A NEW SPECIES OF CHIROPTEROTRITON (AMPHIBIA: CAUDATA) FROM BAJA VERAPAZ, GUATEMALA, WITH COMMENTS ON RELATIONSHIPS AMONG CENTRAL AMERICAN MEMBERS OF THE GENUS

By James F. Lynch and David B. Wake

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A NEW SPECIES OF *CHIROPTEROTRITON* (AMPHIBIA: CAUDATA) FROM BAJA VERAPAZ, GUATEMALA, WITH COMMENTS ON RELATIONSHIPS AMONG CENTRAL AMERICAN MEMBERS OF THE GENUS[1]

By JAMES F. LYNCH[2] AND DAVID B. WAKE[3]

ABSTRACT: *Chiropterotriton veraepacis*, a diminutive species of plethodontid salamander with very large nostrils, is described. It occurs inside bromeliads in an area of montane cloud forest south of Purulhá, Baja Verapaz, Guatemala, and in nearby areas of Alta Verapaz, Guatemala. In most structural features *C. veraepacis* resembles *C. nasalis* of northeastern Honduras, a shorter tailed, wider headed species with larger nostrils. The new species is similar to species of the *bromeliacia* group from Guatemala and Chiapas in ecology and in many structural features but differs from them in osteology. Although *C. nasalis* and *C. veraepacis* are very distinct from the Costa Rican species *C. picadoi* in most morphological and ecological features, they resemble that species in osteology. Some additional information is presented concerning the poorly known species *C. richardi* (Costa Rica) and *C. barbouri* (Honduras), and possible relationships among all of these species are discussed.

INTRODUCTION

In a recent paper (Lynch and Wake 1975) we assigned two new Guatemalan species of *Chiropterotriton* (*C. cuchumatanus* and *C. rabbi*) as well as three previously known Chiapan and Guatemalan forms (*C. megarhinus, C. xolocalcae,* and *C. bromeliacia*) to the *bromeliacia* species group. In that paper we noted the importance of Nuclear Central America as an evolutionary center for *Chiropterotriton* and other tropical plethodontid genera (see also, Wake and Lynch 1976), and remarked that other undescribed *Chiropterotriton* existed in the area.

This paper reports the discovery of a new species of *Chiropterotriton* from the Department of Baja Verapaz, in east-central Guatemala. This form was first encountered in the spring of 1973 by Thomas Uzzell, Academy of Natural Sciences, Philadelphia (ANSP), who collected four individuals in an area of montane cloud forest a few kilometers south of the village of Purulhá. The locality is some 130 km east of the closest populations of *bromeliacia*-group *Chiropterotriton* in Huehuetenango, Guatemala, and is over 100 km west of the nearest known localities for *C. nasalis*

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in Honduras. In 1972 the present authors had collected two species of *Bolitoglossa* at the same locality where Uzzell found *Chiropterotriton*, but we did not encounter salamanders of the latter genus on that visit, nor on a later trip (August, 1973). Because Uzzell's specimens clearly represented an undescribed member of the genus. we returned to the Purulhá area a third time in November, 1974, in hopes of securing additional material. On this occasion we collected a series of eleven *Chiropterotriton*. We name this species for its provenance, a beautiful land of true peace:

Chiropterotriton veraepacis NEW SPECIES

Figure 1

Holotype: MVZ 112499. An adult male from 4.2 km (by road) S Purulhá, Baja Verapaz, Guatemala, collected by James F. Lynch, David B. Wake, and Theodore J. Papenfuss, 14 November 1974. The holotype is one of a series taken at elevations between 1740 and 1780 meters.

Paratypes: MVZ 112495-98 (4 specimens), LACM 123803 same data as holotype. MVZ 112490-112494 (5 specimens) collected at the type locality 13 November 1974. ANSP 28194-28197 (4 specimens) collected at the type locality in early 1973 by Thomas M. Uzzell, Jr.

Diagnosis: Compared to other Central American *Chiropterotriton*, *C. veraepacis* is a rather small species, with an unusually long tail and narrow head. Eight sexually mature individuals of both sexes measure 26.1-31.2 mm (mean 28.6 mm) SL[4]. The tail is 1.26-1.43 times SL in undamaged adult males, whereas head width is 0.13-0.14 times SL. Maxillary teeth are abundant (range 45-57; mean 49.0 for adults), vomerine teeth are few (range 8-11; mean 9.6 for adults), and the nostrils are notably enlarged (diameter equals 0.4-0.6 mm in adults). *C. veraepacis* is distinguished from *C. nasalis* by longer tail, much narrower head, smaller feet, and somewhat smaller nostril[5]; from *C. picadoi* by somewhat longer tail, narrower head, much longer limbs, much larger feet, more maxillary teeth, and much larger nostrils; from *C. bromeliacia* by somewhat smaller average size, narrower head, longer tail, and many more maxillary teeth; from *C. cuchumatanus* by much longer tail, narrower head, more maxillary teeth, and somewhat fewer vomerine teeth; from *C. rabbi* by smaller average size, longer tail, much narrower head, and smaller nostrils; from *C. xolocalcae* by much longer tail, much narrower head, more vomerine teeth, and much larger nostrils; from *C. megarhinus* by much longer tail, much narrower head, and somewhat smaller nostrils. Other species of *Chiropterotriton* from Central America have a light inter-

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

[5] Statements 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.
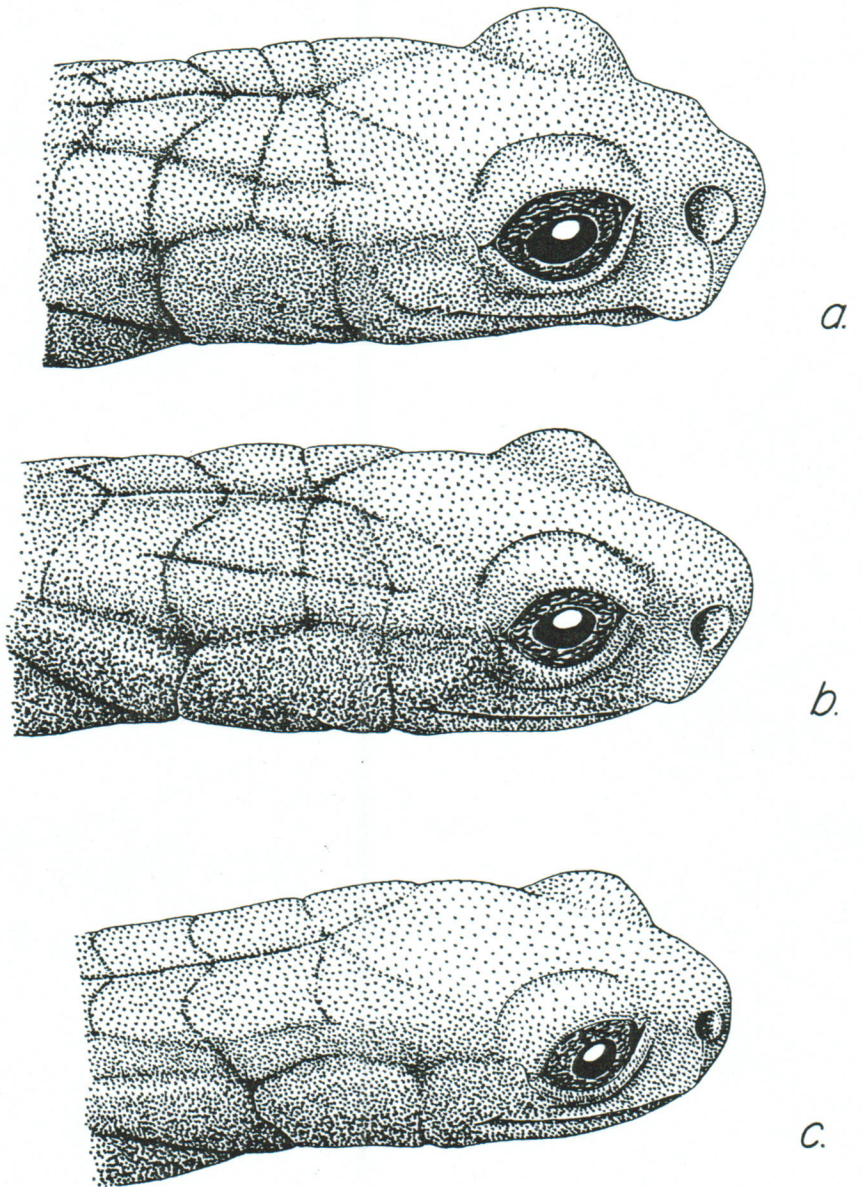
FIGURE 1. Heads of adult males of species of *Chiropterotriton*, drawn to same scale. (a) *Chiropterotriton veraepacis*, (b) *Chiropterotriton bromeliacia*, (c) *Chiropterotriton picadoi*.

orbital pigment band, at least in some specimens, but we have not seen any indication of this feature in *C. veraepacis*. Both *C. veraepacis* and *C. nasalis* have nostrils that are clearly visible by examination of the dorsal surface of the head from directly above the specimen. In *C. picadoi*, *C. richardi* and members of the *bromeliacia* group the nostrils are only slightly, or not at all, visible in dorsal view.

Description: To judge from the limited sample, *C. veraepacis* is a relatively small member of the genus, the largest of fifteen specimens measuring 31.2 SL. The species has the longest relative tail length and the narrowest relative head width of any of the seven other northern Central American *Chiropterotriton* for which we have data (the eighth known species from the region, the rarely collected *C. barbouri* of Honduras, is not considered here). The number of maxillary teeth increases dramatically with SL ($r = 0.82$; $P < 0.01$), but no size related increase in vomerine tooth count is evident ($r = 0.24$; $P > 0.1$). The nostrils are moderately large in juveniles and subadults. Nostrils increase in size in adults, contrary to what is seen in *C. xolocalcae*, *C. rabbi*, and *C. picadoi*. The only adult female in the type series (MVZ 112497) has a shorter tail and more maxillary teeth than have males of equivalent SL. Adult males possess conspicuous oval-shaped mental hedonic glands.

Measurements of the holotype (in mm): Head width 3.9; snout to gular fold (head length) 5.7; head depth at posterior angle of jaw 2.7; eyelid length 2.0; eyelid width 1.0; anterior rim of orbit to snout 1.8; horizontal orbit diameter 1.5; interorbital distance 2.3; distance between vomerine teeth and parasphenoid tooth patch 0.5; snout to fore limb 7.9; distance separating internal nares 0.8; distance separating external nares 0.8; snout projection beyond mandible 0.3; snout to posterior angle of vent (SL) 28.2; snout to anterior angle of vent 25.7; axilla to groin 14.3; tail length 39.8; tail width at base 2.4; tail depth at base 2.6; fore limb length 6.7; hind limb length 7.6; width of right hand 1.9; width of right foot 2.3.

Coloration (in life): The dorsum of the holotype is dark vinaceous brown. A red-orange patch of pigment is present in the sacral region, but in contrast to the situation seen in most Central American *Chiropterotriton*, there is no interorbital bar of light pigment. A pair of obscure, red-brown patches of color are present in the otic region. There is a hint of a jagged-edged dorsal stripe on the tail. The dense dorsal melanin network is lighter laterally. A few small white iridophores are present at the side of the head and trunk. The limb bases are light pink. The venter is slate gray, with the tail somewhat darker than the belly and chin. Small white iridophores are scattered on the chin, with fewer on the belly, and none on the underside of the tail. The animal is fundamentally very dark, with other pigments (save at the tail base) becoming evident only on close examination.

The paratypes generally resemble the holotype in coloration. All fourteen paratypes are dark brown to black dorsally, all possess a light sacral patch (red, red-brown, orange, or obscure red-orange), and all lack an interorbital bar of light pigment. Ventral coloration shows more variation, ranging from medium gray to nearly black. Contrast between the chin and the belly is greatest in those individuals with darker bellies. The number of ventral white iridophores ranges from none to moderately abundant, especially in the gular region. Most individuals show at least a few white

flecks along the side of the head. In most individuals there is an obscure, irregularly bordered caudal stripe, and in some it is faintly visible on the back as well.

Habitat: The type series was collected in an exceptionally humid cloud forest which extends for several kilometers to the west and east of the type locality along the north-facing slopes of the Sierra de Chuacús. According to the vegetational classification of Holdridge (1967), the type locality supports lower montane wet evergreen forest (see also Savage, 1975). Large bromeliads, orchids, and other epiphytes are conspicuously abundant, as are the tree ferns that are typical of cloud forests elsewhere in Guatemala. Low palms are common in the understory of the forest. There are no relevant weather data for nearby sites, but to judge from the aspect of the vegetation and from the generalized precipitation map published by the Instituto Geografico Nacional of Guatemala (1966), annual rainfall probably exceeds 3000 mm. The local topography is extremely rugged, and much of the area is inaccessible to collecting due to the extreme steepness of slope.

Ten of the eleven *Chiropterotriton* collected by the present authors were found inside arboreal bromeliads (*Tillandsia* and *Catopsis* spp) during daylight hours. The eleventh specimen was encountered after dark on the upper surface of a palm leaf approximately 1 m above the ground. Uzzell obtained the four ANSP paratypes and an additional six specimens (ANSP 2885-90, too poorly preserved to measure) from large bromeliads, 2-8 feet off the ground.

Other arboreal amphibians which occur at the type locality of *C. veraepacis* include two species of *Bolitoglossa* (a population tentatively assigned to *B. helmrichi* and a less common, undescribed all-black species), *Hyla bromeliacia,* *Plectrohyla quecchi,* and a large, fringe-limbed hylid similar to *Hyla miliaria.* All of the foregoing species were found in arboreal bromeliads, but some occur under the loose bark of downed logs as well. Terrestrial amphibians and reptiles collected in the vicinity of the type locality include *Eleutherodactylus brocchi, E. rugulosus, Anolis cobanensis, A. crassulus, Barisia moreleti, Sceloporus taeniocnemis,* and *Thamnophis cyrtopsis.*

The cloud forest inhabited by *C. veraepacis* became easily accessible in the summer of 1972 upon completion of an all-weather road through the mountains of Baja Verapaz and Alta Verapaz. This previously undisturbed tract of forest is rapidly being destroyed by lumbering and agricultural activities, and the prospects of continued survival of *C. veraepacis* and other as yet undescribed endemic amphibians are bleak.

Range: Known only from the type locality and a nearby locality in Alta Verapaz, Guatemala. To be sought in montane cloud forest along the humid, north-facing slopes in the Chuacús-Minas mountain ranges of Baja Verapaz and Alta Verapaz. Thomas Uzzell collected two specimens of *Chiropterotriton* in a bromeliad 30 feet above the ground on the top of a ridge above Finca Volcán, Alta Verapaz (ANSP 28198-28199). Stuart (1948) reports an altitude of 925 meters for the finca, and Uzzell's collecting site is somewhat higher. Although these specimens are poorly preserved and cannot be measured, we assign them to *C. veraepacis* on the basis of their general form, large nostrils, light pigment spots at the base of the tail and absence of an interorbital bar of pigment. *C. veraepacis* is the first species of salamander to be reported from Baja Verapaz.

COMPARATIVE OSTEOLOGY

In our previous paper (Lynch and Wake 1975) we reviewed the osteological characters of the five species that comprise the *C. bromeliacia* group. An additional five species of *Chiropterotriton* occur south and east of the Isthmus of Tehuantepec: *C. veraepacis* of Guatemala, *C. nasalis* and *C. barbouri* of Honduras, and *C. picadoi* and *C. richardi* of Costa Rica (Wake and Lynch 1976). These ten species constitute *Chiropterotriton*-beta.

In addition to the skeletal material for the *bromeliacia* group that was available for our previous study, we have examined a second specimen of *C. cuchumatamus*. A partial skeleton of the rare *C. richardi* provided limited information (Wake 1966), and we have had one hand and one foot of an additional specimen (MVZ 99516). We have examined one cleared and stained *C. veraepacis*, two *C. nasalis*, five *C. picadoi*, and one specimen (ANSP 28200) of a population from the mountains south of Pueblo Viejo, Depto. Yoro, Honduras, that is tentatively assigned to *C. barbouri*.

C. veraepacis differs sharply from all members of the *C. bromeliacia* group in having prefrontal bones, in having frontal processes of the premaxillary bone which arise separately and then fuse, separating again near their tips (Fig. 2), in having the

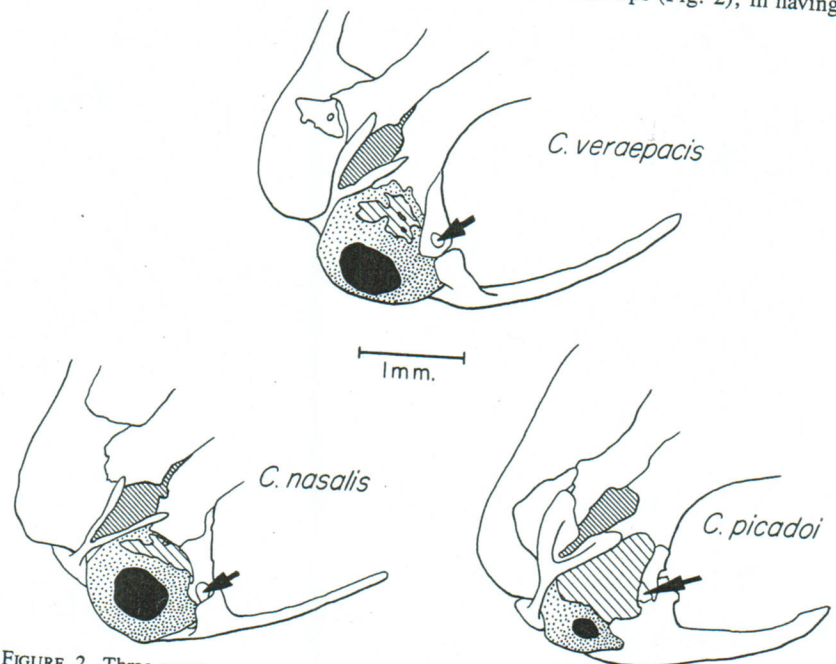FIGURE 2. Three-quarter, anterolateral view of the nasal capsule region of three species of *Chiropterotriton*, illustrating important features. Heavy lines, nasal bone; fine lines, internasal fontanelle; stipple, cartilaginous nasal capsule; blackened area, opening in nasal capsule for external naris. Arrows point to area through which nasolacrimal duct passes ventrally into the nasal capsule.

fourth and fifth distal tarsals fused, and in having reduced numbers of carpal elements, the result of ulnare-intermedium fusions (Fig. 3). In these characters it resembles both *C. nasalis* and *C. picadoi* (Wake 1966, reported prefrontals to be present or absent in *C. abscondens = C. picadoi*. This statement is based on one apparently pathological specimen that has heavy ossification and in which the prefrontals and nasals are fused. In the other four individuals examined the situation illustrated in figure 2 is seen.). *C. veraepacis, C. nasalis,* and *C. picadoi* all lack septomaxillary bones and columellar processes of the opercular apparatus, which are present in some of the *bromeliacia* group. The new specimen of *C. cuchumatamus* has a pair of distinct septomaxillary bones, so the elements have now been found in all members of the *bromeliacia* group except *C. xolocalcae.*

In most osteological features *C. nasalis* and *C. veraepacis* are especially similar. They differ from all members of the *bromeliacia* group in a number of derived characters (the erratically structured, reduced nasal bones, the fused frontal processes of the premaxillary, and the carpal and tarsal fusions). The members of the *bromeliacia* group differ from these two species in one derived character, loss of the prefrontal bones. Additional derived features of *C. nasalis* and *C. veraepacis* distinguish them from some to most members of the *bromeliacia* group; these include loss of the septomaxillary bones and the preorbital processes of the vomers. *C. nasalis* has only a rudimentary tibial spur, while the process is absent in the *bromeliacia* group. *C. veraepacis* has a tibial spur.

The nasal capsules of *C. nasalis* and *C. veraepacis* have an orientation that distinguishes them from the members of the *bromeliacia* group and the other species discussed here. The external nares are shifted so as to have a more dorsal orientation than the nares of most species, which are typically directed anterolaterally in a nearly vertical plane.

C. richardi and *C. barbouri* are the least well known species of *Chiropterotriton*-beta, but we have some useful information. Both species have prefrontal bones, preorbital processes of the vomers, and tibial spurs, but lack septomaxillaries and columellar processes of the operculum. The ulnare and tibiale are fused in both, as are distal tarsals four and five. Frontal processes of the premaxillary are fused for a short distance above their origin in *C. barbouri* but not in *C. richardi.*

In the *bromeliacia* group the nasals are the main bony link between the frontals and the maxillaries, but in *C. nasalis, C. veraepacis* and *C. barbouri* the prefrontals provide that link. The nasals are reduced in the first two species. These features suggest that enlarged nostrils have evolved in different ways in the two species assemblages, and that no constant set of characters accompanies nostril enlargement. Some accommodation for the enlarged nostrils is required in the facial region of the skull, but it may be the result, (a) of prefrontal loss and movement of nasals into the "prefrontal zone", (b) of nasal reduction and increased prefrontal importance, (c) or of both nasal and prefrontal reduction, but with both retaining important connecting functions in the facial part of the skull (as occurs in *C. richardi*).

Both *C. veraepacis* and *C. nasalis* differ from *C. picadoi* and *C. richardi* in lacking preorbital processes on the vomer and in having tear-drop shaped prefrontals that are pierced for passage of the nasolacrimal ducts (Fig. 2). *C. barbouri* has preor-
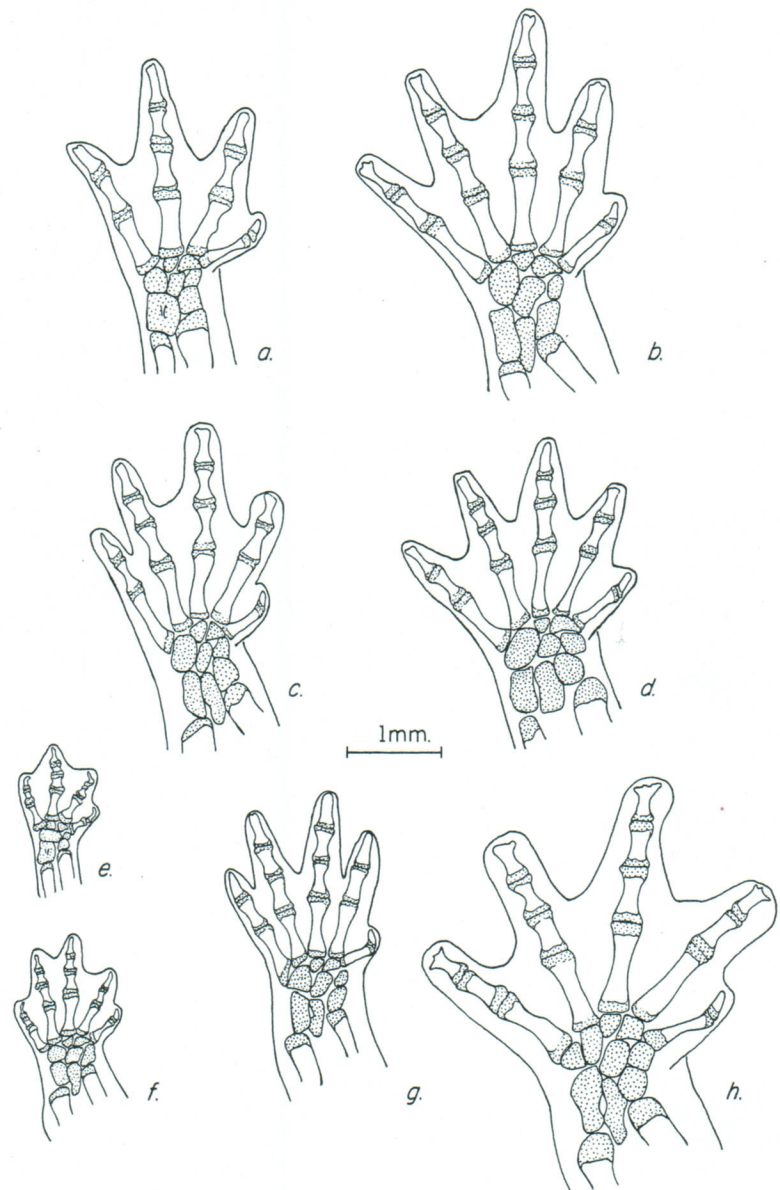
FIGURE 3. Hands and feet of species of *Chiropterotriton*, drawn to same scale from cleared and stained specimens with aid of microprojector. Cartilage stippled. (a) Left hand and (b) foot of *C. veraepacis;* (c) foot of *C. barbouri;* (d) foot of *C. nasalis;* (e) hand, and (f) foot of *C. richardi;* (g) foot of *C. picadoi;* (h) foot of *C. bromeliacia.*

bital processes, but also has prefrontals very similar to those of *C. veraepacis*. The nasal bones of *C. veraepacis* and *C. nasalis* are very reduced in size and irregular in shape; the bones have weak or no articulations. Nasals are large, regular in form, and well articulated in *C. picadoi* and *C. barbouri*. The small nostriled *C. picadoi* has a very solid, strongly articulated skull, while the relatively large nostriled *C. richardi* and the small nostriled *C. barbouri* have the more restricted articulation typical of Guatemalan, Honduran, and Chiapan species of *Chiropterotriton*. In *C. richardi* the nasals are rather small, but less reduced than in *C. veraepacis* and *C. nasalis*.

If the *bromeliacia* group is accepted as a monophyletic assemblage, the osteological data are consistent with a reasonably clear cladistic network for the eight species we are able to consider in detail (Fig. 4). The characters used are as follows (upper case letters indicate primitive states, lower case derived state; see Wake 1966, for detailed analysis of characters):

A. Prefrontal and nasal form the bony connecting link between the frontal or the center of the skull and the maxillary; the nasolacrimal duct passes between the prefrontal and the nasal. a. No prefrontal bone; only the nasal bone is involved in the link, and the nasolacrimal duct passes behind it. a'. Nasal bone reduced in size and does not span frontal and maxillary; only prefrontal involved in link; nasolacrimal duct pierces expanded ventrolateral part of prefrontal. States a and a' represent independent derivations from A in very different directions.

B. Septomaxillary present. b. Septomaxillary absent.

C. Frontal processes of premaxillary arise separately and do not fuse. c. Processes fused at base but separate distally.

D. Distal tarsals 4 and 5 discrete. d. Distal tarsals 4 and 5 fused.

E. Vomer has a preorbital process. e. No process.

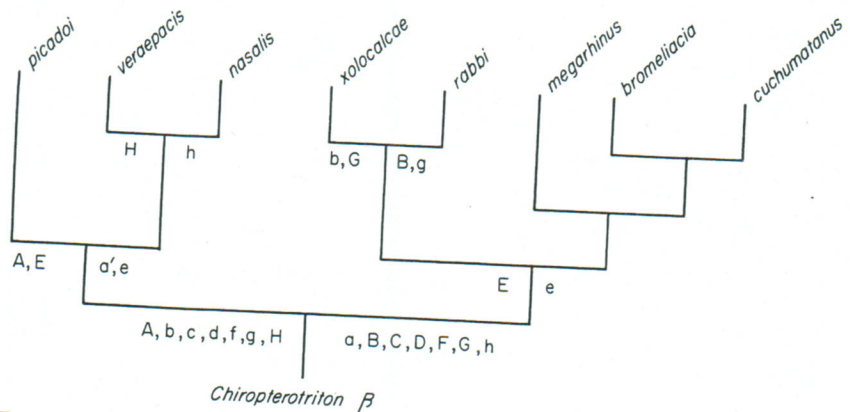F. Intermedium and ulnare discrete in carpus. f. Intermedium and ulnare fused.

FIGURE 4. Cladogram of eight species of *Chiropterotriton*-beta, constructed by use of osteological characters. The character states indicated apply to all species along the branch unless modified states are indicated at a higher level in the dendrogram. See text for explanation.

G. Columellar process of operculum present. g. Process absent.
H. Tibial spur present. h. No tibial spur.

The first branching separates the *bromeliacia* group from all other species. The second branching separates *C. picadoi* from *C. veraepacis* and *C. nasalis* on the basis of loss of the preorbital process of the vomer and piercing of the prefrontals in the latter two species. On osteological grounds *C. nasalis* and *C. veraepacis* are closest to *C. barbouri,* and they are very distinct from the species of the *bromeliacia* group. The osteological formulas for the poorly known species are, for *C. barbouri:* A (but the nasolacrimal duct pierces the prefrontal as in a'), b, c (but the amount of fusion is slight), d, E, f, g, H; for *C. richardi:* A, b, C, d, E, f, g, H. If placed on the cladogram *C. richardi* would be on a branch derived from (but not a sister group of) the main branch leading to *C. picadoi, C. nasalis,* and *C. veraepacis*. A branch leading to *C. barbouri* would be a more primitive, non-sister group of the *C. veraepacis-C. nasalis* line. In osteological formula *C. barbouri* is identical to *C. picadoi,* but when one takes into account additional features, especially the shape of bones such as the prefrontal and the route of the nasolacrimal duct, it seems clear that it is more similar to its more osteologically derived neighbors than to *C. picadoi.*

The cladogram contains four convergences. We have rather arbitrarily coded *C. nasalis* as h, even though a rudimentary tibial spur might be present. We have never seen tibial spur rudiments in the *bromeliacia* group, but with larger samples it would not be surprising to find an occasional rudiment. Septomaxillaries have not been observed in *C. xolocalcae,* but experience has shown that these bones are found in at least a small percentage of other members of the group, and the absence here may reflect the small sample size. It is likely that the remaining two convergences (e and g) are real.

In addition to the easily coded characters which have been used above, the general arrangement and shape of the bones of *C. nasalis, C. veraepacis* and *C. barbouri* are similar, and in some details of foot structure (the shape of the terminal phalanges, fig. 3) these species, *C. picadoi* and *C. richardi* are similar and differ from all members of the *bromeliacia* group.

MORPHOMETRIC ANALYSIS

Methods

Lynch and Wake (1975) used a number of analytical approaches in comparing the five species of the *Chiropterotriton bromeliacia* group. The number of specimens of *C. veraepacis,* while small, is sufficient for some of the same kinds of quantitative comparisons. Specifically, we have undertaken linear regression analysis of single characters as they vary with SL, and multiple discriminant analysis of all characters simultaneously in an attempt to clarify the phenetic and phyletic relationships among eight of the ten Central American species of *Chiropterotriton* (*C. bromeliacia, C. cuchumatanus, C. megarhinus, C. nasalis, C. picadoi, C. rabbi, C. veraepacis, C. xolocalcae*). *C. barbouri,* a poorly known species from western Honduras, and *C. richardi,* a poorly known Costa Rican form, have been omitted due to lack of sufficient comparative material. The reader is referred to our earlier paper for detailed

description of statistical methodology and for discussion of the choice and scaling of individual characters.

Analysis of individual characters: Eight characters are considered: standard length (SL), head width (HW), nostril diameter (ND), combined length of hind limb and fore limb (CL), foot width (FW), tail length (TL), number of maxillary teeth (MT), and number of vomerine teeth (VT). As described in detail in Lynch and Wake (1975), we have used linear regression techniques to project means and 95 percent confidence limits for characters 2-8 to a common value of SL = 30 mm. To eliminate the confusing effects of secondary sexual dimorphism and possibly nonlinear rates of character change across very wide ranges of SL, only post-juvenile males (SL greater than 24 mm) are included in the regression analysis.

Multivariate analysis of characters: The same eight morphological characters examined in the regression analysis were utilized in the discriminant function analysis. The purpose of this exercise was to define the combination of phenetic traits which best distinguishes the Central American species of *Chiropterotriton* from one another, and to eliminate the effects of intercorrelation among characters in assessing morphological similarity among species. This latter aim is realized because discriminant analysis defines statistically independent composite axes, each of which corresponds to independently varying character complexes (see Blackith and Reyment 1971). The Smithsonian Institution's version of the SPSS program for stepwise discriminant analysis was used for all computations.

Phenetic clustering of taxa: The discriminant analysis defines the centroid of each species cluster with respect to each of the seven discriminant axes which exist for an analysis of eight groups and eight characters. Because the distances between points in discriminant space ("D-space") are not biased by intercorrelations among characters, as is the case if phenetic distance is measured in simple Euclidian space, it is often preferable to base phenetic clustering on the scores along the major discriminant axes (for an example of the different results of these two metrics see Robinson and Hoffmann 1975). The latter axes are said to define a "reduced space" because most interspecific differentiation can be expressed using only a few of the maximum possible number of discriminant axes. A two- or three-dimensional representation of the group centroids (or of individual specimens) in discriminant space often suffices as a summary of significant interspecific variation.

With the above in mind, we have used the generalized distance (=Mahalanobis Distance) between the group centroids with respect to the first three discriminant axes as the basis for phenetic clustering. The unweighted pair group method using arithmetic averages (UPGMA), as described by Sokal and Sneath (1963) and Sneath and Sokal (1973) was the clustering algorithm employed. The UPGMA technique is a sequential, agglomerative, hierarchic, non-overlapping method (see Sneath and Sokal, 1973) which begins by defining a cluster (or several clusters) consisting of the least dissimilar Operational Taxonomic Units (OTU's), then adds individual OTU's or other clusters to pre-existing clusters on the basis of average phenetic similarity.

A second technique, the Prim algorithm (see Prim 1957; Farris 1970; Sneath and Sokal 1973), was used to form a minimum-spanning network connecting the eight OTU's, again based on the generalized distance separating them. This algorithm min-

imizes the total length of the internodes connecting the OTU's, and results in closest
phenetic neighbors always being linked by an internode. When superimposed on a
display of group centroids in reduced space, the Prim network provides a useful check
on the adequacy of the visual impression of inter-OTU distances (see Sneath and
Sokal, 1973: 255–256).

Results

Analysis of individual characters: Figure 5 and Table 1 summarize the results
of the regression analysis of single characters in post-juvenile males of the eight spe-
cies of *Chiropterotriton*. *C. veraepacis* has a longer tail and narrower head than the
other species in the comparison. The 95% confidence limits of the projected mean
values of TL and HW at SL = 30 mm show no overlap between *C. veraepacis* and
any of the remaining taxa. Some overlap is evident with respect to the other five
characters considered in the analysis, but *C. veraepacis* differs significantly ($P < 0.05$)
from every other species in from three to six characters. The 95% confidence limits
for projected character values tend to be relatively broad for *C. veraepacis* and *C.
nasalis,* probably reflecting their small sample sizes.

A mosaic pattern of differentiation is found. For example, high maxillary tooth
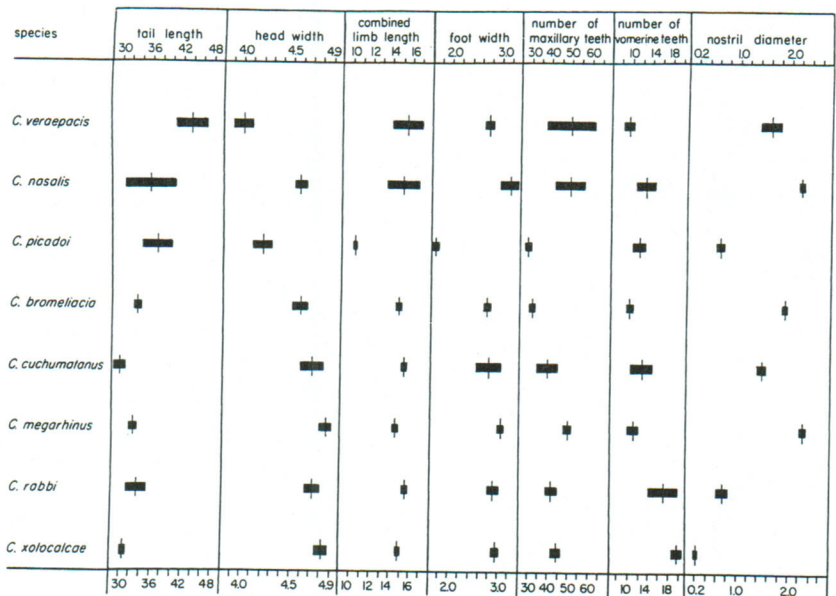counts may be associated with high vomerine tooth counts (*C. xolocalcae*), moderate

FIGURE 5. Predicted mean (vertical line) and 95% confidence limits (solid bar) for eight
characters in post-juvenile males of eight species of *Chiropterotriton*-beta. See text for further
explanation. Note that the column "head width" was incorrectly labeled "head length" in a
similar figure in Lynch and Wake (1975, fig. 7). All figures in mm.

TABLE 1

Predicted mean character values and 95% confidence limits (in parentheses) for post-juvenile male *Chiropterotriton* at SL = 30 mm. Values obtained by linear regression analysis (see text), except where no significant correlation was found between dependent variable and SL. In such instances, indicated by asterisk (*), univariate means and confidence limits are given. Symbols for characters: SL = standard length; TL = tail length; HW = head width; CL = combined limb length; FW = foot width; MT = maxillary tooth count; VT = vomerine tooth count; ND = nostril diameter.

| | | | | | CHARACTERS | | | | |
SPECIES	N	SL	TL	HW	CL	FW	MT	VT	ND
C. veraepacis	8	27.8	43.7 (40.6-46.8)	4.0 (3.9-4.1)	15.6 (14.1-17.1)	2.8 (2.7-2.8)	49.9 (37.8-61.9)	9.4* (8.4-10.4)	0.53* (0.47-0.59)
C. nasalis	7	28.0	35.6 (30.6-40.6)	4.6 (4.5-4.6)	15.2 (13.6-16.8)	2.8 (3.0-3.4)	49.7* (42.4-57.0)	13.1* (11.2-15.1)	0.73 (0.72-0.75)
C. picadoi	16	28.3	37.0 (34.0-40.0)	4.2 (4.1-4.3)	10.4 (10.2-10.6)	1.7 (1.6-1.8)	29.3 (27.5-31.1)	11.8 (10.6-13.0)	0.21 (0.18-0.24)

(*C. nasalis*), or low (*C. veraepacis*) vomerine tooth counts. An exception to the pattern of independent variation of characters is the invariable association of large nostril size with low numbers of vomerine teeth (previously noted in the *bromeliacia* group, Lynch and Wake 1975). *C. picadoi* is exceptional in having both few vomerine teeth and very small nostrils. This species possesses a well-developed preorbital vomerine process, as do the other small-nostriled species (*C. rabbi, C. xolocalcae*) in the analysis, but the presence of the process is not always associated with a large complement of vomerine teeth in other plethodontid salamanders (see Wake 1966; Lynch and Wake 1975: 34-35). Thus, our earlier conclusion that the preorbital vomerine process is necessary, but not sufficient, for the presence of a large number of vomerine teeth, is not affected by the pattern seen in *C. picadoi*.

Discriminant analysis: Figure 6 and Table 2 summarize the results of the stepwise discriminant analysis of interspecific variation. The absolute magnitudes of the standardized discriminant coefficients (Table 2) are proportional to the relative importance of each character in separating the species along each discriminant axis. The first three discriminant axes, representing the first three discriminant functions, together account for 95.7% of the observed interspecific morphological variation. Although the con-

Table 2

Summary of results of stepwise multiple discriminant analysis of variation in post-juvenile male *Chiropterotriton*. Raw (unstandardized) and standardized coefficients are given for the first three discriminant functions, which together account for 95.7% of the observed interspecific variation. The magnitudes of the standardized coefficients are proportional to the relative contribution of each variable on a given discriminant axis. The most important variables on each axis are marked with an asterisk (*).

| | DISCRIMINANT FUNCTION | | | | | |
| | FIRST | | SECOND | | THIRD | |
CHARACTER	Raw	Stand.	Raw	Stand.	Raw	Stand.
SL	0.008	0.022	0.058	0.157*	−0.076	−0.204*
TL	0.003	0.012	0.029	0.128*	0.021	0.092
HW	−0.078	−0.042	−0.083	−0.045	−0.167	−0.090
CL	0.006	0.015	−0.147	−0.362*	−0.040	−0.100
FW	−0.076	−0.046	−0.060	−0.036	0.183	0.111
MT	0.001	0.011	−0.003	−0.028	0.036	0.350*
VT	−0.012	−0.060	−0.007	−0.038	−0.008	−0.041
ND	0.521	0.403*	−0.061	−0.047	−0.050	−0.038
CONSTANT	−0.391		0.280		1.172	
PER CENT VARIATION EXPLAINED	54.13		32.98		8.59	
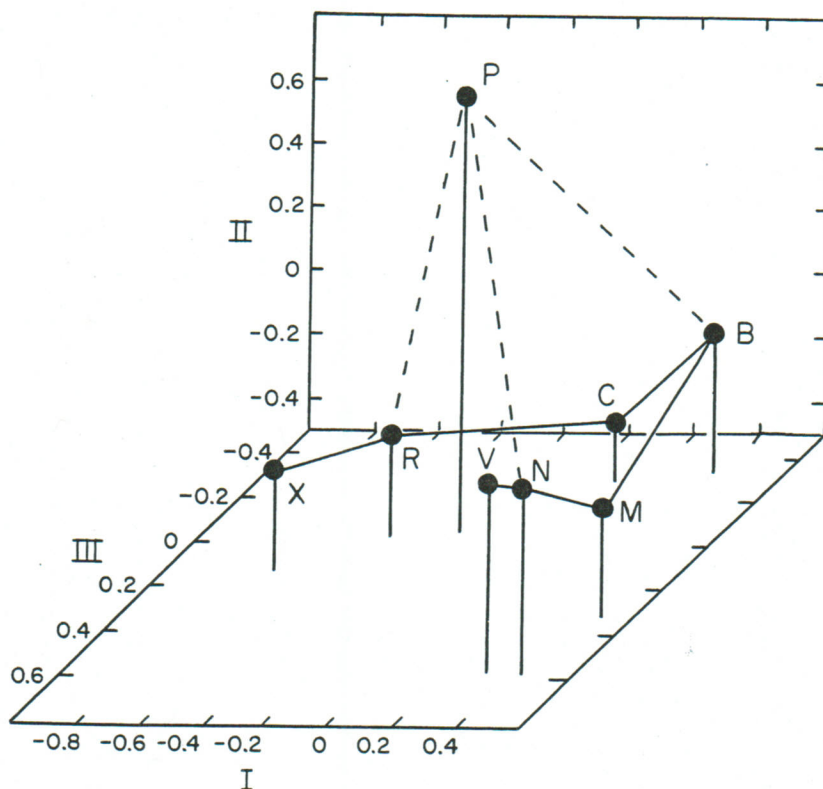
FIGURE 6. Plot of the first three discriminant axes separating post-juvenile males of the species of the *Chiropterotriton bromeliacia* group [*bromeliacia* (B), *cuchumatanus* (C), *megarhinus* (M), *rabbi* (R), *xolocalcae* (X)] plus *C. veraepacis* (V), *C. nasalis* (N), and *C. picadoi* (P). The dots are the positions of the group centroids for each species relative to these three variates. The centroids are connected by a computed Prim network, which links the closest phenetic neighbors. *C. picadoi* is about equally close to three species. See text for further explanation.

tributions of three of the remaining four discriminant axes are statistically significant (P<0.05), their cumulative impact on the discriminatory process is small (4.3%). The first discriminant function accounts for 54.1% of the interspecific variation; nostril diameter (ND) is by far the most important determinant of the score along this axis, as was also found to be the case in our earlier study of the *bromeliacia* group. The second discriminant function (33.0% of interspecific variation) is influenced most strongly by limb length (CL), and its most obvious effect is to sharply distinguish the short-limbed *C. picadoi* from all other species. The third discriminant function (8.6% of interspecific variation) shows high loading for maxillary tooth count (MT) and, to a lesser extent, standard length (SL) and foot width (FW). This axis tends to separate *C. veraepacis* and *C. nasalis* from *C. picadoi* and the *bromeliacia* group species.

TABLE 3

Generalized (Mahalanobis) distance values for centroids of eight OTU's.
$\overline{D}$ = mean generalized distance.

SPECIES	2	3	4	5	6	7	8	$\overline{D}$
1. C. bromeliacia	1.142	0.865	0.368	0.664	0.905	0.912	1.123	0.854
2. C. xolocalcae		0.402	0.871	1.211	1.126	1.214	1.166	1.019
3. C. rabbi			0.595	1.012	0.996	1.073	1.075	0.860
4. C. cuchumatanus				0.725	0.940	0.953	1.226	0.811
5. C. megarhinus					0.406	0.323	1.307	0.807
6. C. veraepacis						0.144	1.124	0.806
7. C. nasalis							1.253	0.839
8. C. picadoi								1.182

A three dimensional projection of the group centroids of each of the eight species in relation to the first three discriminant axes (Figure 6) summarizes the differentiation achieved by these axes. Viewed in D-space, *C. picadoi* appears to be the most isolated of the eight species, mainly by virtue of its very high positive score along the second discriminant axis. A close phenetic relationship between *C. nasalis* and *C. veraepacis* is evident, and these two species appear more similar to *C. megarhinus* than to any of the other *bromeliacia* group.

Table 3 gives the Mahalanobis distances separating the group centroids of the eight species in the D-space defined by the first three discriminant axes. The impressions gained from inspection of the three dimensional plot of group centroids are strengthened by these distance estimates. The most similar pair of species is *C. nasalis* and *C. veraepacis* ($\overline{D}$ = 0.14 units); no other species pair is separated by less than 0.32 units, the latter being the distance between *C. nasalis* and *C. megarhinus*. At the other extreme, *C. picadoi* shows no strong similarity to any of the other species ($\overline{D}$ = 1.18; range 1.07–1.31).

Despite the similarities of most of the species in gross appearance, the discriminant analysis succeeded in assigning 95% of the 130 individual specimens to the "correct" home population on the basis of morphometric criteria alone (Table 4). This result confirms the utility of multivariate approaches in making morphological comparisons among OTU's which show complex patterns of overlap in single characters and which exhibit size-related variation in most morphological traits. Of the seven misidentifications which occurred, three were assignments of *C. bromeliacia* and *C. rabbi* to *C. cuchumatanus*, three were assignments of *C. rabbi* to *C. xolocalcae*, or vice versa, and one is a misclassification of *C. nasalis* as *C. megarhinus*. In spite of the small overall phenetic separation of *C. nasalis* and *C. veraepacis* individuals of both species were not mismatched by the discriminant procedure.

Phenetic clustering; The Prim network linking the eight *Chiropterotriton* species is superimposed over the three-dimensional projection of the group centroids in figure 6. The distortion resulting from the geometry of the projection and from the omission

TABLE 4

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

| | | PREDICTED GROUP MEMBERSHIP | | | | | | | |
Actual Group	N	1	2	3	4	5	6	7	8
1. *C. bromeliacia*	33	32	0	0	1	0	0	0	0
2. *C. xolocalcae*	22	0	21	1	0	0	0	0	0
3. *C. rabbi*	22	0	2	18	2	0	0	0	0
4. *C. cuchumatanus*	9	0	0	0	9	0	0	0	0
5. *C. megarhinus*	13	0	0	0	0	13	0	0	0
6. *C. veraepacis*	8	0	0	0	0	0	8	0	0
7. *C. nasalis*	7	0	0	0	1	0	0	6	0
8. *C. picadoi*	16	0	0	0	0	0	0	0	16

of the fourth and higher discriminant axes evidently is small, for the Prim linkage of OTU's which show the highest phenetic similarity conforms well with the visual impression of similarities gained from the projection. The network is basically a chain which connects seven of the species in the order *xolocalcae-rabbi-cuchumatanus-bromeliacia-megarhinus-nasalis-veraepacis*. The eighth species, *C. picadoi*, lies well off this main sequence, and is about equally as distant from *C. rabbi, C. bromeliacia*, and *C. nasalis*.

The UPGMA phenogram, based on the same matrix of generalized inter-OTU distances used to construct the Prim network, is shown in figure 7. Summarizing, we see a tight cluster formed by *C. veraepacis* and *C. nasalis*, which is connected to the "looser" grouping of four *bromeliacia* group species by *C. megarhinus*, the fifth species in that group. *C. picadoi* shows slightly more similarity to the small-nostriled members of the *bromeliacia* group than to the other OTU's, but it is not very similar to any of the species. The linkage pattern among the five species of the *bromeliacia* group produced by the UPGMA analysis is identical to that derived previously (Lynch and Wake 1975: Fig. 10a) from an 11-character phylogenetic clustering algorithm, the WISS method of Farris, Kluge, and Eckhardt (1970).

DISCUSSION

The species of *Chiropterotriton* considered in this paper have several ecologically important features in common. All are small, arboreal or crevice-dwelling salamanders which inhabit wet montane forest, and all have very limited geographic ranges. Sympatry between congeners is unknown in northern Central American *Chiroptero-*
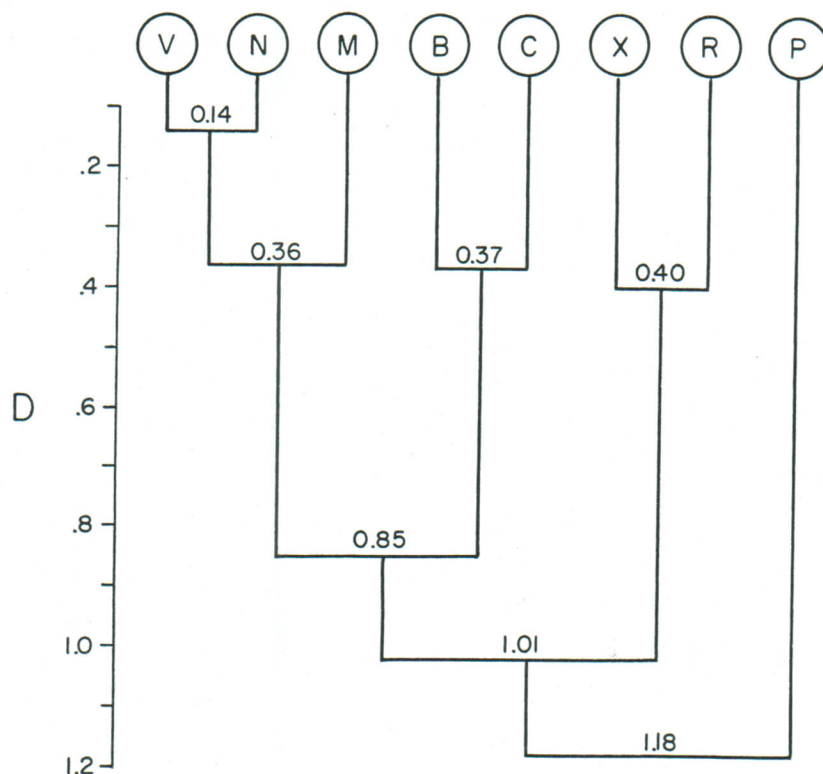
FIGURE 7. UPGMA phenogram of eight species of *Chiropterotriton* based on Mahalanobis Distance between group centroids with respect to the first three discriminant axes. (B) *C. bromeliacia*; (C) *C. cuchumatanus*; (M) *C. megarhinus*; (N) *C. nasalis*; (P) *C. picadoi*; (R) *C. rabbi*; (V) *C. veraepacis*; (X) *C. xolocalcae*. See text for futher explanation.

triton, although co-occurrence of several pairs of species of *Chiropterotriton*-alpha has been documented north of the Isthmus of Tehuantepec in the Sierra Madre Oriental. In addition, *C. picadoi* and *C. richardi* of the beta assemblage are sympatric in Costa Rica. In the absence of a sympatry test, one can always argue that the isolated populations of *Chiropterotriton* in Central America do not merit full specific rank. However, the unique combination of external morphometric traits which characterizes each of the Central American populations, combined with the osteological differences between most of the forms, makes it highly likely that these populations do in fact represent separate evolutionary units. We are actively investigating genetic divergence between species of tropical salamanders, and results to date lend support to our conclusions based on morphology.

The data from morphometrics and from osteology produce somewhat conflicting

pictures of evolutionary relationships. The UPGMA clustering technique based on the external morphology and dentition places *C. nasalis* and *C. veraepacis* well within the *bromeliacia* group. These seven species share more in common ecologically than they do osteologically. All are small species that occur in basically arboreal sites in cloud forests. They appear to be ecomorphs, with similar, adaptive structural responses to similar selective pressures. Certainly one reasonable hypothesis is that they are close relatives, derived from a common stock that was, itself, adapted to climbing in cloud forest habitats.

On osteological grounds this suggestion does not appear to be valid. An alternate hypothesis postulates an early separation between the ancestors of the *bromeliacia* group and the ancestors of all other *Chiropterotriton*-beta. These two lineages are sister groups, in the sense of Hennig (1966), with both lineages displaying both primitive and derived characters. The *bromeliacia* group has remained in Nuclear Central America, and has speciated but not undergone much additional differentiation. In contrast, the other assemblage is rather diverse, and widespread. *C. veraepacis* and *C. nasalis* are close relatives, distinct from each other in morphometric features but not in osteology. The cladistic species pattern of figure 4 leads us to suggest that morphological similarity of these two species to the *bromeliacia* group results from convergence by different stocks in response to similar selective pressures.

On osteological grounds both *C. richardi* and *C. barbouri* seem allied with *C. picadoi*, *C. nasalis*, and *C. veraepacis* rather than with the *bromeliacia* group. *C. barbouri* is a relative of *C. nasalis* and *C. veraepacis* and is somewhat intermediate between these two species and *C. picadoi* in osteological structure. Possibly *C. richardi* is the earliest known derivative of a *Chiropterotriton*-beta stock. It is the only species in Central America with any degree of resemblance to members of the genus *Oedipina*, lives sympatrically with species of that genus, and, like *Oedipina*, has been found living in holes in moss-covered earth banks. This elongate, diminutive animal with very short limbs and a long tail, closely resembles juvenile *Oedipina* in habitus. Possibly it is a semi-fossorial form.

A general character state formula for the genus *Oedipina* is: a, b, c. d, E, f, g, h (one population of one species of *Oedipina* appears to have septomaxillaries but b rather than B is used because of the clear preponderance of that state). This formula is compatible with the hypothesis that an animal rather like *C. richardi* might have given rise to *Oedipina*. Further suggestion of relationship comes from details of the structure of the feet of *C. richardi* and *Oedipina*. In addition to having the carpal and tarsal fusions typical of the *nasalis* group (character states d, f), *C. richardi* also has a fusion of the centrale and distal carpal 4, (Fig. 3). *Oedipina* also typically has all of these fusions, and fusion of distal carpal 4 and the centrale has also been reported in *Parvimolge townsendi* and various species of *Thorius* (Wake 1966). Fusion of the tibiale and centrale occurs in the tarsus of *C. richardi*, but has not been encountered elsewhere.

The relationship of *C. picadoi* to other species of *Chiropterotriton*-beta is obscure. On the basis of sharing many derived states with *C. barbouri*, *C. nasalis*, and *C. veraepacis* (b, c, d, f, g) we are tempted to postulate close relationship. Yet, *C.*

picadoi is very different from these three species in external morphological features and dentition. It has very short limbs and small feet, and in many features resembles the even more elongate and short-limbed *C. richardi*.

We earlier (Wake and Lynch 1976) assigned *C. nasalis, C. barbouri, C. richardi,* and *C. picadoi* to a *nasalis* group, thus placing all *Chiropterotriton*-beta in but two groups. We retain that arrangement here, but note that the *nasalis* group is morphologically far more diverse than the *bromeliacia* group.

Zoogeographic patterns conform well with our hypothesis concerning evolutionary relationships. The *bromeliacia* group is a cluster of species with high phenetic similarity sharing many derived osteological characters. They are so far known from a number of localitites in western Guatemala and Chiapas. The *nasalis* group is far more diverse than the *bromeliacia* group in morphometric and osteological traits. When additional information becomes available it may be possible to subdivide the *nasalis* group into three parts: 1) *C. nasalis, C. barbouri,* and *C. veraepacis,* a mainly northeastern group of arboreal species from Guatemala and Honduras that seems well defined osteologically; 2) *C. picadoi* of Costa Rica, allied to the former three species by derived osteological traits but not by ecology or external morphology; 3) *C. richardi* of Costa Rica, a highly distinctive, diminutive, elongate species with a combination of generalized (skull) and specialized (feet) osteological traits that distinguish it from all other species of *Chiropterotriton*.

The recent (February, 1976) Guatemalan earthquake has led to renewed interest in the structure and history of Nuclear Central America, one of the most complex and seismically active regions of the world. As a result of detailed investigations of land movements during the earthquake, the principal faults have been sharply defined, and the history of the region has been placed in new perspective. The Cocos plate is moving from the southwest and being subducted where it meets the Caribbean and North American plates in what Plafker (1976) calls the Middle American Megathrust. The North American plate is moving mainly westward, and the Caribbean plate is being forced eastward by the combined plate movements. The Motagua fault, clearly outlined by the recent earthquake, lies at the border of the Caribbean and North American plates. The extreme western end of the Caribbean plate is being "squeezed" between the Cocos and North American plates, and Plafker speaks of this region as being "decoupled" from the plate. This is the area of maximum volcanic activity in southern Guatemala. The amount of movement along the Motagua fault has been great, with a probable minimum movement of 200 km since Miocene being estimated by Plafker. Estimates of total movement along the fault range from a few hundred to over 1000 km. The movements are great enough and recent enough to have had profound impact on salamander distribution and evolution in the area. *Chiropterotriton,* for example, is restricted to montane and lower montane cloud forests in Central America. Low mountain ridges of nearly continous cloud forest are required for dispersal of these salamanders. In the present instance, we have shown that *C. veraepacis* and *C. nasalis* are similar in structure and we think that they are close relatives. *C. veraepacis* is found in a region that lies a little over 100 km west of the nearest population of *C. nasalis*. However, *C. veraepacis* occurs to the north of the Motagua fault, right along a branch of the Polochic fault, on the edge of the North American

plate, while *C. nasalis* occurs to the south and east of the fault zone, on the Caribbean plate. Thus there is no continuous montane link between the two areas now, and it is extremely unlikely that one has extended across the fault in the past. It is more likely that the two species populations have dispersed to their present sites by routes extending from the west in both instances. Presumably these populations have been separated for long periods of time.

Chiropterotriton-beta is sufficiently different from *Chiropterotriton*-alpha that the erection of a new genus for the former group might be justified. We choose not to do so at this time, for *Chiropterotriton*-beta is so diverse in structure that it would be difficult to diagnose meaningfully. Further, the osteological evidence presented here suggests that even a finer division of *Chiropterotriton* may be required than a simple two-way split. The key species in any future taxonomic revision of this group is *C. richardi*, a highly specialized species that might be derived from an early stock that gave rise not only to the remainder of *Chiropterotriton*-beta but also *Oedipina*.

The present study supports the view that a great amount of evolutionary differentiation has occurred in the lineages of plethodontid salamanders in the New World tropics.

ACKNOWLEDGMENTS

RESUMEN

En este trabajo se describe una diminuta nueva especie de salamandra plethodóntida de grandes narinas, *Chiropterotriton veraepacis,* que habita en bromeliaceas en la zona de bosque nublado montano al sur de Puruhlá, Baja Verapaz, Guatemala y en las zonas cercanas de Alta Verapaz, Guatemala. *C. veraepacis* muestra semejanzas en muchos caracteres fenéticos con *C. nasalis* del nordeste de Honduras, que es una especie de cola mas corta, cabeza mas ancha y narinas de mayor tamaño. La nueva especie se asemeja en ecología y algunos caracteres estructurales a las especies del grupo *bromeliacea* de Guatemala y Chiapas, pero difiere de ellas en caracteres osteológicos.

A pesar de que *C. nasalis* y *C. veraepacis* son muy distintos en la mayoria de caracteres morfológicos y ecológicos de la especie costarricense *C. picadoi,* estas especies son parecidas en osteología. Tambien se presenta información adicional referente a las poco conocidas especies, *C. richardi* (Costa Rica) y *C. barbouri* (Honduras). Asimismo se tratan las posibles relaciones entre las especies de este género.

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