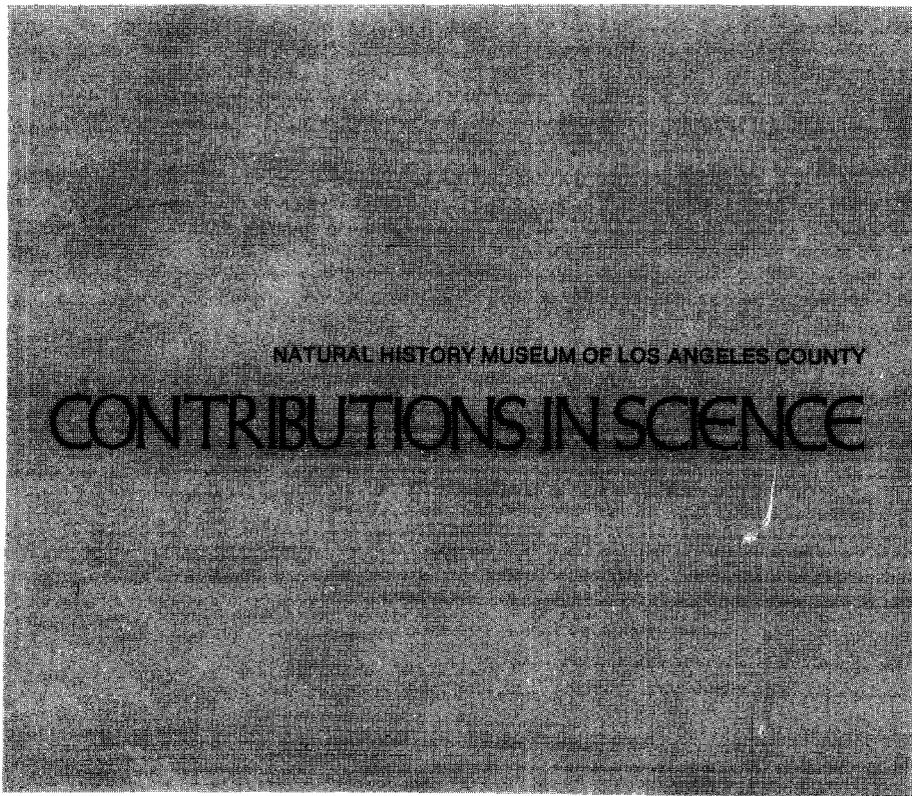


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SYSTEMATICS OF THE *CHIROPTEROTRITON BROMELIACIA* GROUP
(AMPHIBIA: CAUDATA), WITH DESCRIPTION OF TWO
NEW SPECIES FROM GUATEMALA

By JAMES F. LYNCH AND DAVID B. WAKE



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SYSTEMATICS OF THE *CHIROPTEROTRITON BROMELIACIA* GROUP
(AMPHIBIA: CAUDATA), WITH DESCRIPTION OF TWO
NEW SPECIES FROM GUATEMALA¹

By JAMES F. LYNCH² AND DAVID B. WAKE^{2,3}

ABSTRACT: The *Chiropterotriton bromeliacia* group contains five species of plethodontid salamanders with allopatric distributions in Northern Nuclear Central America. *Chiropterotriton xolocalcae* and *C. megarhinus* occur in the Pacific coastal mountains of Chiapas, Mexico. *Chiropterotriton bromeliacia* is known from the vicinity of Volcan Tajumulco in extreme southwestern Guatemala. Two new species described herein occur in western Guatemala, *C. rabbi* in the Montañas de Cuilco, and *C. cuchumatanus* in the Sierra de los Cuchumatanes. Detailed variational analysis of the five species reveals that each is morphologically distinctive, with nostril diameter being the character which best separates all five species. In order of increasing nostril diameter, the species are *C. xolocalcae*, *C. rabbi*, *C. cuchumatanus*, *C. bromeliacia*, and *C. megarhinus*.

There is general agreement in the results of several phenetic and phylogenetic estimates of relatedness among the five species. *Chiropterotriton bromeliacia* appears to be the most derived form, while *C. xolocalcae* seems least modified from the overall morphology of the presumed ancestral stock. The *bromeliacia* group is a distinctive unit within the genus, and occupies a rather isolated position in the phylogeny of neotropical plethodontid salamanders.

INTRODUCTION

Three species of salamanders of the genus *Chiropterotriton* are presently known from Northern Nuclear Central America, that portion of Middle America which lies between the Isthmus of Tehuantepec and the eastern border of Guatemala. All three forms inhabit the Sierra Madre, the rugged mountain chain which dominates the Pacific versant of the region (Fig. 1).

Chiropterotriton bromeliacia was described from material collected on the Pacific-facing slope of Volcan Tajumulco in southwestern Guatemala (Schmidt 1936). *C. xolocalcae* occurs only on Cerro Ovando, Chiapas, Mexico, about fifty kilometers west of Volcan Tajumulco (Taylor 1941). Further west in Chiapas, a few kilometers northeast of Tonolá, is the type locality for *C. megarhinus* (Rabb 1960). Until now, all three species have been known only from the type series, and there is little information concerning them in the literature.

The first section of the present paper reports the discovery of two undescribed species of *Chiropterotriton* in Northern Nuclear Central America, and provides new morphological and ecological information concerning the species previously known. The remainder of the paper is concerned with a phenetic and phylogenetic analysis of the group.

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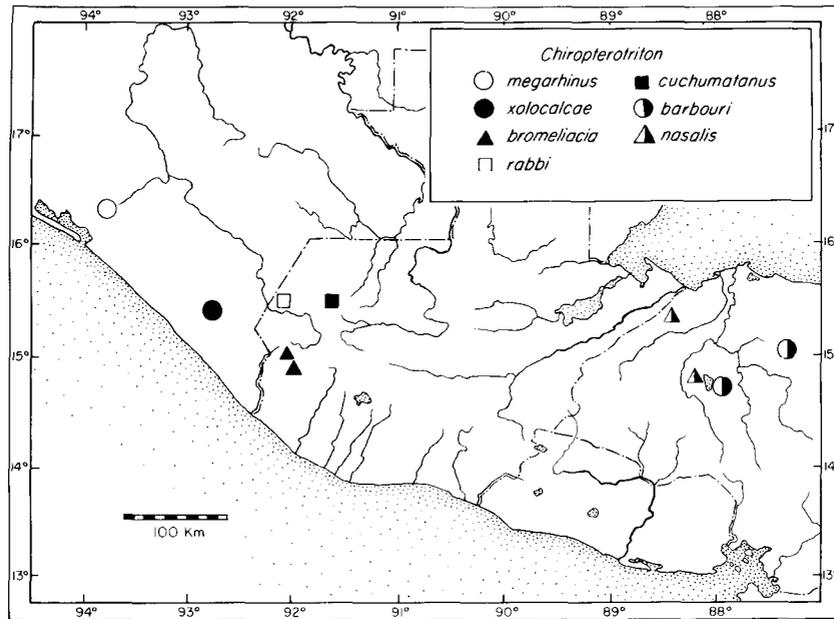


FIGURE 1. The distribution of *Chiropterotriton* in Nuclear Central America.

DESCRIPTION OF NEW SPECIES

The first of the new species was discovered in the Montañas de Cuilco, a rugged and isolated uplift located between the Pan American highway and the Rio Cuilco in westernmost Guatemala. We take pleasure in naming this form in honor of George B. Rabb, foremost student of the genus *Chiropterotriton*:

Chiropterotriton rabbi new species

Figure 2

Holotype: MVZ 103839. An adult male from 9.5 km W, 8.5 km S (airline) La Democracia, Huehuetenango, Guatemala, collected by James F. Lynch and David Bradford, 3 December 1971. The holotype is one of a series taken at elevations between 2100 and 2500 meters.

Paratypes: MVZ 103840-47, 103849-52, 103854-71, 103873-78; LACM 105298-300: all 39 specimens with same data as holotype. MVZ 109297-109301 (5 specimens). Collected at the type locality by James F. Lynch and Lynne D. Houck, 7 August 1972.

Diagnosis: Relative to other Central American *Chiropterotriton*, *C. rabbi* is a moderately large species (females to 37.5 mm, males to 36.7 mm SL²) with moderate to high numbers of maxillary teeth (range 23-64; mean 44.7 in 34 post-juveniles³ of both sexes), high numbers of vomerine teeth (range 13-29; mean 19.8 in 32 post-juveniles), and small nostrils (diameter < 0.2 mm in individuals with

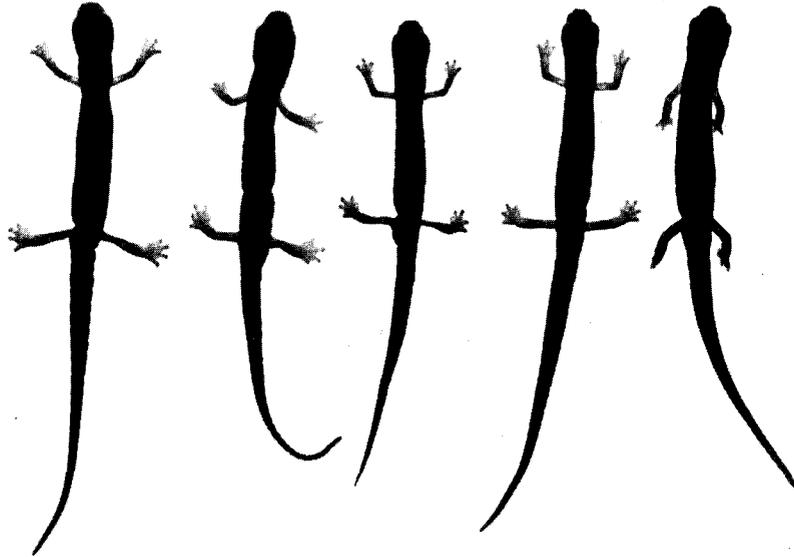


FIGURE 2. Dorsal view of typical adult males of the five species of the *Chiropterotriton bromeliacia* group. From left to right: *C. rabbi*, *C. xolocalcae*, *C. cuchumatanus*, *C. bromeliacia*, *C. megarhinus*.

SL > 30 mm). *C. rabbi* is distinguished from *C. bromeliacia* by larger average size, relatively broader head⁶, longer limbs, more maxillary and vomerine teeth, and much smaller nostrils (Fig 3); from *C. cuchumatanus* by larger size, relatively longer tail, more maxillary teeth, and smaller nostrils; from *C. xolocalcae* by larger size, longer limbs, and larger nostrils; from *C. megarhinus* by larger average size, narrower head, longer limbs, smaller feet, fewer maxillary teeth, more vomerine teeth, and much smaller nostrils.

Description: Compared to other Central American species of the genus, *C. rabbi* is a relatively large, gracile form. The median SL of 37 post-juveniles is 31.7 mm (mean 32.3 mm), and the largest individual (a female) of 45 examined is 37.5 mm

⁶SL = standard length, here defined as the distance from the snout to the posterior angle of the vent.

³Post-juveniles are individuals with SL > 25 mm. In most of the species considered here, 25 mm is approximately the dividing point between sexually mature and immature males, but the post-juvenile designation is intended primarily as an indication of body size, not sexual maturity.

⁶Statements concerning proportional distinctions between species are based on comparisons of adult males at a common projected SL (30 mm). All character differences noted in the diagnoses are significant at the 0.05 level or above. Statistical methods are explained in the section on interspecific comparisons; statistical summaries appear in figure 8, table 2, and the Appendix.

SL. The sexes do not differ appreciably in overall size, but certain other characters are sexually dimorphic. Males have significantly longer limbs and fewer premaxillary teeth than have females of equivalent SL. Tail length tends to be relatively greater in males, but the variance in this character is too high for the sexes to be separated at the 0.05 level. Larger males have moderately well-developed mental hedonic glands which are lacking in females. The following comments apply specifically to post-juvenile males unless otherwise noted.

Head width is moderate (projected mean 0.158 times SL at 30 mm SL); the snout is elongate and slightly protuberant dorsally. There is no detectable sexual dimorphism in the number of maxillary or vomerine teeth. Individual variation is great, but there is a significant ($P < 0.01$) increase in the number of maxillary and vomerine teeth with increasing size. Sixteen large individuals (SL > 32 mm) have 38-64 (mean 48.1) maxillary and 16-29 (mean 20.4) vomerine teeth. Nostril diameter decreases with increasing size, and in the largest individuals (SL > 32 mm) is 0.1 - 0.2 mm (Fig. 4). A sublingual fold is present.

The limbs are slender and relatively long. The coupling ratio (= hind limb + fore limb/axilla-groin length) exceeds unity in males having a SL greater than about 30 mm (range 1.01 - 1.16; mean 1.07), but is somewhat less (range = 0.92 - 1.03; mean = 0.96) in females of that size. Feet are of moderate size and are only slightly webbed (Fig. 5). Digits are relatively long and are rounded and slightly expanded distally. Distinct sub-terminal digital pads are present. The order of decreasing length of the fingers is 3, 4, 2, 1; for the toes the order is 3, 4, 2, 5, 1. The first digit on the hands and feet is short and barely free of the web. The base of the long, evenly tapering tail is only slightly compressed laterally. Tail length generally exceeds SL in animals having SL greater than about 30 mm, but not in juveniles and subadults.

Measurements of the holotype (in mm): Head width 5.3; snout to gular fold (head length) 8.8; head depth at posterior angle of jaw 2.6; eyelid length 2.8; eyelid width 1.3; anterior rim of orbit to snout 2.5; horizontal orbital diameter 1.7; interorbital distance 1.8; distance between vomerine teeth and parasphenoid toothpatch 0.8; snout to fore limb 10.6; distance separating internal nares 1.4; distance separating external nares 2.3; snout projection beyond mandible 0.6; snout to posterior angle of vent (SL) 34.5; snout to anterior angle of vent 31.4; axilla-groin 17.3; tail length 39.4; tail width at base 2.8; tail depth at base 3.1; fore limb length 9.1; hind limb length 9.3; width of right hand 2.6; width of right foot 3.9.

Coloration (in alcohol): The holotype is dark brown dorsally with obscure orange flecks and a general reduction in the intensity of pigmentation mid-dorsally. A distinct orange-tan interorbital bar is present. The rostral area is slightly lightened. A pair of orange-tan spots occurs in the pelvic area. The venter is light gray and has a mottled, "dirty" appearance resulting from a diffuse peppering of small melanophores. The chin is somewhat lighter than the trunk region of the venter, due to greater gaps between melanophores. The ventral surface of the tail is darker gray than the trunk, and becomes increasingly dark distally.

Many of the paratypes correspond to the holotype in general coloration, but considerable variation is evident. In addition to the uniform or faintly mottled pattern characteristic of the majority of specimens, the following modes of dorsal coloration were noted: (1) mid-dorsal light stripe, (2) paravertebral stripes, (3) distinct reticulate blotching. Individuals may combine features of more than one of these modes, and it is difficult to assign the pigmentation of every individual to a discrete category. The overall color of the dorsum varies from black-brown to red-brown to orange-tan. The most common pattern consists of a black-brown ground color interrupted by greater or lesser numbers of obscure tan to red-brown blotches, streaks, or vermiculations. A light-colored interorbital bar (or at least some light mark) is present in all individuals examined, but the intensity of the bar ranges from very conspicuous to barely discernible. Ventral coloration varies from dirty white to medium gray, depending on the abundance and dispersion of melanophores and the degree of contraction of pigment within each cell. A narrow ventrolateral fringe of frosted white pigment is present in many individuals. The chin is consistently lighter than the trunk region of the venter, the greatest contrast being observed in individuals with the darkest trunk pigmentation. Some individuals possess obscure to well-defined white spots in the cheek region of the head. The coloration of the underside of the tail may be uniform dark gray, "salt-and-pepper" gray and white, or dirty cream. In a few individuals (especially MVZ 103841, 103849, 103864) the ventral surface of the tail is coral pink.

The coloration in life was similar to that described for preserved specimens, except that the lighter colors were noticeably more intense. The ventrolateral frosting, which has largely faded in the preserved specimens, was conspicuous and pale green in the living animals.

Habitat: The holotype and all 44 paratypes were collected inside arboreal bromeliads (*Tillandsia*) in an isolated cloud forest on the north-facing slope of a northern outlier of the main ridge of the Montañas de Cuilco. The salamanders were encountered at elevations between about 2100 and 2500 m, but were most abundant between 2200 and 2400 m, where as many as six occurred in a single bromeliad. They were absent from seemingly suitable bromeliads between 2500 m and the 2650 m summit of the ridge. No *Chiropterotriton* were found under or inside logs or bark slabs, despite a careful search. Salamanders were taken as high in the trees as we searched (approximately 8 m). Associated with *C. rabbi*, but less common (five specimens encountered), was *Bolitoglossa resplendens*, a much larger, more robust species which was taken beneath logs as well as in bromeliads. Although the collecting effort was approximately equivalent on both visits to the type locality, many more salamanders were found in December (dry season) than in August (wet season).

Range: Known only from the type locality.

Early in 1973, Thomas Uzzell informed us (personal communication) that he had collected two specimens of *Chiropterotriton* in the Sierra de los

Cuchumatanes, an extensive plateau located north of the Pan American highway in western Guatemala. In July, 1973, we visited the locality described to us by Uzzell, and collected a series of an undescribed form which shall be known as

***Chiropterotriton cuchumatanus* new species**

Figure 2

Holotype: MVZ 113002, an adult female from forest along highway 9N, 8.5 km (by road) SW San Juan Ixcoy, Huehuetenango, Guatemala, at about 2860 m elev, collected 14 July 1973 by James F. Lynch, David B. Wake, Lynne D. Houck, and Albert B. Bennett.

Paratypes: MVZ 113003-05, 113007-19, 113021-22; LACM 105296-97; all 20 specimens with same data as holotype.

Diagnosis: The smallest of the five Central American *Chiropterotriton* considered here (females to 32.0 mm, males to 31.0 mm SL), post-juveniles having moderate numbers of maxillary (28-49; mean 37.8) and vomerine (9-20; mean 12.9) teeth, a relatively short tail, and moderately large nostrils (diameter 0.3-0.5 mm in individuals with SL > 30 mm). *C. cuchumatanus* is distinguished from *C. bromeliacia* by somewhat smaller size, relatively longer limbs, shorter tail, more maxillary and vomerine teeth, and smaller nostrils; from *C. rabbi* by notably smaller size, shorter tail, fewer vomerine teeth, and larger nostrils; from *C. xolocalcae* by somewhat smaller size, longer limbs, fewer vomerine teeth, and larger nostrils; from *C. megarhinus* by longer limbs, shorter tail, fewer maxillary teeth and smaller nostrils.

Description: *C. cuchumatanus* is a small, short-tailed species. Eighteen post-juveniles have a median SL of 29.6 (mean 29.3 mm; maximum 32.0 mm). The data suggest a slightly larger overall size for females (median SL 30.3) than for males (median SL 28.6 mm), but the small sample size precludes reliable assessment of this apparent dimorphism. The sexes do differ significantly in relative limb length, tail length, and foot width; males exceed females in each instance. The number of premaxillary teeth is greater in females (range 5-11; mean 8.1) than in males (range 1-5; mean 3.1), and these teeth are greatly enlarged in males. A mental hedonic gland is present in males larger than about 24 mm SL, but is conspicuous only in males 30 mm or larger. In general, *C. cuchumatanus* is more sexually dimorphic than the other Central American *Chiropterotriton*.

The following comments apply specifically to post-juvenile males except where otherwise indicated. Head width is moderate (projected mean 0.157 times SL at SL = 30 mm). The snout is relatively short and rounded. There is a significant positive correlation ($P < .05$) between the number of maxillary teeth and SL. Individual variation is great, however, and animals between 28 and 32 mm SL have 28-49 maxillary teeth. There is no significant correlation between SL and vomerine tooth number in post-juveniles ($r = 0.03$; $P > 0.1$). The mean number of vomerine teeth for nine post-juvenile males is 12.7 (95% C.L. = 10.5-14.8). The nostrils are moderately large (Figs. 3 and 4). A sublingual fold is present.

The limbs are moderately long in males, with a coupling ratio of 1.03 - 1.21 (mean 1.11) in nine post-juveniles. Females have significantly shorter limbs, with a coupling ratio of 0.82 - 0.99 (mean 0.90) in seven post-juveniles. Feet are of moderate size, and are significantly larger in males. Digits are of medium length

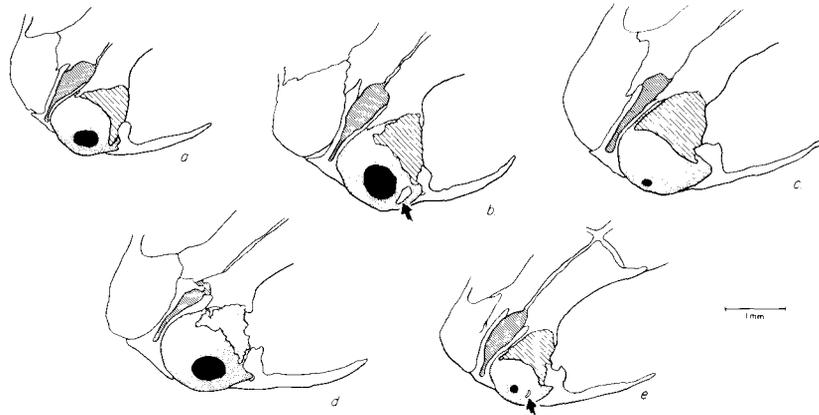


FIGURE 3. Three-quarter, anterolateral view of the nasal capsule region of the five species of the *Chiropterotriton bromeliacia* group showing important cranial elements. Heavy lines, nasal bone; fine lines, internasal fontanelle; stipple, cartilaginous nasal capsule. Opening in nasal capsule for external naris blackened. Arrows point to septomaxillary bones. (a) *C. cuchumatanus*; (b) *C. megarhinus*; (c) *C. xolocaelae*; (d) *C. bromeliacia*; (e) *C. rabbi*.

and are broadly rounded at the tips (Fig. 5). Distinct subterminal pads are present. The order of decreasing length of the fingers is 3, 4, 2, 1; for the toes the order is 3, 4, 2, 5, 1. The first digits of the hands and feet are short and barely extend from the webbing connecting them to the second digits. The overall development of webbing of the hands and feet is moderate (Fig. 5).

The base of the evenly tapered tail is rather stout and is slightly compressed laterally. Tail length is less than, or barely exceeds, SL in post-juvenile males, and is even shorter in post-juvenile females and juveniles of both sexes.

Measurements of the holotype (in mm): Head width 4.7; snout to gular fold (head length) 6.5; head depth at posterior angle of jaw 2.4; eyelid length 2.4; eyelid width 1.0; anterior rim of orbit to snout 1.8; horizontal orbit diameter 1.6; interorbital distance 1.5; distance between vomerine teeth and parasphenoid tooth patch 0.3; snout to fore limb 8.2; distance separating internal nares 1.1; distance separating external nares 1.0; snout projection beyond mandible 0.6; snout to posterior angle of vent (SL) 29.5; snout to anterior angle of vent 26.5; axilla to groin 15.3; tail length 25.3; tail width at base 2.3; tail depth at base 2.4; fore limb length 6.5; hind limb length 6.7; width of right hand 1.8; width of right foot 2.1

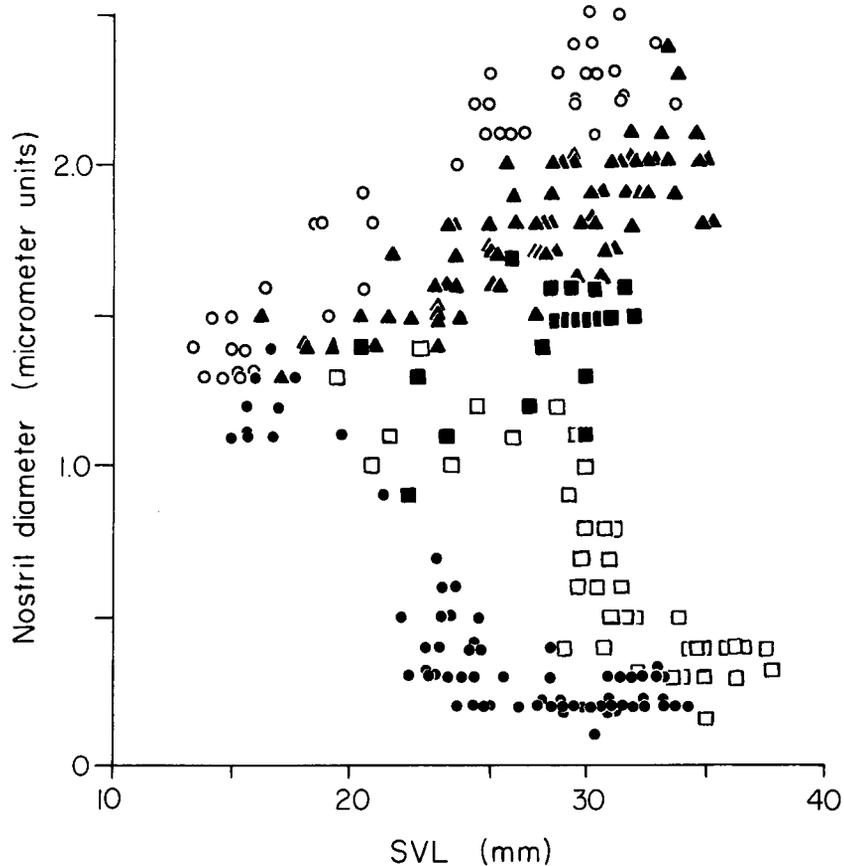


FIGURE 4. Scattergram showing relationship of nostril diameter to standard length in five species of *Chiropterotriton*. Symbols: open circles - *C. megarhinus*; solid circles - *C. xolocalcae*; triangles - *C. bromeliacia*; open squares - *C. rabbi*; solid squares - *C. cuchumatanus*.

Coloration (in alcohol): The holotype has a distinct red-brown mid-dorsal stripe which extends nearly to the tip of the tail. The red color grades into black-brown laterally. A distinct orange-brown interorbital bar is present. The rostral area is lighter than the post-cranial dorsum, but is lighter than the interorbital bar. The trunk and tail regions of the venter are lead gray. A narrow, faint suffusion of white pigment is concentrated in the ventrolateral region. The chin is considerably lighter than the remainder of the venter, due to wider spacing of melanophores and increased concentration of the melanin within each melanophore. There are no guanophores visible on the chin, but a few tiny white flecks are scattered along the side of the head between the jaw angle and the gular fold. The iris is flecked with numerous silvery iridophores. The paratypes show

considerable variation in color and pattern. In about one third of the specimens there is a mid-dorsal stripe of red-brown to tan color, but the intensity, width, and integrity of the stripe vary. Several specimens have a distinctly mottled gray and brown dorsal pattern, whereas some others are essentially uniformly gray-black to brown-black dorsally. Discrete color morphs are not distinguishable. The most consistent feature is the presence of at least some brown pigment, in the form of blotches, streaks, a mid-dorsal stripe, or a combination of these, on a dark gray to black background. All but one of the paratypes have an interorbital bar of lighter pigment. The rostral area is frequently marked with flecks or patches of orange-tan pigment, but is generally set off from the interorbital bar by a narrow dark band. The pelvic area generally lacks distinctive markings, but in some individuals there is a discernible brightening of the dorsal pattern in this region. A patch of dark pigment is located just posterior to the interorbital bar, but this feature is obscured in individuals having generally dark dorsal coloration.

Ventral coloration ranges from medium gray to nearly black. A faint ventrolateral rim of light pigment is visible in about half of the specimens. Chin

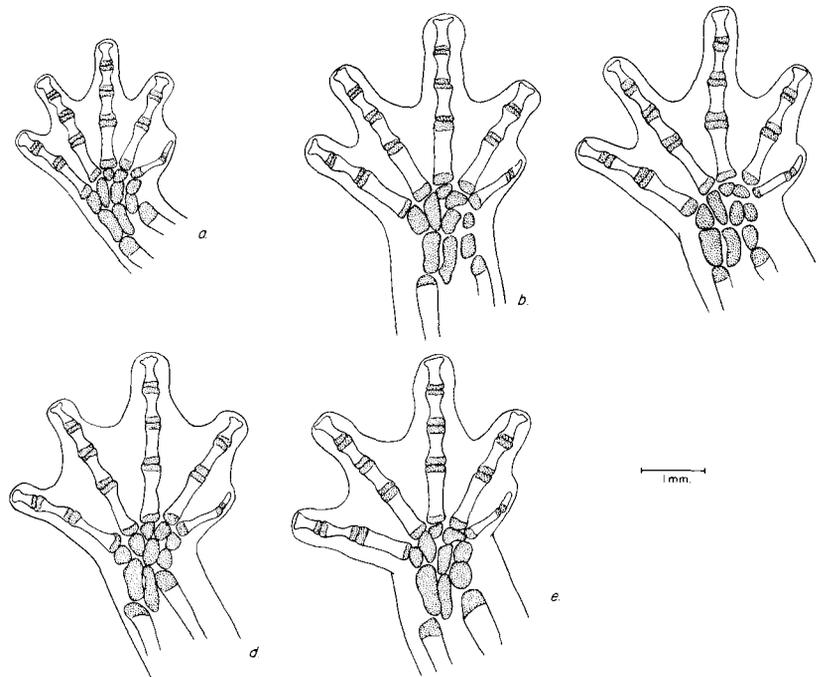


FIGURE 5. Feet of the species of the *Chiropterotriton bromeliacia* group, drawn from cleared and stained specimens with aid of microprojector, cartilage stippled. (a) *C. cuchumatanus*; (b) *C. megarhinus*; (c) *C. xolocalcae*; (d) *C. bromeliacia*; (e) *C. rabbi*.

coloration ranges from pale gray-white to a patchy salt-and-pepper gray-black, but is always distinctly lighter than the trunk region of the venter. In many individuals, irregular melanic patches give the chin a "dirty" appearance. Small white flecks or patches are present in the cheek region of all specimens. In some individuals these spots extend to the upper and lower labial regions. The iris is heavily suffused with silvery iridophores in all specimens. The ventral surface of the tail generally resembles the trunk region in coloration, but in a few individuals there are scattered small interruptions in the melanin network covering the underside of the tail. In one subadult male, the ventral surface of the regenerating tail has a coral pink hue.

The coloration in life was essentially as described here for specimens preserved in ethanol for two months.

Habitat: The type series was collected in a humid, slightly-disturbed forest on the rocky, north-facing slope of one of the main ridges of the Sierra de los Cuchumatanes. Oaks (*Quercus*) are the dominant trees at the type locality, but Madrone (*Arbutus*), Pine (*Pinus*), and Fir (*Abies*) are also present. The slope is strewn with limestone boulders, and there is relatively little undergrowth. To judge from the luxuriant carpet of mosses which covers rocks and tree trunks, the area is characterized by relatively high humidity, but no large bromeliads were noted. This oak forest is quite localized, and gives way to open pine woods and farmland within a few hundred meters of the type locality.

Twenty *C. cuchumatanus* were found beneath the bark of fallen logs and rotting stumps. A single individual occurred on the ground beneath a log. Uzzell (personal communication) reported finding two individuals under moss mats on tree trunks, but logs with loose bark seemed to be the favored microhabitat at the time of our visit. As many as four *C. cuchumatanus* were found under the bark of a single log.

The discovery of *C. cuchumatanus* is noteworthy not only because it is the first record for *Chiropterotriton* in the Caribbean drainage of Guatemala or southern Mexico, but also because *C. cuchumatanus* is the only Central American member of the genus which is not associated primarily with arboreal bromeliads.

Occurring in microsympatry with *C. cuchumatanus* was a larger species of salamander which provisionally has been identified as *Bolitoglossa rostrata*, a widespread form in the highlands of western Guatemala. The *Bolitoglossa*, which was more common than *C. cuchumatanus* (64 specimens taken vs 21 *Chiropterotriton*), was also found almost exclusively under the bark of stumps and logs. No other amphibians or reptiles were seen at the type locality.

Range: Known only from the type locality, but to be expected elsewhere in the uplands along the humid Caribbean-facing slopes of the Sierra de los Cuchumatanes.

REDESCRIPTIONS OF PREVIOUSLY KNOWN SPECIES

Chiropterotriton bromeliacia Schmidt

Figure 2

Oedipus bromeliacia Schmidt 1936:161, fig. 18

Chiropterotriton bromeleacea (sic) Taylor 1944:216

Holotype: CNHM 21062, an adult male from Volcan Tajumulco, at 8000 feet (2460 m) altitude on the trail above El Porvenir, San Marcos, Guatemala, collected 22 February 1934 by Karl P. Schmidt.

Material examined: CNHM 20291, 20294, 20324-26, 20382, 20657, 20693, 20695-7 and 20700 (57 specimens, all topoparatypes); MVZ 102955-64, 102971-77, 102992-3018, 103029-33, 103035-36, 103039-52, 103065-126, 103190-99, 103200-16, 103218-29, 103278-79, 103301-97, 103490-529, 107696-99, 107747-64 (430 specimens, all from Finca Insula, 7.5 km W, 1.5 km S (air line) San Marcos, Depto. San Marcos, Guatemala, elevation 2050-2400 m); MVZ 103230-58, 103280-83, 103286-98, 103468-89, 103575-86, 103706-09, 112960-113001 (126 specimens, all from west-facing slope of ridge 2-4 km (air line) W El Rincon, Depto. San Marcos, Guatemala, elevation 2400-2750 m); LACM 99472-79, MVZ 102965-70, 102978-91, 103019-28, 103034, 103037-38, 103053-64, 103217, 103259-77, 10328-85, 103299-300, 103398-467, 103530-69, 103591-705, 103710-812, 107700-46, 107765-83, 107784-89, 107795-875, 108422, 112939, 112941-59 (250 specimens, all from the vicinity of Ruta Nacional 1, approx 2 km S, 6-7 km W (air line) San Marcos, Depto. San Marcos, Guatemala, elev 2100-2500 m); MVZ 103570-74, 103587-89, 107790-94, 112938, 112940 (15 specimens, all from the vicinity of Ruta Nacional 1, approx 3 km S, 7.5-8.0 km W (air line) San Marcos, Depto. San Marcos, Guatemala, elev 1900-2070 m).

Diagnostic Characters:⁷ A moderate-sized *Chiropterotriton* (mean SL of 56 post-juveniles = 30.3 mm) having relatively few maxillary teeth (range 20-49; mean 33.6 in 53 post-juveniles of both sexes) and vomerine teeth (range 5-15; mean 10.1), and relatively large nostrils (diameter 0.5-1.0 mm in individuals with SL > 30 mm). *C. bromeliacia* is distinguished from *C. rabbi* by its narrower head, shorter limbs, lower numbers of maxillary and vomerine teeth, and larger nostrils; from *C. cuchumatanus* by its larger size, shorter limbs, longer tail, fewer maxillary teeth, and larger nostrils; from *C. xolocalcae* by its narrower head, smaller feet, longer tail, fewer premaxillary and vomerine teeth, and larger nostrils; from *C. megarhinus* by its narrower head, smaller feet, fewer maxillary teeth, and smaller nostrils.

Description: *C. bromeliacia* is a slender, long-tailed species with relatively short limbs and small feet. The maximum SL observed in a sample of 80 individuals is 35.5 mm, but specimens as large as 37.9 mm have been encountered among the more than 800 individuals collected along the Pacific escarpment west of San Marcos, Guatemala. The sexes are not strongly dimorphic in size (median and mean SL for post-juveniles = 30-31 mm for both sexes in the reference sample),

⁷Except where noted, the following comments are based on a detailed examination of a reference series of *C. bromeliacia* (MVZ 107795-875). This series was taken over a two day period in cloud forest west of San Marcos, Guatemala.

but there is a tendency for the largest individuals in any given sample to be females. A larger series (n= 162 post-juveniles) from Finca Insula has a slight, but significant ($P < .001$)⁸, sexual difference in SL (median SL for females 32.2; for males 31.1 mm). Males have significantly longer limbs and tails compared with females of the same SL. The head of *C. bromeliacia* is unusually narrow (projected mean = 0.153 times SL for males at 30 mm SL). The species has fewer maxillary teeth than the other *Chiropterotriton* of northern Central America. The number of maxillary teeth increases significantly with SL ($r = 0.74$; $P < .01$ for post-juvenile males). The projected mean number of maxillary teeth for standard males (SL = 30 mm) is 31.7 (95% C.L. = 30.4-33.0). Males have significantly fewer premaxillary teeth (range 2-8; mean 3.7) than females (range 6-11; mean 7.9), and these teeth are much larger in males. There is no significant relation between the number of vomerine teeth and SL in post-juveniles ($r = 0.17$, $P > 0.1$ for 42 males). The mean number of vomerine teeth in the sample of post-juvenile males is 10.1 (95% C.L. = 9.4-10.8; range 5-15). Nostril diameter increases markedly with SL, in contrast with the extreme ontogenetic reduction in nostril size which characterizes *C. xolocalcae* and *C. rabbi* (Fig. 4). Labial protuberances are poorly developed in females, but are obvious in males. A sublingual fold is present.

The limbs are relatively short. The coupling ratio is not significantly correlated with SL in males ($r = -0.14$, $P > 0.1$), but is weakly correlated in females ($r = -0.45$, $0.1 > P > 0.05$). For standard males the mean coupling ratio equals 0.99 (95% C.L. = 0.98-1.01); for females the corresponding value is 0.91 (0.89-0.93). The rather small feet average slightly larger in males, but the difference between the sexes is not significant at the 0.05 level. The moderately long digits are joined by moderate amounts of webbing, and their tips are rounded and slightly expanded (Fig. 5). Distinct subterminal pads are present. The order of decreasing length of the fingers is 3, 4, 2, 1; for the toes the order is 3, 4, 2, 5, 1. The first digits of the hands and feet are short and largely contained within the webbing. The base of the long, evenly tapering tail is very slightly compressed laterally. Average relative tail length increases with SL, and exceeds SL in post-juveniles of both sexes.

Coloration (in alcohol): Coloration is extremely variable in this species, as in most Central American *Chiropterotriton*. The overall ground color of the dorsum ranges from nearly black through various shades of brown to light tan and brick red, the most common color being black-brown. In most specimens some lighter pigment (light brown, yellow, or red) is present as irregular blotches, streaks, or chevrons. Rarely, a well-formed mid-dorsal stripe or a pair of paravertebral stripes is present. The light dorsal markings are generally rather obscure, but exceptional individuals are strikingly pigmented. A light-colored interorbital bar is almost invariably present, as noted by Schmidt (1936) and Rabb (1960). In some specimens the rostral area is lightened, but a narrow dark band generally separates the rostral patch from the interorbital bar. A darkened triangle of pig-

⁸Sexes compared using the distribution-free Wilcoxon Two Sample test.

ment is usually located immediately posterior to the interorbital bar. The dorsal light pattern (if any) tends to be intensified in the pelvic region.

Ventral coloration ranges from charcoal gray to dirty cream. The chin is generally similar in coloration to the trunk region of the venter, but a few individuals have a slight lightening of the chin. A faint ventrolateral rim of frosted white pigment is present in a minority of the individuals, but, when present, is not as conspicuous as in *C. rabbi*. Some specimens have a few tiny white flecks in the cheek region, but these are barely visible without magnification. The iris is suffused with silvery iridophores. The ventral surface of the tail is most often darker gray than anterior portions of the venter, but exceptional specimens have considerable reduction of melanic pigment, and a few have greater or lesser amounts of orange to brick red coloration. Schmidt (1936) presented photographs of preserved *C. bromeliacia*.

Habitat: Over 90 per cent of more than 800 specimens we have collected in the San Marcos area were taken inside arboreal bromeliads, as were all of Schmidt's (1936) paratypes from nearby Volcan Tajumulco. The species also occurs in fallen bromeliads and under the bark of logs, but has not been found under rocks or logs. Early in the dry season (November, 1974) we found the species to be relatively common in vertical banks of road cuts, especially in association with outcrops of fractured rock. The species seems to be restricted to cool, humid cloud forests where large tank bromeliads (*Tillandsia* and *Vriesia*) are abundant. We have taken as many as 12 individuals from a single bromeliad, and have found the species to be common as high in the trees as we have searched (approximately 10 m). The species has been collected at elevations between about 1900 and 2750 m, but is most abundant between 2200 and 2600 m. Several other species of salamanders occur in sympatry with *C. bromeliacia*. In the lower cloud forest (1900-2400 m) *Bolitoglossa engelhardti* and *B. franklini* are common bromeliad dwellers. *Bolitoglossa flavimembris*, a more terrestrial form, is occasionally taken in fallen bromeliads or under the bark of logs which harbor *C. bromeliacia*. Above 2500 m, most species of salamanders occurring in the same general habitat with *C. bromeliacia* are primarily terrestrial, but the following have been collected at least occasionally in bromeliads containing *Chiropterotriton*: *Bolitoglossa resplendens*, *B. rostrata*, *B. morio*, and a species of *Pseudoeurycea*. *Abronia vasconcelosi*, an arboreal anguid, has been found in microsymbatry with *C. bromeliacia*, as has the hylid frog *Plectrohyla sagorum*.

Distribution: The present report of *C. bromeliacia* from the mountains west of the city of San Marcos is the first record of the species from other than the type locality. The cluster of new localities is less than 10 km (air line) from the type locality, and it is likely that the species occurs continuously throughout the cloud forest between Volcan Tajumulco and the San Marcos area. However, searches for *Chiropterotriton* in seemingly suitable cloud forest on Volcan Chicabál, less than 25 km southeast of San Marcos, have been unsuccessful. Schmidt (1936) failed to find *Chiropterotriton* on the forested slopes of Volcan Atilán, approx-

imately 70 km (air line) SE San Marcos. The absence of *C. bromeliacia* SE of San Marcos is puzzling, for the three species of *Bolitoglossa* which co-occur with *C. bromeliacia* at moderate elevations near San Marcos have been taken at Volcan Chicabál and Volcan Atitlán. Nor does the species appear to range much northwest of the type locality. Collections of bromeliad-dwelling salamanders from Volcan Tacaná, which straddles the Guatemala-Chiapas frontier, and from the vicinity of Motozintla, Chiapas, do not include *Chiropterotriton*. *Chiropterotriton xolocalcae*, a distinctly different species, occurs at Cerro Ovando, approximately 40 km west of Motozintla.

Chiropterotriton xolocalcae (Taylor)

Figure 2

Oedipus xolocalcae, Taylor, 1941: 148

Chiropterotriton xolocalcae, Taylor, 1944: 216

Holotype: USNM 11371, an adult from Cerro Ovando, Chiapas, Mexico, at 7000-8000 feet, collected 16 April 1940 by Hobart M. Smith and wife.

Material examined: USNM 11400-11470 (71 specimens). All topoparatypes.

Diagnostic Characters: A *Chiropterotriton* of moderate size (females to 34.2, males to 33.2 mm SL). Post-juveniles have moderately high numbers of maxillary (31-60; mean 46.9) and vomerine (15-27; mean 20.8) teeth, a relatively short tail, and very small nostrils (diameter < 0.1 mm in individuals with SL > 30 mm). *C. xolocalcae* is distinguished from *C. bromeliacia* by broader head, wider foot, shorter tail, more maxillary teeth, many more vomerine teeth, and much smaller nostrils; from *C. rabbi* by smaller size, shorter legs, and smaller nostrils; from *C. cuchumatanus* by shorter limbs, more vomerine teeth, and much smaller nostrils; from *C. megarhinus* by slightly longer limbs, smaller feet, shorter tail, fewer maxillary teeth, more vomerine teeth, and much smaller nostrils.

Description: *C. xolocalcae* is moderate in size. Thirty-six post-juvenile males have a median SL of 31.0 mm (mean 30.2 mm). The 71 specimens examined include only four females longer than 25 mm SL. Males have significantly longer limbs than females, but there is no indication of sexual dimorphism in other proportional characters. Adult males have a reniform mental gland and fewer, but larger, premaxillary teeth (2.6; mean 3.8) than females (10-11; mean 10.3). The following comments apply specifically to post-juvenile males except where noted otherwise: The head is wide and somewhat flattened (projected mean head width 0.161 SL at 30 mm SL); the snout is somewhat elongate; the diameter of the nostril opening decreases dramatically with SL, and is minute in adults (Fig. 5). There is a significant positive correlation ($r = 0.55$; $P < .01$) between the number of maxillary teeth and SL. Males between 28 and 32 mm SL have 31-58 maxillary teeth (projected mean 44.6 at 30 mm SL). Vomerine tooth number is also correlated with SL ($r = 0.58$; $P < 0.01$). Males between 28 and 32 mm have 16-25 vomerine teeth (projected mean 19.9 at 30 mm SL). A sublingual fold is present.

The limbs are of moderate length; the coupling ratio, which is not correlated with SL, is 0.92-1.12 (mean 1.03) in males and 0.89-1.02 (mean 0.97) in females. The slightly webbed feet are moderately large and bear long, somewhat tapering digits which, although rounded at the tips, lack appreciable terminal expansions (Fig. 5). Distinct terminal subdigital pads are present. The order of decreasing length of the fingers is 3, 4, 2, 1; for the toes the order is 3, 4, 2, 5, 1. The first digit of the foot tends to be better developed and freer from the palmar webbing in *C. xolocalcae* than in the other *Chiropterotriton* of northern Central America, but the first digit of the hand is small and nearly enclosed by the webbing. The tail is slender, evenly tapering, and relatively short (projected mean 1.03 times SL at 30 mm SL).

Coloration (in alcohol): The 71 paratypes examined have faded considerably after long preservation, but they still display considerable variation in dorsal coloration. The most common pattern (29 individuals) consists of light brown to yellow-tan vermicular markings or mottling on a darker brown background. In many individuals the markings form an imperfect but distinct herringbone pattern. This pattern grades on the one hand into a more or less continuously light-colored dorsum (24 individuals), and on the other to an essentially unicolor darker brown dorsum (15 individuals). There is continuous variation between these modes, and the boundaries between them are somewhat arbitrary. Three additional specimens (4.2% of the sample) have cream-colored paravertebral stripes which extend posteriorly from the eye and become confluent in the lumbar region. Rabb (1960) examined 144 paratypes of *C. xolocalcae* and counted seven (4.8%) with paravertebral stripes. He also noted the presence of an interorbital bar or other light marking in 132 (91.7%) specimens, pelvic light markings in 123 (85.4%), and lightening of the rostral area in 22 (15.0%). No iridophores are visible in the cheek region or in the eye, but this may be an artifact of long preservation. A roughly triangular dark patch is present just posterior to the interorbital region in most specimens, and many individuals have a distinct pair of small dark spots in the scapular region.

Ventral color is dirty cream to medium gray, with the lighter tones more typical. The ventral melanophores do not form a continuous net, and individual pigment cells generally have a punctate or only slightly dendritic morphology. The chin is only slightly lighter than the trunk region of the venter. The tail coloration is similar to, or slightly darker than, that of the remainder of the venter.

Habitat: This species has been collected only once (345 specimens), from medium and large-sized bromeliads growing on the slopes of Cerro Ovando, a southern outlier of the Sierra Madre of Chiapas. The salamanders occurred between 5400-7100 feet (1635-2150 m), but the center of abundance was at about 6800 feet (2060 m), where "they were exceedingly numerous, in practically all bromeliads. In one plant 34 were found" (Taylor and Smith 1945:544). Subsequent visits to the type locality by the late Norman Hartweg (*vide* Stuart 1950)

and by one of us (JFL) have failed to yield additional specimens. Whereas the type series was collected late in the dry season, both unsuccessful attempts were made during the summer rainy season, suggesting the possibility of seasonal shifts in microhabitat. Similar, albeit not as dramatic, shifts in seasonal abundance have been observed for *C. rabbi* (see above) and certain other bromeliad-dwelling salamanders (Smith 1941).

Smith collected specimens of *Bolitoglossa nigroflavescens* in microsympatry with *C. xolocalcae* at the type locality, although the distribution of the former species, a larger and more robust bromeliad dweller, was centered at somewhat lower elevations. Subsequently, *B. nigroflavescens* (but not *C. xolocalcae*) has been taken at several localities between Cerro Ovando and the Guatemalan frontier.

Distribution: Known only from the type locality in southeastern Chiapas, Mexico.

Chiropterotriton megarhinus Rabb

Figure 2

Chiropterotriton megarhinus, Rabb, 1960: 304

Holotype: UIMNH 40782, an adult male from "the northern slope of Cerro Tres Picos, about 19 kilometers northeast of Tonala, Chiapas, Mexico. Altitude approximately 7000 feet" (= ca. 2120 m), collected 1 February 1957 by Thomas MacDougall.

Material examined: UIMNH 40777-81, 40783-4 (seven specimens, all topoparatypes); 45 uncatalogued specimens, all collected by Dennis E. Breedlove from Cerro Tres Picos, Chiapas, Mexico, elev 2100-2425 meters.

Diagnostic Characters: A medium-sized species (females to 37.5 mm SL, males to 33.8 mm SL); with high numbers of maxillary teeth (range 41-65; mean 50.3 in 24 post-juveniles of both sexes), low numbers of vomerine teeth (range 7-17; mean 11.8), and greatly enlarged nostrils (diameter of 0.7-1.0 mm in individuals with SL > 30 mm). *C. megarhinus* is distinguished from *C. bromeliacia* by wider head, broader feet, more maxillary teeth, and larger nostrils; from *C. rabbi* by wider head, shorter legs, broader feet, more maxillary teeth, fewer vomerine teeth, and much larger nostrils; from *C. cuchumatanus* by larger size, shorter limbs, longer tail, more maxillary teeth, and larger nostrils; from *C. xolocalcae* by shorter limbs, longer tail, more maxillary teeth, far fewer vomerine teeth, and much larger nostrils.

Description: Occasional individuals of *C. megarhinus* attain as large a size as any Central American member of the genus (maximum observed SL 37.5 mm), but typical individuals are of moderate size (for 18 post-juvenile males, median SL 30.1 mm, mean SL 29.7 mm; for 6 post-juvenile females, median SL 29.6, mean 31.0 mm). Sexual dimorphism in body proportions is not conspicuous, but males do have significantly larger feet and fewer (but larger) premaxillary teeth than

females of equivalent size. Males have well-developed mental hedonic glands. The following characterizations apply to post-juvenile males, except where noted: The head is broad (projected mean 0.162 times SL at 30 mm SL); the elongate snout protrudes considerably beyond the mandible. There is a significant positive correlation ($r = 0.81$; $p < 0.01$) between maxillary tooth count and SL, but not between vomerine tooth count and SL ($r = 0.10$; $P > 0.1$). There is no indication of important sexual differences in maxillary or vomerine tooth counts. Individuals between 28 and 32 mm SL have 44 to 56 maxillary teeth (for post-juvenile males, projected mean is 49.8 at 30 mm SL.) and 7 to 14 vomerine teeth (mean 10.9). The nostrils are very large (Fig. 4). A sublingual fold is present.

Limbs are short, with a coupling ratio of 0.92 to 1.08 (mean 0.99) in 17 post-juvenile males and 0.85 to 1.02 (mean 0.93) in seven post-juvenile females. This ratio shows no consistent relationship to SL in males, but is negatively correlated with SL in females ($r = 0.45$; $P < 0.05$). The hands and feet are large, moderately webbed, and bear moderately long digits which are rounded and slightly expanded distally (Fig. 5). The first digit of each hand and foot is short and nearly enclosed by the webbing connecting it to the second digit. Distinct subterminal pads are present. The order of decreasing length of the fingers is 3, 4, 2, 1; for the toes the order is 3, 4, 2, 5, 1. The evenly tapering tail is of moderate length, equal to or slightly exceeding SL in post-juveniles of both sexes.

Coloration (in alcohol): Color notes are based on examination of 45 individuals which had been preserved in 40% per cent isopropanol for approximately 15 months. The dorsal pattern is extremely variable in this species. The overall color of the dorsum ranges from very dark brown-black to yellow-tan. In about one-third of the specimens the dorsum is essentially unicolor and dark. In about one-fifth of the animals the dorsum is more or less mottled with light brown or gray, sometimes with the lighter pigment forming indistinct chevrons. In the remainder of the sample, light pigment is either concentrated into an irregular dorsal stripe (12 individuals) or a pair of paravertebral stripes (nine individuals). The dorsal stripe or stripes may be cream-colored or yellow-tan. In all but six of the 45 specimens an interorbital bar is present, but in most instances the bar is faint or discontinuous, or both. Individuals having a strong interorbital bar also tend to show at least slight lightening of the rostral area. The dorsal pattern tends to be somewhat brighter in the pelvic region, and a few individuals have distinct paired streaks or patches of light pigment in that area. The trunk region of the venter varies in color from dirty white to gray, the lighter tones being more typical. In general, the ventral melanophores are discrete and have a punctate or slightly dendritic morphology. The chin is slightly to considerably lighter than the remainder of the venter, due to larger gaps between the melanophores. The underside of the tail is generally similar in coloration to the trunk region of the venter, but in exceptional individuals it may be black or slightly yellow. There are no white spots evident in the cheek region. Preservation has clouded the eyes of the specimens, but at least some light iridophores are visible in the irises of most individuals.

Habitat: According to Rabb (1960), Thomas MacDougall collected the type series of *C. megarhinus* "from large terrestrial bromeliads (either *Tillandsia grandis* or *Vriesia* (sic) (*werckliana*) containing water. These were situated in somewhat dwarfed cloud forest within a thousand feet (3000 m) of the summit of Cerro Tres Picos." The 45 specimens examined in the present study were collected on the southeast slope of Cerro Tres Picos (elevation 2100-2425 m) by Dennis E. Breedlove on 28 May 1972. According to his notes, all of the salamanders were taken inside tank bromeliads (*Tillandsia* and *Vriesia*) in a cloud forest. Evidently, *C. megarhinus*, like *C. bromeliacia*, *C. rabbi*, and *C. xolocalcae*, is primarily a bromeliad-dweller. The only other salamander known to occur in sympatry with *C. megarhinus* is an underscribed *Bolitoglossa*. Three specimens of this large, black species have been collected (two by Breedlove, one by MacDougall) on the ground beneath logs or duff.

Distribution: Known only from the type locality, an isolated pocket of cloud forest in the Sierra Madre of southwestern Chiapas.

COMPARATIVE OSTEOLOGY

The five species discussed in this paper differ from all other *Chiropterotriton* in several important features. It is therefore appropriate to describe their osteology in some detail, and to consider their systematic status.

Rabb (1960) stated that species of *Chiropterotriton* from south of the Isthmus of Tehuantepec differ from those to the north in lacking septomaxillary and prefrontal bones. Based on examination of additional specimens, Wake (1966) reported that one species which occurs north of the Isthmus lacks septomaxillaries and one species in the south has the bones. Further, prefrontal bones were noted in one of the southern species. Thus, the two groups are not completely discrete on the basis of the characters used by Rabb.

In order to understand relationships within *Chiropterotriton*, it is first necessary to consider some aspects of the morphology of *Pseudoeurycea*, the most closely related genus. The two genera are not easily separable by discrete character differences, but all recent workers have recognized that two rather different kinds of salamanders are represented. In general, the species of *Pseudoeurycea* are large, stout, terrestrial salamanders. The hands and feet are unwebbed and are generalized in the arrangement of carpal and tarsal elements and the proportional relationships of the digits. Typically, the outer four digits of the feet are highly disparate in length, the third being clearly the longest and the fifth the shortest. In *Chiropterotriton* the species tend to be smaller and more slender. They are frequently arboreal or scansorial, and their hands and feet typically have a specialized tarsal arrangement (Wake 1966, and below). In addition, the digits often have bulbous tips which include expanded terminal phalanges, in contrast to the generally tapering digits characteristic of *Pseudoeurycea*. In *Chiropterotriton*, the four outermost toes are similar in length, although digit three is still somewhat longer, and digit five shorter, than the

others. Many species have moderate to considerable webbing of both hands and feet.

While Wake (1966) considered the two genera to be distinct, he was unable to find a single feature which would separate all species along traditionally accepted generic lines. Perhaps the most fundamental difference which separates the northern species of *Chiropterotriton* from all *Pseudoeurycea* is the presence in the former of a specialized tarsal configuration, which may be functionally related to an arboreal way of life (Wake 1966). The relatively large fifth tarsal articulates with the central element in these species. This differs from the generalized plethodontid pattern, present in all *Pseudoeurycea*, in which the fifth tarsal is small and is excluded from contact with the central by an extensive articulation of the relatively large fourth tarsal and the fibulare. In some southern *Chiropterotriton* (*nasalis*, *abscondens*) the fourth and fifth tarsals are fused, but others, including the five species discussed in this paper, have the arrangement typical of *Pseudoeurycea*. These observations led Wake (1966) to conclude that *Chiropterotriton* differs from *Pseudoeurycea* in having a derived arrangement of tarsal elements (by virtue of rearrangement or fusion of elements), or, for species with the generalized tarsal pattern, in lacking prefrontal bones. At that time only *C. bromeliacia* and *C. xolocalcae* were known to fall into the latter category; here we add three more species (*C. megarhinus*, *C. rabbi*, *C. cuchumatanus*) and define the *bromeliacia* species group as follows: salamanders of the genus *Chiropterotriton* which differ from all other members of the genus in having a generalized tarsal arrangement and from all *Pseudoeurycea* in lacking prefrontal bones. We retain the species of the *bromeliacia* group within the genus *Chiropterotriton*, rather than assigning them to *Pseudoeurycea*, on the basis of their small size, arboreal way of life, and because they have hands and feet which resemble those of northern species of *Chiropterotriton* (e.g., *multidentatus*, *arboreus*, and *chiropterus*) in all respects, save the tarsal arrangement. This action requires either, 1) that ancestral *Chiropterotriton* had mesopodial patterns of the primitive type, which have been retained only in the *bromeliacia* group among modern *Chiropterotriton*, or, 2) that ancestral *Chiropterotriton* had, from their earliest divergence from the *Pseudoeurycea* lineage, specialized mesopodial patterns, and that ancestors of the *bromeliacia* group experienced a reversal to the primitive condition. A third possibility is that the genus *Chiropterotriton*, as currently recognized, is polyphyletic.

The following cleared and stained salamanders were used for the osteological portion of this study: *C. bromeliacia* 15, *C. cuchumatanus* 1, *C. megarhinus* 2, *C. rabbi* 6, *C. xolocalcae* 2. Most specimens are adults, but juveniles of both *C. bromeliacia* and *C. rabbi* were available. In addition, one small *C. bromeliacia* was embedded in paraffin, sectioned in the frontal plane, and stained by the Van Gieson method. Although the five species are closely similar in general osteology, each possesses a unique combination of features.

Skulls of these species are well-articulated, except in the region of the snout. Premaxillaries, maxillaries and dentaries are all rather slender and weak in comparison with larger northern species such as *Chiropterotriton priscus*. As is typical

for many neotropical salamanders, the dental portion of the premaxillary is small. It is smaller in males than in females, and is offset anteriorly from the anteriorly extended curve formed by the maxillaries. No neotropical plethodontids consistently have paired premaxillaries, and a bony bridge joining the two dental portions is normally present (the only exception known is a single specimen of *Thorius pennatulus*; Wake 1966). In *C. xolocalcae* this bridge is very thin and the bone is nearly divided (Wake 1966). Frontal processes are separated for their entire length in all specimens examined of all five species of the *bromeliacia* group. These processes are rather slender, except in *C. bromeliacia*. The latter is the only one of the five species in which the distal tips of the processes are consistently expanded to the point that the internasal fontanelle is nearly enclosed. Facial portions of the maxillary bones are small and articulate weakly (if at all) with the nasals. The facial processes are largest in *C. xolocalcae* and *C. rabbi*.

The cartilaginous nasal capsules (Fig. 3) protrude moderately (*C. xolocalcae*, *C. cuchumatanus*, *C. rabbi*) to greatly (*C. bromeliacia*, *C. megarhinus*). The latter two species have the largest nostrils. The nasal bones lie over the dorsal and dorsolateral surfaces of the nasal capsules, their shape conforming to that of the underlying capsule. In general, nasal bones of all species are somewhat reduced in size, but interspecific differences are evident. *Chiropterotriton xolocalcae* has large, well-formed nasal bones, in which the anterior-posterior length approximates the width. The bones are nearly as large in *C. rabbi*, but in the latter species the anterior border is more deeply concave than in *C. xolocalcae*. In the other three species the bones are somewhat too much shorter and the anterior border of the nasal bone has the appearance of having been eroded. Actually it has failed to develop as fully as in *C. rabbi* and *C. xolocalcae*. In the latter two species and (to a lesser extent) in *C. cuchumatanus*, the nasal bone is well-articulated with its neighboring elements. In *C. bromeliacia* and *C. megarhinus* there is little contact with surrounding bones.

In *C. rabbi* and *C. xolocalcae*, where the facial portion of the maxillary is fairly large, the foramen of the nasolacrimal duct impinges on the posterolateral margin of the nasal and the dorsoposterior margin of the maxillary. In other species the duct lies behind the nasal, and the posterolateral margin of the bone sometimes bears a concavity. In *C. cuchumatanus* the nasal bone follows the nasal capsule ventrolaterally for a considerable distance. The nasal of *C. bromeliacia* is the least well-developed; in this species the bone is highly variable in shape, and has very irregular margins.

In many primitive plethodontids septomaxillary bones are present in the walls of the nasal capsules behind the nostril in contact with the nasolacrimal duct. The bones are absent in most neotropical salamanders (Wake 1966), but are found in the majority of *Chiropterotriton* north of the Isthmus of Tehuantepec. Of the five southern species considered here, *C. megarhinus* possesses the best developed septomaxillaries; in fact, its septomaxillaries are nearly as large as in any neotropical species. This is a rather unexpected find, for the species also has the largest nostrils of any member of the genus. One might have predicted

that an increase in nostril size would have been accompanied by septomaxillary loss, through erosion of the bone. Actually, as is apparent in figure 3, the septomaxillary bone does not border the nostril in these species; rather, it is located about midway between the nostril opening and the facial process of the maxillary. The bone is present and well-developed in both specimens of *C. megarhinus*, and we presume that it is a consistent feature of the species. This is not true of any of the remaining species. Minute, crescentic septomaxillary bones are present in two of the six specimens of *C. rabbi* (Fig. 3). They are absent in the largest individual as well as in the three smallest specimens. There are no septomaxillaries in 13 of 15 *C. bromeliacia*. In the two exceptional specimens a septomaxillary is present on one side only. In one individual the bone is minute, as in *C. rabbi*. In the other it is well-developed, and only a little smaller than in *C. megarhinus*. This latter individual was one of the two available to Wake (1966) and is the basis for his report of the presence of septomaxillaries in this species. The other specimen available to him in 1966 has been re-examined. It has a small, possibly bony heterotopic mineralization in the vicinity of the nostril on one side only, but it is not in the normal position for a septomaxillary. No sign of septomaxillary bones can be seen in *C. cuchumatanus* or *C. xolocalcae*.

The frontal and parietal bones are well-articulated to each other, and there are only small dorsal fontanelles. The frontals have well-defined, relatively large lateral tabs, which overlap the parietals. Facial portions of the frontals are small, and there is little lateral excursion. The medial edge of the facial portion is emarginate, following the outline of the internasal fontanelle. Typically the frontal is drawn into a sharply pointed process, which extends forward between the nasal and the frontal process of the premaxillary. The face region of the skull of *C. bromeliacia* is foreshortened, relative to the other four species, and the facial portion of the frontal is especially small.

There are no diagnostic features of the occipito-otic, squamosal, or quadrate bones. There are no otic crests. The squamosals are broad dorsally, where they lie against the otic capsule, below a small ridge, and they extend anteroventrally to a blunt point. Neotropical salamanders characteristically lack columellar processes of the opercular apparatus, but they are present in many species of *Chiropterotriton*. Very short and inconspicuous processes are present in *C. cuchumatanus* and *C. megarhinus*. The processes are even smaller, but still discrete, in *C. xolocalcae*. Similarly inconspicuous processes are present in three *C. bromeliacia*, but absent in ten others. There are no processes in any of the specimens of *C. rabbi*.

Vomers of the five species are similar in that the body portion is relatively small and flat. The paired vomers are in direct contact from the vicinity of the inner margin of the tooth row to the posterior margin of the intervomerine fontanelle, at the level of the middle of the internal nares. The preorbital process of the vomer is present in *C. rabbi* and in *C. xolocalcae*, but is absent in the remaining species (Fig. 6). Some individuals of *C. bromeliacia* may have a very minute projection, but none has a true process. In *C. rabbi* the process bears teeth nearly to its tip, but in *C. xolocalcae* the teeth extend only to about the midpoint

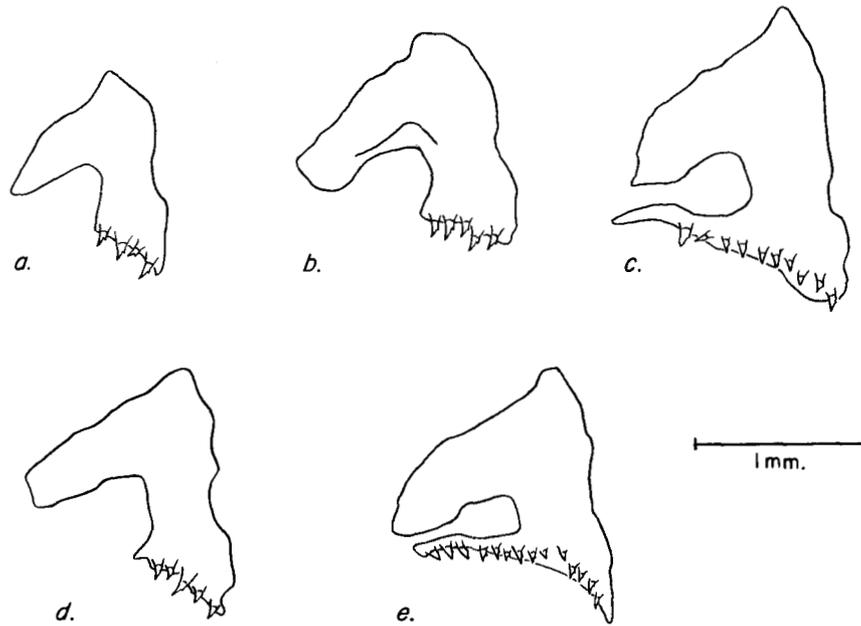


FIGURE 6. Vomers of the species of the *Chiropterotriton bromeliacia* group. (a) *C. cuchumatanus*; (b) *C. megarhinus*; (c) *C. xolocalcae*; (d) *C. bromeliacia*; (e) *C. rabbi*.

of the process, or slightly beyond. Those species which lack the process have relatively large nostrils, but the internal naris is not notably enlarged.

There are no especially distinctive features of the paraphenoid or the posterior patches of vomerine teeth which it bears. There are about 100 vomerine teeth in the larger specimen of *C. xolocalcae*. Ankylosed teeth cannot be counted without damaging the specimens, but these appear to be typical numbers for adult specimens. The patches are separated moderately from each other.

The hyobranchial apparatus has not been studied in detail. This can only be done effectively with sectioned material. It is clear, however, that the apparatus has a rather generalized structure, compared to what is found in other neotropical groups (Wake 1966). The epibranchials are by far the longest element in the apparatus, but they are not exceptionally elongated relative to other neotropical species. Rami are of moderate length. The apparent presence of a lingual cartilage, based on examination of cleared material, is confirmed for *C. bromeliacia* by examination of the sectioned individual. However, the element is very small.

Vertebrae of neotropical salamanders typically have small centra which are virtually nonexistent at the midvertebral level (Wake 1970). Relative to the anterior portion of each centrum, the posterior is more extensive and more

generalized structurally. Posteriorly, a bony "husk" surrounds a spindle-shaped intervertebral cartilage, which extends into the anterior part of the next vertebra. However, the anterior part of each vertebra is relatively small, and the cartilage appears to be at least partially mineralized. In none of these species is the posterior portion of any intervertebral cartilage converted into a condyle, such as is seen in some tropical plethodontids (Wake 1970). In respect to other features the vertebrae have generalized structure. The rib bearers are paired on each side of all but the last (and sometimes even on that) trunk vertebra. Ribs are clearly two-headed, and of intermediate length for the genus (Wake 1966). There are 15 trunk vertebrae. All but the last invariably bear ribs; the last vertebra often bears small ribs. The single sacral vertebra has well-developed paired rib bearers and stout, short ribs. The two caudosacral vertebrae bear long transverse processes, which generally extend laterally nearly perpendicular to the body axis, with only a slight posterior slant. The first caudal vertebra bears simple, elongate transverse processes which are directed anterolaterally from their attachment at the anterior end of the vertebra. On succeeding vertebrae the transverse processes retain their orientation and position, but become progressively shorter. They are present on most of the vertebrae of the tail. The number of caudal vertebrae is difficult to determine with accuracy in our material, and is probably subject to some ontogenetic increase. Adults of the five species have from 25 to 36 tail vertebrae.

Limb elements are simple and unspecialized in structure in all five species. There are no tibial spurs or crests.

Hands and feet of the five species generally have similar cartilaginous and bony structure. The eight carpal elements are arranged in a standard, generalized pattern. The outermost distal tarsal is very large relative to its neighbor. The primitive arrangement of the tarsal elements has been discussed above. The first metatarsal and first metacarpal are the shortest of their respective groups by a wide margin, and they are also relatively slender elements. The fifth metatarsal is shorter than the three middle elements. The phalangeal formulas are 1, 2, 3, 2 and 1, 2, 3, 3, 2 for the hand and foot, respectively. The only phalanx of the small first digit is short, slender and pointed. Terminal phalanges of the other digits are expanded considerably; each has a ventral projection on its distal end which serves as a ligament attachment. The terminal phalanges of the third finger, and of the third and fourth toes, are longer than the penultimate phalanges. In some individuals other terminals may be as long as, or slightly longer than, the penultimate phalanges. In a given foot, the combined length of the bony parts of all terminal phalanges is between about 0.65 and 0.80 of the length of all non-terminal phalanges combined. The total amount of phalangeal bones is 1.1 to 1.3 times greater than the total metatarsal bone in the few specimens in which it was directly measured (one to two specimens of each species). In order to give some idea of the relative lengths of digits, the combined length of the metatarsals and phalanges of the third digit was divided by the same measurements for the fifth digit. For the five species of *Chiropterotriton* this index of relative digital length ranges from 0.69-0.76. For *Pseudoeurycea* the corresponding figures are typically lower, indicating a greater differential in the length of the third and fifth digits.

OTHER INTERSPECIFIC COMPARISONS

The first part of this section is an evaluation of morphological differentiation in the five species of *Chiropterotriton* inhabiting northern Nuclear Central America. In the second part, these morphological data are used as a basis for speculation about the phylogenetic relationships within the group. A relatively detailed account of our phenetic and phylogenetic methodology is presented, for we intend to employ similar techniques in a forthcoming series of systematic studies of neotropical salamanders.

Because insufficient numbers of juveniles and post-juvenile females of four species are available, the analysis is mainly restricted to post-juvenile males (i.e., those with a standard length of at least 24 mm).

METHODS

Analyses of individual characters: The 11 characters considered here include six proportional measurements—(1) standard length, (2) head width, (3) nostril diameter, (4) combined length of hind limb and fore limb, (5) foot width, (6) tail length; two meristic characters—(7) number of maxillary teeth, (8) number of vomerine teeth; and three presence-absence characters—(9) condition of septomaxillaries, (10) condition of preorbital vomerine process, (11) condition of the columellae. Characters 2-8 generally vary significantly with overall size, so simple summary statistics cannot be used to compare populations. Instead, we computed simple least-squares regression statistics relating variation in each "dependent" (i.e. size-correlated) morphological feature to variation in a single "independent" indicator of body size. Standard length (character 1) was chosen as the best available independent index to overall size. The choice is reasonable for this group, since the number of trunk vertebrae is fixed at 15 (Wake 1966). This means that standard length is not subject to important variation that is unrelated to differences in overall body size. Computational formulas are as given in Draper and Smith (1966).

Regression Statistics: The linear equation expressing the covariance of a size-dependent character (Y) with variance in standard length (X) can be written

$$\hat{Y}_i = \bar{Y} + b_1 (X_i - \bar{X}) \quad (1)$$

where \hat{Y}_i = the predicted mean value of Y at $X = X_i$

b_1 = constant = computed estimate of the regression coefficient

The estimated standard error of Y at a particular $X = X_k$ is given by

$$\text{est. S.E. } (Y_k) = \frac{s^2}{n} + \frac{(X_k - \bar{X})^2 s^2}{\sum_i (X_i - \bar{X})^2} \quad (2)$$

where n = sample size. For a given sample size (n) and sample variance about the regression (s^2), the standard error of Y is smallest at $X_k = \bar{X}$.

In many problems involving comparison of regressions, particularly in morphological studies, the Y -intercept (i.e. the $X_k = 0$ line) is outside the range of observed X 's, and far from \bar{X} . In the samples of post-juvenile male salamanders considered here, the smallest X -values are 25 mm, and \bar{X} varies between 29-32 mm. Because the Y -intercept is so far removed from the data points on which the regression relationship is based, the confidence limits around $b_0 (= Y_0)$ are broad, making discrimination between species on the basis of b_0 values impossible in many instances. However, when the same regressions are compared at the grand mean of the individual sample means ($X_k = 30$ mm), many significant interspecific differences are evident. All comparisons were therefore standardized to $X_k = 30$ mm, and \hat{Y}_{30} was tested for interspecific differences. Hereafter these idealized 30 mm males are termed *standard* males. The 95 per cent confidence limits of the \hat{Y}_{30} values for each character are obtained by multiplying the standard error by the appropriate t -value for $(n-2)$ degrees of freedom. In those instances where the correlation between standard length and a proportional or meristic morphological character was found to be non-significant at the 0.05 level, simple univariate means and their confidence limits were substituted for the regression predictions. Standard length was used as a population character by averaging the standard lengths of the post-juvenile males in each sample (Fig. 7).

This mode of analysis has certain deficiencies. It does not include an assessment of variation in the growth process itself. Allometric differences could result in convergence toward a common adult morphology in species which differ significantly as juveniles. It is also possible that some aspects of the morphology of the two sexes vary independently, leading to different patterns of sexual dimorphism from species to species. Larger sample sizes would allow these and other possibilities to be explored, and additional useful systematic characters might well result from such an analysis. Thus, the present methodology is considered conservative in respect to its ability to detect interspecific morphological differences.

Osteological Characters: Characters 9-11 are osteological features (see above, Comparative Osteology) of adult individuals of both sexes. Although osteological characters are commonly thought to be more conservative (and, hence, more reliable) indicators of relationships than limb proportions and tooth counts, we found some variation in all three osteological traits within a series of twelve *C. bromeliacia*. In view of the small number of cleared specimens of the other species, we have been conservative regarding the significance of minor interspecific differences in characters 9-11. It is therefore possible that, as more extensive comparative osteological material becomes available, we may have to modify our estimates of what constitutes the typical character states for each species.

Discriminant Analysis: The analysis of size-correlated characters through simple linear regression techniques is but one step advanced from the classical univariate

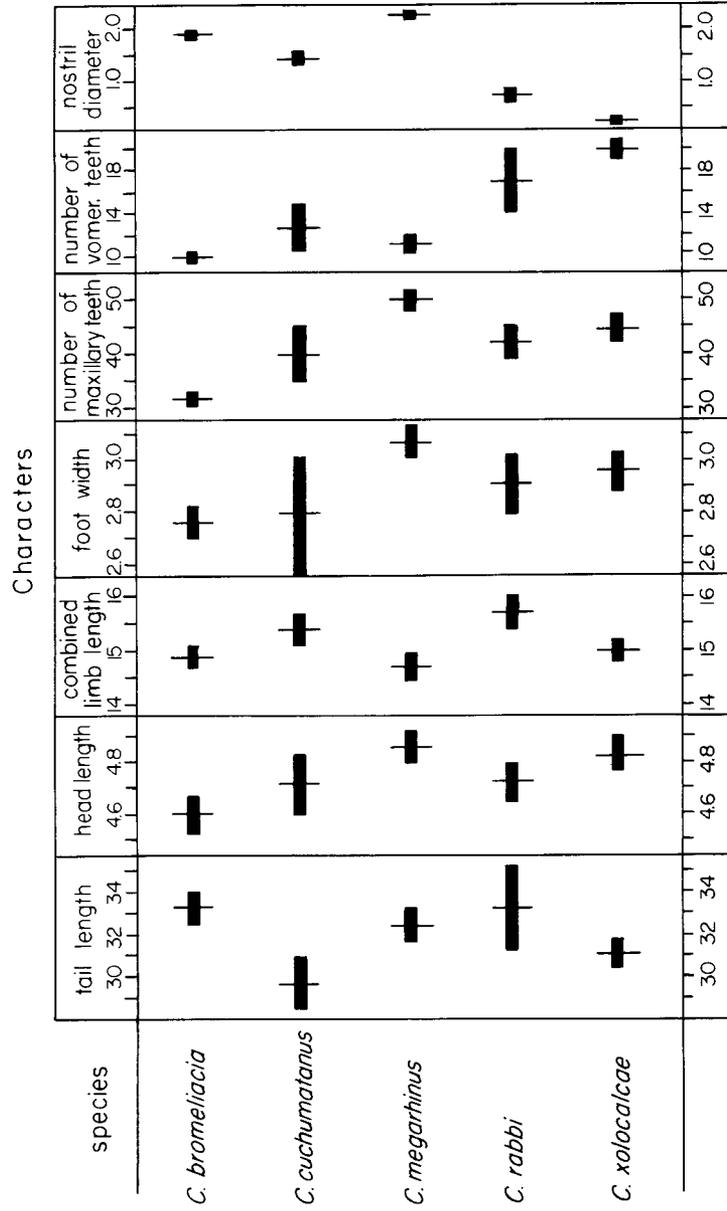


FIGURE 7. Predicted mean (vertical line) and 95% confidence limits (solid bar) for eight characters in post-juvenile males of the *Chiropterotrifon bromeliacia* group. See text for further explanation.

approach to character analysis. A multivariate approach, by which *all* morphologic characters are considered simultaneously, can provide additional information about the underlying major components of variation which often are obscured by confusing patterns of variation in single characters.

Canonical variate analysis (Seal 1964; Blackith and Reyment 1971) was employed in an attempt to sort the key components of interspecific differentiation among the five populations of *Chiropterotriton*. We utilized the University of California, Berkeley, version of the BMD07M program for stepwise discriminant analysis.

The stepwise procedure involves selection of variables from the original set (in this case, characters 1-8 were considered in 99 post-juvenile males for which complete sets of measurements and counts were available) in the order of their decreasing ability to maximize the ratio of between-group to within-group variance. Here, the "groups" are the five samples of post-juvenile males.

The first morphological variable entered is the one which allows the greatest degree of differentiation between groups. Taken singly, each successive variable is a less efficient discriminator, but combinations of increasing numbers of variables allow increasingly efficient separation of the groups. At each "step" in the procedure, the statistical significance of the contribution made by the entering variable is evaluated, using the F-test. After the entry of a variable into the discriminant function, the F-values for the variables previously entered, and for those not yet entered, are recomputed. The stepwise procedure continues until either 1) none of the remaining unentered variables satisfy a predetermined criterion for statistically significant contribution to intergroup discrimination, or 2) all variables have been entered. A useful feature of the BMD07M program is that it computes the "posterior probabilities" which give the likelihood of each individual specimen being a member of each of the designated populations. These data are summarized in a classification matrix which gives the number of "correct" and "incorrect" assignments of individuals to their proper populations. In our study, where each sample of salamanders was taken from a geographically disjunct population, an "incorrect" designation for any given individual simply means that no reliable morphological grounds exist for assigning the specimen to its actual "home" population. In other situations (e.g. where sympatric taxa are involved) the "incorrect" designations might represent actual misidentifications.

Finally, coefficients for the canonical axes (i.e., eigenvectors, or latent roots), which represent the main independent trends in interspecific variation, were computed. The positions of all specimens were plotted relative to the first two of these axes.

Phenetic clustering: The predicted mean character values for each population were used as a basis for clustering the species according to overall morphological similarity. The Prim method and the Wagner method, two related clustering techniques, were utilized. General descriptions of these, together with computational algorithms, can be found in a useful paper by Farris (1970); further discussions and examples are presented by Wagner (1961), Kluge and Farris (1969), Farris (1972), Lundberg (1972), and Estabrook (1972).

The five populations of *Chiropterotriton* will be referred to as OTU's (operational taxonomic units). The Prim method yields a network which links each OTU to whichever other one it most resembles morphologically, resemblance being determined by summing inter-OTU differences over the entire array of standardized character values.

The Wagner method uses the same matrix of inter-OTU differences as a starting point, but differs from the Prim method in generating hypothetical taxonomic units (HTU's) wherever their presence on the network will shorten the total linkage distance (i.e., the "Manhattan distance") between neighboring triads of taxa.

The Prim and Wagner methods are termed *parsimonious* because they produce the shortest possible networks linking the OTU's, given the absence or presence of hypothetical intermediate forms. If the evolution of a group has not involved reversals, parallelisms, or convergences in the development of any characters, the Wagner method will not generate HTU's, and the two clustering schemes will produce identical networks of OTU's. However, when any of these events has occurred, the Wagner network will always be shorter than the corresponding Prim network.

The Prim and Wagner Networks are said to be unrooted because they are not oriented with respect to evolutionary direction (Farris 1970). Construction of these networks does not require designation of primitive or derived OTU's (or character states). However, assuming that closest phenetic neighbors are also closest phylogenetic neighbors (this assumption is by no means self-evident, as noted by Estabrook 1972), and assuming that evolution proceeds parsimoniously (Camin and Sokal 1965), the "correct" evolutionary linkage will be expressed by one or the other network, depending on whether HTU's are allowed in the phylogeny. If, by whatever means, one is able to designate a particular OTU (or HTU) as ancestral, the previously unrooted Prim or Wagner Network is converted into a rooted (i.e., directed) evolutionary tree.

An unresolved problem common to all attempts at clustering OTU's is whether or not to weight characters differentially. Various weighting schemes have been proposed (e.g., Farris 1966, 1973; Eades 1970), but after considering the alternatives we decided that the least arbitrary procedure in the present instance was to give equal weight to all eleven characters at the outset. It is probably correct (but not necessarily enlightening) to state that some characters are more reliable indicators of relationship than others. In practice, it is difficult to decide *a priori* which characters are good, and even more so to determine just how much emphasis to give them, without invoking circular reasoning. Mayr (1969) has noted that equal weighting of characters is most justifiable at the species level.

As is discussed in the following section, certain aspects of our character analysis do involve *intrinsic* weighting. For example, examination of the interspecific pattern of correlations between character states in apparently distinct characters led to the deletion of some characters because they are non-independent expressions of the same integrated functional system. Similarly,

phylogenetic analysis of characters ignores inter-OTU similarities in primitive features, thereby imparting a high weight to derived aspects of the phenotype. However, aside from these relatively simple deletions we decided to proceed under the operational assumption that all characters were potentially of equal usefulness in indicating relationships among the five species of *Chiropterotriton*.

The next problem encountered was that of coding and standardizing the characters, a difficulty which is related to that of differential weighting. The most commonly utilized method, standardization of the original data to zero mean and unit standard deviation (Sokal and Sneath 1963; Farris 1967), would appear to solve the coding and standardizing problem simultaneously. Unfortunately, this computationally straightforward procedure has important drawbacks which have been overlooked by workers who seem overly impressed by its aura of statistical rigor. Any spurious detail in the original data will be preserved in subsequent clustering if one computes standardized character differences from raw character scores without evaluating the statistical significance of apparent differences in character values. The problem is especially troublesome for continuous characters, because all OTU's are likely to appear to differ (at least slightly) in their mean expression of such characters. A reasonable solution would be to recode the original data so that no two populations are assigned different states for a character unless they actually differ at a level of $P < 0.1$. Our data were recorded so that the number of character states did not exceed the number of statistically distinct subgroups into which the five OTU's could be divided. In most instances, this reduced the number of character state values to two or three per character. Only nostril diameter (character 8) provided sufficient discriminatory power to warrant the assignment of different character states to each of the five OTU's.

As pointed out by Colless (1967) and Eades (1970), an undesirable feature of standardizing the mean and standard deviation is that this procedure introduces consideration of an irrelevant feature, namely the *distribution* of character states among OTU's. The crucial feature is actually the difference between the character states *per se*, and we agree with Colless that a more meaningful way of standardizing characters for phenetic analysis is to constrain the range of variation to unity. Character states can then be coded fractionally in accordance with their position or rank along this range. This convention has certain other advantages (see below), and we therefore recoded character values to the range (0, 1), a procedure termed condensation by Crovello (1968).

Phylogenetic clustering: Phenetic methods of clustering, of which the Prim and Wagner methods are examples, yield graphic structures which may serve as a basis for phylogenetic speculation. However, in the absence of additional information, phenetic constructs are not in themselves evolutionary hypotheses; they are simply summaries of morphological differentiation compiled according to a specified algorithm. Colless (1967) and Estabrook (1972) have discussed the distinction between a phenogram, which is a datum, and a phyletic tree, which is a hypothesis. As was noted earlier, the former can be transformed into the latter by specifying the ancestral-derived relationship, either among the OTU's as whole

units, or among individual characters. Because parsimony has been invoked as an evolutionary principle (Camin and Sokal 1965; Estabrook 1968; Farris, Kluge and Eckhardt 1970), one is tempted to postulate an evolutionary interpretation of linkage systems, such as the Wagner and Prim methods, which give parsimonious networks.

Other criteria also may be used to optimize phylogenetic trees. Hennig (1966) proposed a radical method of phylogenetic analysis which clusters taxa based on the number of shared derived characteristics. The Hennigian system rests on the assumption that in any group of organisms one can find characters which have evolved in a single direction. Such characters provide reliable information concerning cladistic relationships. Hennig and his proponents have been criticized severely by some orthodox systematists (e.g., Mayr 1969; Darlington 1970), but much of the dispute has concerned the application of cladistic arguments to problems of taxonomic classification and zoogeography. These controversies, although important, do not detract from what is, in our view, the main strength of Hennigian phylogenetic systematics; namely, the straightforward (if largely unverified) methodology it provides for determining cladistic relationships. Gould (1973) has voiced a rather similar opinion.

Farris, Kluge and Eckhardt (1970) presented a quantitative codification of Hennigian phylogenetic analysis which offers the possibility of combining some of the best features of the phenetic and phylogenetic schools of evolutionary analysis. Their clustering technique, termed the Weighted Invariant Step Strategy (WISS), begins with the same kinds of phenetic data used in the Prim and Wagner analyses, but requires either that the ancestral form be known *a priori*, or that the direction of evolution in each individual character be well enough understood to allow different character states to be designated as more or less removed from the primitive condition. Thus, direction as well as magnitude enters the computation of character differences. Taxa are clustered according to the maximum number of derived character steps (not just identical character states) shared. Because ancestral (i.e. primitive) characteristics may be retained haphazardly by very distantly related taxa, shared primitive character states are not considered in the clustering procedure. At each branching point, the WISS procedure creates an HTU which is assigned character values equal to the most derived condition shared by the two taxa immediately above it on the tree. The result of this convention is that, in keeping with the previously noted assumption of the Hennigian method, no character reversals are present on the WISS tree; convergence and parallelism are permitted, however. If the restriction against evolutionary reversals is removed, the WISS procedure gives the same results as the Wagner procedure (Farris, Kluge and Eckhardt 1970). In order to apply the WISS technique to the present data set, it was first necessary to postulate an evolutionary sequence leading to the observed pattern of variation in each of the characters. This is perhaps the most difficult problem of judgment in any phylogenetic analysis, and one is forced to generate a number of basically untestable evolutionary hypotheses. Various criteria have been proposed (and criticized) for the detection of primitive character states (e.g., Inger 1967; Kluge and Farris 1969; Lundberg

1972, 1973; Throckmorton 1968; Wake and Özeti 1969; Nelson 1972, 1973a, 1973b; Marx and Rabb 1970, 1972). There appears to be general agreement that the most reliable indication of primitiveness is derived from reference to related out-groups, the "outside primitives" of Throckmorton (1968). Character states widespread in groups related to the one being clustered are likely to be primitive, particularly if one of the out-groups is known on other grounds to be ancestral.

In the present analysis, unambiguous comparisons with out-groups were difficult for many of the characters. External proportions, which are known to be subject to relatively rapid and reversible evolutionary change, were a particular problem. However, a few features do seem orderable on the basis of their occurrence (or lack thereof) in other species of *Chiropterotriton* and in members of the closely related genus *Pseudoeurycea*. For example, small nostrils characterize the adults of all *Pseudoeurycea* and almost all *Chiropterotriton* outside northern Nuclear Central America, the only exceptions being *C. nasalis* of nearby Honduras and *C. dimidiatus* of east-central Mexico. We consider it highly probable that large nostril size in adult *Chiropterotriton* is a derived paedomorphic feature (Rabb 1960; Wake 1966), and we coded the observed nostril sizes as representing greater or lesser deviations from the presumed ancestral condition. Characters 7, 9, 10 and 11 can also be ordered on a primitive-derived scale by reference to out-groups. The presence of septomaxillaries, preorbital vomerine processes, columellae, and abundant vomerine teeth all appear to be primitive features by this criterion (Wake, 1966).

For proportional characters, we assumed that the ancestor which gave rise to the Central American *Chiropterotriton* was relatively generalized in its overall habitus (i.e., that it was neither extremely attenuate, nor especially heavy-bodied, and that it possessed moderately proportioned legs, tail, and feet). We chose the median character state for each proportional character as likely to be the most similar to the presumed ancestral condition. It is, of course, possible that we are mistaken, and that the actual ancestor of these species possessed such specialized traits as a broad head, very long (or short) legs, or an especially long tail. However, in the absence of evidence to that effect, and keeping in mind the evolutionary patterns observed in other groups of salamanders, it seems reasonable to suppose that a salamander having unspecialized morphology was the ancestor of these five species.

Once an evolutionary sequence had been inferred for each set of character states, two sets of WISS trees were computed. For one of these, characters were standardized to a total range (0,1) as in the Wagner analysis. For the other set, the previous coding scheme was modified by assigning the zero value to the presumed ancestral state, and constraining the range of variation in *each direction* of character evolution to one. If only a single direction of change is involved, the standardization will not change the previous (0,1) range of variation. However, where character evolution has been bidirectional (as where an ancestor of moderate size has given rise to both larger and smaller descendants), the maximum absolute difference between end members of the two lineages is *two* units rather than one. Such a character would be coded as varying between zero and

TABLE I

Character states recoded for WISS analysis. "0" indicates presumed ancestral state; maximum range of variation in any direction from ancestral state is one. Character symbols: (1) standard length; (2) tail length; (3) head width; (4) combined limb length; (5) foot width; (6) number of maxillary teeth; (7) number of vomerine teeth; (8) nostril diameter; (9) condition of septomaxillaries; (10) condition of preorbital vomerine process; (11) condition of columella. The advancement index (AI) is the sum of the absolute values of the individual character states divided by the number of characters.

SPECIES	CHARACTERS											AI	
	1	2	3	4	5	6	7	8	9	10	11		
<i>bromeliacia</i>	0	1	-1	0	-1	-1	1	0.75	1	1	1	1	0.80
<i>cuchumatanus</i>	-1	0	0	1	-1	0	1	0.5	1	1	1	0	0.68
<i>megarhinus</i>	0	1	1	0	1	1	1	1	0	1	1	0	0.73
<i>rabbi</i>	1	1	0	1	0	0	0	0.25	0.5	0	1	1	0.43
<i>xolocalcae</i>	0	0	1	0	0	0	0	0	1	0	0.5	0	0.23

one in one direction, and zero and minus one in the other (see Camin and Sokal 1965).

As noted earlier, there are several advantages to standardizing characters to unit range when performing a phylogenetic analysis. First, data for all kinds of characters (ordered and unordered, binary and multistate, discrete and continuous) can be combined easily and naturally. Secondly, the method provides a convenient means of assessing the relative overall phenetic divergence of taxa from each other and from their presumed ancestor. A formula for the overall distance coefficient (OD) relating two taxa (p and q) on the basis of n characters coded to range (0,1) is,

$$OD = \frac{1}{n} \sum_{i=1}^n \left| a_{p_i} - a_{q_i} \right| \quad (3)$$

Where a_{p_i} and a_{q_i} are the standardized values for character i in taxa p and q, respectively. This measure is the complement of the association coefficient (S_G) of Colless (1967). If one of the taxa being compared (say, q) is the ancestor of the group, then, by definition, *all* of its character states will have the primitive value (0), and equation (5) becomes an advancement index (AI), where

$$AI = \frac{1}{n} \sum_{i=1}^n \left| a_{p_i} \right| \quad (4)$$

Thus, a simple summation of the absolute values of the standardized character states, divided by the number of characters (n) provides a convenient index of the overall morphological derivativeness of an OTU. The minimum value ($AI = 0$) will be observed only in OTU's which have no change from the ancestral condition in any character. The maximum value ($AI = 1$) will be found in forms which possess the maximally derived condition in *every* character. Obviously, most real taxa will not approach these extremes, but will combine various proportions of primitive and more-or-less derived features.

It should be emphasized that the OD and AI indices are *relative* measures of divergence. They are subject to change if taxa are added to, or deleted from, the analysis, particularly if the changes involve OTU's which possess extralimital or peripheral character state values for one or more characters.

RESULTS

Predicted Mean Character Values: Figure 8 and Appendix I summarize the most important aspects of the analysis of individual characters. Each population of *Chiropterotriton* is separable from every other by at least seven of the eleven characters. Every character serves to separate at least some of the species from others, and one character (nostril diameter) is distinctive in each of the five populations. These data suggest a mosaic pattern of variation, i.e. a relatively low degree of inter-character correlation from taxon to taxon. A species with relative-

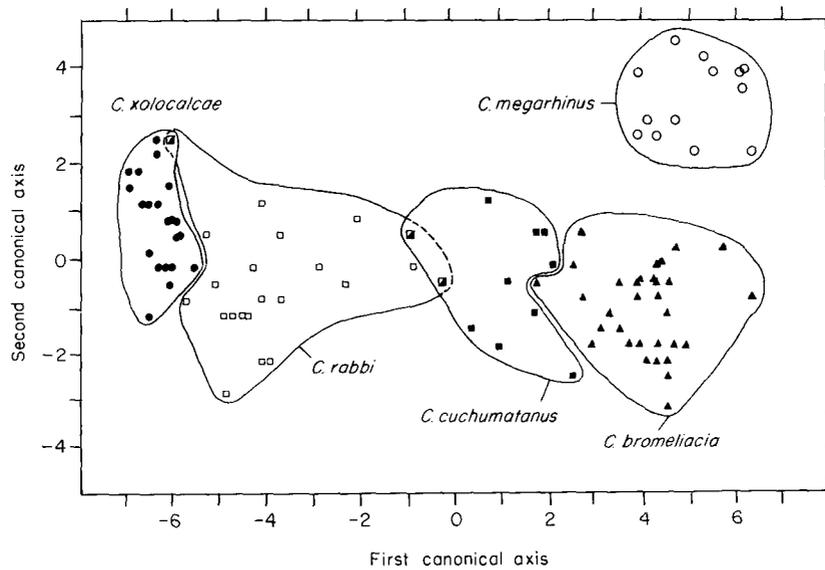


FIGURE 8. Plot of the first two canonical variates separating post-juvenile males of the species of the *Chiropterotriton bromeliacia* group. Eight characters are considered. The first variate (abscissa) accounts for about 88% of the observed interspecific variance.

ly short legs may have either small feet (*C. bromeliacia*), or very large feet (*C. megarhinus*). Similarly, high maxillary tooth counts may be associated either with low (*C. cuchumatanus*) or high (*C. rabbi*) numbers of vomerine teeth. An exception to this general pattern of independent variation is found in characters 7, 8, and 10. Examination of the recoded character states (Table 1) reveals that a high vomerine tooth count (state 0 of character 7) is invariably associated with the presence of the preorbital vomerine process (state 0 of character 10) and small nostril size (states 0 and 0.25 of character 8). Conversely, populations having low vomerine tooth counts (state 1) always lack the vomerine process (state 1), and, as adults, possess enlarged nostrils (states 0.50, 0.75, 1.0). *A posteriori* consideration of the structural and functional relationships among these three characters suggests that a functional relationship, rather than a chance correlation, is involved. In this group, the preorbital vomerine process bears teeth; other things being equal, species possessing the process will tend to have more teeth than those lacking it. However, several species of other plethodontid genera which have a well-developed vomerine process have few vomerine teeth. Evidently, the structure is necessary, but not sufficient, to support a large complement of vomerine teeth.

The relationship of vomerine structure to nostril size is somewhat less obvious. The internal nares are located just in front of the preorbital processes of the vomers, and the narial openings border on these processes. We have been unable to detect any correlation between the diameter of the internal nares, which is

similar in all species, and the diameter of the nostrils. Nevertheless, the fact that species with large nostrils lack the preorbital process implies a functional involvement, given the proximity of the process to the internal nares. Further, other *Chiropterotriton* with large nostrils (*nasalis*, *dimidiatus*; Wake 1966) also lack preorbital processes, but the processes are invariably present in species of *Chiropterotriton* with small nostrils.

Reference to outgroups reveals that the correlation between small nostril size and the presence of an enlarged preorbital vomerine process is not invariable. Species with large nostrils (e.g., certain *Chiropterotriton* and most *Thorius*) invariably lack the process, but species with small nostrils (e.g., *Bolitoglossa orestes*, and certain *Thorius* and *Batrachoseps*) may also lack it.

To allow for the possible effects of varying degrees of functional interconnectedness, we prepared two sets of phenetic and phylogenetic diagrams. The first set shows the result of treating all eleven characters as independent. The second set represents the clustering patterns obtained when two characters (7 and 10) are interpreted as being completely redundant measurements of a single character complex represented by character 8, and are omitted from the analysis. Thus, the alternate set of figures is based on only nine of the original eleven characters.

Discriminant Analysis: Table 2 gives the raw and standardized coefficients for the first three canonical variates. These compound variables represent the three main independent modes of interspecific differentiation, and together account for 99 per cent of the observed interspecific variance. For each axis the magnitude of the standardized coefficients are proportional to their contributions

TABLE 2

Raw and standardized coefficients for the first three canonical axes of variation. The main contributors to variation along each axis are italicized. Character symbols as in Table 1.

CHARACTER	FIRST CANONICAL AXIS		SECOND CANONICAL AXIS		THIRD CANONICAL AXIS	
	Raw	Standardized	Raw	Standardized	Raw	Standardized
1	.061	.142	-.166	-.388	-.267	-.623
2	-.003	-.012	.066	-.265	-.400	<i>-1.605</i>
3	-.436	-.148	.295	.100	.272	.092
4	.235	<i>.312</i>	-.425	<i>-.564</i>	1.626	<i>2.159</i>
5	-.481	-.186	1.101	.425	-1.309	-.505
6	-.015	-.091	.199	<i>1.202</i>	.032	.193
7	-.096	-.018	-.033	-.097	.027	.079
8	5.205	<i>.869</i>	.600	.100	.792	.132

to variation. The scores of 99 individuals with respect to the first two canonical variables are plotted in figure 8.

The first canonical axis accounts for 88 per cent of the observed variation between species. This dimension separates *C. xolocalcae*, *C. rabbi*, and *C. cuchumatanus* from *C. bromeliacia* and *C. megarhinus*. As indicated by the magnitudes of the standardized coefficients in Table 2, the first axis expresses interspecific differences in nostril diameter, with lesser contributions being made by limb length and foot size. Body size, which is usually the dominant factor on the first canonical axis in analyses involving organisms of different sizes (see Blacklith and Reymont 1971), is of relatively minor importance here due to the broad interspecific overlap in body size.

The second canonical variate, which accounts for 8 per cent of the observed interpopulation variation, mainly expresses differences in the number of maxillary teeth, with limb length, foot size, and standard length having lesser importance. This axis serves to distinguish *C. megarhinus* from *C. bromeliacia*.

The third and successive canonical axes do not provide important insights into additional significant modes of interspecific differentiation, and together these axes account for only 4 per cent of the between-species variance.

The classification matrix (Table 3) shows that only three of 99 post-juvenile males would be assigned to the wrong population on morphological grounds. All three mistakes involve individuals of *C. rabbi*, two of which were identified as *C. cuchumatanus* and one as *C. xolocalcae*. That the remaining 96 individuals were correctly assigned to their home populations on the basis of external morphology alone demonstrates that seemingly minor interspecific character differences, when taken in combination, are consistent enough to allow reliable identification of virtually all individual post-juvenile males of the five species.

TABLE 3

Classification matrix based on discriminant analysis of 99 post-juvenile male *Chiropetrotriton* from five populations. Entries along the main diagonal are "correct" matches of individual to their source populations based on eight morphological characters. See text for further explanation.

SPECIES	NUMBER OF INDIVIDUALS CLASSIFIED INTO GROUP				
	1	2	3	4	5
1. <i>bromeliacia</i>	33	0	0	0	0
2. <i>cuchumatanus</i>	0	9	0	0	0
3. <i>megarhinus</i>	0	0	13	0	0
4. <i>rabbi</i>	0	2	0	19	1
5. <i>xolocalcae</i>	0	0	0	0	13

Phenetic clustering and phylogenetic relationships: Some features of the networks produced by the Prim and Wagner algorithms vary depending on 1) the method used to standardize characters, and 2) the *de facto* weighting (through inclusion or rejection) of possibly redundant characters (Fig. 9). In view of this instability,

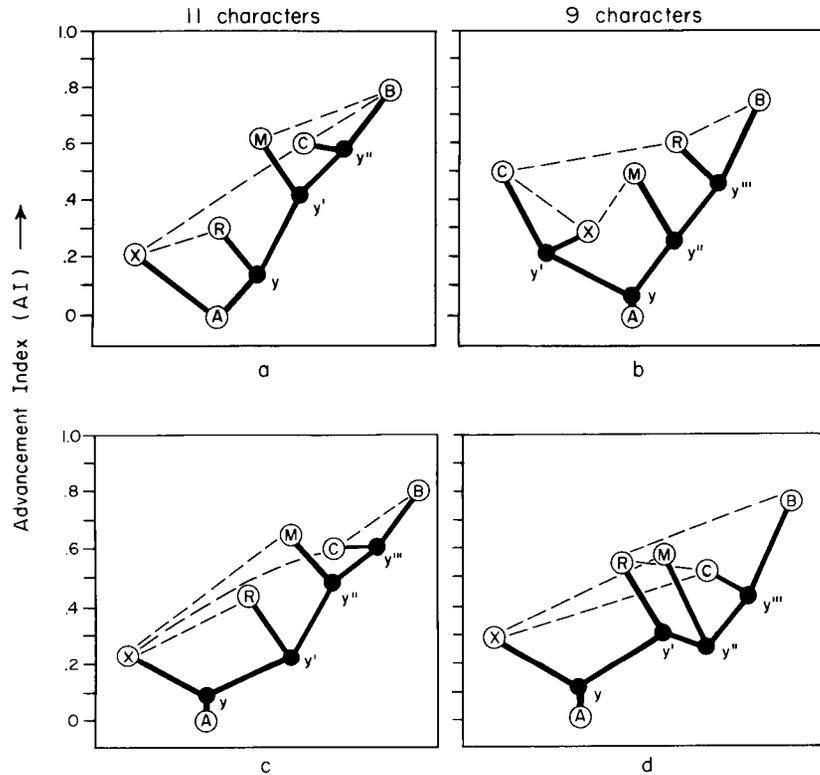


FIGURE 9. Relationships among the species of the *Chiropterotriton bromeliacia* group, indicated by Wagner trees (solid lines) and Prim networks (dashed lines). In (a) and (b) the total range of variation is standardized in each of 11 characters. In (c) and (d) the range of variation is standardized in each direction of change from the inferred ancestral condition. The Prim networks link the five extant species according to overall phenetic similarity; the Wagner trees represent suggested phyletic sequences, and include a hypothetical ancestor (A) as well as several hypothetical intermediate taxa (Y, Y', Y'', etc.). The advancement index (AI) of each taxon is indicated on the ordinate. The location of taxa on the abscissa is arbitrary. Symbols: B = *C. bromeliacia*; C = *C. cuchumatanus*; M = *C. megarhinus*; R = *C. rabbi*; X = *C. xolocalcae*.

one cannot be certain which (if any) of the particular configurations is an accurate representation of the actual relationships among the five species of *Chiropterotriton*. Nevertheless, certain features are common to most or all of the

clustering patterns illustrated in figure 10, and some tentative conclusions can be drawn.

First, it is clear that a number of morphological convergences or reversals, or both, have occurred during the evolution of the group. The phenetic distances separating OTU's (Tables 4 and 5) tend to be shorter than the patristic distances (i.e., the distances measured along the internodes of the network), implying the

TABLE 4

Overall phenetic distances separating five species of *Chiropterotriton*. Entries are summed character state differences. Characters are standardized to the range (0,1). Upper half-matrix gives results when all eleven characters are included; in the lower half-matrix two possibly redundant characters (nos. 7 and 10) have been deleted. Symbols: A = hypothetical ancestor; B = *C. bromeliacia*; C = *C. cuchumatanus*; M = *C. megarhinus*; R = *C. rabbi*; X = *C. xoloccalcae*.

	B	C	M	R	X	A	Mean Distance	
							11	9
B	-	4.25	5.75	5.5	5.75	6.75	5.6	4.4
C	4.25	-	6.0	6.25	5.5	5.5	5.5	4.3
M	5.75	6.0	-	7.25	6.5	5.5	6.2	5.0
R	3.5	4.25	5.25	-	3.25	3.25	5.1	3.9
X	3.75	3.5	4.5	3.25	-	2.0	4.6	3.4
A	4.75	3.5	3.5	3.25	2.0	-	4.6	3.4

TABLE 5

Overall phenetic distances separating five species of *Chiropterotriton*. Characters recoded so that the absolute value of the range is one in each direction of change from the implied ancestral state. See legend to Table 4 for further explanation.

	B	C	M	R	X	A	Mean Distance	
							11	9
B	-	7.25	9.25	8.0	8.25	8.75	8.3	7.1
C	7.25	-	10.5	8.75	8.0	7.5	8.4	7.4
M	9.25	10.5	-	10.25	8.5	8.0	9.3	8.1
R	6.0	6.75	8.25	-	5.25	4.75	7.4	6.2
X	6.25	6.0	6.5	5.25	-	2.5	6.5	5.3
A	6.75	6.5	6.0	4.75	2.5	-	6.3	5.3

existence of homoplasy (*sensu* Farris 1972). If one applies LeQuesne's (1969) criterion for the detection of homoplasy, one finds that primitive and derived features exist in combinations which cannot be the result of uniquely derived character evolution. As an example, characters 2 and 4 occur in the combinations (0,0), (0,1), (1,0), and (1,1) in *C. xolocalcae*, *C. bromeliacia*, *C. cuchumatanus*, and *C. rabbi*, respectively. No matter which state is considered primitive for each character, there is no way these four combinations could have arisen without at least a single reversal or convergence having occurred.

A second general conclusion involves the relative primitiveness and derivedness of the overall phenotype of some of the species. Assuming the correct direction of character-state evolution has been inferred for most of the characters, *C. xolocalcae* shows the least phenotypic divergence from the hypothetical ancestor. At the other extreme, *C. bromeliacia* consistently has the largest advancement index, regardless of differences in character standardization and weighting. *C. bromeliacia* possesses advanced states in all of the characters whose evolution can be inferred confidently (e.g. characters 7, 8, 9, 10, and 11).

The relative positions of the remaining three species vary depending on the method of standardizing characters and the inclusion of possibly redundant characters, but *C. cuchumatanus* tends to be linked most closely to *C. bromeliacia* by both the Prim and the Wagner algorithms in the 11-character analyses. Much of the apparent similarity between these two species is related to their scores for the triad of highly correlated nostril-vomer characters 7, 8, and 10; when characters 7 and 10 are deleted from the analysis, *C. rabbi* replaces *C. cuchumatanus* as the species with closest phenetic similarity to *C. bromeliacia* (Fig. 9 b and d). Finally, the relatively large inter-OTU phenetic differences (Tables 4 and 5) reinforce the previous impression that each of the species is distinct morphologically. Of the group, *C. megarhinus* is, on the average, the most distinctive in overall morphology, i.e. it has the greatest mean phenetic separation from the other species. As a result of the rather low degree of similarity between *C. megarhinus* and the other species, its position on the Prim and Wagner networks tends to shift with practically every modification of the clustering procedure.

Figure 10 shows the branching pattern resulting from the WISS analysis of morphological similarities. The WISS trees are not affected by the two methods of standardizing character variation, but there are differences between the 11-character and nine-character trees. As would be expected from the fact that the WISS clusters are formed solely on the basis of the number of shared *derived* character steps, the general advancement level of the HTU's connecting pairs of species tends to be lower than was the case for HTU's generated by the Wagner algorithm.

In the 11-character analysis (Fig. 10a), the species fall into two basic groups which share no derived character states. The *C. rabbi*-*C. xolocalcae* group is based on a single shared derived step (actually fractional steps in characters 9 and 11). Apart from this rather tenuous association of *C. rabbi* with *C. xolocalcae*, the WISS tree in figure 10a is essentially identical to the Wagner trees in figures 9a and 9b.

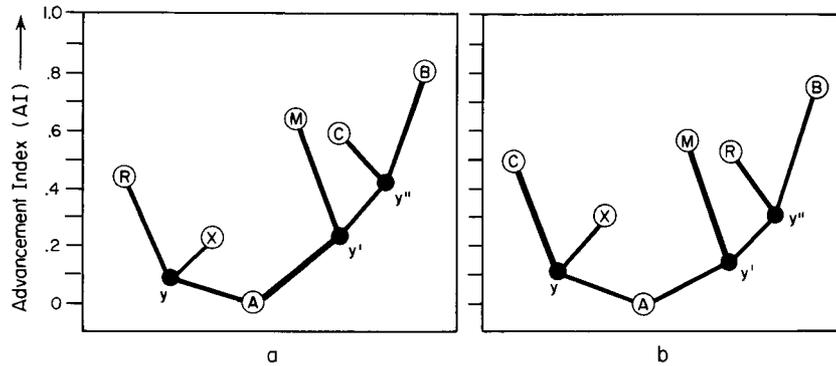


FIGURE 10. WISS trees constructed from data standardized as in Fig. 9 c-d. Clusters formed on the basis of shared derived characteristics. Symbols as given for Fig. 10.

The nine-character WISS tree (Fig. 10b) corresponds even more closely to the equivalent Wagner trees (Figs. 9b and 9d). The branching sequence produced by the two algorithms are identical when all characters in the Wagner analysis are standardized to a total range (0,1), and differ only slightly when the range is standardized in each direction of change from the ancestral state. Thus, whether we consider overall phenetic similarity (Wagner algorithm) or similarity in derived characteristics (WISS algorithm), the results are much the same. Given the relatively small number of characters, the presence or absence of correlated characters has a more important effect on the results than does the inclusion or exclusion of primitive character states. Colless (1967) has cautioned against interpreting agreement in the classifications produced by different clustering methods as evidence of the correctness of the classification. However, concordance is at least evidence that the classification is robust given the set of characters used in the analysis. As Colless rightly comments, the way to confirm the phylogenetic relevance of a given classification is not to apply additional clustering methods to the same data, but rather to examine additional characters.

DISCUSSION

Morphological and phyletic relationships among the five species: The results of the bivariate, multivariate, phenetic, and phyletic analyses all indicate a pervasive (if subtle) pattern of morphological differentiation within the group, despite the obvious similarities in gross appearance (Fig. 2). Not only can each population be distinguished on the basis of a number of morphological features, but even individual specimens can be assigned to the correct population with a high degree of certainty (97 per cent correct identifications in a sample of 99 individuals). Because the two new populations appear to be as well-differentiated as the three species previously known, and because all five populations are geographically isolated evolutionary units, we believe we are justified in designating the new forms as full species (see Mayr 1969: 193-197).

It would appear that each population has experienced a distinctive combination of evolutionary changes in a number of morphological characteristics, and no two species are especially similar phenetically. Within the group, *C. bromeliacia* apparently has the most highly derived phenotype (although it preserves the presumed ancestral state in a few characters), while *C. xolocalcae* retains the greatest number of ancestral character states. The remaining species are intermediate, with *C. megarhinus* being, on the average, the least similar to the other forms. Convergences or reversals, or both, must have occurred in the evolution of several characters.

Unfortunately, morphological differences between the species cannot be correlated with obvious ecological differences on the basis of our present knowledge of the biology of the group. All five species occur in sympatry with larger *Bolitoglossa* (but not with other *Chiropterotriton*), all live at relatively high elevations (1800 - 2900 m) in wet, forested habitats, and all except *C. cuchumatanus* are restricted mainly to bromeliads. The two species living in closest geographic proximity (*C. xolocalcae* and *C. bromeliacia*) are very dissimilar phenetically. Any adaptive significance of observed morphological differences remains problematical.

Further refinement of our knowledge of the relationships within this group will depend on the examination of new suites of characters. Biochemical techniques, especially electrophoresis and immunochemistry, appear to offer the best prospects for such an advance.

EVOLUTIONARY AND ECOLOGICAL RELATIONSHIPS WITH OTHER GROUPS

The relationships of these five species to other *Chiropterotriton* remains uncertain. It has been suggested (Rabb 1958; Wake and Lynch In Press) that the *Chiropterotriton* of northern and central Mexico may comprise a group derived independently from the Trans-Isthmian species referred to the genus. Although we have not yet undertaken a review of the entire genus, it appears that the closest relatives of the five species considered here are found to the southeast in Honduras (*nasalis*, *C. barbouri*). Whether the Costa Rican forms (*C. picadoi*, *C. abscondens*) also are closely related to the other Central American species or represent still another independent radiation is unclear.

It is possible that the *Chiropterotriton* of Chiapas, Guatemala, and Honduras, rather than being remnants of a past migration of ancestral *Chiropterotriton* south across the Isthmus of Tehuantepec, actually represent an autochthonous evolutionary radiation from a generalized *Pseudoeurycea*-like ancestor. The fact that the arrangement of tarsal elements in the *Chiropterotriton* of northern Central America is identical to that in *Pseudoeurycea*, but different from that found in *Chiropterotriton* of central and northern Mexico, lends support to this hypothesis. It is also relevant to note that Taylor (1944) originally assigned *C. barbouri* to the genus *Pseudoeurycea*. Of the four species of *Pseudoeurycea* currently known to inhabit northern Central America, *P. rex* is the smallest and most generalized. It is perhaps somewhat similar to the

hypothetical link between the two genera. Future papers by us will examine the question of the relationships of *Pseudoeurycea* and *Chiropterotriton* more directly.

We know of several additional undescribed species of salamanders of the *Chiropterotriton-Pseudoeurycea* group which have been taken by collectors in the upland of Chiapas and Guatemala, and it appears that northern Nuclear Central America has been the site of a significant burst of evolutionary activity by this group, as it has been for salamanders of the genus *Bolitoglossa* (Wake and Brame 1969). Elsewhere (Wake and Lynch In press) we have discussed the zoogeographic significance of the region in the evolutionary history of neotropical salamanders.

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We wish to thank Joseph Copp for making available to us a large series of *C. megarhinus* from his personal collection. These salamanders were collected by Dennis E. Breedlove, who also provided useful and expert information concerning the plant associations in which the animals were found. Thomas Uzzell first informed us of the existence of *Chiropterotriton* in the Sierra de los Cuchumatanes of western Guatemala. George Zug of the National Museum of Natural History arranged the loan of a large series of *C. xolocalcae*. Albert Bennett, David Bradford, Lynne D. Houck, and John E. Woods provided invaluable assistance in the field work. The Spanish summary was prepared by Fernando Ortiz-Crespo.

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RESUMEN

Cinco especies de salamandras pletodóntidas componen el grupo *Chiropterotriton bromeliacia*; estas especies viven en la parte norte de América Central nuclear donde tienen distribuciones geográficas alopátricas. *Chiropterotriton xolocalcae* y *C. megarhinus* ocurren en las montañas de la costa del Pacífico de Chiapas, México. *Chiropterotriton bromeliacia* es conocida de la vecindad del Volcán Tajumulco en el extremo sud-occidental de Guatemala. Dos especies nuevas que son descritas en este artículo provienen de Guatemala occidental, *C. rabbi* de las montañas de Culico y *C. cuchumatanus* de la Sierra de los Cuchumatanes. Un análisis varacional detallado de las cinco especies revela que cada una es separable morfológicamente de las demás; el diámetro de las ternillas es la característica que sirve mejor para este objeto. Las especies en orden de creciente diámetro de ternillas son: *C. xolocalcae*, *C. rabbi*, *C. cuchumatanus*, *C. bromeliacia* y *C. megarhinus*. La última nombrada tiene ternillas enormes ovaladas. Hay una buena correspondencia general entre varios estimados fené-

APPENDIX

Predicted mean character values and 95% confidence limits (in parentheses) for post-juvenile male *Chiropterotriton* at SL = 30 mm. Figures for characters 2-8 obtained by regression analysis, except where no significant correlation found between character and SL. In such instances, indicated by an asterisk (*), simple means are shown. Symbols for characters are as in Table 1. Symbols for states of characters 9-11: A = absent; p = minutely or occasionally present; P = present, well-developed. Values for characters 1-7 are in mm; value for character 8 is in micrometer ocular units (1 unit = approx. 0.33 mm).

SPECIES	n	CHARACTERS										
		1	2	3	4	5	6	7	8	9	10	11
<i>bromeliacia</i>	42	30.2	33.2 (32.5-33.9)	4.60 (4.52-4.67)	14.9 (14.7-15.1)	2.76 (2.70-2.83)	31.7 (30.4-33.0)	10.1* (9.4-10.8)	1.89 (1.84-1.94)	a	a	a
<i>cuchumatanus</i>	9	28.8	29.7 (28.5-30.9)	4.72 (4.60-4.83)	15.5 (15.2-15.7)	2.80 (2.55-3.06)	40.1 (35.0-45.2)	12.7* (10.5-14.8)	1.47* (1.37-1.57)	a	a	a
<i>megarhinus</i>	18	29.7	32.4 (31.7-33.2)	4.86 (4.80-4.92)	14.7 (14.4-14.9)	3.07 (3.01-3.13)	49.8 (48.2-51.5)	10.9* (9.8-11.9)	2.27 (2.21-2.34)	P	a	P
<i>rabbi</i>	27	32.3	33.2 (31.3-35.2)	4.73 (4.65-4.81)	15.7 (15.4-16.0)	2.91 (2.80-3.02)	41.9 (39.2-44.6)	17.1 (14.2-20.0)	0.72 (0.59-0.84)	p	P	a
<i>xolocotcae</i>	38	30.1	31.1 (30.4-31.7)	4.83 (4.77-4.90)	15.0 (14.8-15.2)	2.96 (2.88-3.03)	44.6 (42.2-47.0)	19.9 (19.0-20.9)	0.21 (0.19-0.23)	a	P	P

ticos y filogenéticos de parentesco de las cinco especies. *C. bromeliacia* consistentemente parece ser la forma más derivada, mientras que *C. xolocalcae* parece ser la menos modificada desde el punto de vista de la morfología general del supuesto linaje ancestral. El grupo *bromeliacia* es una unidad distintiva dentro de su género, y ocupa una posición más bien aislada en la filogenia de las salamandras plelodóntidas neotropicales.

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