

**NEW GENERA AND A NEW SPECIES OF  
CENTRAL AMERICAN SALAMANDERS, WITH A REVIEW  
OF THE TROPICAL GENERA  
(AMPHIBIA, CAUDATA, PLETHODONTIDAE)**

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**ABSTRACT.** A new genus and species of plethodontid bolitoglossine salamander is described from material collected in northwestern Guatemala. *Bradytriton silus* new genus, new species, is unique in a combination of structural characteristics that includes a laterally compressed tail, stocky body with no clearly defined neck, and short, slender limbs bearing syndactylous hands and feet. To diagnose the new genus, an analysis of the entire neotropical assemblage of plethodontid salamanders was undertaken. Approximately 138 species belong to the supergenus *Bolitoglossa* and 11 genera are recognized. The genus *Chiropterotriton* is shown to be polyphyletic; thus, two new genera are described. *Nototriton* new genus, includes the *picadoi* group of *Chiropterotriton* beta. *Dendrotriton* new genus, includes the *bromeliacia* group of *Chiropterotriton* beta. Those species formerly called *Chiropterotriton* alpha remain as the sole representatives of the genus. Eight of the eleven neotropical genera are shown to be monophyletic. Of the three exceptional genera, both *Dendrotriton* and *Nototriton* are nonparaphyletic relative to all genera except *Oedipina*, but *Dendrotriton* is easily distinguished from *Oedipina*. *Nototriton* may be paraphyletic relative to *Oedipina*, but the two genera can be readily distinguished on the basis of major differences in ecology and shape. *Pseudoeurycea* comprises morphologically generalized species that may not be far removed from the morphology of the ancestral stock of the entire neotropical group. Only *Nyctanolis* and *Chiropterotriton* are more plesiomorphic than *Pseudoeurycea*. Lists of species assigned to the genera are provided. Potential relationships within the supergenus *Bolitoglossa* are discussed, but parallelism and convergence have been so extensive that no definitive statement concerning generic affinities is possible.

**RESUMEN.** Un nuevo género y especie de salamandra plethodóntida bolitoglossina se describe en base a material recolectado en el noroeste de Guatemala. *Bradytriton silus*, nuevo género, nueva especie, es peculiar por su combinación de caracteres que incluye una cola comprimida lateralmente, un cuerpo macizo con cuello escasamente definido, y patas delgadas y cortas provistas de manos y pies syndáctilos. Para diagnosticar este nuevo género se realizó un análisis del grupo completo de salamandras plethodóntidas neotropicales. Las aproximadamente 138 especies pertenecen al supergénero *Bolitoglossa*, en el cual se reconocen 11 géneros. El género

*Chiropterotriton* se señala como polifilético y por lo tanto dos nuevos géneros se describen. *Nototriton*, nuevo género, incluye el grupo *picadoi* de *Chiropterotriton* beta. *Dendrotriton*, nuevo género, incluye el grupo *bromeliacia* de *Chiropterotriton* beta. Las especies previamente incluídas en *Chiropterotriton* alfa permanecen como las únicas representantes de este género. Ocho de los once géneros neotropicales se señalan como monofiléticos. De los tres géneros restantes, tanto *Dendrotriton* como *Nototriton* son monofiléticos en relación a todos los géneros excepto *Oedipina*, aunque *Dendrotriton* es fácilmente distinguible de *Oedipina*. *Nototriton* podría ser parafilético en relación a *Oedipina*, pero estos dos géneros pueden ser rápidamente reconocidos en base a sus marcadas diferencias en ecología y forma corporal. *Pseudoeurycea* comprende especies morfológicamente generalizadas que podrían estar no muy alejadas de la morfología del grupo ancestral del ensamble neotropical analizado. Sólo *Nyctanolis* y *Chiropterotriton* son más plesiomórficos que *Pseudoeurycea*. Listas de las especies asignadas a cada género se presentan. También se discuten las potenciales relaciones dentro del supergénero *Bolitoglossa*, pero paralelismos y convergencias han sido tan prevalentes que ninguna opinión definitiva puede plantearse en cuanto a afinidades genéricas.

### INTRODUCTION

In the summer of 1974, the junior author collected several species of salamanders in a remote area in northwestern Guatemala. Included in this collection were three species that obviously were undescribed. Subsequent morphological analysis showed that two of the new species have combinations of traits that require them to be placed into two new genera. One of these (*Nyctanolis*) has been described elsewhere (Elias and Wake, 1983). In this paper we describe the second new genus. We also report the results of a detailed

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analysis of all of the currently recognized genera of tropical salamanders. As a result of this analysis, which was a necessary background for the description of the new genera and species, two additional new genera are erected. These are described herein, and diagnostic characters are given for all existing genera of tropical salamanders. In addition, all recognized species of tropical salamanders are referred to a genus, and relationships among the genera are examined. This analysis reinforces previous views (Wake, 1966; Wake and Lynch, 1976) that there has been very extensive parallelism and convergence during the adaptive radiation of plethodontid salamanders in the New World tropics.

## BACKGROUND

Although several genera of New World tropical salamander species were described in the nineteenth century, and some knowledge of the diversity of the group was available at that time, the most authoritative taxonomic work on these salamanders during the early part of the twentieth century (Dunn, 1926) placed all tropical species in a single plethodontid genus, *Oedipus*. Dunn considered *Oedipus* to be "a large, modern genus of some 30 species. The extremes are quite different but there are many connecting links." There was little increase in knowledge of tropical salamanders until the mid-1930's, when Schmidt, Taylor, and other workers began publishing their results (for historical summary, see Wake, 1972, and Smith and Smith, 1976). Taylor (1940) showed that *Oedipus* was a preoccupied name, and substituted the old name *Bolitoglossa* for the entire assemblage, except for a group of diminutive species, which he placed in Cope's (1869) old genus *Thorius*. Shortly thereafter, Taylor (1944) undertook a radical revision of all the neotropical salamanders, in which he described four new genera (*Chiropterotriton*, *Parvimolge*, *Magnadigita*, *Pseudoeurycea*), resurrected *Oedipina* and *Haptoglossa*, and continued to recognize *Bolitoglossa* and *Thorius*. Since that time, there has been relative stability in the generic classification of the group. *Lineatriton* was established by Tanner (1950), *Magnadigita* was placed in the synonymy of *Bolitoglossa* by Wake and Brame (1963), and *Haptoglossa* was placed in the synonymy of *Oedipina* by Brame (1968). The entire assemblage was characterized and the genera defined by Wake (1966), who established the supergenus *Bolitoglossa* for this group. This supergenus, and the supergenera *Hydromantes* and *Batrachoseps*, were included in the tribe Bolitoglossini, subfamily Plethodontinae, of the family Plethodontidae. Many species have been discovered since 1926; herein, we recognize 138.

The most recent comprehensive treatment of the supergenus *Bolitoglossa* (Wake and Lynch, 1976) dealt mainly with ecology, distribution, and biogeography and offered little new morphological or taxonomic analysis. Since the publication of that paper, major new discoveries have been made; here, we attempt to give phylogenetic perspective to the available information.

The present effort is not definitive, for continued new discoveries indicate that our knowledge of the group, even at the generic level, remains incomplete. We are aware of many

undescribed species, and a number of described species—including some crucially important ones—are known from only one or a very few individuals. Nevertheless, we believe that the broad outlines of relationship are sufficiently clear to justify the substantial revision we undertake here.

## MATERIALS AND METHODS

We have not considered in detail the species of *Bolitoglossa*, *Oedipina*, and *Thorius*, all large, monophyletic genera, which are either under intense study presently (*Bolitoglossa* by D.B. Wake, P. Alberch, A. Larson, and colleagues, *Thorius* by J. Hanken), or have been analyzed recently (*Oedipina* by Brame, 1968). Instead, we have emphasized apparently polyphyletic and paraphyletic groups, as well as newly discovered species that do not easily fit into any existing genus. In these critical cases, we have analyzed doubly cleared and stained specimens, histological sections, and dissections of fixed material. As a point of departure for the choice and analysis of characters, we have relied on the literature, which will be cited where appropriate.

We have had access to adequate samples of most of the species. Important species for which we have lacked sufficient material but nevertheless can offer useful information include (present generic designation used): *Chiropterotriton barbouri*, *C. richardi*, and *Parvimolge praecellens*. These are discussed in appropriate places in the following account.

As noted above, one of the new genera has recently been described (Elias and Wake, 1983). We begin this work with an account of the characters that are used in our generic revision. We then describe a newly discovered genus and species and erect two new generic names to encompass previously known species. Finally, we present a preliminary phylogenetic analysis.

## CHARACTERS USED FOR ANALYSIS

A necessary first step in the process of phylogenetic reconstruction is the identification of monophyletic taxa (*sensu* Eldredge and Cracraft, 1980). Our goal is to deduce monophyletic groups from a matrix of morphological character states. There are incomplete data for too many species to justify an extensive analysis at the species level. Accordingly, we have relied on the literature and our own previous work to recognize groups of species. We have treated these groups as hypotheses and have investigated whether or not each is a monophyletic taxon. A group that is found to be monophyletic is then treated as a genus. We believe that the generic level of classification should combine species into monophyletic units that are separated from other such units by morphological gaps. Ideally, the gaps will coincide with ecological and behavioral differences as well. Thus, our objective is to define generic-level units that are meaningful in both phylogenetic and ecological terms.

In the analysis that follows, each genus is scored for eighteen characters (Table 1). In certain genera, there is some variation in these characters among, or even within, species. Only if a derived condition is characteristic of every known population and species (i.e., only if it appears in most adults)



is the genus as a whole scored as derived. Thus, our character scoring should reflect the most primitive common denominator for each genus discussed and should represent the situation in the common ancestor of the included species. The disadvantage of this conservative approach is that it masks a certain amount of parallelism.

The characters used in our analysis are described below. All of the characters are treated as two-state characters, with primitive (plesiomorphic) and derived (apomorphic) states identified on the basis of outgroup analysis (Eldredge and Cracraft, 1980). Our outgroups are the genera *Hydromantes* and *Batrachoseps*, the other members of the tribe Bolitoglossini; and the members of the tribe Plethodontini. Most of the osteological characters have already been discussed in detail by Wake (1966) and Lynch and Wake (1978). By convention, we code the characters (0) to indicate primitive and (1) to indicate derived states.

1. *Mesopodial mineralization*. Mesopodials are cartilaginous throughout life (0) or are mineralized in adults (1).

2. *Tibial spur*. A well-developed rodlike structure, free from the shank of the bone, is present proximally (0) or is absent or reduced to a low ridge (1).

3. *Carpal fusion*. The ulnare and intermedium are discrete (0) or fused (1).

4. *Tarsal fusion*. Distal tarsals four and five are discrete (0) or fused (1).

5. *Mental glands*. Clusters of individual glands form a small patch located near the tip of the chin in male tropical salamanders (Truffelli, 1954). The patch is either externally visible, and ovoid, circular, or subtriangular, with rounded or low columnar individual internal glands (0), or is externally obscure, with long, tubular individual internal glands that are oriented posteriorly from their openings near the chin (1). The tubular glands extend posteriorly as twisted tubes covered by the skin of the gular area.

6. *Stylus of operculum*. The stylus, or columella, is not well developed in any of the tropical species, but it may be present, with a distinct rodlike shape (0) or reduced to a broad bulge or be entirely absent (1).

7. *Preorbital processes of vomers*. These slender processes, which may or may not bear teeth, are either present between the internal nares and the orbit (0) or absent (1).

8. *Prefrontal bones*. These bones are either present in varying degrees of development (0) or absent (1).

9. *Septomaxillary bones*. These bones are not well developed in any tropical salamanders, but small ossicles may be present (0) or absent (1).

10. *Frontal processes of premaxillary bone*. Where only a single premaxillary bone is present, the frontal processes are either fused together at the point of origin on the dorsal surface of the pars dentalis and for some distance dorsoposteriorly (1) or separated for their entire length (0). We score those few instances in which the processes arise separately and subsequently fuse as 0.

11. *Premaxillary bones*. The pars dentalis of plethodontid salamanders is either divided (0) or fused so that only a single bone is present (1).

12. *Skull roof*. The parietal bones may either meet or ap-

proach each other very closely on the midline, thus forming a complete skull roof (0), or be widely separated and joined by a connective tissue sheet, thus forming an incomplete skull roof (1).

13. *Sublingual fold*. A small to large fold of glandular skin underlying the tongue may be present (0) or absent (1).

14. *Limb length*. Limbs are moderate to short in length, so that they overlap slightly or not at all when adpressed (0), or are very long, so that they overlap by more than two costal interspaces (1).

15. *Tarsal arrangement*. Distal tarsal four is discrete from and larger than distal tarsal five and articulates with the fibulare (0), or distal tarsal five is discrete from and larger than four and articulates with the centrale (1). When distal tarsals four and five are fused, the character is scored as 0.

16. *Trunk vertebral shape*. The ratio of centrum length to posterior centrum diameter is low (2.5–4), and the vertebrae are relatively wide and short (0), or the ratio is high (greater than 4), and the vertebrae are relatively narrow and elongate (1).

17. *Number of trunk vertebrae*. There are either 14 (0) or 18 or more (1).

18. *Tail shape*. The tail is either round or ovoid in cross section (0) or strongly compressed laterally, with a dorsal, glandular ridge (1).

The eighteen characters are listed in Table 1, along with the states that characterize each of the 11 genera we recognize in this paper. This table alone can be used to diagnose all of the genera. In most instances the genera are diagnosed by autapomorphies (derived characters unique to a given taxon), combinations of synapomorphies (derived characters shared by two or more taxa), or both. In some instances, determination that a given genus is monophyletic requires an analysis of the distribution of character states over all taxa; such cases are detailed in the Discussion. All 11 genera can be readily diagnosed on the basis of unique combinations of traits, including both apomorphic and plesiomorphic states. *Bolitoglossa* probably should be divided into at least two taxa (Wake and Lynch, 1976), but it is a well-defined (if unwieldy), monophyletic taxon as currently recognized. However, our generic concept does require that we recognize four new generic taxa. One of these, *Nyctanolis*, is a recently discovered monotypic genus that has been described elsewhere (Elias and Wake, 1983). A second newly discovered genus, also monotypic, is described immediately below. The other two new genera result from subdivision of an existing genus and are described below in the context of our generic diagnoses.

## DESCRIPTION OF A NEW GENUS AND SPECIES

### *Bradytriton* new genus

**TYPE SPECIES.** *Bradytriton silus* new species.

**DIAGNOSIS.** A plethodontid salamander belonging to the subfamily Plethodontinae, tribe Bolitoglossini, supergenus *Bolitoglossa*. *Bradytriton* is a short-snouted, stout-bodied, short-tailed taxon with small limbs and diminutive, syn-



**Table 1.** Distribution of character states in genera of neotropical plethodontid salamanders. See text for listing of characters. 0 = primitive state; 1 = derived state.

Genus	Character																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>Bolitoglossa</i>	0	0	0	1	0	1	0	0	1	0	1	0	1	0	0	0	0	0
<i>Bradytriton</i>	0	0	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1
<i>Chiropterotriton</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0
<i>Dendrotriton</i>	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
<i>Lineatriton</i>	1	0	0	1	0	0	0	0	1	1	1	0	0	0	0	1	0	0
<i>Nototriton</i>	0	0	1	1	0	1	0	0	1	1	1	0	0	0	0	0	0	0
<i>Nyctanolis</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
<i>Parvimolge</i>	1	0	1	1	1	1	1	0	1	0	1	0	0	0	0	0	0	0
<i>Pseudoeurycea</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Oedipina</i>	0	1	1	1	1	1	0	1	1	1	1	0	0	0	0	0	1	0
<i>Thorius</i>	1	0	1	1	0	1	1	0	1	0	1	1	0	0	0	0	0	0

dactylous hands and feet, readily distinguished from most other members of the supergenus on the basis of those features. It differs from all other members of the supergenus in having a laterally compressed tail with a relatively massive dorsal glandular ridge. *Thorius* and *Parvimolge* have short limbs, but these genera are much smaller and differ in other ways as well: *Thorius* has an incomplete brain case, and both genera frequently have mineralized mesopodial and hyobranchial ossifications as adults. *Nototriton* and *Dendrotriton* have long, slender tails. All *Bolitoglossa* lack sublingual folds. Most *Pseudoeurycea* have long tails and long limbs, and all lack the mesopodial fusions (ulnare-intermedium in manus; fourth and fifth distal tarsal in pes) that characterize *Bradytriton*.

**ETYMOLOGY.** From *bradys*, Gr., referring to the slow and lethargic movements of the living animals, and *triton*, Gr., a commonly used term for salamanders.

### ***Bradytriton silus* new species**

Figures 1 through 6

**HOLOTYPE.** Museum of Vertebrate Zoology (MVZ) 131587, an adult female from Finca Chiblac, 15 km NE Barillas, Depto. Huehuetenango, Guatemala, elevation 1,310 m (4,300 ft), collected by P. Elias, 6 September 1974.

**PARATYPES.** MVZ 131586, LACM 134566, same data as the holotype; MVZ 131589–131594 (6 specimens), same locality and collector as holotype, collected 7 September 1974; MVZ 134635–134637 (3 specimens), El Rayo, elevation 1,370 m (4,500 ft), 3 km S buildings of Finca Chiblac, 10 km NE Barillas, Huehuetenango, Guatemala, collected by J. Jackson and P. Elias on 1 September 1975; MVZ 134638, same locality and collectors as preceding series, collected on 31 August 1975; MVZ 173063, Finca Chiblac, 10 km NE Barillas, Depto. Huehuetenango, Guatemala, elevation 1,370 m (4,500 ft), collected by H.B. Shaffer and P. Elias on 2 July 1977; MVZ 173064, same data as preceding number, collected between August 1975 and October 1977 by J. Jackson and P. Elias.

**DIAGNOSIS** (measurements in millimeters). See Generic Diagnosis. A stout species of moderate size (standard length, SL, in four adult males, 39.1–53.3, mean 45.3; seven adult females 44.5–53.0, mean 49.0; Table 2) with a very stout, short tail (SL/tail length in three adult males is 1.3–1.7, mean 1.4; in six adult females, 1.2–1.7, mean 1.4), short limbs (when adpressed, fore and hind limbs leave 2–3, mean 2.3, costal interspaces uncovered in four adult males; 2.5–3, mean 2.9, in seven adult females), and small, syndactylous hands and feet. The relatively broad head (SL/head width in four adult males is 5.9–6.1, mean 6.1; in seven adult females, 5.7–6.6, mean 6.2) is essentially continuous with the body, and there is no neck. Maxillary teeth (41–50, mean 44.0, in four adult males; 40–59, mean 47.9, in seven adult females) and vomerine teeth (16–22, mean 18.5, in four adult males; 17–25, mean 20.6, in seven adult females) are moderate in number. The species is reddish brown in color, with obscure streaking and flecking of lighter and darker pigments.

**DESCRIPTION.** This stout, short-limbed species has a very short, truncate snout and diminutive hands and feet.

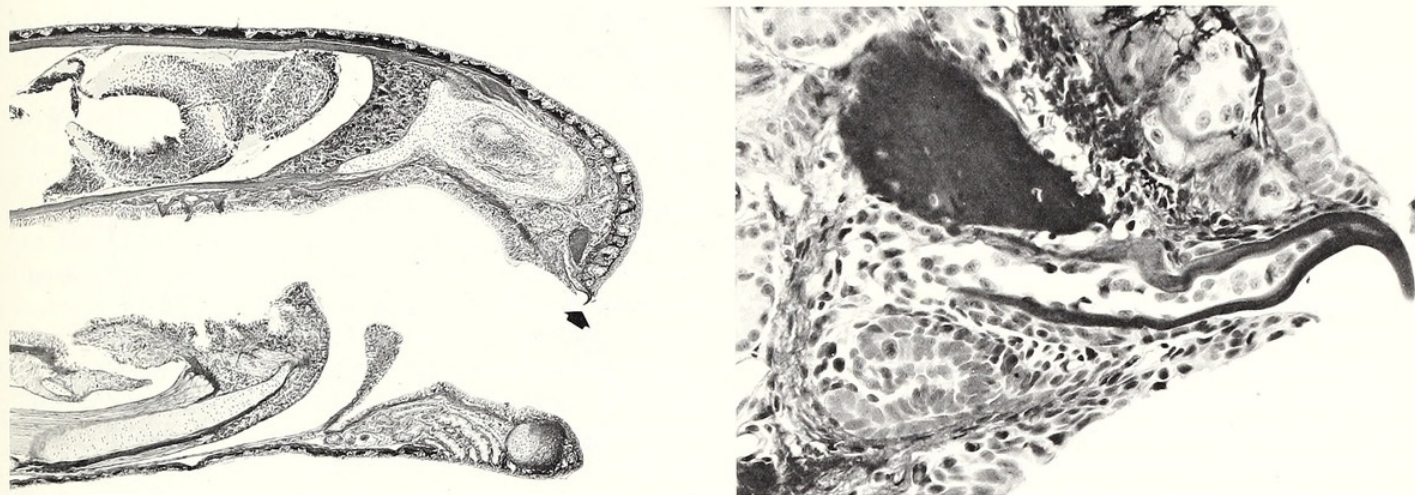


**Figure 1.** Dorsal view of MVZ 131587, the holotype of *Bradytriton silus* new genus and species.



The nostrils are small. Labial protuberances are poorly developed in females, which have an especially short snout, but are large and wide in adult males; the protuberances produce a broad muzzle rather than the elongate snout typical of other tropical salamanders. Mental glands are present in

males but are not externally demarcated; the glands consist of a cluster of moderately long tubules that converge in the region of the mandibular symphysis, where they open individually to the ventral surface of the anterior intermandibular region. The tongue is adetoglossal, with a distinct small pad.



**Figure 2.** Parasagittal section through the head of a specimen (MVZ 134637) of *Bradytriton silus* new genus and species. The section is near the midline and passes through the mandibular symphysis.

Left. The arrow points to an enlarged premaxillary tooth and indicates the part of the section that is magnified in the view on the right. When the mouth is closed, the premaxillary teeth extend outside the mouth and lie near the ventral and anterior parts of the lower jaw, near the openings of the mental gland. The long, tubular ducts of the mental gland are evident immediately posterior to the mandible. Note that no external ventral swelling is present. Also well displayed in this section is the complex free tongue characteristic of the tribe Bolitoglossini. The hyoglossal muscles are attached to the apparently flexible anterior tip of the basibranchial. Immediately anterior to the tongue is the large sublingual fold, characteristic of all of the tropical salamanders except *Bolitoglossa*.

Right. Enlargement of the premaxillary tooth at the end of the arrow in the left part of this figure. The pedicel of the tooth is attached to the posteroventral border of the premaxillary bone (here oriented so that the border appears to be ventral). The crown is relatively large and is unicuspid. The cusp is strongly hooked.

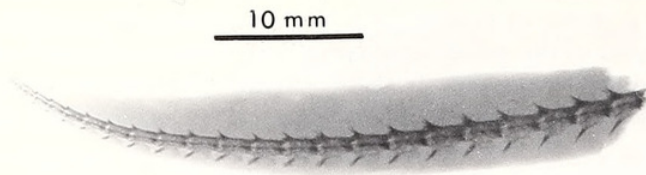
**Table 2.** Data for type series of *Bradytriton silus* new genus and species.\*

	Sex	Standard length	Head length	Head width	Foot width	Hind limb length	Fore limb length	Tail length	Maxillary tooth number	Premaxillary tooth number	Vomerine tooth number	Limb interval
MVZ 131589	♂	53.3	11.3	8.7	3.3	12.1	9.4	—	50	3	17	3.0
MVZ 134636	♂	46.4	10.3	7.6	3.1	11.0	9.5	36.0	41	5	16	2.0
MVZ 134637	♂	42.3	8.8	6.8	2.3	9.6	8.7	31.6	43	6	19	2.0
MVZ 134638	♂	39.1	9.0	6.6	2.3	8.7	8.0	23.2	42	8	22	2.0
MVZ 131591	♀	53.0	10.4	8.7	3.2	10.7	9.5	30.6	59	8	22	3.0
MVZ 131593	♀	51.5	10.3	8.8	2.5	9.2	9.6	—	48	8	20	3.0
MVZ 131586	♀	50.1	9.7	7.8	2.9	11.0	10.1	40.4	46	9	19	3.0
MVZ 134635	♀	48.8	10.1	7.4	2.7	11.0	9.2	34.1	46	9	25	3.0
MVZ 131587**	♀	48.5	9.5	7.5	2.5	9.4	9.5	36.6	52	6	17	3.0
MVZ 131592	♀	46.6	9.7	8.2	2.9	11.0	9.5	34.5	44	10	23	2.5
LACM 134566	♀	44.5	9.3	6.8	2.5	8.6	8.9	33.3	40	9	18	3.0
MVZ 131590	J	35.6	8.1	6.7	2.2	7.5	7.3	21.5	31	8	16	2.5
MVZ 131594	J	34.4	7.8	6.1	1.4	7.2	7.1	22.3	37	8	18	2.0

\* All measurements are in millimeters.

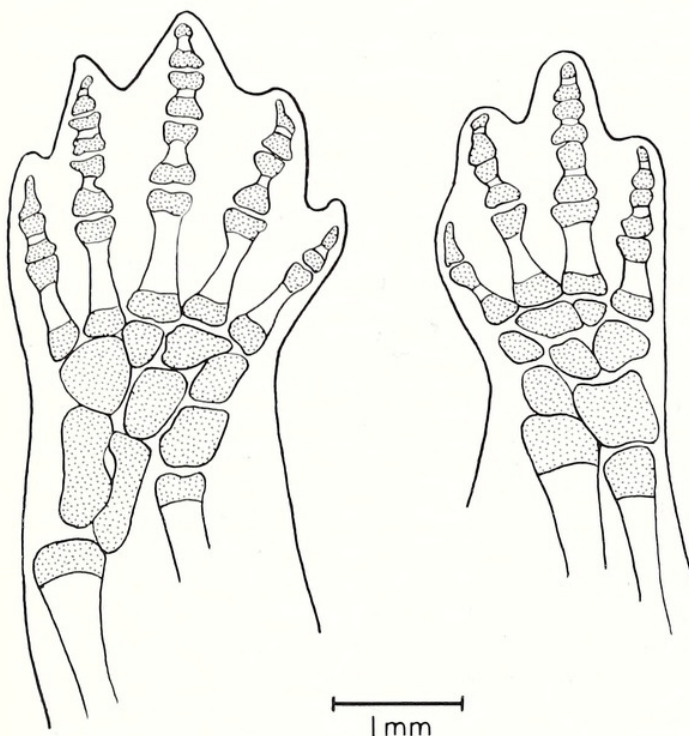
\*\* Holotype.



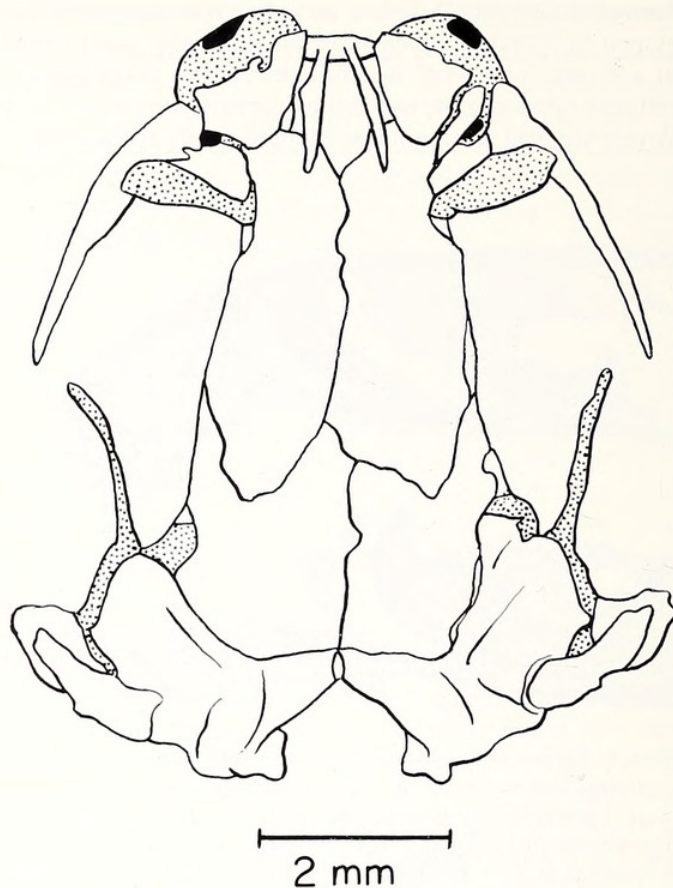


**Figure 3.** Radiograph of the broken tail of a specimen (MVZ 131586) of *Bradytriton silus* new genus and species. Dorsal to the top. Note the large glandular mass above the vertebral column.

The sublingual fold is well developed. The profile of the rounded head is undifferentiated from the trunk, and there is no apparent neck region. A deep unpigmented groove extends beneath the eye, following its curvature, but does not extend to the lip. The eyes are moderate in size and protrude slightly beyond the margin of the jaw. The postorbital groove is an indistinct furrow that extends posteriorly from the eye and intersects a deep vertical groove at right angles. The latter groove passes behind the base of the mandible and becomes a clearly defined nuchal groove. The gular fold is pronounced. Vomerine teeth are few to moderate in number and are arranged in a single, curved row that extends laterally beyond the lateral margin of the internal nares. Maxillary and vomerine teeth increase in number to some extent with increasing body size. The maxillary tooth row extends back to



**Figure 4.** Dorsal views of the left foot (left) and of the right hand (right) of an adult male (MVZ 173064) *Bradytriton silus* new genus and species. Cartilage is stippled. The phalangeal elements are very poorly ossified and are less distinct than illustrated here (see text). Note the syndactylous nature of the digits.



**Figure 5.** Dorsal view of the skull of an adult male (MVZ 173063) *Bradytriton silus* new genus and species. Bone is outlined, and cartilage is stippled. The external nares and the nasolacrimal foramina are black.

a point nearly posterior to the eyeball. Premaxillary teeth are 3–8, mean 5.5, in four adult males, 6–10, mean 8.4, in seven adult females; the teeth of males are very large and hooked and protrude under or through the lip (Fig. 2). The trunk is stout and cylindrical. The tail is of moderate length and is strongly tapered near its tip. It has a marked basal constriction and is strongly compressed laterally. The tail appears stout when viewed laterally but seems narrow from a dorsal perspective (Figs. 1, 3). Postiliac glands are distinct. The limbs are short and slender. Hands and feet are diminutive and syndactylous; the greatest foot width is about  $\frac{1}{5}$  SL and the foot is barely wider than the lower limb. The digital tips are free, but adjacent digits are fused for most of their length (Fig. 4). There are no subdigital pads. The toes, in order of decreasing length, are 3, 2, 4, 5, 1; the fingers, 3, 2, 4, 1.

**MEASUREMENTS OF THE HOLOTYPE** (in millimeters). Head width 7.5; snout to gular fold (head length) 9.2; head depth at posterior angle of jaw 4.6; eyelid width 1.9; anterior rim of orbit to snout 2.0; horizontal orbit diameter 2.4; interorbital distance 2.3; vomerine teeth virtually continuous with parasphenoid tooth patch; snout to fore limb 12.6; distance separating internal nares 1.8; distance separating external nares 1.9; snout projection beyond mandible 0.3; snout to posterior angle of vent (standard length) 48.5;



snout to anterior angle of vent 44.4; axilla to groin 28.1; tail length 36.6; tail width at base 3.4; tail depth at base 4.8; fore limb length (to tip of longest toe) 9.5; hind limb length 9.4; hand width 1.7; foot width 2.5.

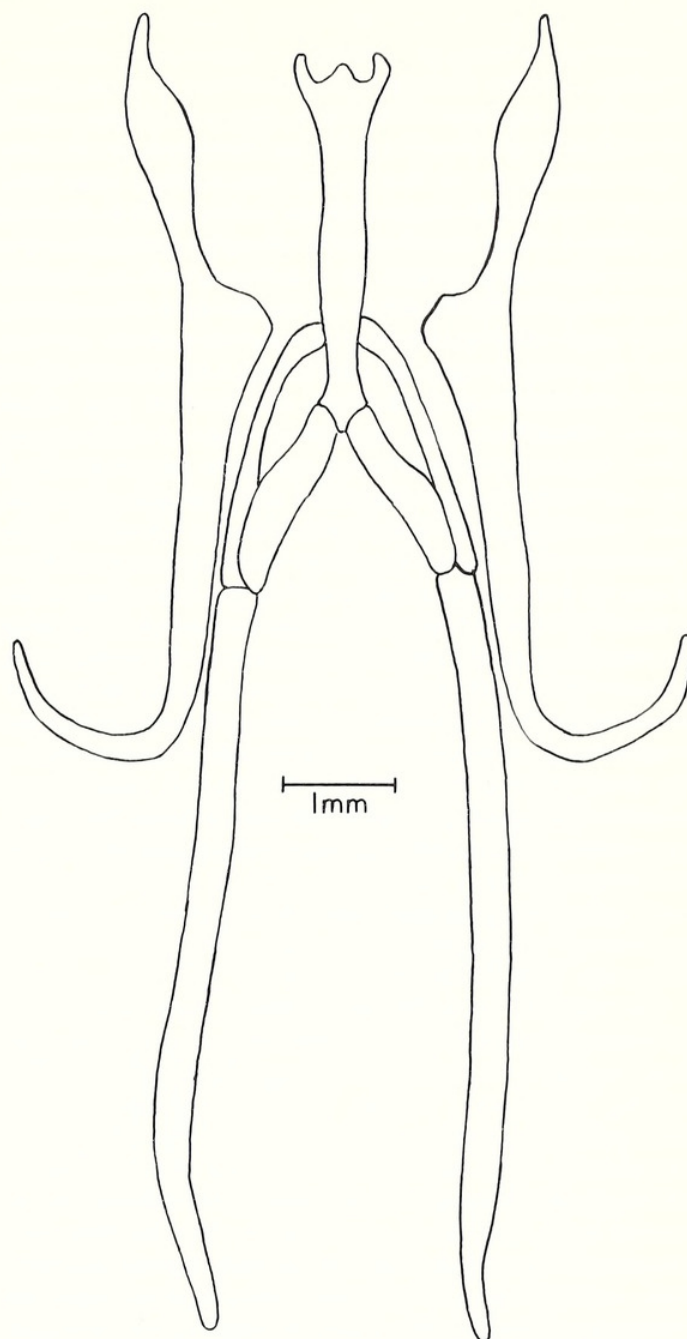
**COLORATION IN LIFE.** The dorsal coloration of this species is reddish brown. This color is broken by irregular flecks of black on the anterior trunk and dominated by black on the head. Brown coloration extends halfway down the lateral surfaces. The cheeks, sides of the tail, and lower flanks are black, overlain with dense white flecks. The legs are brown proximally but grade distally to black with white flecking. The feet are black marked with white flecks dorsally. The eye is chestnut brown.

**COLORATION IN ALCOHOL.** The dorsal surfaces of the head and trunk are dark gray. This color gives way to lighter gray and then to brown on the tail. Black flecks are superimposed on the brown at the tail tip. The arms and legs are dark gray with some light flecks. The lips, chin, throat, and undersides of the legs are dark gray with light gray flecks. The ventral surface of the trunk is unmarked dark gray. The ventral surface of the tail lightens distally to brown interrupted by darker flecks. The palmar surfaces and the tips of the nasal cirri are pale gray.

**HABITAT.** This species lives in an area of very humid cloud forest that received 5 to 6 meters of rainfall annually. All specimens were taken within 2 km of the type locality and were found in direct contact with the substratum under cover objects. Sympatric with *Bradytriton* were three species of *Bolitoglossa*, one species of *Nyctanolis*, various hylid and leptodactylid frogs, lizards of the genera *Anolis*, *Sceloporus*, and *Lepidophyma*, and one member of the snake genus *Lep-todeira* (Elias, in press).

**OSTEOLOGY AND RELATED MORPHOLOGY.** Information has been derived from two cleared and stained male specimens, from radiographs of the entire sample, and from histological sections of the head and neck of one male.

The skull (Fig. 5) is short and very broad. The facial portion of the skull is poorly developed and is little expanded in front of the eyes. The anterior cranial elements are surprisingly weak for a moderate-sized species, and the bones are highly variable in shape, position, and number from one individual to the next, and even from one side to the other in the same individual. The premaxillary is relatively broad and has a large pars dentalis. However, the bone virtually "floats" at the anterior end of the skull; in most individuals, it does not contact the maxillaries, and in some it is separated from those bones by a sizeable gap. Even when a contact exists, the articulation is tenuous. The palatal portions of the premaxillary are greatly reduced or absent and do not contact the anterior extensions of the vomers. The frontal processes arise separately from the pars dentalis and are separated for their whole length. They are very narrow and columnar basally but become markedly compressed vertically to form the lateral margins of the gland-filled internasal fontanelle. The processes are generally divergent for their entire length and become flattened and slightly expanded near their distal tips. These tips overlap the expanded facial portions of the frontals in relatively firm (for this species) articulations. The frontal



**Figure 6.** Dorsal view of the hyobranchial apparatus of an adult male (MVZ 173063) *Bradytriton silus* new genus and species. The entire structure is cartilaginous. The paired ceratohyals ordinarily lie closer together but have been moved somewhat laterally for clarity of illustration.

processes terminate distinctly posterior to the posterior tip of the nasals, a little behind the osseous anterior margin of the orbit. The internasal fontanelle is relatively narrow, except near its posterior terminus. In three adult males the nasals are strongly protuberant, extending well anterior to the jaw outline, but they are only slightly to moderately protuberant (Fig. 5) in the other males. The nasals protrude slightly in two females, including the holotype. Nasals are very irregular in size, shape, and degree of ossification but



tend to be roughly triangular to quadrangular. The posterior tip is poorly defined, and the anterior margin is very irregular. Tiny fragments of disconnected bone frequently occur around the anterior and lateral margins of the nasal. In one cleared and stained individual, one of these fragments is very large and is situated as if it were an entirely separate bone intercalated between the nasal and the prefrontal (Fig. 5). This fragment is only slightly smaller than the prefrontal. The nasals only slightly overlap the anterior parts of the frontals. They have a variable degree of contact with the maxillary facial processes but a very narrow contact with the prefrontals. The posterolateral margin of the nasals may be slightly evacuated for the passage of the nasolacrimal duct, which passes through a shallow but distinct channel in the lateral part of the prefrontal and enters the nasal capsule through a foramen in the anterior margin of the prefrontal. The foramen may form a half-circle in the prefrontal. The prefrontals are about one-third the size of the nasals. Some small, bony fragments are present in some individuals at the anteroventral end of the prefrontals. The prefrontals are relatively long and narrow and are extensively overlapped by the facial processes of the maxillary. The prefrontals overlap the frontals only slightly. The maxillaries are relatively short and straight with narrow, pointed anterior and posterior projections on the dental portion. The posterior tips extend nearly to the posterior margin of each eyeball. Maxillary teeth are bicuspid and moderate in size. They are borne along all but the tip of the dental portion of the maxilla. The relatively well-developed palatal portion of the maxillaries is separated by a strong articulation from the lateral-most part of the vomerine body. There are no septomaxillary bones.

The large, morphologically specialized premaxillary teeth of males are attached to the premaxillary in such a way that their elongate crowns project directly anteriorly and pierce the lip (Fig. 2). Once through the lip, the unicuspid (apparently only the lingual cusp is retained) makes a sharp 90° turn caudad before terminating in a point. When the mouth is closed, the tooth tip is very close to the opening of the mental gland. This gland, which has a restricted exit at the mandibular symphysis, is a cluster of tubules converging to form a small cluster of apertures (Fig. 2). The glands and teeth constitute a functional complex that serves to transfer the glandular secretion to females during courtship in a manner analogous to vaccination (Arnold, 1977). Teeth of similar shape occur in some species of *Pseudoeurycea* (Taylor, 1941).

The large, strong vomers are in limited contact only at their extreme tips, posterior to the large intervomerine fontanelle. A distinct, narrow process at the anterior end of the vomer extends toward the premaxillary but does not touch that bone; rather, it is appressed against the ventral surface of the nasal capsule and follows that structure to curve upwards at its anterior tip. Immediately medial and anterior to the internal naris, the body of the vomer is strengthened by a dorsal bony ridge that is apparently unique among bolitoglossine salamanders. The large, stout, but relatively short, preorbital process falls far short of the lateral margin of the vomerine body. The process is blunt tipped, and it has a dorsal dimension that is very unusual in that it seems to

become continuous with the antorbital cartilage. The vomerine teeth are borne in a single curving row along the base of the vomer body and nearly to the tip of the preorbital process. The bicuspid teeth are about the size of the maxillary teeth.

Frontals are well developed and articulate firmly with each other middorsally, except at their anterior end. The posterior part of each bone is a large, broad lobe that broadly overlaps the parietal. A small, anterior lobe of the parietal abuts the lateral margins of the posterior lobe of the frontal but does not significantly overlap the frontal. The facial portion of the frontal is rather poorly developed. Anteriorly, the frontal is drawn into a narrow point lying ventral or lateral to the frontal processes of the premaxillary.

The parietals are large bones, firmly articulated to each other and to all surrounding bones. The stout, well-developed lateral spurs extend anteroventrally, overlapping the cartilaginous insertion of the ascending process of the palatoquadrate cartilage into the braincase. The semicircular canals produce prominent bulges in the relatively large otic capsules. A small but prominent spinous process is present at the extreme lateral margin of each capsule. A fibrous mass of connective tissue extends from this process to the quadrate. The squamosal lies in a distinct depression in the lateral wall of the capsule. The large parasphenoid is relatively broad and blunt-tipped anteriorly; the orbitosphenoids are relatively widely separated. Posterior vomerine teeth are in two bilateral patches that diverge posteriorly. The patches in two males contain 36–39 and 44–48 small, bicuspid teeth, respectively. The operculum has no stilus, although a slight protrusion is present. The well-developed quadrate is attached to the otic capsules by relatively large, strong squamosals. A small process extends posteriorly from the squamosal and is connected by a ligament to the proximal tip of the ceratohyal.

The lower jaw is rather weak. The prearticular is relatively large, but low, and the dentary is very slender. The arc of the lower jaw is relatively flat and broad.

The hyobranchial apparatus is typical of that of generalized members of the supergenus *Bolitoglossa* in being cartilaginous and lacking a urohyal (Fig. 6). The rather slender ceratohyals have a discrete and well-developed medial process. The very narrow anterior process is drawn into a point that extends upward into the sublingual fold. The long and slender epibranchials are slightly more than twice the length of the basibranchial. The basibranchial is slightly less than twice the length of the second ceratobranchial. The second ceratobranchials are much stouter than the slender first ceratobranchials. The first ceratobranchials are relatively well developed in comparison with those of other tropical plethodontids. The radii of the first basibranchial are continuous with the main part of the element, and there is no sign of a fibrocartilage joint. The broad-based and relatively short radii are joined by a distinct connective tissue strand. The most distinctive feature of the entire hyobranchial apparatus is the very well-developed anterior projection that is unique among the tropical genera (Figs. 2, 6). This broad-based and relatively stout projection is apparently somewhat flexible, for the cartilage cells at its base are surrounded by less intercel-



lular matrix than are the cells either proximal or distal to it. This process apparently represents a primitive condition and is reminiscent of the process seen in *Ensatina* (Lombard and Wake, 1977), although the process in *Ensatina* is less continuous with the basibranchial. The anterior basibranchial process is clearly a less-derived homologue of the lingual cartilage that is present in many tropical plethodontids.

The vertebral column consists of relatively stout vertebrae, with well-developed centra. There are one cervical, fourteen trunk, one sacral, two caudosacral, and a varying number of caudal vertebrae (from 20 to 26 in individuals having complete tails). The atlas has no special features, but the neural arch is barely completed in both cleared and stained adults. The first trunk vertebra is distinctly shorter than the remaining vertebrae and has a high, well-developed neural crest. Lower crests are present on the next few trunk vertebrae. The centrum is large and may be largely filled with mineralized cartilage, for only the terminal concavities are clearly filled by unmineralized intervertebral cartilage. All trunk vertebrae have well-developed, separated, pointed processes (hyperapophyses) on the posterior border of the neural arch. The nerve route pattern is typical of bolitoglossine salamanders (Edwards, 1976): the first trunk vertebra has a single foramen in front of the transverse processes, the second has single foramina both in front of and behind the transverse processes, and the third and succeeding vertebrae (to the end of the tail) have single foramina behind the transverse processes. The transverse processes of the trunk vertebrae are well developed. The dorsal and ventral rib bearers are separated for their entire lengths. The long, relatively straight processes extend beyond the lateral margins of the zygapophyses. They are sharply angled posteriorly in the first few vertebrae but are nearly perpendicular to the column over most of its length. The dorsal bearer is immediately dorsal to the ventral bearer, but it tends to be slightly more posteriorly oriented. Moderately long ribs with distinctly separated heads are present on all but the last trunk vertebra. Transverse processes of the first caudosacral vertebra are stout and blunt-ended and are swept somewhat posteriorly. Transverse processes of the second caudosacral vertebra are short, stout, and blunt-ended; they are nearly perpendicular to the column or are slightly anteriorly oriented. The first caudal vertebra is short and is associated with a distinctly constricted tail base. The relatively short transverse processes located at the extreme anterior end of the centrum are sharply oriented in an anterior direction. The transverse processes of succeeding caudal vertebrae are progressively shorter and barely exceed the anterior zygapophyses in length; they are borne on the extreme anterior end of each vertebra, at the base of the zygapophyses. The sharply tapered tail is deep as a result of a thick glandular layer lying dorsal to the vertebral column but is relatively narrow. Caudal vertebrae generally lack neural crests, although there may be low and irregularly formed crests on the first one or two vertebrae; however, the caudal vertebrae have very well-developed hyperapophyses.

The small hands and feet are highly distinctive (Fig. 4). They are very reduced in size and have relatively little ossified tissue. The digits are fused to one another for most of their

lengths but are free at their tips. Indeed, the digits are so poorly developed that it is somewhat artificial to present a phalangeal formula. Some phalanges are entirely cartilaginous, others may have a tiny speck of ossified tissue, and only the proximal phalanx of the longest finger and toe is consistently well ossified. An unusual feature is the cartilaginous tip of many terminal phalanges. In other plethodontid salamanders, these tips are well ossified and often specialized in structure. The poor degree of development suggests that *Bradytriton* does not use its limbs for specialized locomotory activity. A few individuals can be scored as having a phalangeal formula of 1, 2, 3, 2, for the hand and 1, 2, 3, 3, 2, for the foot, based on the presence of tiny specks of radio-opaque material visible in radiographs. Even the metapodial elements, which are cylindrical in shape, are small and poorly ossified, and the first digit of the hand has an especially small element. As a result of the fusion of the ulnare and intermedium, there are seven carpals; similarly, there are eight tarsals as a result of the fusion of distal tarsals 4 and 5. A distinct spur projects from the shank of the tibia for nearly its entire length, and there is a low but distinct tibial crest.

**RANGE.** *Bradytriton silus* is known only from the immediate vicinity of the type locality on the eastern slopes of the Sierra de los Cuchumatanes in extreme northwestern Guatemala.

**ETYMOLOGY.** From *silus*, L. for "pug-nosed" referring to the characteristic truncated appearance of the snout.

#### GENERIC SYNOPSSES

#### *Bolitoglossa* Duméril, Bibron, and Duméril

*Oedipus* Tschudi

*Eladinea* Miranda-Ribeiro

*Magnadigita* Taylor

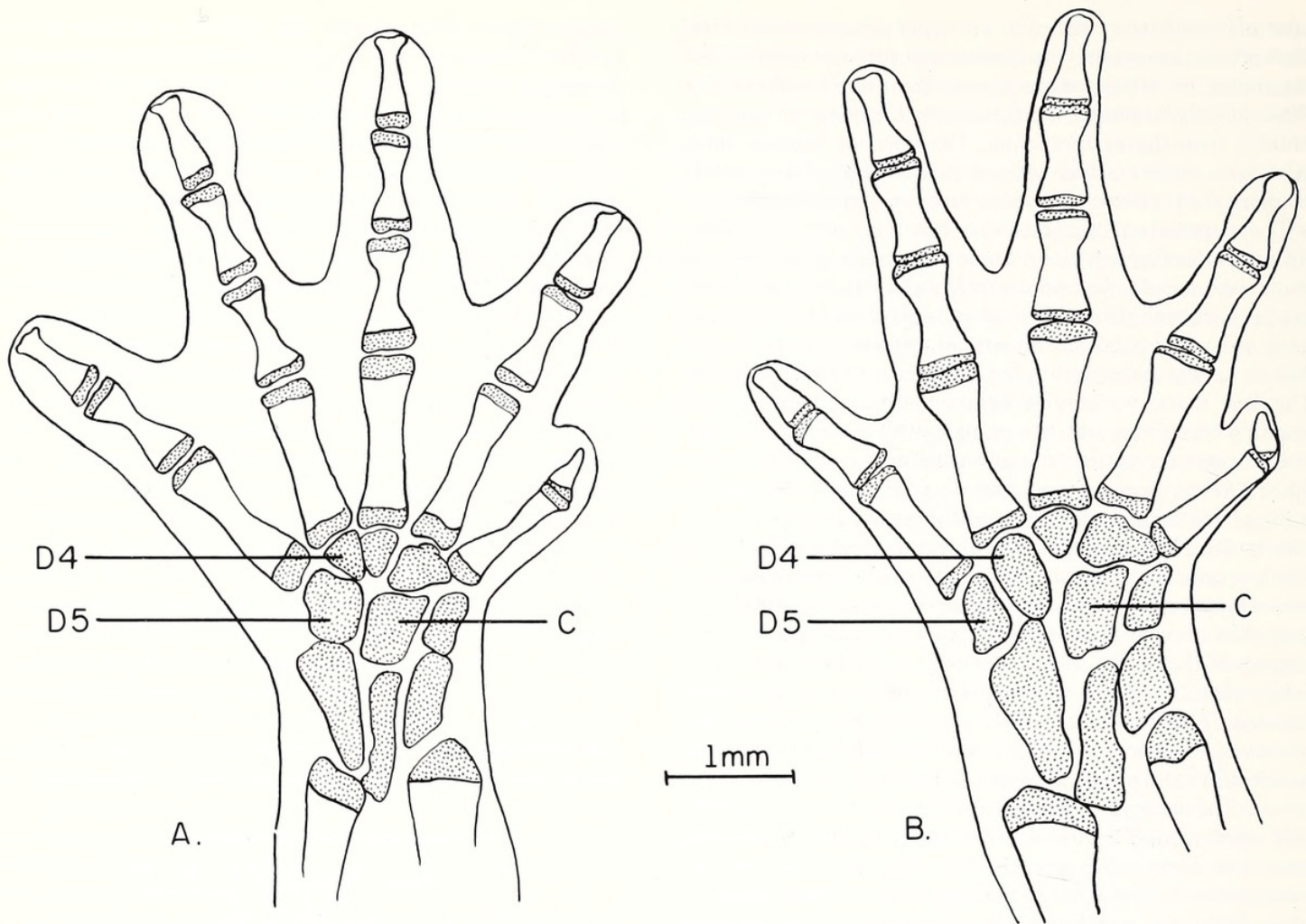
*Palmatotriton* Smith

**TYPE SPECIES.** *Bolitoglossa mexicana* Duméril, Bibron, and Duméril.

**DIAGNOSTIC CHARACTERS.** Small to very large salamanders with partially to fully webbed hands and feet, distinguished from members of all other tropical salamander genera in lacking a sublingual fold.

**REFERRED SPECIES.** *Bolitoglossa adspersa* (Peters); *B. altamazonica* (Cope); *B. alvaradoi* Taylor; *B. arborescens* Taylor; *B. biseriata* Tanner; *B. borburata* Trapido; *B. capitana* Brame and Wake; *B. cerroensis* Taylor; *B. chica* Brame and Wake; *B. colonnea* (Dunn); *B. compacta* Wake, Brame, and Duellman; *B. cuchumatana* (Stuart); *B. cuna* Wake, Brame, and Duellman; *B. dofleini* (Werner); *B. dunni* (Schmidt); *B. engelhardti* (Schmidt); *B. epimela* Wake and Brame; *B. equatoriana* Brame and Wake; *B. flavimembris* (Schmidt); *B. flaviventris* (Schmidt); *B. franklini* (Schmidt); *B. hartwegi* Wake and Brame; *B. helmrichi* (Schmidt); *B. hypacra* (Brame and Wake); *B. lignicolor* (Peters); *B. lincolni* McCoy and Walker; *B. macrinii* (Lafrentz); *B. marmorea* (Tanner and Brame); *B. medemi* Brame and Wake; *B. meliana* Wake and Lynch; *B. mexicana* Duméril, Bibron and





**Figure 7.** Feet of *Chiropterotriton* and *Pseudoeurycea*.

A. Left foot of an adult *Chiropterotriton multidentatus* (39.6 mm SL) from Hidalgo, Mexico. Cartilage is stippled. Note that distal tarsal 5 is larger than distal tarsal 4 and articulates with the centrale. This arrangement is unique to *Chiropterotriton* within the supergenus *Bolitoglossa*.

B. Left foot of an adult *Pseudoeurycea leprosa* (53.9 mm SL) from Veracruz, Mexico. Cartilage is stippled. Note that distal tarsal 5 is smaller than distal tarsal 4 and that it does not articulate with the centrale; this is the primitive pattern in plethodontid salamanders. The foot of this species is relatively much smaller than that of *C. multidentatus*, for although the feet as illustrated are about the same size, the specimen of *Pseudoeurycea* is much larger. Note that the fifth toe is smaller in *Pseudoeurycea* than in *Chiropterotriton*.

Duméril; *B. minutula* Wake, Brame, and Duellman; *B. morio* (Cope); *B. mulleri* (Brocchi); *B. nicefori* Brame and Wake; *B. occidentalis* Taylor; *B. odonnelli* (Stuart); *B. orestes* Brame and Wake; *B. palmata* (Werner); *B. pandi* Brame and Wake; *B. peruviana* (Boulenger); *B. phalarosoma* Wake and Brame; *B. platydactyla* (Gray); *B. ramosi* Brame and Wake; *B. resplendens* McCoy and Walker; *B. riletti* Holman; *B. robusta* (Cope); *B. rostrata* (Brocchi); *B. rufescens* (Cope); *B. salvinii* (Gray); *B. savagei* (Brame and Wake); *B. schizodactyla* Wake and Brame; *B. schmidtii* (Dunn); *B. silverstonei* Brame and Wake; *B. sima* (Vaillant); *B. sooyorum* Vial; *B. striatula* (Noble); *B. stuarti* Wake and Brame; *B. subpalmata* (Boulenger); *B. taylori* Wake, Brame, and Myers; *B. valleculea* Brame and Wake; *B. veracruzis* Taylor; *B. walkeri* Brame and Wake; *B. yucatanica* (Peters).

**RANGE.** *Bolitoglossa* has by far the widest range of any of the tropical salamander genera. It occurs almost continuously from the lowlands of eastern San Luis Potosi, Mexico,

in the north, south to the Amazonian lowlands of southern Peru, the mountains near Cochabamba, Bolivia, and southern Minas Gerais, Brazil.

**COMMENT.** Many species have been added to this large genus during the past two decades, but no revisionary study has been undertaken. A number of undescribed species are known to us. We here place *Bolitoglossa omniusanctorum* in the synonymy of *B. morio* on the basis of close similarity of the type specimens of *B. omniusanctorum* to specimens of *B. morio* in size, form, and coloration.

Wake and Brame (1969) and Wake and Lynch (1976) discussed a possible subdivision of this large, cumbersome genus. Wake and Lynch (1976) referred to "alpha" and "beta" sister groups and suggested that these might eventually be recognized as separate genera. The beta group is defined on the basis of an apomorphic character, a tail base specialization (Wake and Dresner, 1967). Members of the alpha group frequently have osteological reductions and foot specializa-



tions, but we know of no apomorphic character or combination of characters that would unambiguously define the alpha group. These diagnostic problems, combined with the absence of marked ecological or phenetic differentiation between the two groups, lead us to postpone formal division.

### *Bradytriton* new genus

**TYPE SPECIES.** *Bradytriton silus* new species.

**DIAGNOSTIC CHARACTERS.** This is a short-snouted, stout-bodied salamander with small limbs and small, syndactylous hands and feet. It differs from all other tropical salamander genera in having a laterally compressed tail with a well-developed dorsal glandular ridge.

**REFERRED SPECIES.** *Bradytriton silus* new species.

**RANGE.** The unique species is known only from the immediate vicinity of the type locality on the northeastern slopes of the Sierra de los Cuchumatanes in northwestern Guatemala.

### *Chiropterotriton* Taylor

**TYPE SPECIES.** *Oedipus multidentatus* Taylor.

**DIAGNOSTIC CHARACTERS.** Small to moderately large salamanders with relatively broad, partially webbed hands and feet and broad-tipped fingers and toes. *Chiropterotriton* differs from all other tropical salamander genera in its arrangement of tarsal cartilages: in *Chiropterotriton*, distal tarsal five is larger than distal tarsal four and articulates with the centrale; in other genera, four is larger than five, and five is excluded from articulation with the centrale (Fig. 7).

**REFERRED SPECIES.** *Chiropterotriton arboreus* (Taylor); *C. chiropterus* (Cope); *C. chondrostega* (Taylor); *C. dimidiatus* (Taylor); *C. laevis* (Taylor); *C. magnipes* Rabb; *C. mosaueri* (Woodall); *C. multidentatus* (Taylor); *C. priscus* Rabb.

**RANGE.** The genus is restricted to eastern Mexico, from west-central Tamaulipas in the north to the mountains of northern Oaxaca in the south.

**COMMENT.** Most species of this genus have been studied in some detail by Rabb (1955, 1958, 1965). The major unstudied unit is that comprising *C. chiropterus* and *C. laevis*.

### *Dendrotriton* new genus

**TYPE SPECIES.** *Oedipus bromeliacia* Schmidt.

**DIAGNOSIS.** Small, slender, long-tailed, arboreal salamanders with long legs, broad hands and feet, and long, broad-tipped digits. *Dendrotriton* differs from *Oedipina* by its short trunk (14 vs. 18 or more trunk vertebrae) and long limbs; from *Nyctanolis* in having a single premaxillary; from *Chiropterotriton* in having a larger fourth than fifth tarsal; from *Bolitoglossa* in possessing a sublingual fold; from *Bradytriton*, *Nototriton*, *Parvimolge*, *Oedipina* and *Thorius* by its lack of carpal and tarsal fusions; from *Lineatriton* by its short vertebrae and long legs; and from *Pseudoeurycea* by its lack of prefrontals and tibial spurs.

**REFERRED SPECIES.** *Chiropterotriton bromeliacia*

(Schmidt); *C. cuchumatanus* Lynch and Wake; *C. megarhinus* Rabb; *C. rabbi* Lynch and Wake; *C. xoloccalcae* (Taylor).

**ETYMOLOGY.** From *dendron*, Gr. for tree, referring to the arboreal habits of all known species, and *triton*, Gr., a commonly used term for salamanders.

**RANGE.** Southwestern Chiapas, Mexico, through western Guatemala.

**COMMENT.** This group has recently been studied in detail by Lynch and Wake (1975), who presented photographs of all five species.

### *Lineatriton* Tanner

**TYPE SPECIES.** *Spelerpes lineolus* Cope.

**DIAGNOSTIC CHARACTERS.** A very slender, elongate, fossorial form with diminutive limbs, hands and feet, and an extremely long tail. *Lineatriton* is distinguished from all other tropical salamander genera in having very elongated, narrow vertebrae. *Oedipina* has a similar body form and ecology but differs from *Lineatriton* in having 18 or more, rather than 14, trunk vertebrae.

**REFERRED SPECIES.** *Lineatriton lineola* (Cope).

**RANGE.** *Lineatriton* is restricted to two disjunct areas of the Gulf slope of Mexico: along the lower slopes of the mountains of west-central Veracruz and the area around Los Tuxtlas in eastern Veracruz.

**COMMENT.** This is one of the most distinctive of the tropical genera and is apparently monotypic. It has been little studied since the work of Tanner (1950).

### *Nototriton* new genus

**TYPE SPECIES.** *Spelerpes picadoi* Stejneger.

**DIAGNOSIS.** Small, long-tailed salamanders of arboreal, terrestrial, or semifossorial habitats. The species have moderately long to short legs and small hands and feet. The intermedium and ulnare of the manus and distal tarsals four and five of the pes are fused. The genus is distinguished from other genera with similar fusions as follows: from *Oedipina* by having only 14 rather than 18 or more trunk vertebrae; from *Bradytriton* by having a long, slender tail and slender body; from *Parvimolge* by having the tail longer than the body, by having frontal processes fused together at their base (all species but *richardi*), and by lacking mesopodial and hyobranchial mineralizations; from *Thorius* by having a complete skull roof over the brain case; from *Bolitoglossa* by having carpal fusions and a sublingual fold.

**REFERRED SPECIES.** *Chiropterotriton barbouri* (Schmidt); *Bolitoglossa diminuta* Robinson; *Chiropterotriton nasalis* (Dunn); *C. picadoi* (Stejneger); *C. richardi* (Taylor); *C. veraepacis* Lynch and Wake.

**ETYMOLOGY.** From *notos*, L., referring to the southerly distribution of the genus, and *triton*, L., Gr., a commonly used term for salamanders.

**RANGE.** *Nototriton* ranges from eastern Guatemala to the Meseta Central of Costa Rica.

**COMMENT.** Most of *Nototriton* consists of what has been



called the *picadoi* group (Wake and Lynch, 1976) or the *nasalis* group (Lynch and Wake, 1978) of *Chiropterotriton*. The species *richardi* may not be referable to this genus; it was originally described as a member of the genus *Parvimolge* and has been considered problematic by Rabb (1955), Wake (1966), Wake and Lynch (1976), and Lynch and Wake (1978). It is more appropriately placed in *Nototriton* than elsewhere, but it differs from other members of the genus in possessing an unusual combination of ancestral and derived characters (Lynch and Wake, 1978). Table 2 was constructed by ignoring *N. richardi*, but we have nonetheless tentatively assigned the species to this genus because it does not come as close to fitting into any other genus. Further, we are reluctant to establish a new genus for such a poorly known form.

The species described as *Bolitoglossa diminuta* by Robinson (1976) is also most appropriately placed in *Nototriton*. Radiographs of the holotype reveal that it has frontal processes of the premaxillary that are fused, and it has a very long tail for its small body size (53% of total length). It was reported to lack a sublingual fold, and we have been unable to see one; however, the holotype, a mature female, is very small (31.1 mm SL), and it may be impossible to determine the status of this character without histological sections. *Nototriton richardi* has a very reduced sublingual fold. It was on the basis of the apparent absence of this fold in the holotype of *B. diminuta* that the senior author urged Robinson to describe the species as a *Bolitoglossa*, even though Robinson had originally intended to place it in the genus *Chiropterotriton*.

### *Nyctanolis* Elias and Wake

**TYPE SPECIES.** *Nyctanolis pernix* Elias and Wake.

**DIAGNOSTIC CHARACTERS.** This is a large, long-legged, long-fingered, long-toed, long-tailed taxon that differs from all other tropical salamander genera in having paired premaxillary bones.

**REFERRED SPECIES.** *Nyctanolis pernix* Elias and Wake.

**RANGE.** The unique species is known from the north-eastern slopes of the Sierra de los Cuchumatanes in NW Guatemala; near the Lagos de Montebello in nearby Chiapas, Mexico; and from the Sierra de las Minas in eastern Guatemala.

### *Oedipina* Keferstein

*Oedipina* Keferstein  
*Ophiobatrachus* Gray  
 ? *Haptoglossa* Cope  
*Oedipinola* Hilton

**TYPE SPECIES.** *Oedipina uniformis* Keferstein.

**DIAGNOSTIC CHARACTERS.** Slender, elongate salamanders of moderate to large size with very small limbs, hands, and feet, and a very long tail. *Oedipina* is distinguished from all other tropical salamander genera, including *Lineatriton*, the only genus that resembles it externally, by having 18 to 22 (rather than 14) trunk vertebrae.

**REFERRED SPECIES.** *Oedipina alfaroi* Dunn; *O. altura* Brame; *O. carablanca* Brame; *O. collaris* (Stejneger); *O. complex* (Dunn); *O. cyclocauda* Taylor; *O. elongata* (Schmidt); *O. grandis* Brame and Duellman; *O. ignea* Stuart; *O. parvipes* (Peters); *O. paucidentata* Brame; *O. poelzi* Brame; *O. pseudouniformis* Brame; *O. stuarti* Brame; *O. taylori* Stuart; *O. uniformis* Keferstein.

**RANGE.** *Oedipina* ranges from south-central Chiapas, Mexico, through all of Central America and western Colombia to northwestern Ecuador.

**COMMENT.** This is an exceptionally well-defined genus. Since the revision by Brame (1968), only one additional species, *O. grandis*, has been described, and there have been no other taxonomic changes.

### *Parvimolge* Taylor

**TYPE SPECIES.** *Oedipus townsendi* Dunn.

**DIAGNOSTIC CHARACTERS.** Diminutive salamanders with relatively stocky bodies, short legs with small hands and feet, and short, stout tails. It is distinguished from other genera with small species as follows: from *Bolitoglossa* in having a sublingual fold; from *Dendrotriton* and *Chiropterotriton* in having distal tarsals four and five fused and the intermedium and ulnare fused; from *Nototriton* in having a short tail and lacking fused frontal processes of the premaxillary; from *Thorius* in having a complete skull roof over the braincase.

**REFERRED SPECIES.** *Parvimolge townsendi* (Dunn).

**COMMENT.** Two other species, *praecellens* and *richardi*, have been included in the genus. Neither seems to be closely related to *townsendi*, and we here refer them to the genera *Pseudoeurycea* and *Nototriton*, respectively.

### *Pseudoeurycea* Taylor

**TYPE SPECIES.** *Spelerpes leprosus* Cope.

**DIAGNOSTIC CHARACTERS.** A diverse group of moderate-sized to very large salamanders with moderate to long limbs, well-developed hands and feet in which the middle digits are markedly longer than the outer ones (Fig. 7), and a tail about as long as the body. The species are very generalized in morphology. The genus differs from *Nyctanolis* in having a single premaxillary and shorter limbs and tail; from *Dendrotriton* in having prefrontals and tibial spurs; from *Bolitoglossa* in having a sublingual fold; from *Chiropterotriton* in having a fourth distal tarsal that articulates with the fibulare and is larger than the fifth (Fig. 7); from all other genera in having separate distal tarsals four and five.

**REFERRED SPECIES.** *Pseudoeurycea altamontana* (Taylor); *P. anitae* Bogert; *P. bellii* (Gray); *P. brunnata* Bumzahem and Smith; *P. cephalica* (Cope); *P. cochraniae* (Taylor); *P. conanti* Bogert; *P. exspectata* Stuart; *P. firscheini* Shannon and Werler; *P. gadovii* (Dunn); *P. galeanae* (Taylor); *P. goebeli* (Schmidt); *P. juarezi* Regal; *P. leprosa* (Cope); *P. melanomolga* (Taylor); *P. mystax* Bogert; *P. nigromaculata* (Taylor); *P. praecellens* (Rabb); *P. rex* (Dunn); *P. robertsi* (Taylor); *P. scandens* Walker; *P. smithi* (Taylor); *P. unguidentis* Smith and Taylor; *P. werleri* Darling and Smith.



**RANGE.** The genus ranges from eastern Sonora, Mexico, in the northwest, and west-central Tamaulipas, Mexico, in the northeast, through most of eastern and south-central Mexico into western and southern Guatemala.

**COMMENT.** Few characters bind this assemblage of generalized species together. The genus lacks any autapomorphies and is mainly defined by exclusion. A few species stand out from the rest as distinct morphological entities (e.g., *P. bellii*, *P. praecellens*, *P. werleri*). The *gadovii*, *rex*, and *leprosa* groups are the core of the genus and appear to be closely interrelated (Maxson and Wake, 1981). We here assign *praecellens* to *Pseudoeurycea*. Rabb (1955) placed it in the genus *Parvimolge* with some hesitation. It differs from *P. townsendi* in that it is larger and stouter and has prefrontal bones. Rabb (1955) reported that *P. praecellens* had some mineralization of the hyobranchial apparatus, as in *P. townsendi*; however, we have been unable to see this feature in our radiographs of the unique holotype. The species fits reasonably well in *Pseudoeurycea*, and Rabb suggested that it might prove to be a relative of *P. cephalica*.

### *Thorius* Cope

**TYPE SPECIES.** *Thorius pennatulus* Cope.

**DIAGNOSTIC CHARACTERS.** Diminutive, slender salamanders with short limbs and small hands and feet. *Thorius* is distinguished from all other tropical salamanders by two characters: the suborbital groove intersects the lip, and the skull is incompletely ossified, leaving the braincase uncovered by bone (the parietal bones have an especially large gap separating them).

**REFERRED SPECIES.** *Thorius dubitus* Taylor; *T. macdougalli* Taylor; *T. maxillabrochus* Gehlbach; *T. minutissimus* Taylor; *T. narisovalis* Taylor; *T. pennatulus* Cope; *T. pulmonaris* Taylor; *T. schmidtii* Gehlbach; *T. troglodytes* Taylor.

**RANGE.** The genus ranges from the eastern margins of the Mexican Plateau into the mountains of northern and central Oaxaca, and in the Sierra Madre del Sur of southern Oaxaca and Guerrero, Mexico.

**COMMENT.** The genus has recently been studied in detail by Freeman (1977) and Hanken (1980), but the taxonomic results of these unpublished theses are not yet available. All of the described species (except perhaps *T. maxillabrochus*) are valid, but there are numbers of additional undescribed species.

### DISCUSSION

The supergenus *Bolitoglossa* was redefined by Elias and Wake (1983) on the basis of hyobranchial and tail base characteristics. All genera considered here have the features of the supergenus. Our main departure from Wake (1966) is that two formerly diagnostic features are deemphasized. First, *Nyctanolis* has two premaxillary bones; thus, the supergenus *Bolitoglossa* can no longer be characterized by the presence of a single, fused bone. Second, *Nyctanolis* and some species of *Pseudoeurycea* have a lateral parietal spur that is only

poorly developed: in *Nyctanolis* the spur may be little more than a low ridge on the underside of the bone, and in some *Pseudoeurycea* the "spur" is really only a small lateral lobe. Still, at least some form of parietal "spur" is present in all members of the supergenera *Batrachoseps* and *Bolitoglossa*.

With the new genera, the supergenus *Bolitoglossa* includes 11 genera. *Nyctanolis*, *Bradytriton*, *Parvimolge*, and *Lineatriton* are monotypic; the other genera include from five (*Dendrotriton*) to over sixty (*Bolitoglossa*) species. Additional undescribed species that are known to us will increase the number of species in such large genera as *Bolitoglossa*, *Pseudoeurycea*, and *Thorius* but will not affect the monotypic genera.

The genera *Bolitoglossa*, *Lineatriton*, *Oedipina*, *Pseudoeurycea*, and *Thorius* are essentially unchanged by our analysis. The content of *Parvimolge* is reduced to a single species by transfer of the species *praecellens* to *Pseudoeurycea*. The genus most strongly affected is *Chiropterotriton*. As a result of the shift of the old *bromeliacia* species group (Lynch and Wake, 1975) to the new genus *Dendrotriton* and of the old *picadoi* (Wake and Lynch, 1976) or *nasalis* (Lynch and Wake, 1978) species group to the new genus *Nototriton*, *Chiropterotriton* has been reduced to a group of nine species that inhabit eastern Mexico. The species formerly known as *Bolitoglossa diminuta* is included in *Nototriton*. The other two new genera, *Nyctanolis* and *Bradytriton*, are based on newly discovered species.

Hecht and Edwards (1976a, 1976b) and Hecht (1976) discuss the relative information content of different types of shared derived character states (synapomorphies) for the reconstruction of phylogeny. Ordered by increasing significance (basically, the degree of confidence one has in their interpretation) in phylogenetic reconstruction are five classes of synapomorphies:

- “(I) Shared and derived character states which are the result of loss. Such loss characters are the zero state because there is no developmental evidence.
- (II) Shared and derived character states which are the results of simplification or reduction of complex structures as indicated by comparative or developmental anatomy.
- (III) Shared and derived character states which are the result of growth and developmental processes dependent on size, age, and hormonal and other physiological relationships. Characters related to allometric functions are the best examples.
- (IV) Shared and derived character states which are highly integrated functionally and are subject to directional selection.
- (V) Shared and derived character states which are unique and innovative in structure (the most important type of information).” (From Hecht and Edwards, 1976a.)

Our analysis in this paper is based on the 18 characters outlined earlier. The apomorphic characters we have chosen include seven that are autapomorphic (Table 1). These are not useful in phylogenetic analysis but are included because they aid in diagnosing genera. The 11 remaining characters vary in degree of utility. Six involve morphological transformation, and five involve losses of elements. We interpret



our loss characters as falling into the third category of Hecht and Edwards (1976) rather than the first, for we have some ontogenetic information concerning the way in which four of the five characters are lost. We believe that loss of septomaxillaries, prefrontals, preorbital processes of vomers, and columellae (or styler processes of the opercula) are all pae-domorphic characters (Lynch and Wake, 1978; Alberch et al., 1979; Alberch and Alberch, 1981; Elias, in press), but whether they should all be counted as independent characters or considered to be parts of a single "global" paedomorphic process is unresolved.

The six remaining characters (1, 3, 4, 5, 10, 11) all involve transformations. Characters 10 and 11 relate to ontogenetic phenomena and fall into Hecht and Edwards's third category. Transformation characters 1, 3, 4, and 5 are parts of integrated, functionally significant systems; they fall in the fourth category of Hecht and Edwards.

Other authors have used additional characters in generic diagnoses of tropical salamanders. Some of these characters (e.g., a posteriorly directed spur on the squamosal in *Thorius*) are autapomorphies and of little use in phylogenetic analysis. Others occur in all members of one genus but also appear irregularly in one or a few species in some other genera (e.g., the complex tail base present in some *Pseudoeurycea*). Other characters, such as the shape and degree of ossification of the intervertebral articulation (used by Taylor, 1944), are subject to extreme ontogenetic variation (Wake, 1970), and we have not had sufficient material to perform a complete analysis. Still other characters, such as external shape of hands and feet, shape of terminal digits, length of ribs, and fusion or nonfusion of transverse processes, have proven impossible to codify consistently for all neotropical species, but these may well have utility for finer analysis of intra- and inter-generic relationships in the future. The hyobranchial apparatus (features of the tip of the first basibranchial, including length and shape of radii and detailed structure of the lingual cartilage and associated musculature) holds much promise as a source of additional characters (Tanner, 1952; Lombard and Wake, 1977). However, this structure requires detailed histological study, and we have examined too few species to discern broad patterns. Future studies should involve comparative ontogenetic analyses, for heterochronic modes of evolution have been strongly implicated in salamanders (Wake, 1966; Alberch et al., 1979; Alberch and Alberch, 1981).

Biochemical, immunological, and cytological characters are useful in analyzing phylogenetic relationships in the supergenus *Bolitoglossa*. Recently Maxson and Wake (1981) used immunological approaches to study albumin evolution in *Pseudoeurycea* and *Chiropterotriton* (*sensu lato*). Extensive evolution of albumin has taken place in these groups, and immunological methods will be most useful at the intrageneric level of comparison. In reference to the present generic review, the principal result of interest from the immunological work is the finding that *Chiropterotriton* (antisera from *C. multidentatus*) and *Dendrotriton* (antisera from *D. bromeliacia*) are more similar to *Pseudoeurycea* (antisera from five species) than they are to each other. This finding cor-

roborates our conclusion that the two genera are distinct. No antisera were prepared for species of *Nototriton*, but one-way tests were made to some species of the genus. Immunological distances between species of *Chiropterotriton* and *Dendrotriton* are about equivalent to those between *Chiropterotriton* and *Nototriton*, but immunological distances between *Dendrotriton* and *Nototriton* are considerably less. Distances within *Dendrotriton* (maximum 21) are much less than between *Dendrotriton* and *Nototriton* (minimum 64).

Some data on chromosomes are available (Leon and Kezer, 1978; J. Kezer and S. Sessions, pers. comm.). All members of the supergenus *Bolitoglossa* so far examined have a haploid chromosome number of 13, as do members of the genus *Batrachoseps*. All other plethodontids examined have a haploid number of 14. The species of *Dendrotriton* (*D. bromeliacia*, *D. cuchumatanus*, *D. rabbi*) and *Nototriton* (*N. picadoi*, *N. veraepacis*) so far examined have a distinct heteromorphism (presumably XY) in the thirteenth pair of chromosomes. This pattern has been found in some species of *Thorius* and *Oedipina* but not in *Chiropterotriton*, *Pseudoeurycea*, *Lineatriton*, *Bolitoglossa*, or *Parvimolge* (chromosomes of *Nyctanolis* and *Bradytriton* have not been examined). These data lend further support to our decision to separate *Dendrotriton* and *Nototriton* from *Chiropterotriton*.

From the 18 characters analyzed we are unable to conclusively demonstrate the monophyletic status of 3 of the 11 bolitoglossine genera: *Dendrotriton*, *Nototriton*, and *Pseudoeurycea* (Table 1). A genus appearing in Table 1 must have at least one apomorphic character (a synapomorphy for the species of the genus) that is not shared with any other given genus in order for us to consider it to be monophyletic.

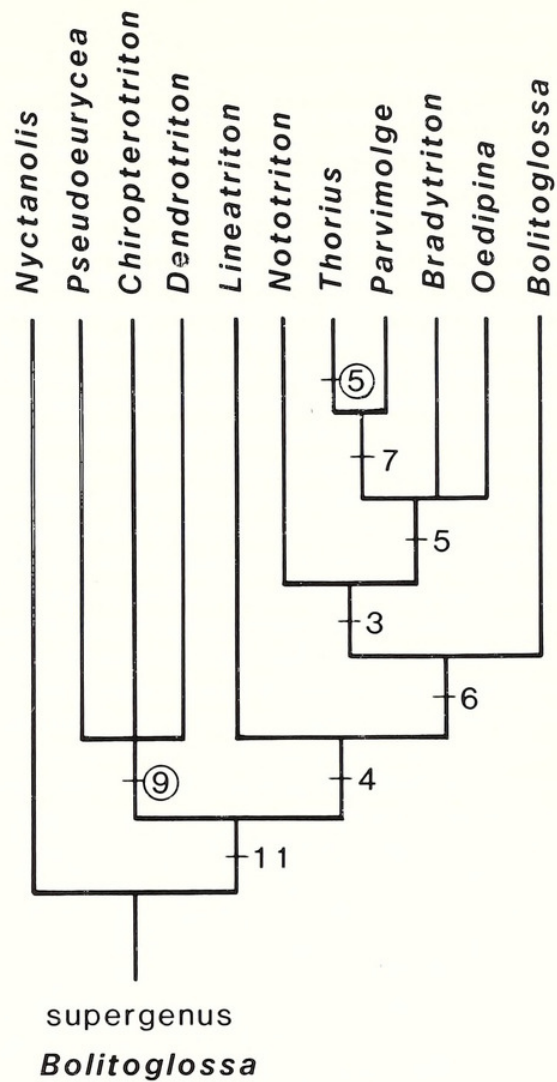
All of the apomorphies shown for *Dendrotriton* in Table 1 are shared with *Oedipina*; nevertheless, in other characters, which proved impossible to score for all neotropical genera, *Dendrotriton* shows derived states not found in *Oedipina*. Species of *Dendrotriton*, all of which are arboreal, show such derived features as relatively long legs, with long, well-developed digits and expanded terminal phalanges. *Oedipina*, all of which are semi- to fully fossorial, have very short legs, with short, erratically developed digits and unspecialized phalanges. The limb states of the two genera are derived in opposite directions from the ancestral state. Thus, despite the absence of defining synapomorphies in our formal tabulation, we consider *Dendrotriton* to be a well-defined, monophyletic assemblage.

The situation with *Pseudoeurycea* is far more complex. This genus is something of a "waste-basket," notwithstanding arguments of Baird (1951) to the contrary. It has only a single apomorphy (fused premaxillaries, character 11, Table 1), and this is shared with all genera of the supergenus except *Nyctanolis*. All of the other genera are easily distinguished from *Pseudoeurycea* on the basis of a variety of synapomorphies and autapomorphies. The species of *Pseudoeurycea* are relatively diverse in external structure and behavior but are basically similar in their generalized osteology, such that there is no clear osteological basis for subdividing the genus into monophyletic assemblages. The generotype is *P. leprosa*; it and some allied species have a plesiomorphic character



(septomaxillary bones) and an apomorphic character (a complex tail base, not coded here, but rather similar to the tail base seen in *Bolitoglossa* beta, Wake and Lynch, 1976). It may eventually be possible to formally recognize this group taxonomically, but the remaining species in the present genus *Pseudoeurycea* would still constitute a very disparate assemblage. Maxson and Wake (1981) have shown that species of *Pseudoeurycea* are greatly divergent in albumin structure. One group that is not well defined morphologically can be defined reasonably well on a biochemical basis (the combined *gadovii* and *rex* groups of Wake and Lynch, 1976, together with some members of other groups). However, an electrophoretic analysis in progress (Yang and Wake, unpublished data) discloses that most species are very distinct from one another and that groups of species are not readily apparent. *Pseudoeurycea* may be a paraphyletic taxon, the members of which have retained relatively conservative morphologies. In this respect, the genus presents a taxonomic problem similar to that encountered in the genus *Plethodon* (Larson et al., 1981), another taxon based largely on plesiomorphic characteristics. We do not think that *Pseudoeurycea*, as presently constituted, represents the remnants of the ancestral stock of all tropical salamanders, for in many respects members of *Nyctanolis* and *Chiropterotriton* are more generalized osteologically. For example, *C. priscus* has relatively large, well-developed septomaxillary bones, primitive elements that occur only occasionally in the few species of *Pseudoeurycea* that have them. Thus, our character scorings must be used cautiously when making phylogenetic interpretations.

*Nototriton*, although it is readily distinguished from most genera, has no apomorphies that are not shared with *Oedipina*. This situation is superficially similar to the problem of *Dendrotriton* versus *Oedipina*, but the three synapomorphies shared by *Nototriton* and *Oedipina* are a different set. Further, unlike *Dendrotriton*, *Nototriton* may be a paraphyletic group that includes lineages of a pre-*Oedipina* stock (see Lynch and Wake, 1978). For example, *N. richardi*, a poorly known species of which fewer than ten specimens have been collected, appears to be more primitive than other *Nototriton* in some respects but more derived in others. It could be placed in *Oedipina*, but it lacks an increased number of trunk vertebrae (character 17), the synapomorphy that most strongly distinguishes the species of *Oedipina* from all other tropical plethodontids. The remaining species of *Nototriton* form a well-defined assemblage (see Lynch and Wake, 1978). As recognized here, *Nototriton* is a diverse group consisting of several rare, secretive, and poorly known species. At this time we are unable either to define autapomorphies for the genus or to subdivide it into clearly monophyletic sublineages. By joining *Oedipina* and *Nototriton* to form a single genus, we could claim monophyly for the group as a whole, but this would severely blur the limits of the present genus *Oedipina*, one of the most tightly knit, well-diagnosed, and highly apomorphic genera of salamanders. Species of *Nototriton* share a number of structural and ecological similarities, and they are sharply distinguished from *Oedipina* by the synapomorphies of the latter group. Accordingly, we choose to recognize both *Oedipina* and *Nototriton*, although the lat-



**Figure 8.** Maximum parsimony cladogram of genera in the tribe Bolitoglossini. The numbered characters (Table 1) are present in their derived condition in all taxa above the point in the dendrogram where the lines occur. Reversals are circled. The tree treats character 9 as if it were a synapomorphy in its reversed form (i.e., resembling the presumed primitive condition). Parallelisms are not illustrated.

ter genus may ultimately not prove to be a monophyletic assemblage.

We used the data in Table 1 to compute Wagner trees, using the method of cladistic inference by parsimony (Farris, 1970), but with one modification. We fixed the root of the tree *a priori* by declaring *Nyctanolis* to be the first derivative branch. We believe that the premaxillary character is considerably more substantial than any other in the matrix (because it is conservative and relatively well understood; see Wake, 1966), and we accordingly used the rooting method to weight this character heavily. The resulting tree is presented in Figure 8.

There are reasons for questioning the validity of this maximum parsimony tree. Although there are six stems characterized by synapomorphies, two of these are reversed later in the dendrogram. Only three of the six synapomorphic



characters (3, 4, 5) are "high-quality" characters, i.e., characters that fall into Hecht and Edwards's (1976a) category 4 and constitute parts of integrated systems. The significance of character 5 is unclear; the long, tubular mental glands of certain of the genera (e.g., *Oedipina*, *Bradytriton*) are unusual but may represent extreme cases of subtler variation that would require histological documentation. Note that the dendrogram requires a reversal of this character in the stem leading to *Thorius*. It seems more likely that tubular glands have evolved in parallel, a hypothesis that is supported by the observation that some species of the unrelated North American genus *Eurycea* have such glands. Characters 3 and 4 involve fusions of carpals and tarsals. Although these characters may be more complex than those that involve loss of elements, they nevertheless require little more than simple developmental modifications. We know that character 3 has evolved independently in extra-tropical plethodontids (e.g., *Aneides hardii* and some species of *Batrachoseps*; Wake, 1966). However, among plethodontids character 4 (tarsal fusions) appears to be unique to the genera reported here. It is possible that distal tarsals 4 and 5 are fused in *Batrachoseps*, rather than 5 being lost as Wake (1966) has suggested.

Because we have fixed the root of the tree with *Nyctanolis*, character 11 will be a common feature of most possible dendrograms. Characters 6 and 7 fall into Hecht and Edwards's third weighting category, for we have some ontogenetic information concerning them (unpublished and Elias, in press). We think that both characters 6 and 7 reflect parallel evolution, for both characters refer to features that appear relatively late in the development of related species. Character 7 (loss of preorbital processes of the vomer) has evolved independently in some species of *Batrachoseps* (Marlow et al., 1979). Scoring for character 6 (loss of stylus of the operculum) requires a certain degree of subjectivity, because the process, where it appears at all, is invariably very small in members of the supergenus *Bolitoglossa*.

The final significant character in Figure 8 is the presence or absence of septomaxillary bones (character 9). Most members of the supergenus *Bolitoglossa* lack septomaxillaries, and a questionable feature of this tree is that it contains a stem for which the synapomorphy is a postulated reversal (reappearance of septomaxillaries). This reversal unites *Pseudoeurycea*, *Chiropterotriton*, and *Dendrotriton*, three genera that share no additional synapomorphies and have little else in common. Because the first two of these genera are extensively plesiomorphic, no system of analysis can deal with them easily.

Septomaxillary bones are not well developed in any tropical salamander. They appear regularly in some *Chiropterotriton* (Rabb, 1956; Wake, 1966) but are absent in others (e.g., *C. dimidiatus*). Septomaxillary bones are extremely small and variably present in four of the five species of *Dendrotriton* (Lynch and Wake, 1975, 1978). Septomaxillaries also occur in at least some individuals of several species of *Pseudoeurycea* (*P. cephalica*, *P. leprosa*, *P. werleri*, and *P. nigromaculata*) and occasionally in other bolitoglossine genera. Wake (1966) reports their presence in individuals of *Parvimolge townsendi*, *Oedipina uniformis*, *Thorius pennatulius*,

and three species of *Bolitoglossa*. We hypothesize that tropical salamanders as a group have undergone osteological reduction, and that such reduction may have characterized the ancestral stock. Loss of the septomaxillaries can be interpreted as a manifestation of a general paedomorphic trend in the group (Wake, 1966; Alberch and Alberch, 1981). Because these bones are so well developed in *Chiropterotriton* relative to other members of the supergenus *Bolitoglossa*, we consider it unlikely that a reversal of this character (i.e., re-evolution of septomaxillaries following their loss in an ancestor) has occurred in the genus. *Chiropterotriton* is the only tropical genus in which the presence of septomaxillaries is universal in adults of most species (all but the paedomorphic *C. dimidiatus*). The loss of septomaxillaries in certain *Chiropterotriton* species parallels the loss of the bones in other genera, and the same underlying mechanism could be involved in all cases.

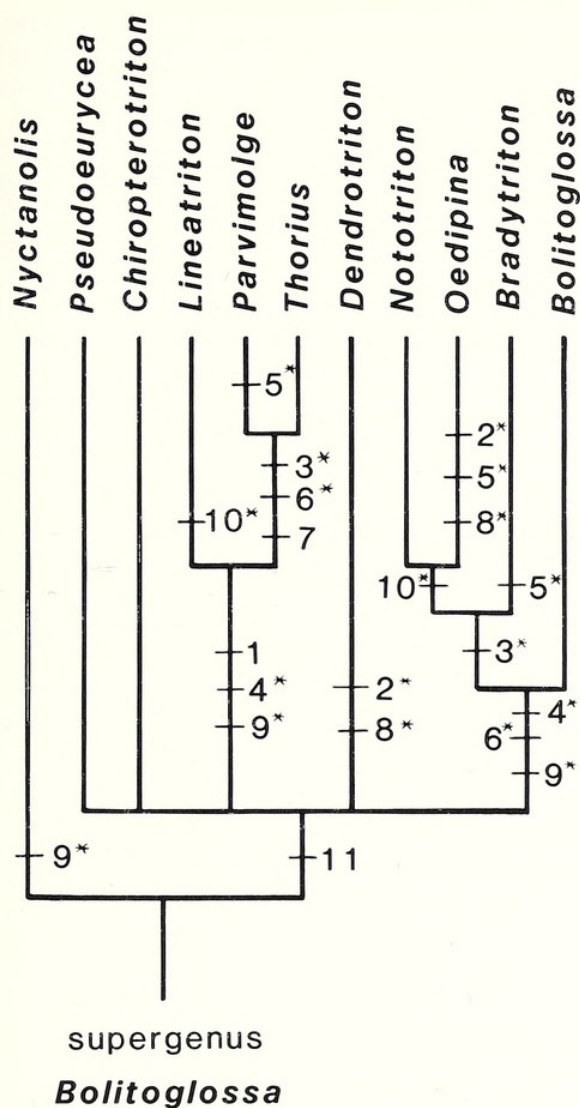
Paedomorphosis is not necessarily a unidirectional process, and some reversals are to be expected. Thus, septomaxillaries may have reappeared in *Dendrotriton* and *Pseudoeurycea*, following their loss in the respective ancestral stocks. The bones occur irregularly even in those species where they are found at all. The rare appearance of septomaxillaries in other genera is likely to be atavistic, i.e., based on a reversal of an original paedomorphic event.

Summarizing our arguments, linkage of *Chiropterotriton*, *Dendrotriton*, and *Pseudoeurycea* on the basis of a postulated shared reversal of a single character is not warranted. If the septomaxillary character is omitted from the Wagner analysis, the resulting dendrogram includes a stem uniting these same three genera. This time the stem is based on another shared reversal, separation of tarsal elements (character 4). We consider such a reversal to be unlikely but not impossible. Instances are known in which species with fused tarsals show polymorphism for the trait, so reversals could occur (Wake, 1966; Wake and Brame, 1969; Alberch and Alberch, 1981). We conclude that parsimony methods must be used cautiously where extensive parallelism pervades an evolutionary radiation.

An alternative method of analyzing our data is illustrated in Figure 9. This dendrogram is based on the zoogeographic and phyletic arguments of Wake and Lynch (1976, fig. 32), who recognized a "Mexican Group" of genera including *Pseudoeurycea*, *Chiropterotriton* (*sensu stricto*), *Parvimolge*, *Lineatriton*, and *Thorius*. Using the present suite of osteological characters, we can find no justification for recognition of a clade including these five genera; so we have indicated a five-way division separating them at the second level of the dendrogram and grouping them to the left of the figure. Although this dendrogram has relatively little internal structure, it does distinguish two groups of three and four genera, respectively.

The dendrogram in Figure 9 differs from that in Figure 8 in several respects. The former dendrogram contains fewer unique synapomorphies (three rather than six) and more parallelisms (ten rather than five), but it has no reversals. A five-way division occurs above the first synapomorphy. The three characters involved in unique synapomorphies (1, 7, 11) fall





**Figure 9.** An alternative tree of the genera in the tribe Bolitoglossini. There are no reversals in this tree, but all parallelisms (asterisks) are indicated.

into Hecht and Edwards's (1976a) third and fourth categories, the kinds of characters that they consider to have relatively high systematic value. The stem uniting *Lineatriton*, *Parvimolge*, and *Thorius* has three synapomorphies. For illustrative purposes, we have indicated all parallelisms in Figure 9, and it can be seen that two of these three synapomorphies evolved in parallel with other stems. The stem uniting *Bradytriton*, *Nototriton*, *Oedipina*, and *Bolitoglossa* also has three synapomorphies (4, 6, 9), but none of them is unique.

The tropical plethodontid genera constitute a highly derived lineage. The species are so specialized, in fact, that little further morphological innovation seems possible. Rather, variation on similar themes has occurred repeatedly, with the result that characters useful in the taxonomy of other salamander groups have been subject to extensive parallel evolution. We have long known that such features as elongation of body and tail, diminution in body size, changes in

relative limb length and foot size, and increased digital webbing have evolved several times in the group (Wake, 1966; Wake and Lynch, 1976; Alberch and Alberch, 1981). Apparently the evolution of other morphological traits is also complex, and close evolutionary interlinking of seemingly unrelated traits is a possibility (see Alberch et al., 1979; Alberch and Alberch, 1981). The incorporation of biochemical and immunological approaches to phyletic analysis holds promise for unraveling the complex history of this group, but the long evolutionary history of the neotropical salamanders poses serious problems for all known analytical techniques. At one time, the tropical salamanders were considered to form a reasonably compact congeneric group (Dunn, 1926). The intervening years have seen a steady erosion of this concept as new salamanders have been discovered and novel analytical techniques have been applied. Based primarily on its possession of a common tongue projection mechanism (Lombard and Wake, 1977), the supergenus *Bolitoglossa* does appear to be monophyletic, but the group is more ancient and highly diverse than was thought previously. The present effort is but one more developmental stage in our attempt to understand the complex history of the tropical salamanders.

#### ACKNOWLEDGMENTS

Work reported in this paper has been under way for several years and has involved examination of specimens housed in a number of collections. We especially thank the curators of the collections of the Museum of Natural History, University of Kansas; National Museum of Natural History; American Museum of Natural History; Field Museum of Natural History; Museum of Comparative Zoology, Harvard University; Museum of Zoology, University of Michigan; and the Natural History Museum of Los Angeles County for loan of specimens and for hospitality and access to their collections during our visits. Monica Frelow assisted in several phases of our study. Gene M. Christman of the Museum of Vertebrate Zoology and James Hendel of the Scientific Photographic Laboratory, University of California, Berkeley, assisted in preparation of the figures. We have benefitted from discussions concerning several aspects of this study with Arden H. Brame, James Kezer, James F. Lynch, Stanley Sessions, Marvalee H. Wake, and Kay P. Yanev. We are indebted to several colleagues for extensive help in our field work, especially Jeremy L. Jackson, James F. Lynch, Theodore J. Papenfuss, Robert Seib, and H. Bradley Shaffer, but also to others too numerous to mention. The work of this laboratory on tropical salamanders has been supported by the National Science Foundation (current grant DEB-78 03008). Finally, we thank the Guatemalan Forest Service for making it possible for us to work in Guatemala, and the Direccion General de la Fauna Silvestre for collecting permits for Mexico.

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Submitted 6 October 1981; accepted 15 December 1982.





Wake, David B. and Elias, Paul. 1983. "New genera and a new species of Central American salamanders, with a review of the tropical genera (Amphibia, Caudata, Plethodontidae)." *Contributions in science* 345, 1–19.  
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