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THE SYSTEMATIC STATUS AND RELATIONSHIPS
OF THE HYLID FROG
NYCTIMANTIS RUGICEPS BOULENGER

By

WILLIAM E. DUELLMAN¹ AND LINDA TRUEB²

Boulenger (1882:421) described and illustrated a distinctive new genus and species of tree frog, *Nyctimantis rugiceps*, from Amazonian Ecuador. The genus was characterized by having a vertical pupil and integumentary-cranial co-ossification. Boulenger stated: "The erect pupil distinguishes this genus from *Hyla*, and the adherence of the tongue in nearly its whole extent from *Agalychnis*." Boulenger (1897:12) named *Nyctimantis papua* from New Guinea; this species also was characterized by a vertical pupil, but it was noted to differ from *N. rugiceps* by the absence of integumentary-cranial co-ossification. Stejneger (1916:85) remarked on the taxonomic arrangement of the two species and stated: "There is not the faintest probability that these two tree-toads are directly phylogenetically related, thus constituting a natural genus, and as they differ in *N. rugiceps* having the derm of the top of the head involved in the cranial ossification, while in *N. papua* it is free, I propose as a generic term for the latter the name *Nyctimystes*." The genus *Nyctimystes* is now known to include 24 species in New Guinea and northern Australia. Zweifel (1958) redefined the genus and emphasized two features—the vertical pupil and the pigmented network on the lower eyelid.

¹ Curator, Division of Herpetology, Museum of Natural History, and Professor, Department of Systematics and Ecology, University of Kansas, Lawrence, Kansas 66045.

² Adjunct Curator, Division of Herpetology, Museum of Natural History, and Adjunct Professor, Department of Systematics and Ecology, University of Kansas, Lawrence, Kansas 66045.

Meanwhile, *Nyctimantis rugiceps* has been ignored, although the name has been included in checklists by Nieden (1923) and Goin (1961), both of whom reiterated the vertical shape of the pupil. The species is known in the literature only from the four specimens in the British Museum (Natural History) and one from Alpayacu, Ecuador (Goin, 1961:13). Duellman (1970:18) listed *Nyctimantis* in the Amphignathodontinae, which was characterized by a horizontal pupil.

During the past six years we have collected *N. rugiceps* and have examined the type specimens and the few other specimens that have found their way into museums. We have prepared one of these 19 specimens as a skeleton. The purposes of this paper are to (1) redescribe the external morphology of *N. rugiceps* and in so doing correct certain "distinguishing features," (2) report on the osteology of the species, (3) present the accumulated biological data on this previously poorly known species, and (4) present evidence for the phylogenetic position of the species.

DESCRIPTION OF THE SPECIES

External Morphology.—The following description is based on 11 adult males and three adult females. The snout-vent length is 55.3-67.6 ($\bar{x}=61.87\pm 2.94$) mm in males and 59.7-63.0 ($\bar{x}=61.3$) mm in females. The head is slightly broader than long in males; the ratio of head length to snout-vent length is 0.342-0.367 ($\bar{x}=0.355\pm 0.008$) in males and 0.360-0.382 ($\bar{x}=0.372$) in females, whereas the ratio of head width to snout-vent length is 0.354-0.378 ($\bar{x}=0.365\pm 0.010$) in males and 0.353-0.380 ($\bar{x}=0.364$) in females. The snout is long and truncate in dorsal view and bluntly rounded in lateral profile. The internarial area is depressed; elsewhere the top of the head is flat with the skin co-ossified with the underlying dermal bone. In a juvenile (UIMNH 90071) having a snout-vent length of 28.4 mm the skin is barely co-ossified. The canthus is angular, and the loreal region is slightly concave. The lips are barely flared. The width of the eyelid is much less than the interorbital distance; the ratio of interorbital distance to head width is 0.321-0.392 ($\bar{x}=0.349\pm 0.020$) in males and 0.352-0.374 ($\bar{x}=0.367$) in females, whereas the ratio of eyelid width to head width is 0.176-0.250 ($\bar{x}=0.207\pm 0.019$) in males and 0.181-0.208 ($\bar{x}=0.193$) in females. The upper edge of the tympanum is covered by a thin supratympanic dermal fold that curves posteroventrally from the posterior corner of the eye; a well-developed tympanic annulus is present. The tympanum is about two-thirds of the diameter of the eye; the ratio of tympanum to eye is 0.538-0.698 ($\bar{x}=0.626\pm 0.048$) in males and 0.636-0.754 ($\bar{x}=0.678$) in females.

The body is moderately slender. The skin on the throat, chest, belly and proximal ventral surfaces of the thighs is granular; else-

where the skin is smooth. The anal opening is directed postero-ventrally at the midlevel of the thighs and is covered by a short flap; anal tubercles and folds are absent. The limbs are slender. The hands are immense; the length of the hand (from the base of the inner palmar tubercle to the end of the third finger) is about equal to the width of the head. The discs are slightly larger than the tympanum, and the fingers are barely webbed basally. The first finger is shorter than the second. The inner palmar tubercle is large and ovoid; the outer palmar tubercle is small and inconspicuous. The subarticular tubercles are large and flat; a few low, inconspicuous supernumerary tubercles are present on the proximal segments of the digits. The ratio of tibia length to snout-vent length is 0.474-0.556 ($\bar{x}=0.503\pm 0.023$) in males and 0.514-0.544 ($\bar{x}=0.525$) in females. The ratio of foot length to snout-vent length is 0.392-0.453 ($\bar{x}=0.426\pm 0.019$) in males and 0.421-0.454 ($\bar{x}=0.433$) in females. Tarsal folds are absent; the inner metatarsal tubercle is large and elliptical, whereas the outer metatarsal tubercle is absent. The subarticular tubercles are large and subconical; minute, low supernumerary tubercles are present on the proximal segments of the digits. The discs are slightly smaller than those on the hand. The toes are about two-thirds webbed; the webbing formula (number of free digits) is: I 2-2 II 1.5-2.3 III 1.5-1.8 IV 1.5-1.5 V.

The prevomerine teeth are situated on prominent elevations that are closely approximated medially and divergent posterolaterally between large, ovoid choanae. Males have a total of 17-24 ($\bar{x}=19.9\pm 1.70$) prevomerine teeth, whereas females have 20-21 ($\bar{x}=20.3$). The tongue is broadly ovoid, slightly indented posteriorly, and barely free behind. The vocal slits extend from the midlateral base of the tongue nearly to the angles of the jaws. The large vocal sac is single and median.

Coloration.—In life the dorsum normally varies from gray to tan, but one individual was dark brown at night. In some individuals the periphery of the dorsum has a bronze tint. The flanks, hidden surfaces of the limbs, and all ventral surfaces are dark chocolate brown. One to three large ovoid, bright yellow spots are present on each flank, and there is one large spot on the posterodorsal surface of each thigh and on the proximal upper surface of each arm (Fig. 1). In some frogs the spots are lemon yellow. The pupil is horizontal, and the iris is dark brown. In preservative the dorsum is dull grayish tan; the flanks, venter, and limbs are dark brown, and the spots are creamy white.

Osteology.—Some features of the cranial osteology of *Nyctimantis* are reminiscent of those of amphignathodontines. The frontoparietal is expanded posterolaterally to form a supraorbital flange, the frontoparietal fontanelle is covered with bone, and the



FIG. 1.—An adult male *Nyctimantis rugiceps*. 63.0 mm; KU 125960 from Santa Cecilia, Provincia Napo, Ecuador.

frontoparietals, nasals, pars facialis of the maxillary and zygomatic and otic rami of the squamosal are exostosed (Figs. 2-3). Aside from these similarities, the skull of *Nyctimantis* possesses a suite of characters which renders it quite distinct from any other known hylid. Dermal ornamentation is limited to a moderate amount of casquing and exostosis of a simple reticulate pattern modified to produce low spines on the pars facialis of the maxillary and a vague series of radial ridges along the distal margin of the frontoparietal. The skull is slightly broader than long and widest at the articulation of the maxillary and quadratojugal. Anterior to the orbits the skull narrows and terminates in a truncate snout. The dermal sphenethmoid is absent. The premaxillary and maxillary are well-developed elements bearing pedicellate teeth and narrow palatine shelves. The palatine process of the premaxillary is inconspicuous, and the alary process is about three times as high as the pars dentalis. The alary processes are nearly vertical and, in frontal view, slightly divergent. The quadratojugal is present and fully articulated. The cultriform process of the parasphenoid is edentate and moderately short, terminating well posterior to the palatines at the level of the lateral articulation of the nasal and frontoparietal. The lateral wings are indistinct and juxtaposed to the medial rami of the pterygoids. The prevomers are diffuse with indistinct margins which lie adjacent to the pars palatine anteriorly; they are separated medially and form the medial, anteromedial and posteromedial borders of the internal choanae. The dentigerous processes are widely separated medially and oriented at a slight angle to the midline. The ptery-

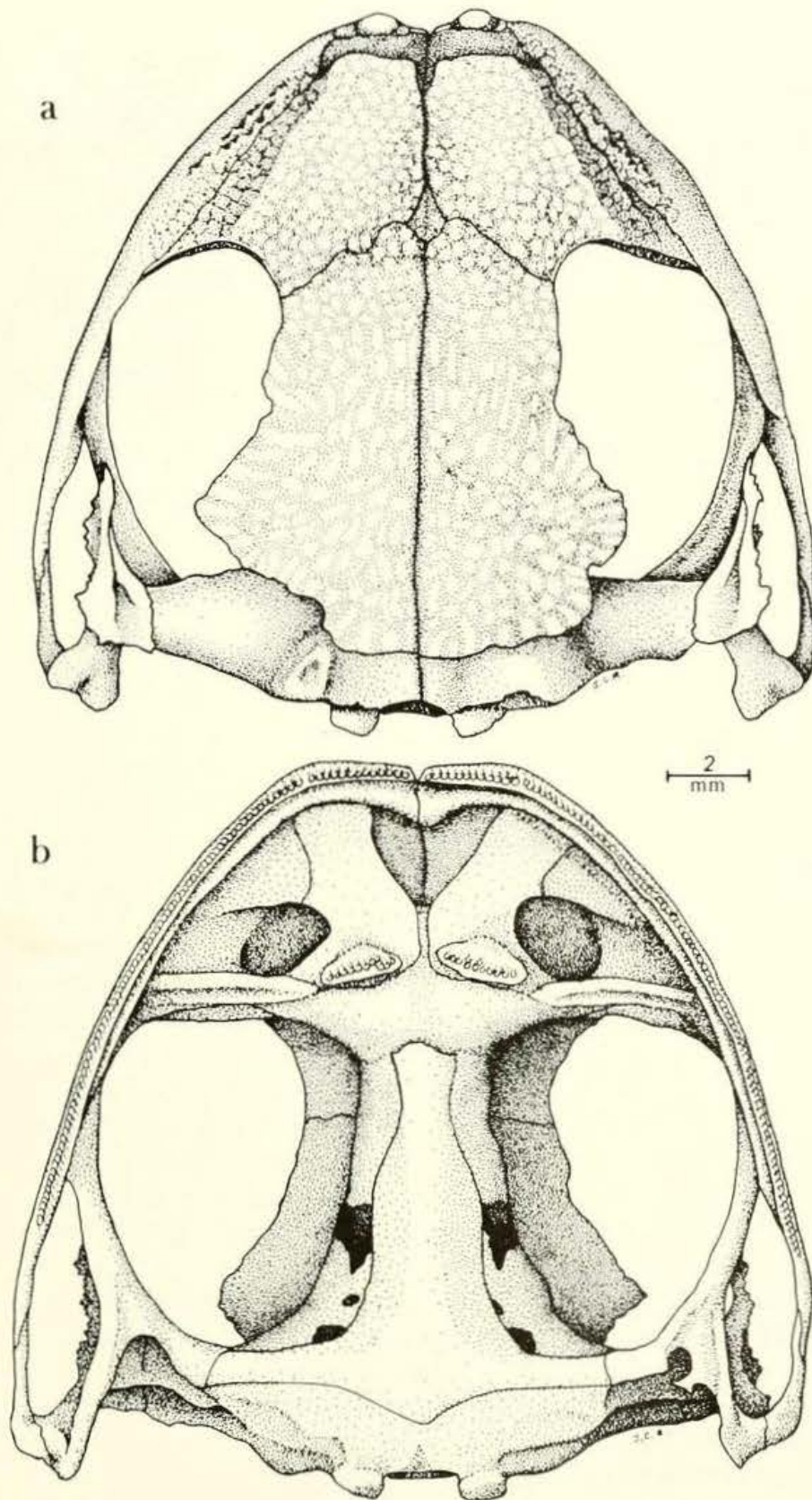


FIG. 2.—Dorsal (a) and ventral (b) views of the skull of *Nyctimantis rugiceps*, KU 125960.

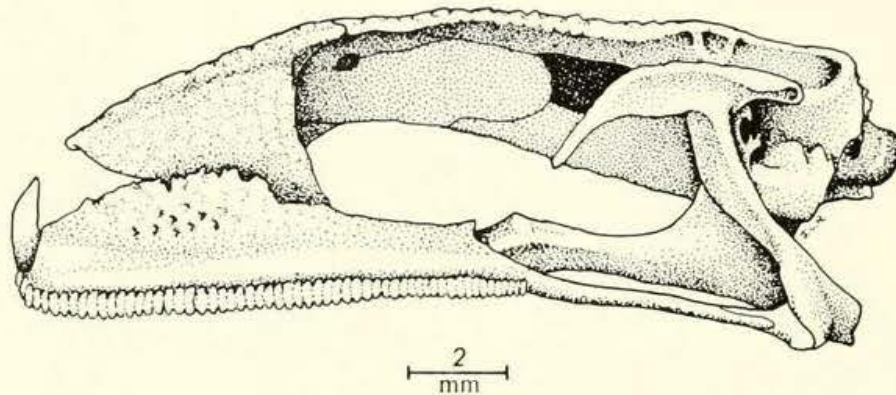


FIG. 3.—Lateral view of the skull of *Nyctimantis rugiceps*, KU 125960.

goids are robust, edentate elements that are fully articulated. The medial ramus articulates with the anterolateral corner of the otic capsule without overlapping the anterior edge; the anterior ramus bears a strong articulation with the maxillary at the midlevel of the orbit. The mandible is edentate and smooth, and Meckel's cartilage is ossified into a symphyseal bone.

The pectoral girdle is arciferal (Fig. 4a). The epicoracoid cartilages are well developed, wide and unfused posterior to the precoracoid bridge. The omosternum is small, cartilaginous and spatulate. The sternum is represented by a small plate of cartilage. The clavicle is robust, characterized by a strong anterior concavity, juxtaposed medial ends and a bicapitate lateral terminus; the anterolateral clavicle articulates with the scapula, whereas the posterolateral clavicle articulates with the coracoid. The coracoids bear a moderate medial separation and double articulations laterally. The anterolateral portion of the coracoid articulates with the clavicle; the posterolateral portion forms part of the glenoid cavity and thereby articulates with the slightly crested humerus. The scapula is a well ossified, long element with a proximal bicapitate head which articulates with the clavicle anteriorly and the humerus, by way of the glenoid cavity, posteriorly. The suprascapula is about one-half ossified by virtue of the presence of the cleithrum which invests the base of the suprascapula and extends along most of the length of the anterior edge.

There are eight procoelous, presacral vertebrae, the most anterior of which bears widely spaced cervical cotyles (Fig. 4b). Neural spines are poorly developed and only clearly distinct on presacrals I-III. Presacrals I-II are imbricate whereas III-VIII are non-imbricate. The transverse processes are moderately well developed, their widths in decreasing order of size being III, IV, and II=V=VI=VII, respectively. The transverse processes of presacral III are moderately expanded and slightly wider than the sacral diapophyses. The latter are moderately expanded. The anterior edge of the sacral diapophysis is straight, whereas the

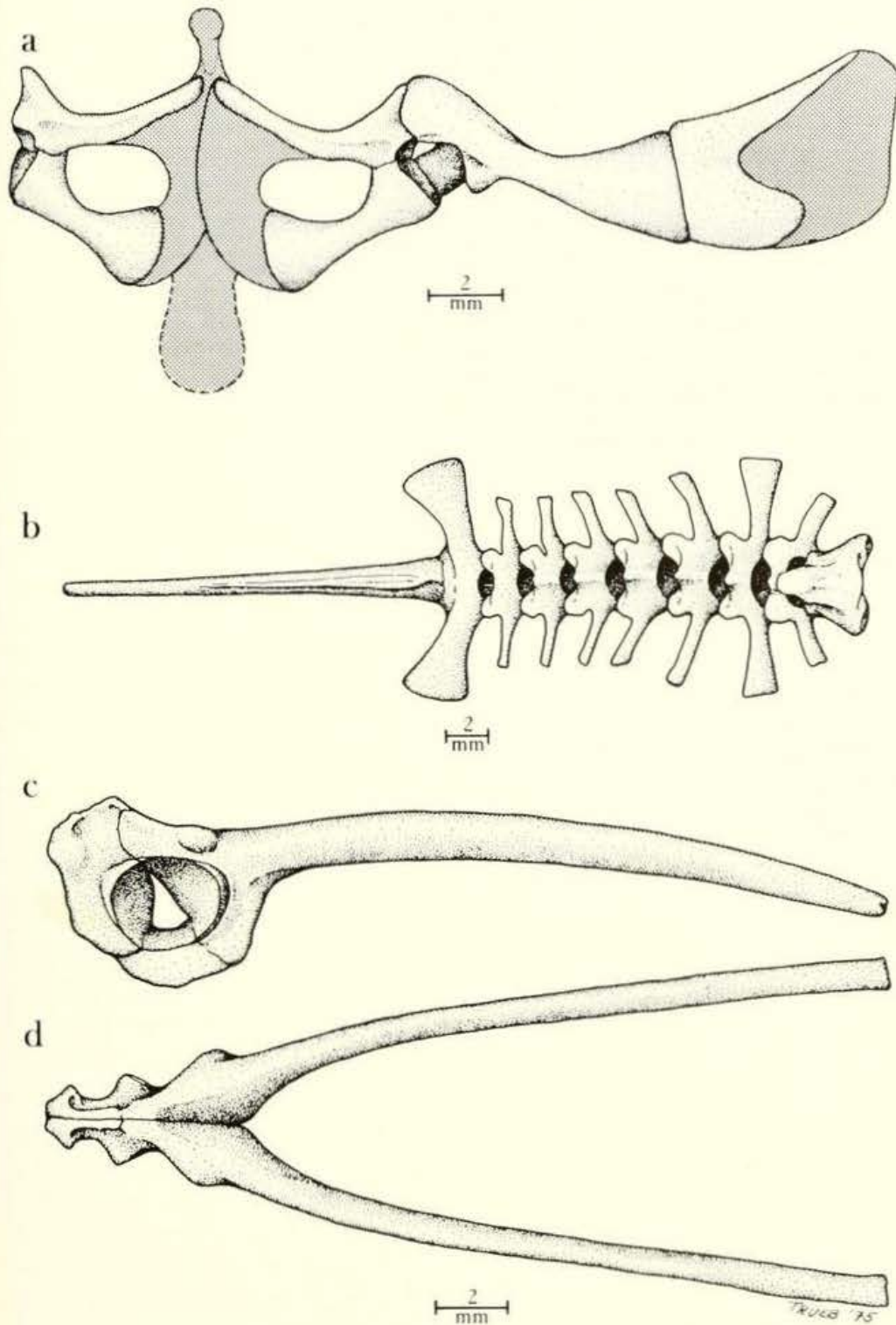


FIG. 4.—Postcranial skeleton of *Nyctimantis rugiceps*, KU 125960: a. Ventral view of pectoral girdle; b. Dorsal view of vertebral column; c and d. Lateral and dorsal views of pelvic girdle.

posterior edge is strongly concave; the diapophysis bears a slight posterolateral orientation. The coccyx bears a bicondylar articulation with the sacrum and a low crest which extends over the proximal half of the element.

The ilia are relatively short, uncrested, and proximally flattened at the articular surface with the sacral diapophyses (Fig. 4c-d). A small dorsolateral protuberance invests the posterior end of the bone above the acetabulum. In dorsal view the ilia enclose a V-shaped area with a sub-acuminate base. The ischia are more expanded dorsally than posteriorly, and the pubis is cartilaginous.

The phalangeal elements of the hand and foot conform to the anticipated patterns of 2-2-3-3 and 2-2-3-4-3, respectively. The distal elements are claw shaped. The prepollex is a flat, expanded element with a straight leading edge and curved posterior edge which produce a distal point. In contrast to the prepollex, the prehallux is scarcely developed.

FIELD OBSERVATIONS

Our observations on this rare, enigmatic tree frog were made at Santa Cecilia, Ecuador, where the frogs were found in primary and secondary lowland tropical rainforest; most of the frogs were in or near clumps of large bamboo. Except for one female obtained from a tree felled by day, all of the frogs were found at night. Two subadults were on bushes about 1.5 m above the ground; all others were calling males. Apparently the males are widely scattered throughout the forest; they seem to call from approximately the same sites night after night for periods of up to at least two weeks. Some calling sites are more than 10 m above the ground.

Calling males were found in bamboo stumps (3), in bamboo sections (2), and in a cavity in a tree (1). The bamboo stumps were about 10 cm in diameter, and each contained 10-20 cm of water. The frogs call from the inner walls of the bamboo; upon being disturbed, they submerge. Some large bamboos at angles of about 45° have wide cracks in the walls, and the frogs are able to enter the hollow stalks, which contain some water. In September 1973 Ronn Altig found a clutch of 773 unpigmented eggs in a bamboo stump inhabited by a calling male; an attempt to raise the eggs was unsuccessful. The diameter of the ova in five of these eggs is 1.1-1.4 (\bar{x} =1.28) mm. The association of the eggs solely due to the presence of the male does not definitely identify them as belonging to *Nyctimantis*. Nevertheless, no other frog at Santa Cecilia is known to deposit eggs in bamboo, nor is any other species known to utilize this calling site. The tadpoles are unknown.

At Santa Cecilia the distinctive mating call was heard throughout the year, although the number of individuals calling was highly variable. On some nights three or four were heard, whereas on other nights none was calling. The call consists of two or three loud notes, "knock-knock." Analysis of four recordings made at Santa Cecilia reveals that the call rate is 2.3-2.4 calls per minute, with 4.7-9.1 (\bar{x} =5.8) notes per minute. Three individuals produced only

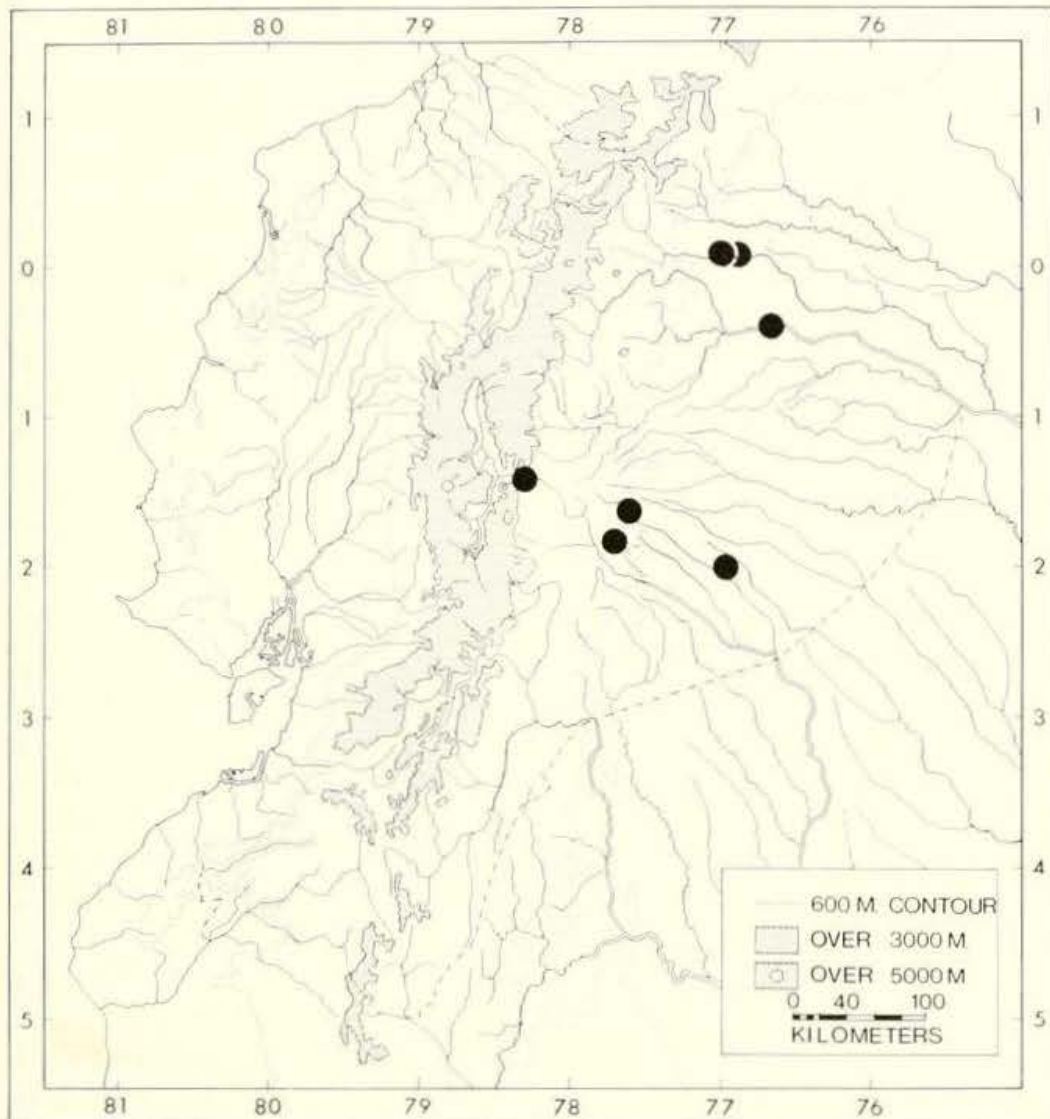


FIG. 5.—Map of Ecuador showing localities from which *Nyctimantis rugiceps* is known.

two notes per call group, whereas the fourth frog produced sequences of two or three notes. Usually the second note is much longer than the first, which has a duration of 0.04-0.15 (\bar{x} =0.105) of a second; the duration of the second notes is 0.05-0.76 (\bar{x} =0.256) of a second. There are approximately 100 pulses per second. The fundamental frequency at 478-1130 (\bar{x} =847) Hz is dominant.

Nyctimantis rugiceps is known from only seven localities in Amazonian Ecuador (Fig. 5). One locality, Alpayacu, is at an elevation of 1100 m; all other localities are elevations of 300-600 m. Presumably the frog is endemic to the westernmost part of the Amazon Basin; although presently it is known only from Ecuador, its occurrence in the Río Putumayo drainage of southern Colombia and in the Río Morona-Santiago-Pastaza region of northern Perú is anticipated. Conversely, extensive collections farther eastward in

the basin (Iquitos, Perú, and Leticia, Colombia) have not revealed the presence of *Nyctimantis*.

DISCUSSION

Duellman (1970) included eight genera in the subfamily Amphignathodontinae. All are characterized by having extensively ossified crania and horizontal pupils. Additionally, *Amphignathodon*, *Cryptobatrachus*, *Flectonotus*, *Fritziana*, *Gastrotheca* and *Stefania* are similar in that the females of these genera carry the eggs on their back or within a dorsal pouch. The other two genera of this sub-family, *Anotheca* and *Nyctimantis*, lack this specialized mode of reproduction; *Anotheca* is known to deposit eggs in bromeliads (Taylor, 1954) and in water-filled tree cavities (Robinson, 1961; Duellman, 1970), and it is assumed that *Nyctimantis* utilizes water-filled cavities in trees and bamboo for this purpose (see Field Observations).

The osteology of *Cryptobatrachus* is not known; however, of the remaining seven genera, there are obvious similarities among four—*Amphignathodon*, *Anotheca*, the *argenteovirens* and *plumbea* groups of *Gastrotheca*, and *Nyctimantis*, all of which occur in northwestern South America, except *Anotheca*, an inhabitant of cloud forest in Central America and southern México. These frogs are distinguished from *Flectonotus*, *Fritziana*, *Stefania* and other *Gastrotheca* by the presence of more extensive casquing, exostosis, and the tendency toward development of cranial co-ossification. The frontoparietals tend to be expanded posterolaterally to form supraorbital flanges, the frontoparietal fontanelle is covered with bone and the frontoparietals, nasals, pars facialis of the maxillary and zygomatic and otic rami of the squamosal are exostosed. *Amphignathodon* is distinct from other members of the subfamily in having mandibular "teeth." Despite the spectacular, bony spines which ornament the skull of *Anotheca* (Duellman, 1970, Fig. 53), the basic architecture of the skull of this species is similar to that of members of the *argenteovirens* and *plumbea* groups of *Gastrotheca* and *Nyctimantis*. Cranially, *Nyctimantis* and *Anotheca* share one character which distinguishes them from *Gastrotheca*. In both of the former species the medial ramus of the pterygoid is juxtaposed squarely against the anterolateral corner of the ventral ledge of the otic capsule, whereas in all *Gastrotheca* observed the medial ramus of the pterygoid articulates with the ventral ledge of the otic capsule along its anterior or leading edge.

Other pertinent osteological similarities prevail between *Anotheca* and *Nyctimantis*. Their cranial proportions are similar, that is the heads are broader than long and terminate in a truncate snout anteriorly. The snout shape is somewhat more accentuated in *Anotheca* because of the casqued, exostosed condition of the

nasals. Save for a slightly shorter anterior pterygoid ramus and smaller dentigerous prevomerine processes in *Anothea*, the ventral aspect of the skull is very similar to *Nyctimantis*. The pectoral girdles are nearly identical, as are the vertebral columns except for a few minor features. In *Anothea* presacrals I-III are imbricate, the leading edge of the sacral diapophysis is anteriorly concave and the crest on the urostyle is somewhat better developed than in *Nyctimantis*. The only notable differences in the pelvic girdles are that the ilial shafts are cylindrical throughout their lengths and somewhat longer in *Anothea*. The latter disparity probably is correlated with the differences in structure of the sacral diapophyses.

Both frogs are of a comparable size. The average snout-vent length of 20 male *Anothea* is 60.7 and eight females 62.2 mm (Duellman, 1970); comparable figures for *Nyctimantis* are 61.9 (N=11) and 61.3 (N=3), respectively. Only two body proportions seem to differ significantly. In *Nyctimantis* the tibia is slightly longer relative to the snout-vent length (48.6% in male *Anothea*; 50.3% in male *Nyctimantis*), and the tympanum is smaller with respect to the eye (81.0% in male *Anothea*; 62.6% in male *Nyctimantis*). The morphology of the tongue, condition of the skin, position of the cloaca and gross morphology of the hands (*i.e.* relative finger lengths and webbing) are the same. The first finger is shorter than the second in hylines, *Anothea*, and *Nyctimantis*, but longer than the second in the amphignathodontines. There are discernible differences in the tuberculation of the hands and feet, the amount of foot webbing, the presence (*Anothea*) versus the absence (*Nyctimantis*) of a tarsal fold, and the external morphology of the cloacal opening. *Anothea* is provided with an elongate anal sheath and vertical skin folds flanking the cloaca, whereas *Nyctimantis* has only an abbreviated anal flap and tubercles around the cloaca instead of folds. Male *Anothea* lack vocal slits and apparently a vocal sac also; both structures are well developed in *Nyctimantis*. Despite these morphological differences, both species have a similar, simple repetitive type of call, not unlike some *Gastrotheca*. The species have similar ovarian egg complements (650 in *Anothea* and 773 in *Nyctimantis*) and ovarian size factors (Duellman and Crump, 1974) of 15.16 (*Anothea*) and 16.00 (*Nyctimantis*). Ovarian size factors for three species of *Gastrotheca* having direct development are 0.96-1.47 ($\bar{x}=1.21$), for three species of *Gastrotheca* having free-swimming tadpoles 5.33-6.30 ($\bar{x}=5.83$), and for six species of pond-breeding *Hyla* in the upper Amazon Basin 13.1-37.1 ($\bar{x}=26.1$).

Clearly, distributional, reproductive, life history and morphological data for *Anothea* and *Nyctimantis* describe two remarkably similar but distinct monotypic genera. We are confronted with two, or possibly three, questions—what, if any, is the relationship

between *Anotheca* and *Nyctimantis*, and how are they, separately or together, allied to the amphignathodontines? The similarities of habitus, habit and life history are sufficiently pervasive to argue for a relationship, albeit a distant one, between these taxa rather than what otherwise would have to be considered a remarkable example of convergence. Their reproductive habits and osteology ally them more closely with the amphignathodontines than any other group of hylids. And, as discussed previously, among the amphignathodontines they are morphologically most similar to the *argenteovirens* and *plumbea* groups of *Gastrotheca*. It is worthwhile to note that although eggs are carried in a maternal pouch in *Gastrotheca*, all members of the *argenteovirens* and *plumbea* groups have free-swimming tadpoles (Duellman, 1974). This feature must be considered primitive in contrast to most other *Gastrotheca* in which the young undergo their entire development within the maternal pouch (Trueb, 1974). Given the foregoing premises, it seems most parsimonious to suggest that *Anotheca* and *Nyctimantis* represent early, but independent, offshoots from an ancestral stock that was destined eventually to give rise to primitive members of *Gastrotheca*. However, for purposes of classification they must be placed in the Hyliinae.

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RESUMEN

El género de sapos hylidos *Nyctimantis* contiene una especie, *N. rugiceps* Boulenger, 1882. Este gran sapo arborícola (♂, 67 mm de longitud hocico-ano) está caracterizado por tener la piel del dorso de la cabeza co-osificada con los huesos dermales inmediatos

y por un dorso de color gris pálido o marrón claro y un vientre de color marrón oscuro con grandes manchas amarillas sobre los flancos y muslos.

A *Nyctimantis* sólo se lo conoce desde las selvas húmedas tropicales de la hoya amazónica del Ecuador. Los machos cantan esporádicamente a lo largo del año desde arboles y bambúes. El canto consiste en dos o tres notas altas simulando "nok-nok." Se presume que el desarrollo larval ocurre en cavidades de troncos y bambúes llenos de agua.

Basado en caracteres estructurales externos, en la osteología, y en el factor tamaño del ovario, *Nyctimantis rugiceps* es similar a *Anothea spinosa* (Steindachner) de México y Centroamérica. Estos dos géneros comparten varios caracteres con los grupos *argenteovirens* y *plumbea* de *Gastrotheca*. Sin embargo, los sapos del género *Gastrotheca* (subfamilia Amphignathodontinae) llevan los huevos en una bolsa dorsal. Ambos, *Nyctimantis* y *Anothea*, se consideran como antiguos derivados independientes del tronco que evolucionó hacia *Gastrotheca*. *Nyctimantis* y *Anothea* pueden ser clasificados como hylidos hylinos.

SPECIMENS EXAMINED

ECUADOR: No further data, BMNH 80.12.5.152. *Napo*: Lago Agrio, KU 126259; Limoncocha, UIMNH 90071; Santa Cecilia, KU 109559, 125960 (skeleton), 126311, 143207, 150488-91. *Pastaza*: Alpayacu, UMMZ 90432; Canelos, BMNH 80.12.5.163-4 (3); Río Copataza, USNM 198708; Alto Río Pucayacu, KU 142861-2, USNM 198707.

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