth 2, maxillary teeth 2, vomerine teeth 9, costal grooves 17, limb interval $7\frac{1}{2}$, standard length 47.5, axilla-groin length 31.0, head width 4.4, snout-gular fold length 7.7, tail length 78.1, hind limb length 9.2.

The holotype has more teeth than any of forty other members of the species examined by us. The other Colombian specimen resembles Panamanian *parvipes* in having low numbers of maxillary teeth, an elongate and narrowly tipped snout, and relatively small eyes. The two Colombian specimens are much darker than individuals from the Canal Zone which are light brown dorsally and gray to white ventrally. Dark *parvipes* are known from far western Panamá.

Range—Western Panamá to southwestern Colombia.

Oedipina complex (Dunn, 1924)

Figure 2

Oedipus complex Dunn, 1924. Occ. Papers Boston Soc. Nat. Hist., 5: 94.

Holotype—MCZ 9408; a young male from Las Cascadas, near Gamboa, Canal Zone, Panamá.

Material Examined—Medem field number 641 (to be deposited in USNM), just above sea level near the Penal Colony on Isla Gorgona, 25 miles west of the mainland, Departamento de Cauca, Colombia; BM 1901.3.29.115, Paramba, 800 meters (2500 feet), Provincia de Imbabura, Ecuador.

Diagnosis—A small species (maximum: 45.6 standard length) distinguished from *O. elongatus* by its less robust habitus, presence of maxillary teeth, and less contrasting light and dark coloration; from *O. parvipes* by short and rounded to blunt-tipped snout, large eyes, 13-45 maxillary teeth that extend beyond the internal choanae posteriorly, and 13-32 vomerine teeth arranged either in patches or series; from all *Oedipina* except *elongatus* and *parvipes* by 17 (rarely 18) rather than 19 costal grooves.

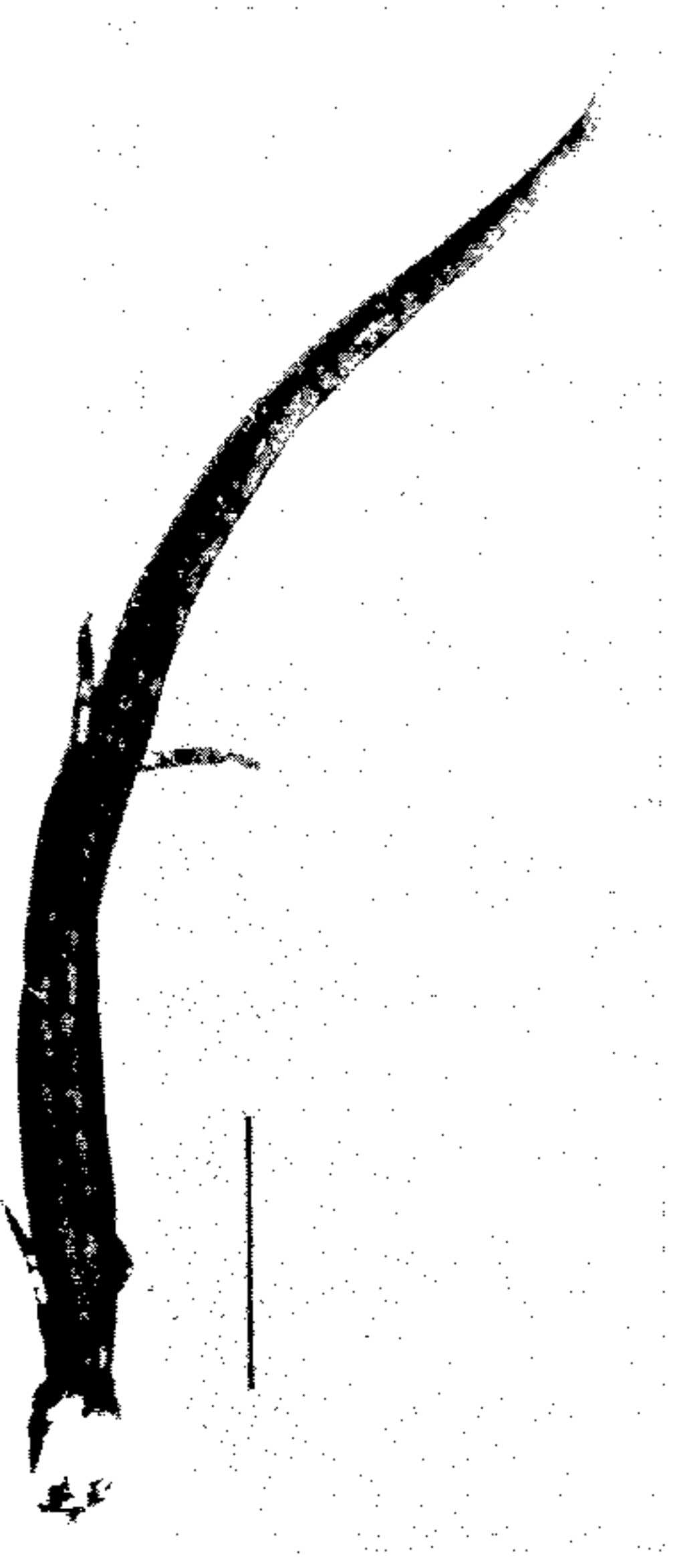


Fig. 2. *Oedipina complex* USNM, Isla Gorgona, Colombia. Female. Line equals 1 cm.

Remarks—The two specimens reported here represent the first records of the species from South America. It is of value, therefore to present the following information concerning them.

Medem 641. Female. Counts and measurements: premaxillary teeth 3, maxillary teeth 13, vomerine teeth 16, costal grooves 18, limb interval $8\frac{1}{2}$, standard length 32.4, axilla-groin length 20.2, head width 3.6, snout-gular fold length 5.4, tail length 33.0, hind limb length 5.9. Coloration: black laterally and gray ventrally with a light brown band dorsally from the neck onto the tail; white blotches on last $\frac{1}{2}$ of tail; head with a large white patch between the eyes and posteriorly onto neck, some white spots on snout; dorsum of proximal portions of fore and hind limbs whitish.

BM 1901.3.29.115. Male. Counts and measurements: no premaxillary teeth, maxillary teeth 17, vomerine teeth 32, costal grooves 17, limb interval 9, standard length 45.6, axilla-groin length 29.3, head width 4.9, snout-gular fold length 7.5, tail length 79.2, hind limb length 8.2. Coloration: dark brown dorsally and laterally, gray-brown ventrally; head with large white patch from anterior edge of eyes to level of gular fold, white coloration on snout; dorsum of proximal portions of fore and hind limbs whitish.

The Ecuadorian specimen (BM 1901.3.29.115) was examined by Dunn (1926) who called it *parvipes*. We think the specimen is a very large *complex* based on the following points: 1) The snout is somewhat intermediate between the pointed snout of typical *parvipes* and the blunt snout of typical *complex*. It resembles *complex* more than *parvipes*, however. 2) Although the holotype of *parvipes* has more maxillary teeth (19) than this individual (17), these numbers are more typical of *complex* than of *parvipes*. 3) The number of vomerine teeth (32) is higher than the highest number we have seen in either *complex* (28) or *parvipes* (19), but is closer to the number normally found in *complex*. 4) The vomerine teeth are in a patch. Patched vomerine teeth are occasionally found in large *complex*, but the teeth are in single rows in all *parvipes*. 5) It is larger (by 2.5 mm. standard length) than the largest *complex* but well within the known size range of *parvipes*. 6) The foot is less syndactylous than that of *parvipes* and is shorter with broader digits. The foot closely resembles that of *complex* but is proportionately larger. 7) Both *complex* and *parvipes* in South America have similar coloration consisting of a dark ground color with a large whitish patch on the head and often some scattered whitish coloration on the tail.

The Colombian specimen closely resembles Panamanian *complex* in all features, but has one more costal groove than is normally found. This specimen and a single individual of *Bolitoglossa biserialis* also collected on Isla Gorgona are the only insular records of salamanders south of Isla Tigre, an island close to the mainland in the Golfo de Fonseca, Provincia de Valle, Honduras.

Range—Western Panama thru western Colombia to northern Ecuador.

Brame and Wake (1962b) reexamined the type of *palnata* and concluded that it was a species distinct from *altamazonica*. Finally, Wake and Brame (1963) demonstrated the invalidity of the genus *Magnadigitia* and assigned all nominal members of that genus to *Bolitoglossa*. At the present time two genera, *Bolitoglossa* and *Oedipina*, are recognized in South America.

In 1875, Jiménez de la Espada described *Urotripsis platensis* from a single specimen that he believed had been collected near Montevideo, Uruguay. The species was shown to be a member of the genus *Ensatina* by Dunn (1923) and has been discussed by Myers and Carvalho (1945) and by Stebbins (1949). It is now generally accepted that *platensis* was based on California salamanders that somehow reached Spain by way of Uruguay.

MATERIALS AND METHODS

Materials for the present study have been obtained from the major collections of the world, and number 671 specimens. All material was thoroughly examined and measurements were taken in the following manner, unless otherwise stated. Standard length is measured from the tip of the snout to the posterior edge of the vent. Head width is measured at the broadest point. Snout-gular fold distance is measured from the tip of the snout to the gular fold on the mid line. Limb length is measured from the axilla or groin to the tip of the longest digit of the straightened limb. All measurements were made by the senior author with the same vernier calipers and are in millimeters. Limb length is expressed in terms of limb interval units. Limb interval refers to the number of costal folds between the tips of the longest digits of the fore and hind limbs when the limbs are appressed to the sides of the trunk. All maxillary, premaxillary, and vomerine teeth have been counted and counts are based on totals of ankylosed teeth per individual. Dentary teeth have not been counted because the specimen must be mutilated in order to obtain accurate counts, and because numbers of dentary teeth have not proved to be taxonomically significant in *Bolitoglossa*. The parapsphenoid tooth patch has not been counted for the same reasons. Data is presented in the following manner: measurement (number of adults examined: smallest adult—mean—largest adult); teeth (number of adults examined: lowest number—mean—highest number). Color descriptions are based on alcoholic material, unless otherwise stated.

Museum numbers of all material examined are presented under each species. Certain species occur in Central as well as South America; only specimens from South America are listed under material examined, but the range of each species is clearly stated.

GENUS *OEDIPINA*

SPECIES ACCOUNT

Two closely related species of *Oedipina* occur in South America. Both are known also from southern Central America. Only four individuals of the genus have been collected from Colombia and Ecuador (Fig. 11)

Oedipina parvipes (Peters, 1879)

Figure 1

Speleperes (*Oedipus*) *parvipes* Peters, 1879. Monatsb. Königl. Preufs. Akad. Wissensch., Berlin, 1879: 778.

Holotype—ZMB 9518; from Laceres (Cáceres), Cenia (on the Cauca River), Departamento de Antioquia, Colombia.

Material Examined—BM 1914.5.21.90, Peña Lisa, Condoto, Departamento de Chocó, Colombia; and holotype.

Diagnosis—A medium sized species (maximum: 57.7 standard length) distinguished from *O. elongatus* by its less robust habitus and less contrasting light and dark coloration; from *O. complex* by its long and pointed snout, small eyes, 0-19 maxillary teeth that do not extend past the internal nares posteriorly, and 9-19 vomerine teeth arranged in series and never patched; from all species of *Oedipina* except *elongatus* and *complex* by 17 rather than 19 costal grooves.



Fig. 1. *Oedipina parvipes* BM 1914.5.21.90, Peña Lisa, Colombia. Male. 1 line equals 1 cm.

Remarks.—No information concerning the holotype has been available since the original description. Brame recently examined the holotype and it is worthwhile to present the following data. Counts and measurements: premaxillary teeth 2, maxillary teeth 19, vomerine teeth 15, costal grooves 17, limb interval 8½, standard length 40.4, axilla-groin length 27.9, head width 3.9, snout-gular fold length 6.3, tail length 48.7, hind limb length 7.3. Maxillary teeth do not extend past the level of the internal choanae. The holotype is in poor condition and head shape and eye size are impossible to determine due to desiccation. Dunn (1926) translated the color description by Peters (1879) as follows: "black, upper side of head mainly white, gular fold white, sides of belly and tail sprinkled with white; on the upper arm, on the elbow, and on the base of the thigh, a white spot."

ran, United States National Museum (USNM); James E. Böhlke, Academy of Natural Sciences of Philadelphia (ANSP); Ernest E. Williams, Museum of Comparative Zoology, Harvard College (MCZ); Robert G. Crippen, Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); Heinz Werdmuth, formerly of the Zoologisches Museum, Berlin (ZMB); Alice G. C. Grandison and J. C. Battersby, British Museum (Natural History) (BM); K. Klemmer, Senckenberg Museum, Frankfurt am Main (SM); Jean Guibé, Muséum National de l'histoire Naturelle, Paris (MNHP); Neil T. Richmond, Carnegie Museum, Pittsburgh (CM); Charles M. Bogert and Richard G. Zweifel, American Museum of Natural History (AMNH); John M. Legler, University of Utah (UU); Lothar Forcart, Naturhistorisches Museum, Basel (NMB); Werner Ladiges, Zoologisches Staatsinstitut und Zoologisches Museum, Hamburg (ZSZMH); Josef Eiselt, Naturhistorisches Museum, Wien (NMW); L. D. Brongersma, Rijksmuseum van Natuurlijke Historie, Leiden (RNHL); and James A. Peters, San Fernando Valley State College (JAP). The fine series of living *Bolitoglossa adspersa* supplied by Fred Medem and Jorge Hernández C. of the Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá (ICNB), were of great use. We especially thank Fred Medem (ICNB), Hermanno Nicéforo María of the Instituto de La Salle, Bogotá (MLaS), and Gustavo Orcés V. of the Escuela Politécnica Nacional, Quito (EPN) for enabling us to borrow and examine important specimens from Colombia and Ecuador, and M. A. Carriker, Jr. of Bucaramanga, Colombia for information concerning Colombian localities. The abbreviation MNRJ is for the Museu Nacional, Rio de Janeiro, and MP is for the Museu Goeldi, Pará. The four drawings were made by Pamela L. Immel of the Los Angeles County Museum (LACM) and the photographs were taken by the staff photographer, Armando Solís (LACM). Both did excellent work despite the lack of uniformly preserved material. Robert J. Lavenberg also assisted with illustrations. The key to the South American salamanders was checked by Arnold G. Kluge and Norman J. Scott, Jr., and portions of the manuscript were read by Kluge and Roy W. McDiarmid. We are grateful to Jay M. Savage (USC) for his encouragement and for reading and critically appraising the completed manuscript. The study of southern Central and South American salamanders was initiated by the senior author while studying in Costa Rica under the sponsorship of the National Science Foundation (G-6089). The junior author gratefully acknowledges support received from the National Science Foundation in the form of Cooperative Graduate Fellowships.

HISTORICAL REVIEW

Fifteen names have been proposed for South American salamanders. In the following list are indicated authors, dates, and type localities for all names based on South American material, and Panamanian forms found later to occur in South America.

Speleperes adspersus Peters, 1863; Bogotá (Departamento de Cundinamarca), Colombia

- Oedipus altamazonicus* Cope, 1874, Nauta (Departamento de Loreto), Peru
- Speleperes (Oedipus) parvipes* Peters, 1879; Laceros (Cáceres?), (Departamento de Antioquia), Colombia
- Speleperes peruvianus* Boulenger, 1883; Moyabamba (Departamento de San Martín), Peru
- Speleperes palmatus* Werner, 1897; Cordillera, Ecuador
- Geotriton andicola* Posada Arango, 1909; Colombia
- Speleperes sinus* Vaillant, 1911; Ecuador
- Oedipus complex* Dunn, 1924; Las Cascadas, near Gamboa, Canal Zone, Panama
- Oedipus paraensis* Unterstein, 1930; Pará (Estado do Pará), Brazil
- Eladinea estheri* Miranda Ribeiro, 1937; Belém (Estado do Pará), Brazil
- Bolitoglossa borburata* Trapido, 1942; Río Borburata, Estado de Carabobo, Venezuela
- Bolitoglossa phalarosoma* Wake and Brane, 1962; Medellín, Departamento de Antioquia, Colombia
- Magnadigitia hypactra* Brane and Wake, 1962; Páramo Frontino, Departamento de Antioquia, Colombia
- Bolitoglossa biseriata* Tanner, 1962; Río Tuira at mouth of Paya tributary, Provincia de Darén, Panamá
- Bolitoglossa oresies* Brane and Wake, 1962; Culata, Estado de Mérida, Venezuela
- At the time of Dunn's monograph of the Plethodontidae (1926), the latest review of the South American forms, seven species had been described from South America. Dunn synonymized *peruvianus*, *palmatus*, and *sinus* with *altamazonicus*, and *andicola* with *adspersus*. He placed all recognized species (*adspersus*, *altamazonicus*, and *parvipes*) in the genus *Oedipus*.
- Upon re-examination of the holotype of *peruvianus* and comparison with other Amazonian species, Parker (1939) concluded that *peruvianus* and *altamazonicus* were distinct species, and in the same paper he suggested that *Eladinea estheri* was a synonym of *altamazonicus*.
- Taylor (1944) reviewed the generic status of Central and South American salamanders and referred *adspersa* to the genus *Magnadigitia* (with a query), *parvipes* to the genus *Oedipina*, *borburata* to *Bolitoglossa*, and tentatively placed *altamazonica*, *peruviana*, and *paraensis* in *Bolitoglossa*. Taylor considered the validity of the genus *Eladinea* to be in question.
- In 1944, Dunn, on the basis of newly collected material, removed *andicola* from the synonymy of *adspersa*, but placed both in the preoccupied genus *Oedipus*.
- Myers and Carvalho (1945) pointed out similarities between *estheri*, *altamazonica*, and *paraensis*, but stated that certain identification of *estheri*, even to genus, was premature.
- Wake and Brane (1962) showed that *andicola* was a synonym of *adspersa*.

THE SALAMANDERS OF SOUTH AMERICA

By ARDEN H. BRAME, JR.¹

and

DAVID B. WAKE²

ABSTRACT: A resumé of all previous work on South American salamanders, including an historical taxonomic survey, is given. All recognizable taxa are described or redescribed. Two genera (*Bolitoglossa* and *Oedipina*) and 18 species of plethodontid salamanders occur in South America. *Bolitoglossa sima*, previously synonymized with *B. altamazonica*, is recognized, and *Oedipus parvus* is shown to be a synonym of *B. altamazonica*. Six new forms are described, five from Colombia (*Bolitoglossa pombi*, *B. capitata*, and *B. nicefori* from the Cordillera Oriental; *B. valleculla* from the Cordillera Central; and *B. savagai* from the Sierra Santa Marta) and one from Ecuador (*Bolitoglossa chica* from the 1,000 foot level northwest of Quito, Ecuador). Evolutionary relationships are discussed and a hypothesis concerning the origin of Latin American salamander genera of the family Plethodontidae is presented with special emphasis upon the entry into South America.

INTRODUCTION

South American salamanders are the classical exception to the idea that salamanders are an exclusively north-temperate group, for only in the neotropics do they penetrate south of the equator. Biologists have always been intrigued with organisms living under novel or unusual conditions, or in unexpected regions, and it is surprising that South American salamanders virtually have been ignored for so long. When we initiated this study we were under the impression, along with most herpetologists, that the South American salamander fauna was small and insignificant. As we began to accumulate the widely scattered preserved material we discovered that the fauna, to the contrary, was varied and of considerable systematic and biogeographic importance. We have had the unique opportunity of examining and directly comparing virtually all specimens collected from the South American continent, and can now present a comprehensive review of the South American salamander fauna, its evolutionary relationships, and its origins.

ACKNOWLEDGMENTS AND ABBREVIATIONS

We appreciate the loan of materials and assistance in other ways from the following persons and institutions: Norman E. Hartweg and Charles F. Walker, University of Michigan Museum of Zoology (UMMZ); Robert F. Inger and Hymen Marx, Chicago Natural History Museum (CNHM); Doris M. Coch-

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