# *Nyctanolis pernix*, A New Genus and Species of Plethodontid Salamander from Northwestern Guatemala and Chiapas, Mexico

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ABSTRACT. A new bolitoglossine salamander, *Nyctanolis pernix*, from the Cordillera de los Cuchumatanes of Guatemala and neighboring Mexico has been discovered. It differs from all other neotropical plethodontids in its spotted color pattern, long legs, and divided premaxilla. The osteology of *Nyctanolis* is the most plesiomorphous of any member of the supergenus *Bolitoglossa*. Except for the apomorphies characterizing the supergenus, *Nyctanolis* retains a morphology ancestral to the entire tribe Bolitoglossini and one more generally primitive than found in the other supergenera of the tribe, *Batrachoseps* and *Hydromantes*. The morphological features of the new genus place it as a sister group to the rest of the supergenus *Bolitoglossa*. The apparently ancient lineage represented by the new form occurs today in the oldest landpositive area in all of Central America.

## INTRODUCTION

> The remarkable radiation of the Bolitoglossini that has occurred in Mexico includes 7 genera and 63 species as at present understood. . . . Beyond question other genera and dozens of other species remain to be discovered. . . .
>
> —Smith and Smith, 1976

Our understanding of the evolutionary history of tropical salamanders is still in its infancy, and undescribed species are found with regularity. No new genera have been described for thirty years (Tanner, 1950), but despite this seeming stability several of the presumed lineages are poorly defined (Wake and Lynch, 1976). In the summer of 1974 the senior author visited a remote area on the eastern slopes of the Sierra de los Cuchumatanes, in extreme northwestern Guatemala. There, in a limited area, he discovered five species of salamanders living in sympatry in a cloud forest at intermediate elevations. Three of these species proved to be undescribed. In this paper we present a description of the most distinctive of the new species. It is so unusual in its combination of ancestral and derived morphology that it requires its own genus. It is the only tropical plethodontid that has two premaxillary bones, and it differs from all other tropical salamanders as well in its body form and behavior. This long-legged, large, colorful salamander, with its long, whip-like tail, and high level of scansorial activity reminds us more of an anoline lizard than a typical salamander.

We name the new genus for its anoline aspect and nocturnal habits (Gr., *nyktos*, night) and the species (L., quick, agile) for its gymnastic behavior.

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## TAXONOMY AND MORPHOLOGY

### *Nyctanolis* new genus

*Type species. Nyctanolis pernix* sp. nov.

*Diagnosis.* A plethodontid salamander belonging to the subfamily Plethodontinae, tribe Bolitoglossini, supergenus *Bolitoglossa;* distinguished from all other members of the supergenus by the presence of paired premaxillary bones and extremely long tail, limbs, and digits. The genus is easily distinguished from the diminutive species of *Parvimolge* and *Thorius* by its large size, and from the elongate species of *Lineatriton* and *Oedipina* by its long limbs and large, broad head. Most species of both *Chiropterotriton* alpha and beta are much smaller, but it is further distinguished from the former by having a fifth distal tarsal that is smaller than the fourth, and from the latter in having a distinct lingual cartilage and a well-developed columella. It differs from *Bolitoglossa* in having a distinct sublingual fold, nine tarsal elements, a well-developed columella, and a lingual cartilage. It differs further from *Bolitoglossa* alpha in having a well-defined tibial spur, and from *Bolitoglossa* beta in having only a slightly constricted tail base and unspecialized transverse processes on the first caudal vertebra. *Nyctanolis* most closely resembles species of *Pseudoeurycea,* but is distinguished from that genus by being more extreme in limb, hand, and foot specializations and by having a more fully developed columellar stylus and lingual cartilage, in addition to its unique premaxillae.

### *Nyctanolis pernix* sp. nov.
Figures 1-4

*Holotype.* Museum of Vertebrate Zoology (MVZ) 134641, an adult female from Finca Chiblac, 10 km (air) NE Barillas, Huehuetenango, Guatemala, (91°16'W, 15°53'N), 1,370 m (4,500 ft) elevation, collected 29 August 1975, by P. Elias and J. Jackson.

*Paratypes.* MVZ 131583-85, 134639-40, 134642-44, 149370, 149372-73, 173062 (cleared and stained), MCZ 100154, same data as holotype but collected at different times by P. Elias, J. Jackson, H. B. Shaffer, and A. Diaz. United States National Museum 206925, cave near stream that empties the main lake, Lagunas de Montebello, Chiapas, Mexico, (91°32'W, 16°5'N), collected by Scott Belfit, 8 July 1972.

*Diagnosis.* A large, slender species (standard length, SL, in four adult males 43.2–68.1, $\bar{x}$ 54.9; nine adult females 57.8–73.6, $\bar{x}$ 67.9) with a very long tail (SL/tail length in three adult males is 0.73–0.84, $\bar{x}$ 0.79; three adult females 0.80–0.94, $\bar{x}$ 0.87) and long limbs and digits (when appressed fore and hind limbs overlap in four adult males by 3–4 costal grooves, $\bar{x}$ 3.6; in eight adult females by 1.5–4.0 costal grooves, $\bar{x}$ 2.5). The head is broad (SL/head width in four adult males 5.8–6.3, $\bar{x}$ 6.0, in nine adult females 6.0–6.6, $\bar{x}$ 6.2) and relatively flat, and contains large numbers of maxillary-premaxillary (88–119, $\bar{x}$ 103 in four adult males; 82–131, $\bar{x}$ 110 in nine adult females) and vomerine teeth (29–47, $\bar{x}$ 41.5 in four adult males; 38–53, $\bar{x}$ 45.7 in nine adult females). The species has highly distinctive coloration, and typically animals are shiny dark black with bright red spots on the eyelids that become red-orange, then orange, then yellow, and finally cream-colored posteriorly on the limbs, body, and tail.

*Description.* This large and long-legged but slender species has a short snout. Both males and females grow to a large size. The nostrils and labial protuberances are small in both sexes but are largest in adult males, whose snouts are generally expanded forward to considerably overhang the mandible. The mental hedonic gland is large and pronounced in adult males, attaining a width half that of the entire head. The head is wide and flattened, always markedly broader in dorsal aspect than the broadest point on the trunk. The ratio of maximum head width to head depth at the angle of the

jaw varies in adults from 2.1 to 2.3. A deep unpigmented groove extends below the eye, following its curvature, to near the posterior border of the eye opening, but does not communicate with the lip. A marked angle in the line of the mouth beneath the eye cocks the posteriormost section of the lip gently ventrad to the angle of the jaw. The large and prominent eyes bulge upward from the flattened head, especially in males, but do not extend lateral to the jaw margins. An indistinct postorbital groove extends posteriorly and gently ventrad from behind the eye as a shallow depression turning sharply directly ventrad as a deep crease which, passing behind the jaw articulation, disappears below the level of the mandible. No trace of a nuchal groove is evident, but the gular fold is strongly developed and arches slightly forward at the midline. Vomerine teeth increase in number with increasing size (Table 1) but there are many even in small individuals. These teeth are arranged in a long gently arched row which extends laterally to far beyond the small internal nares, nearly to the jaw line. The many maxillary teeth extend in a long row to the interior angle of the jaw and slightly beyond the posterior margin of the eye. The maxillary teeth are smoothly continuous with the premaxillary teeth so that there is no break except for a slight discontinuity in the largest male. The premaxillary teeth are numerous (up to 15) but are only slightly sexually differentiated and do not pierce the upper lip in males. The tongue pad is nearly round and lies at the end of a pedicel. There is no anterior attachment, and the tongue has the boletoid form characteristic of the supergenus. A large, fleshy sublingual fold is present. The trunk and tail are slender and cylindrical in this species and no strong basal constriction is evident. The tail may be autotomized at any point along its length. The tail is relatively long. No postiliac gland is visible. The limbs are extremely long, and when fore and hind limbs are stretched along the flank they overlap extensively. Hands and feet are large and unwebbed, with distally expanded, quadrangular digital tips. The fingers are, in order of decreasing length, 3,4,2,1; the toes, 3,4,2,5,1.

*Measurements of the Holotype (in mm).* Head width 11.6; snout to gular fold (head length) 15.2; head depth at posterior angle of jaw 5.4; eyelid length 5.0; eyelid width 3.7; anterior rim of orbit to snout 4.4; horizontal orbit diameter 3.5; interorbital distance 3.5; distance between vomerine teeth and parasphenoid tooth patch 0.5; snout to forelimb 21.1; distance separating internal nares 3.3; distance separating external nares 3.4; snout projection beyond mandible 0.3; snout to posterior angle of vent (standard length, SL) 70.5; snout to anterior angle of vent 64.4; axilla to groin 36.9; tail length 79.7; tail width at base 4.8; tail depth at base 5.6; forelimb length (to tip of longest toe) 21.6; hindlimb length 23.7; width of hand (across from tip of innermost to tip of outermost toe when spread) 7.6; width of foot 9.7.

*Coloration (in alcohol).* All ventral surfaces are slate black except palmar and plantar surfaces and tips of the nasal cirri which are less saturated with pigment and thus appear lighter grey. One large adult male (MVZ 134642) is uniformly dark black dorsally as well as ventrally, with the exception of a small, indistinct spot middorsally. All other specimens have essentially the same, almost gaudy coloration. Bright, discrete spots extend from eyelids to tail tip in these 13 animals. One of these has been cleared and stained; variation in 12 other specimens is as follows. A series of large, round, pale yellow spots with irregular margins, each about equal in diameter to the eye, is present on the black dorsum. These spots are almost symmetrically arranged. One spot covers each eyelid in all animals. One spot covers the dorsal surface of each elbow in all but one animal, which has a spot on one side only. All animals have a large spot covering each knee. A pair of spots lies over the shoulders in 11

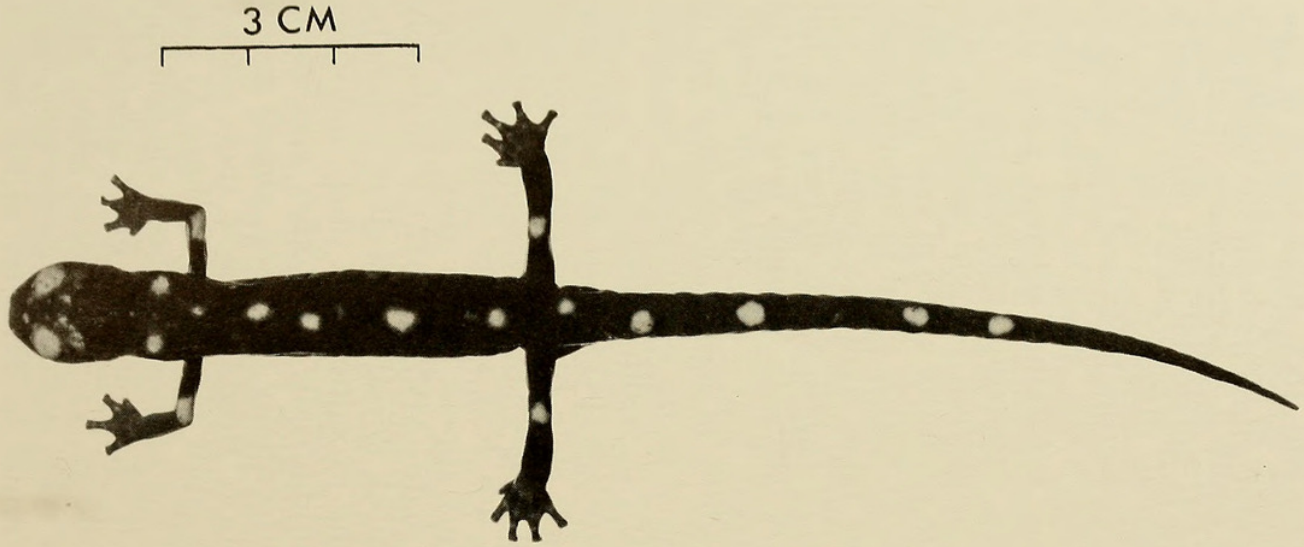


Figure 1. Dorsal view of the holotype of *Nyctanolis pernix*, MVZ 134641.

TABLE 1. VARIATION IN *NYCTANOLIS PERNIX*.

| | Sex | Standard Length | Head Length | Head Width | Foot Width | Hind Limb Length | Fore Limb Length | Tail Length | Maxillary and Premaxillary Tooth Number | Vomerine Tooth Number | Limb Interval |
|---|---|---|---|---|---|---|---|---|---|---|---|
| MVZ 134642 | M | 68.1 | 16.8 | 11.8 | 9.3 | 23.1 | 20.6 | 86.4 | 119 | 45 | −4.0 |
| MVZ 134644 | M | 58.0 | 13.4 | 9.5 | 7.1 | 18.8 | 18.0 | 69.2 | 105 | 45 | −3.0 |
| MVZ 131585 | M | 50.1 | 11.3 | 8.6 | 6.4 | 16.2 | 16.0 | 68.3 | 88 | 29 | −4.0 |
| MVZ 149370 | M | 43.2 | 9.8 | 6.9 | 5.1 | 14.1 | 14.2 | - | 100 | 47 | −3.5 |
| MVZ 134640 | F | 73.6 | 15.9 | 12.3 | 9.9 | 25.2 | 23.5 | - | 117 | 43 | −1.5 |
| MVZ 134639 | F | 71.7 | 16.1 | 11.5 | 7.9 | 22.7 | 20.7 | 89.9 | 110 | 49 | −2.0 |
| MVZ 134641* | F | 70.5 | 15.2 | 11.6 | 9.7 | 23.7 | 21.6 | 79.7 | 112 | 42 | −3.0 |
| MVZ 134643 | F | 69.9 | 15.3 | 11.4 | 9.8 | 21.2 | 19.9 | - | 131 | 53 | −2.5 |
| MVZ 149373 | F | 68.2 | 15.1 | 10.4 | 8.8 | 21.6 | 21.6 | - | 82 | 51 | −4.0 |
| MVZ 131583 | F | 67.6 | 15.4 | 10.9 | 8.3 | 20.8 | 19.6 | 72.1 | 115 | 47 | −2.0 |
| USNM 206925 | F | 67.3 | 15.5 | 10.9 | 9.1 | 22.0 | 21.4 | - | 107 | 40 | - |
| MVZ 173062 | F | 64.1 | 13.5 | 10.2 | 8.4 | 20.3 | 19.9 | - | 104 | 38 | −2.5 |
| MVZ 149372 | F | 57.8 | 12.3 | 9.1 | 6.9 | 19.5 | 18.6 | - | 109 | 48 | −2.5 |
| MVZ 131584 | J | 27.5 | 7.3 | 5.7 | 3.2 | 9.1 | 7.5 | - | 50 | 13 | −0.5 |

*Holotype.

animals, and the 12th has a single shoulder spot. Many individuals have one spot over the pelvis (five have one, one has two, and six are unspotted). Most individuals (nine) have some sort of spot, variable in size and position, in the caudosacral region. Full-sized (i.e., the size of the eyelids) dorsal spots on the trunk between shoulder and pelvis occur in all individuals, and range in number from two to eight. Included among the trunk spots of four specimens is a pair placed symmetrically behind the shoulder. Three animals show variable numbers of small, obscure spots on the trunk. Most individuals lack complete tails, but large spots occur only on the proximal one third of the tail and the first third is complete in 11 specimens. Of these 11, all have some distinct tail spots, ranging from one to eight in number. In addition four of the seven with over one-half the tail present show clusters of up to nine small indistinct spots on the second half of the tail. Miscellaneous small spots occur in many animals: seven have spots on the temple; two have parietal spots; two have paired wrist spots; one has a foreleg spot; one has a flank spot; one has a mandibular spot.

*Coloration (in life).* These animals were patterned as they are in preservation, but the coloration of the dorsal spotting differed. The spots on the eyelids and neck are a deep crimson, those on the elbows and knees are orange, and the trunk and tail spots are light yellow, becoming cream at the tail tip.

*Habitat.* The series from the type locality was collected in a large clearing surrounded by virgin cloud forest. The locality is extremely humid as indicated by rainfall records taken within 5 km of the spot. These records show rainfall of 5 to 6 m annually, but they were taken below the cloudline and thus may underestimate precipitation at the type locality.

The animals at the type locality were collected under both moss and bark on felled cloud forest hardwoods. They were active on rainy nights. Rarely were more than two individuals taken per man-day collecting.

Also occurring at the site were four other salamanders: *Bolitoglossa hartwegi, Bolitoglossa cuchumatana,* a new species of *Bolitoglossa* (Elias, in preparation), and another undescribed species belonging to an as yet undetermined genus of plethodontid salamanders. The three *Bolitoglossa* were taken in the same microhabitats as those in which *Nyctanolis* was found, but the disturbed nature of the habitat leaves ecological relationships vague.

Various hylid and leptodactylid frogs were also taken at the site as was one snake *(Leptodeira)* and lizards of the genera *Anolis, Sceloporus, Scincella, Barisia,* and *Lepidophyma.*

*Range.* The species is known from the type locality and one other locality about 20 km NW of Finca Chiblac just across the border in Chiapas, Mexico.

*Osteology.* Information concerning osteology has been derived from one cleared and stained specimen (MVZ 173062), an adult female, and from radiographs of all of the specimens. Dorsal and ventral views of the skull are illustrated (Fig. 2).

The relatively broad and low skull is compact and well ossified, with well-organized articulations and well-defined bones. Premaxillary bones are distinctly separate in all individuals in which they can be seen; the smallest individual is insufficiently ossified for the bones to be resolved in radiographs. The premaxillary bones are large, relative to the small, fused bones characteristic of other members of the supergenus *Bolitoglossa.* They are well articulated with each other, and are tightly articulated laterally to the maxillaries, which dorsally overlap the dental portions of the premaxillaries. The premaxillaries of both males and females are part of a continuous maxillary-premaxillary arcade, rather than being discontinuously projected anteriorly as in many other tropical salamanders. The palatal process of each premaxillary bone

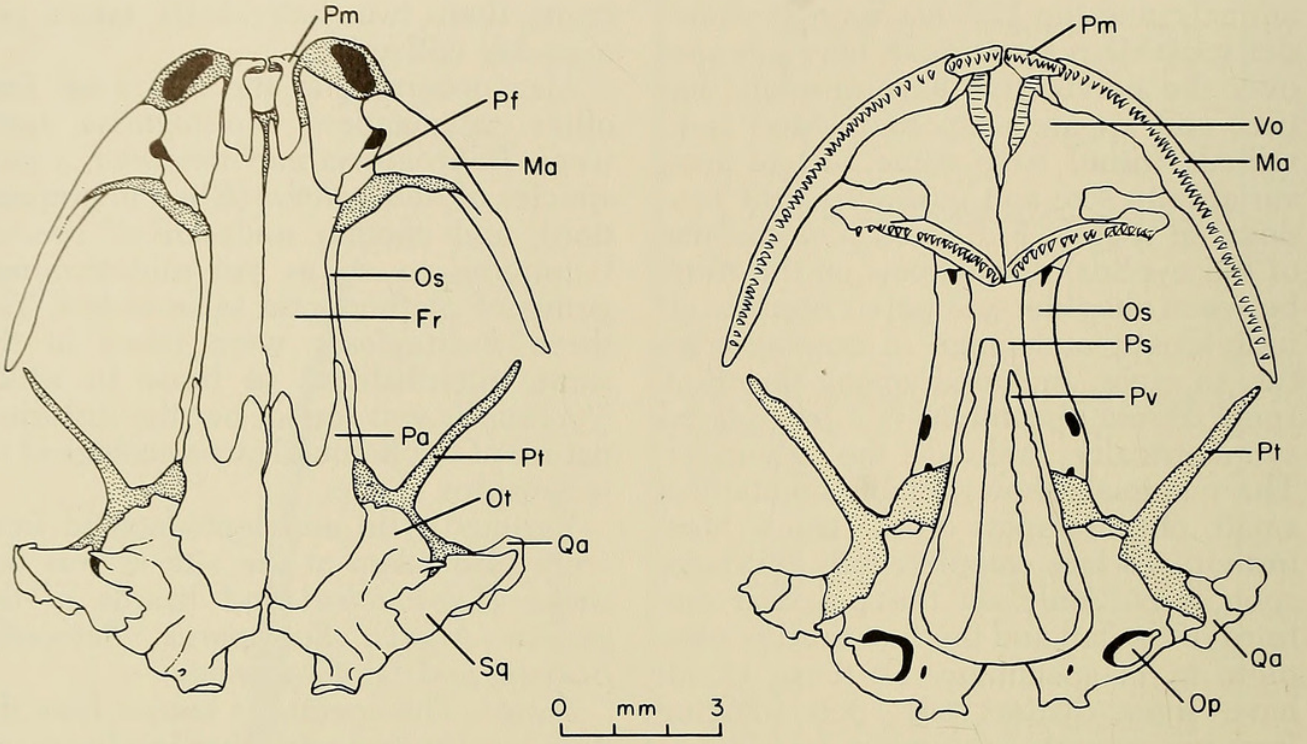


Figure 2. Dorsal (left) and ventral (right) views of the skull of *Nyctanolis pernix*, drawn from cleared and stained specimen with aid of microprojector. Cartilage stippled.

*Abbreviations:* Fr, frontal; Ma, maxillary; Op, operculum; Os, orbitosphenoid; Ot, otic-occipital; Pa, parietal; Pf, prefrontal; Pm, premaxillary; Ps, parasphenoid, Pt, pterygoid portion of palatopterygoid cartilage; Pv, posterior vomerine tooth patch (outline only, teeth not drawn); Qa, quadrate, Sq, squamosal; Vo, vomer.

is narrow and well separated from the vomer behind it. Frontal processes of the premaxillaries are stout and well developed; they arise from a narrow base as columnar structures, then immediately diverge around the large, internasal fontanelle. As the processes rise dorsally and posteriorly they flatten and form the borders of the fontanelle. As they flatten they become somewhat expanded. Laterally the processes closely abut the large nasals, and posteriorly they broadly overlap the anterior extensions of the facial portions of the frontals. The frontal processes do not contact each other behind the fontanelle, but in some individuals they come very close. The frontal processes terminate rather far forward, well in advance of the orbit, and of the posterior tip of the nasals. Nasals are large, but they are nonprotuberant in all females and in all but the largest male; in that individual the premaxillary bones are larger than in any other specimen and the nasal bones extend anteriorly slightly beyond the premaxillaries. The large nasals are triangular in shape, and they have strong, overlapping articulations with the facial processes of the frontals. The nasals slightly overlap the prefrontals, and are overlapped by the anterior part of the facial processes of the maxillaries. The nasals are not domed, but are rather flattened or slightly concave. No septomaxillaries can be seen in any specimen (a slight shadow on one side of the skull in radiographs of one of the smaller specimens might conceivably be a septomaxillary). Prefrontal bones are discrete but relatively small. The bones are only about one-quarter or less the area of the nasals. The prefrontals broadly overlap the facial parts of the frontals, and are overlapped rather narrowly by the pos-

terior and dorsalmost parts of the facial processes of the maxillaries. The foramen for the nasolacrimal duct lies at the extreme anterolateral tip of the prefrontals and is indented into the dorsal margin of the facial processes of the maxillaries. There is a slight indentation of the posterolateral border of the nasals as well. The nasolacrimal duct proceeds from the orbit across the lateral parts of the prefrontals, which are depressed and almost grooved. The maxillary bones are very large and well developed. The bones extend posteriorly to terminate in sharp points at the level of the posterior margin of the eye. The maxillaries bear small but well-developed, bicuspid teeth from the premaxillary nearly to the posterior tip; these teeth are about the same size as the premaxillary teeth in females, but are somewhat smaller in males. The facial processes of the maxillaries are relatively very large and well developed; they are larger in area than the nasals. The palatal processes are moderately well developed and extend as shelflike processes to the margins of the vomer bodies, against which they tightly abut.

The vomers are large bones which are well separated from each other by the intervomerine fontanelle anteriorly. This fontanelle contains a large glandular mass, present also in other plethodontid salamanders but frequently not so well developed. The vomers abut dorsally and posteriorly to this mass, and the posterior parts of the two vomers are tightly articulated. The preorbital processes of the vomers are long and stout; they extend beyond the lateral margins of the vomer bodies, and bear teeth in a long, curving series nearly to their tips, well beyond the lateral border of the internal nares.

Frontals and parietals are well developed and firmly articulated with each other in an extensive interlocking contact. The paired elements are tightly articulated to each other along the midline as well. Anterior parts of the frontals are moderately large and contribute importantly to the facial part of the skull. The overlapping posterior lobes of the frontals are relatively very large. The frontals appear to be relatively narrow, but we believe that this is simply an illusion that results from the unusual (for a tropical salamander) full development of the outer bones of the skull. Parietals are well developed, but they do not have the distinct lateral spurs that are characteristically present (but sometimes very poorly developed) in tropical salamanders (Wake, 1966). The region of the lateral spur is somewhat expanded and ventrally directed, but is not spurlike. The otic capsules are large and well developed, but they do not appear to be relatively as large as in other tropical genera, in which the other portions of the skull are frequently reduced in size. Two or three spinelike projections arise from the anterodorsal parts of the capsules, and are directed laterally; these form a kind of rudimentary crest. The large parasphenoid is narrow anteriorly, but the orbitosphenoids are well separated from each other. The tip of the parasphenoid is blunt. Posterior vomerine teeth are borne in long, relatively narrow patches that are well separated from each other and from the anterior vomerine teeth. The teeth in these patches are somewhat smaller than the maxillary teeth. In the cleared and stained specimen there are 81 (left) and 92 (right) bicuspid, ankylosed teeth. The operculum has a small but well-developed stilus that is as large as this structure ever becomes in any of the other tropical genera (it is absent in the vast majority of tropical species). Well-developed, stout quadrates are connected to the otic capsules by the very large, broad squamosals, and by the cartilaginous suspensorium.

The lower jaw has a long, slender dentary bearing a very long series of small teeth, about the size of those on the maxillary. The prearticular is relatively small and low.

The hyobranchial apparatus (Fig. 3) is very generalized for the supergenus *Boli-*

*toglossa* (cf. Tanner, 1952; Lombard and Wake, 1977). It is typical of the group; there is no urohyal, and the radii are essentially continuous with the basibranchial. There is a well-developed lingual cartilage, but it is represented by what is essentially a direct anterior continuation of the basibranchial, although there is a change from hyaline to fibrocartilage in the joint region between the cartilage and the basibranchial. We have also had available one sectioned head of the species, and detailed examination of it reveals that in all respects the hyobranchial apparatus and associated musculature fits the morphological features of Mode VI of Lombard and Wake (1977). Specifically, the entire apparatus is greatly elongated, and the proportions of the elements are unequal. The epibranchials are very long, more than three times the length of the basibranchial (minus lingual cartilage), and about six times the length of the second ceratobranchials. The diameters of the basibranchial, second ceratobranchial, and base of the epibranchial are about equal, and all are greater than that of the relatively slender first ceratobranchial. The first ceratobranchial is not so slender as is characterisitc of that element in many members of the supergenus *Bolitoglossa*. The radii are of moderate length for a member of the supergenus, but are relatively stout. The ceratobranchials are relatively long, but generalized in form; there is a distinct, but narrow, flattened blade distally, and there is no anterior filament. The point of attachment of the suprapeduncularis muscle is drawn medially into a broad-based process.

Vertebral structure is generalized. Individual vertebrae have centra with hollow, tapered, bony husks, and are joined to one another by the spindlelike intervertebral cartilages and the zygapophyses. There is a single atlas, 14 trunk vertebrae, one sacral vertebra, two caudosacral vertebrae, and a variable number of caudal vertebrae. The trunk vertebrae all have transverse processes that

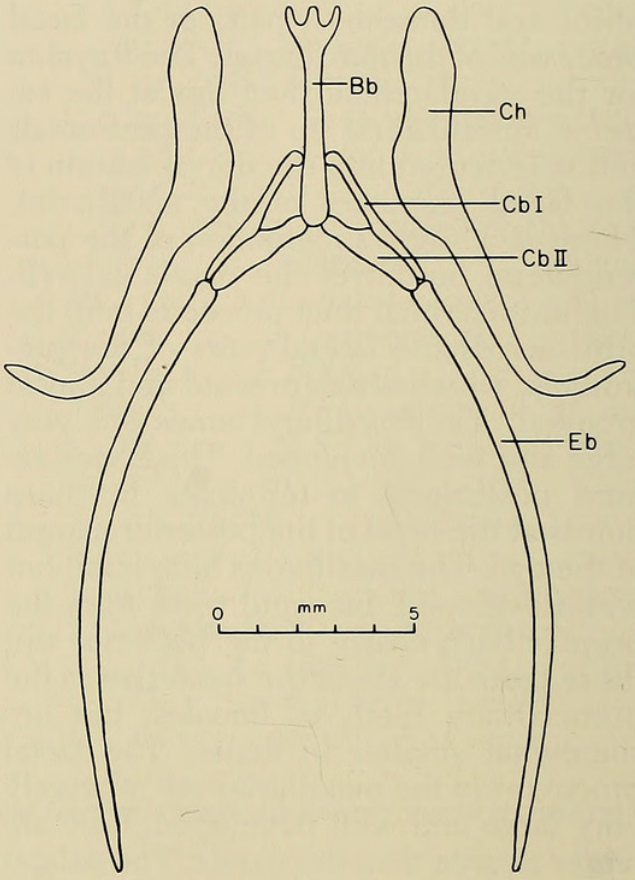


Figure 3. Dorsal view of the cartilaginous hyobranchial apparatus of *Nyctanolis pernix*.

*Abbreviations:* Bb, basibranchial; CbI, first ceratobranchial; CbII, second ceratobranchial; Ch, ceratohyal; Eb, epibranchial.

arise and remain separated until their tips. These processes are relatively long, and extend well beyond the limits of the zygapophyses. The upper transverse process is a little anterior in placement relative to the lower one. Relatively long, slender ribs are borne on all but the last trunk vertebra; rib heads are relatively widely separated. Spinal nerve routes are similar to those reported by Edwards (1976) for this group: a ventral root issues from the neural arch of the atlas; dorsal and ventral roots issue from separate foramina in the anterior, pre-transverse process part of the neural arch of the first trunk vertebra; there is a very large foramen in the anterior, pre-transverse process part of the neural arch of the second trunk vertebra, and a set of dorsal and

ventral roots emerge through a common, small foramen in the posterior, post-transverse process part of the neural arch of the same vertebra; dorsal and ventral roots emerge through a common, small foramen in the posterior, post-transverse process part of the third and all succeeding trunk vertebrae.

The first caudosacral vertebra has relatively long, nearly straight transverse processes. The second is a smaller vertebra, with processes that are much shorter than those of the first; these processes may be straight, but are more frequently oriented anteriorly. The origin of the processes on the first caudosacral vertebra is about midcentral, but those of the second vertebra arise in advance of the midpoint of the centrum. The second caudosacral vertebra bears rudiments of the haemal arch, not joined to each other, on the posterior part of the ventral surface of the centrum. The foramen for the spinal nerves is located behind the processes, about midcentrally.

The tail base region is not nearly as specialized for tail autotomy as in most other members of the supergenus (Wake and Dresner, 1967), but fundamentally it qualifies as a constricted-based tail even if the constriction is only slight. The first caudal vertebra is slightly, but not obviously, shorter than the second. It differs from the second caudal in having a complete haemal arch that lacks an anterior keel. It differs from the second caudosacral immediately in front of it in having transverse processes that arise at the very anterior end of the vertebra, essentially as extensions of the bases of the prezygapophyses. The transverse processes are short, and extend only a short distance anterior and lateral to the edge of the prezygapophyses. The musculature extending between the first caudal and the second caudosacral vertebrae is visibly shortened, relative to adjacent segments, but the tail is slender and the shortened segment is not obviously constricted. The smallest juvenile lost its tail at the base during capture, between the second caudosacral and the first caudal vertebrae. The skin of the shortened segment has collapsed over the wound in the preserved animal, in the typical wound-healing specialization that characterizes salamanders with constricted and slender-based tails (Wake and Dresner, 1967).

Complete tails are rare. The only large specimen with a complete tail has 39 caudal vertebrae, a very large number for the supergenus, with the exception of the exceptionally elongate species of *Lineatriton* and *Oedipina*. Other large specimens show signs of earlier breaks, always away from the basal region. We cannot rule out tail base breaks in juveniles, with subsequent regeneration. One specimen has a tail broken at vertebra 39. Another has a total of 45 vertebrae, regenerated from vertebra 24. There are 49 vertebrae in the tail of another specimen, regenerated from vertebra 24. The holotype has 34 caudal vertebrae, but its tip is missing; further, it shows signs of an initial break at vertebra 18, and a subsequent break at vertebra 27. The caudal vertebrae are narrow and elongate; transverse processes are very short and are little more than small projections of the prezygapophyses. The spinal foramina are located midcentrally.

The hands and feet are highly distinctive (Fig. 4). The digits are very long, with terminal expansion. All phalangeal elements are well developed. The phalangeal formula is 1, 2, 3, 2 for the hand and 1, 2, 3, 3, 2 for the foot; this is the primitive formula for the supergenus *Bolitoglossa*. The long metapodial elements are cylindrical, as are all but the terminal phalanges. Terminal phalanges are specialized, and resemble those of *Aneides lugubris* (Wake, 1963); they are greatly expanded distally, and the expanded portion is slightly recurved and nearly bifurcated in the larger specimens. The expanded portion of each terminal phalanx is distinctly flattened. On the ventral surface of each phalanx, near the base, a well-defined projection is

present which serves as the site of insertion of a digital tendon. Even the phalanx of the first digit displays some distal expansion.

The carpal and tarsal arrangements are those characteristic of primitive plethodontids. There are eight carpals and nine tarsals. Distal tarsal 5 is smaller than distal tarsal 4 and does not articulate with the centrale.

Limb bones are very elongate, slender, and cylindrical. There is a well-defined, distinct tibial spur near the proximal end of the tibia, and the bone has a sharply defined crest distally.

*Relationships.* The tribe Bolitoglossini is characterized by seven unique apomorphies relative to all other plethodontids. All members of the tribe have 1) lost the urohyal; 2) radii fused to the basibranchial; 3) long epibranchials relative to the ceratobranchials; 4) a second ceratobranchial modified for force transmission; 5) a cylindrical muscle complex around the tongue; 6) lost the circumglossus muscle (all discussed in Lombard and Wake, 1977); and 7) a juvenile otic capsule configuration (Lombard, 1977).

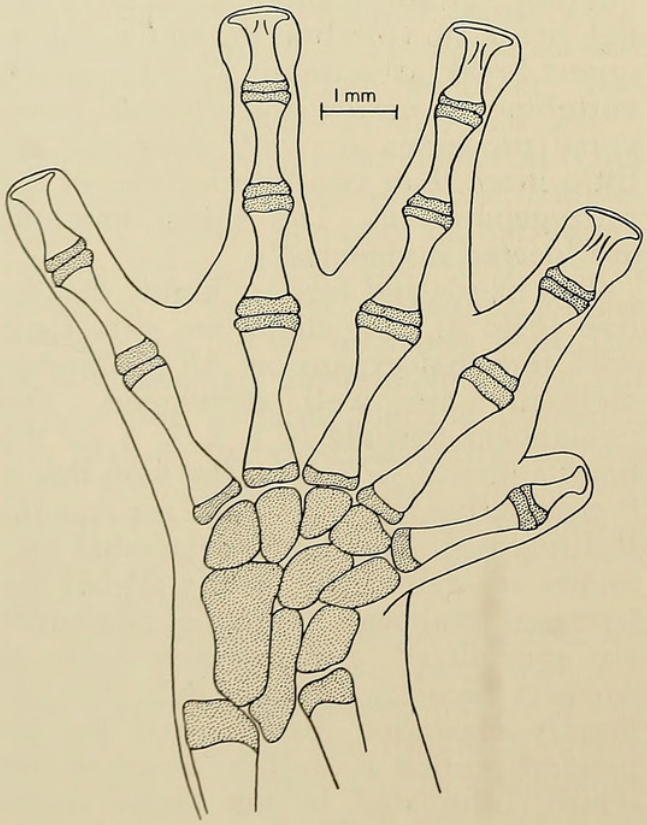


Figure 4. Dorsal view of the left foot of *Nyctanolis pernix*, cartilage stippled.

The supergenus *Bolitoglossa* is characterized by having a specialized autotomy area in the tail base that follows two caudosacral vertebrae (Wake and Dresner, 1967), and by some modifications of the throat and tongue musculature (Lombard and Wake, 1977).

The morphology of *Nyctanolis* includes all of the unique apomorphies characteristic of both the tribe Bolitoglossini and the supergenus *Bolitoglossa* and we therefore consider it to be a member of both taxa.

In most of its characters *Nyctanolis* is generalized within the supergenus *Bolitoglossa* and is similar to generalized members of related genera. Because of its generalized structure the phylogenetic position of the new genus relative to the other members of the supergenus is suggested by only two characters: absence of septomaxillary bones, and presence of paired premaxillaries. The absence of septomaxillary bones from most specimens of *Nyctanolis* (one of fourteen *may* have one septomaxillary) is a derived state that would place the new genus somewhere among the other genera. However, the erratic occurrence of these bones in species in which they are typically found (Wake, 1966), combined with the possible occurrence of septomaxillaries in one *Nyctanolis* specimen, weakens the value of this character. In having paired premaxillaries *Nyctanolis* is more primitive than any other member of the supergenus *Bolitoglossa*. Among neotropical salamanders only *Nyctanolis* has the premaxillary divided. This division is occasionally seen in an individual or two of some other species (Wake, 1966), but nowhere else is it characteristic of a taxon. This plesiomorphy argues strongly for the cladistic isolation of *Nyctanolis;* the new genus appears to be a sister

group to the rest of the supergenus (Fig. 5).

In many respects *Nyctanolis* preserves more plesiomorphic character states than any other member of the tribe Bolitoglossini; only those characters which diagnose the supergenus *Bolitoglossa* distinguish *Nyctanolis* from the ancestral state of all bolitoglossines. Members of the genus *Hydromantes* have the most primitive tail base region in the tribe, and have paired premaxillaries and well-developed septomaxillaries; however, they have a host of apomorphous characters, including a highly specialized projectile tongue and associated features, and they have lost prefrontals (Wake, 1966; Lombard and Wake, 1977). The species of *Batrachoseps* mainly have apomorphous characters, including only four toes, widely separated frontals and parietals, and a strongly developed lateral parietal spur. All *Batrachoseps* are plesiomorphic relative to the other bolitoglossine supergenera in retaining genioglossus muscles as tongue retractors (although in a highly specialized form, see Lombard and Wake, 1977). While most *Batrachoseps* lack prefrontals and have but a single premaxillary, *B. wrighti* gains prefrontals and divided premaxillaries when it gets very large, and *B. campi* has these characters almost from the time of hatching (Marlow, Brode, and Wake, 1979). *Batrachoseps* has two or three caudosacral vertebrae and a wound-healing specialization, and in these respects is more apomorphic than *Hydromantes* but less than supergenus *Bolitoglossa*, all members of which have two caudosacral vertebrae and provision for autotomy of the tail at the base. In fact, only in this respect, and in the absence of well-developed septomaxillaries, is *Nyctanolis* less plesiomorphic than *B. campi*.

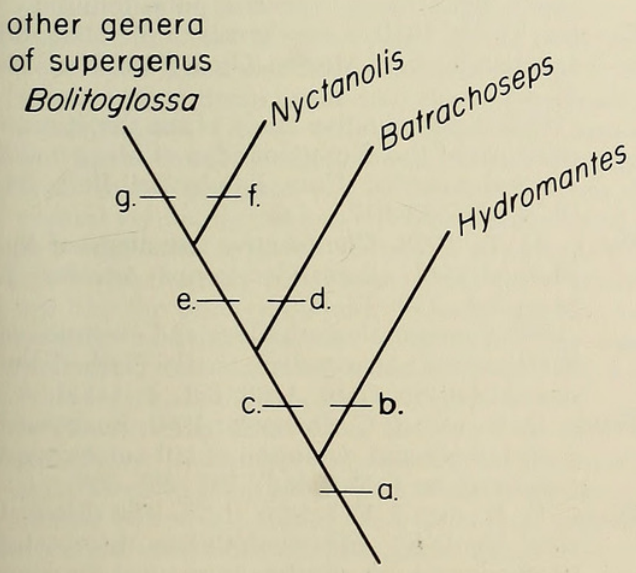


Figure 5. Cladogram showing the relationships of the members of the tribe Bolitoglossini. Principal synapomorphies characterizing each branch are as follows: a. Tribe Bolitoglossini, seven apomorphies discussed in text. b. Radii lost. c. Reduction in number of caudosacral vertebrae to two (three are still found in certain *Batrachoseps* but in these same species animals with two are common). d. Toe number reduced to four. e. Supergenus *Bolitoglossa*, tail base with complex of breakage specializations. f. See generic and species diagnoses in text. g. Characterized within the supergenus *Bolitoglossa* by fused premaxillae.

A feature uniting *Batrachoseps* and the supergenus *Bolitoglossa* is the reduction in number of pairs of diploid chromosomes from 14 to 13; unfortunately, we have no chromosomal information for *Nyctanolis*.

*Nyctanolis* probably represents the earliest surviving offshoot from the ancient ancestral stock of the supergenus *Bolitoglossa*. From a biogeographic perspective this is especially interesting, for this ancient group occupies not the northernmost part of the tropical distribution of bolitoglossines, where the most generalized forms have been found previously, but the eastern slopes of the mountainous core of Nuclear Central America. This area is one of three foci of evolutionary activity in tropical salamanders, and geographic isolates associated with it are thought to have been important in the adaptive radiation of tropical plethodontids (Wake and Lynch, 1976). The area in which *Nyctanolis* survives, now in a highly specialized ecological and

behavioral form, is the oldest land-positive area in all of Central America (Wake and Lynch, 1976; Rosen, 1978).

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For many years the work of Ernest E. Williams on the evolution of anoline lizards has been an inspiration for our work on the evolution of tropical salamanders. It is a privilege to be able to describe this anoline-like salamander in a volume dedicated to Professor Williams.

## ADDENDUM

Since preparation of this paper, *Nyctanolis pernix* has been discovered at a third locality. Jonathan Campbell has collected one juvenile specimen (KU 189586) 2.4 mi. SE Purulha, Depto. Baja Verapaz, Guatemala, 1,615 m elevation. This is approximately 125 km ESE of the type locality (by air).

## LITERATURE CITED

Edwards, J. L. 1976. Spinal nerves and their bearing on salamander phylogeny. J. Morphol., **148:** 305–327.

Lombard, R. E. 1977. Comparative morphology of the inner ear of salamanders (Caudata: Amphibia). Contrib. Vert. Evol., **2:** viii + 140 pp.

Lombard, R. E., and D. B. Wake. 1977. Tongue evolution in the lungless salamanders, family Plethodontidae. J. Morphol., **153:** 39–79.

Marlow, R. W., J. M. Brode, and D. B. Wake. 1979. A new salamander, genus *Batrachoseps*, from the Inyo mountains of California, with a discussion of relationships in the genus. Contrib. Sci. Nat. Hist. Los Angeles Co., **308:** 1–17.

Rosen, D. E. 1978. Vicariant patterns and historical explanation in biogeography. Syst. Zool., **27:** 159–188.

Smith, H. M., and R. B. Smith. 1976. Synopsis of the herpetofauna of Mexico, Vol. IV. Source analysis and index for Mexican amphibians. North Bennington, Vermont, John Johnson.

Tanner, W. W. 1950. A new genus of plethodontid salamander from Mexico. Great Basin Nat., **10:** 37–44.

———. 1952. A comparative study of the throat musculature of the Plethodontidae of Mexico and Central America. Univ. Kansas Sci. Bull., **34,** pt. 2(10): 583–677.

Wake, D. B. 1963. Comparative osteology of the plethodontid salamander genus *Aneides*. J. Morphol., **113:** 77–118.

———. 1966. Comparative osteology and evolution of the lungless salamanders, family Plethodontidae. Mem. So. Calif. Acad. Sci., **4:** 1–111.

Wake, D. B., and I. G. Dresner. 1967. Functional morphology and evolution of tail autotomy in salamanders. J. Morphol., **122:** 265–306.

Wake, D. B., and J. F. Lynch. 1976. The distribution, ecology, and evolutionary history of plethodontid salamanders in tropical America. Nat. Hist. Mus. Los Angeles Co., Sci. Bull., **25:** 1–65.