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SYSTEMATIC RELATIONSHIPS OF NEOTROPICAL HORNED FROGS, GENUS *HEMIPHRACTUS* (ANURA: HYLIDAE)

By

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In the minds of all but the most resolute and devoted systematic biologists, taxonomic study frequently is viewed as a necessary tedium, economically dispatched so that one can move on to more interesting aspects of the biology of an organism. However, occasionally one chances upon an animal that because of its literary antiquity, bizarre appearance and habits, and questionable relationships is of intrinsic interest. Such is the case of the extraordinary horned frogs of the genus *Hemiphractus*. These Neotropical frogs are denizens of undisturbed cloud forests, montane and lowland tropical rainforests from Panamá south to Bolivia. Mating calls are unknown in the group, as are breeding congregations. Solitary individuals are found perched on low vegetation in the forest at night, and, only rarely, a fortunate collector has found a female carrying eggs or young upon her back. Although these frogs have been known for 150 years, only about 200 preserved specimens exist, and more than 50 percent of these have been obtained in the course of extensive field work in Panamá, Ecuador, and Perú within the last eight years. The familial association of this genus has been subject to constant debate since the first species was named in 1824. The morphological peculiarities have been described, redescribed, and largely misinterpreted for an equal length of time. And, virtually nothing is known about the breeding biology, habits, or population structure of these frogs. In view of the uniqueness

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and relative rarity of *Hemiphractus* and the apparent restriction of its species to the rapidly diminishing, undisturbed tropical forests, I feel that it is appropriate to review the systematic status of these unusual frogs. Hopefully, this constitutes only a preface to discovery and subsequent study of other aspects of their biology.

The specific objectives of this study are threefold: (1) to define the genus *Hemiphractus* and the various species that properly are allocated to it; (2) to assess the intrageneric relationships and probable phylogenetic history of the group; and (3) to discuss the possible intergeneric relationships of this anuran genus. A historical résumé provides a synopsis of the taxonomic history of these frogs. Morphological characters judged to be of systematic importance are discussed in an analysis of characters. Finally, within each species account, I have included available information concerning the habitat, habits, food, color in life, and reproduction.

MATERIALS AND METHODS

Specimens examined include 182 preserved frogs inclusive of the type specimens of all nominal taxa except *Hemiphractus scutatus*, for which the type no longer exists. Osteological observations were based on 13 dry skeletal preparations and one cleared and stained specimen; these were supplemented by radiographs of three additional individuals. I have observed living individuals of all species except *Hemiphractus johnsoni* and *H. scutatus*. Colored photographs were available for all species. Specimens are identified throughout the text by their catalogue numbers preceded by the appropriate museum abbreviation, as follows:

AMNH	American Museum of Natural History
ANSP	Academy of Natural Sciences of Philadelphia
AUM	Auburn University Museum
BMNH	British Museum (Natural History)
BYU	Brigham Young University
CAS	California Academy of Sciences
CAS-SU	Stanford University Collection (In California Academy of Sciences)
FMNH	Field Museum of Natural History
KU	The University of Kansas Museum of Natural History
LACM	Los Angeles County Museum of Natural History
MCZ	Museum of Comparative Zoology, Harvard University
MNCN	Museo Nacional de Ciéncias Naturales, Madrid
NHRM	Naturhistoriska Riksmuseet, Stockholm
UIMNH	University of Illinois Museum of Natural History
UMMZ	University of Michigan Museum of Zoology
USC-CRE	University of Southern California—Costa Rica Expedition
USNM	United States National Museum (=National Museum of Natural History)
ZSM	Zoologisches Sammlung München

Because *Hemiphractus* lack any obvious, external secondary sexual characteristics, the sexes of all adult and subadult specimens

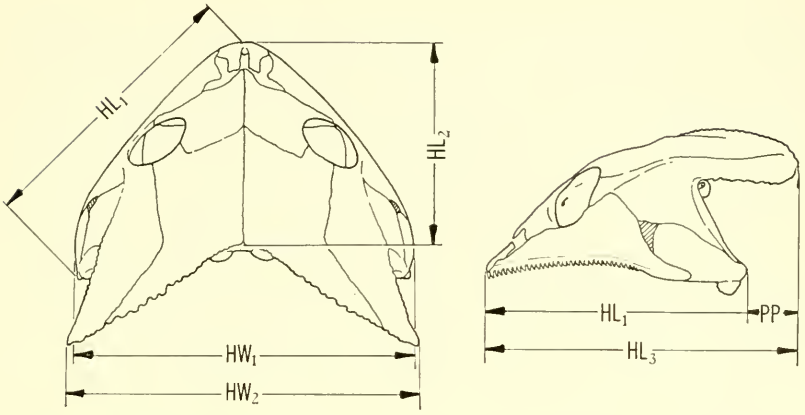

FIG. 1. Schematic dorsal and lateral views of skull of *Hemiphractus scutatus* showing various cranial dimensions measured. Skull approximately natural size; subtemporal fenestra indicated by hatching. Abbreviations: *HL*, head length; *HW*, head width; *PP*, posterior projection of paraoccipital process. See text for explanation of subscript notations.

were determined by examining the gonads. As a result, frogs less than 30 mm snout-vent length were classified as juveniles, whereas those with poorly developed gonads and snout-vent lengths less than the observed ranges for sexually mature individuals (see Table 2) were classified as subadults. Adult females were divided into three classes depending upon the size of ovarian eggs which varied from minute (less than 1 mm diameter) to moderate-sized (between 1 and 3 mm diameter) to large (greater than 3 mm diameter). In several individuals the oviducts were distended but empty; usually such a female either had eggs or young associated with her or showed evidence (depressions on the back) of having recently carried young. When the information was available, date (month) of specimen collection was plotted with respect to reproductive state to determine what, if any, reproductive cycles seem to prevail. These data are summarized in the Remarks section of each species account.

Although most measurements taken on these frogs are standard and self-explanatory, a number of additional cranial dimensions have been recorded that require brief explanation. These are shown schematically in figure 1. Standard head length (HL_1) was measured from the angle of the jaw to the medial articulation of the premaxillaries; unless otherwise noted, all references to head length denote this measurement. Medial head length (HL_2) represents the distance from the posteromedial articulation of the fronto-parietals to the medial articulation of the premaxillaries anteriorly. Lateral head length (HL_3) is a measurement from the distal tip

of the paraoccipital process to the premaxillaries. The length of the paraoccipital process projection (PP) beyond the angle of the jaw was computed as follows: $(HL_3 - HL_1)/HL_1$. Standard head width (HW_1) represents the greatest head width measured across the maxillary arch; unless otherwise noted, all references to head width denote this measurement. The distance between the distal tips of the paraoccipital processes is noted as HW_2.

A number of new and/or special names or phrases are employed in this paper to describe certain cranial features. The most important of these and their definitions are listed below. Most, together with the general structures of the hemiphractine skull, are illustrated and labeled in figure 2.

1. *Postorbital indentation.*—(Fig. 2a); the emargination of the posterodorsal rim of the orbit.
2. *Paraoccipital process.*—(Fig. 2a, b, c); the posterior, projecting horns composed of the squamosal and frontoparietal bones.
3. *Otic margin.*—(Fig. 2a); the lateral edge of the paraoccipital process and the squamosal.
4. *Subtemporal fenestra.*—(Fig. 2a, c); the lateral fenestra bounded anteriorly by the maxillary, dorsally by the squamosal and posteriorly by the quadratojugal.
5. *Supraorbital ridge.*—(Fig. 2a); the bony frontoparietal ridge located at or near the dorsal margin of the orbit and the lateral edge of the frontoparietals; variable in presence, shape and length.
6. *Preoccipital ridge.*—(Fig. 8); transverse frontoparietal ridge lying parallel to the occipital flange and uniting the posterior termini of the supraorbital ridges.
7. *Postorbital ridge.*—(Fig. 2a); the bony frontoparietal ridge located along the posteromedial margin of the postorbital indentation.
8. *Zygomatic ridge.*—(Fig. 2c); a bony ridge variable in degree of development and extent; ridge is constituted by squamosal posteriorly and maxillary anteriorly, and usually extends diagonally ventrad from the posterior border of the ventral arm of the squamosal to the posteroventral margin of the orbit.
9. *Canthus in section.*—a phrase used to describe the configuration of the snout-loreal region in transverse section; thus, the canthus may be rounded (*i.e.*, obtusely angular) or angular (*i.e.*, acutely angular).

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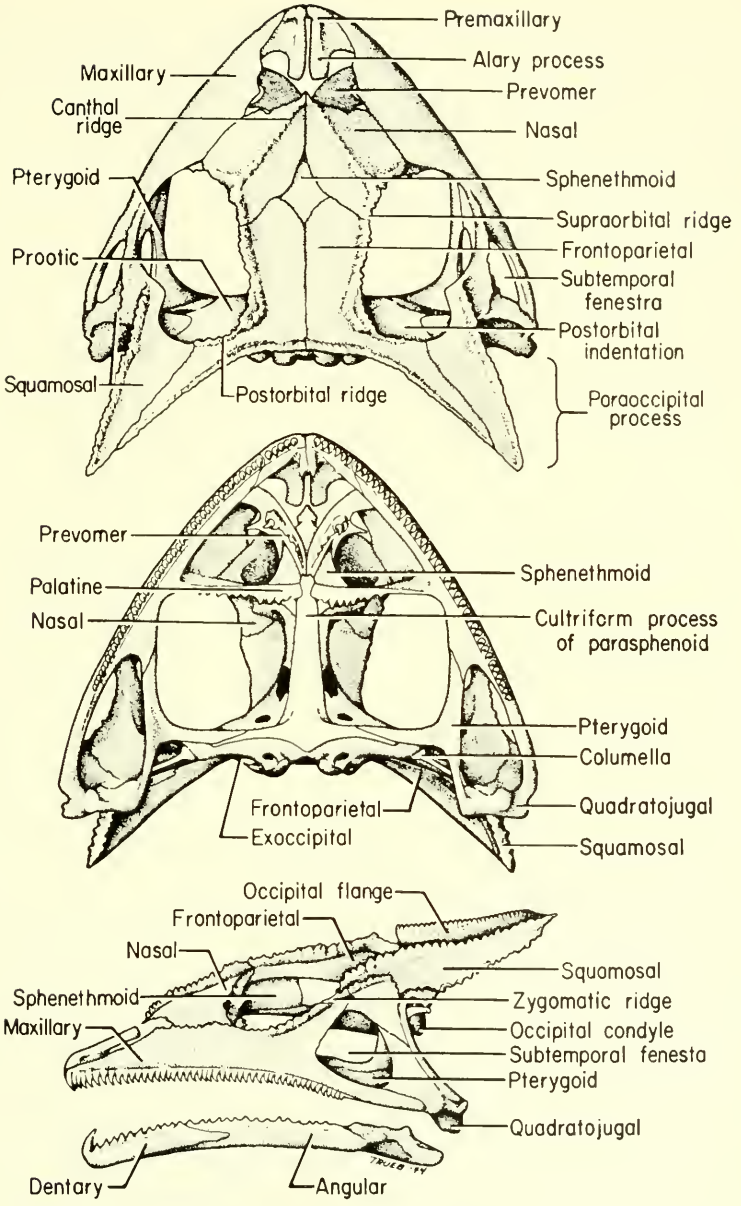

FIG. 2. Skull of *Hemiphractus proboscideus* (KU 124139, ♀; *ca.* × 1.5). Top: dorsal view. Middle: ventral view. Bottom: Lateral view of skull and mandible. Dermal ornamentation not shown.

to measuring preserved specimens. The success of my own and my colleagues' field work in Ecuador was significantly enhanced through the provision of transportation by the Texaco Petroleum Company and the hospitality of Ing. Ildefonso Muñoz B. of Santa Cecilia, Ecuador. William E. Duellman, Alan E. Leviton and John D. Lynch critically reviewed the manuscript. Juan León graciously provided a Spanish translation of the Summary.

Although this manuscript is a result of my long-standing interest in the systematics and biology of casque-headed hylids, I wish to extend special thanks to George S. Myers and Alan E. Leviton who share my interest in these peculiar frogs and who generously contributed the unpublished results of their earlier investigations of *Hemiphractus*. I gratefully acknowledge their generosity and the impetus provided by both gentlemen towards the completion of this contribution to an understanding of these enigmatic frogs.

HISTORICAL RÉSUMÉ

Frogs of the genus *Hemiphractus* are among the most bizarre of anurans. Taxonomically, they have been known since the first species was described and illustrated by Spix in 1824. Because of their extraordinary aspect and adventitious appearance in early collections (namely those of Spix, Jiménez de la Espada, and Moritz Wagner in the early to mid-19th Century), commentary on this peculiar group of anurans occurred quite frequently in the literature of the late 1800's and early 1900's. There was an early proliferation of specific names associated with the genus, and a spate of misinformation has been perpetuated throughout the literature of the past 150 years. In an attempt to clarify the history of this genus, a review is presented below.

Spix (1824:28, Pl. IV, Fig. 2) described *Rana scutata;* perhaps the most significant statement in his brief description is as follows, "*maxillae ensiformes, superior denticulata, inferior non dentata, apice intus subaculeata.*" Gravenhorst (1825:920) proposed a new leptodactylid genus, *Stombus*, and included three species in it—*Rana cornuta* Linné, *R. megastoma* Spix, and *R. scutata* Spix. Subsequently, Wagler (1828:735 and 743, Pl. X, Figs. 1-5) provided a short description and set of illustrations of the type specimen of *scutatus*. As opposed to Spix's statement, Wagler contended that the frog had mandibular teeth; on that basis he erected a new genus, *Hemiphractus*. Furthermore, he proposed the substitute name *Hemiphractus spixii*. Subsequently, Wagler (1830) gave a more complete description of the type specimen, placing it in the order "Ranae" within the family "*R. phaneroglossae.*" Only passing mention was made of this single specimen of *Hemiphractus* in the succeeding 32 years, and in several herpetological works of this period, it was suggested that *Hemiphractus* was allied with lepto-

dactylids and, in particular, the genus *Ceratophrys* (*e.g.*, see Duméril and Bibron, 1841:430, and Günther, 1858:26).

The first substantial contribution to our knowledge of *Hemiphractus* is that of Peters (1862). In this paper he proposed that the genus was allied to "climbing" or "treefrogs." Peters (p. 146) reinstated the specific name *scutatus*, which has priority over Wagler's substitute name, *spixii*, and on the basis of his examination of Spix's specimen, provided a detailed morphological account and illustrations of the frog (pp. 146-149, Pl. 1, Figs. 1-6). To my knowledge, this is the last detailed published description of *scutatus* that is based on examination of the type specimen, although Noble (1926:18) briefly mentioned it. Presumably, the type, which was housed in the zoological collections at Munich, was destroyed or lost during World War II. Peters described and illustrated (1862: 149-152, Pl. 2, Figs. 1-4) a second species, *Hemiphractus fasciatus*. He provided (p. 145) the first adequate definition of *Hemiphractus* and placed the genus within the family Hemiphractidae, which he distinguished from other anuran families on the basis of the following combination of characters: 1) absence of parotoid glands; 2) small transverse processes of the sacral vertebrae; 3) presence of teeth on the palatine bones; 4) presence of rudimentary interdigital webbing; 5) presence of a round, attached tongue; and 6) presence of flattened digital tips. Significantly, Peters did not include the "presence of 'growing' teeth on the mandible" in his definition of the family, but this character is included in the generic definition (p. 145) preceding that of the family.

In his paper on the structure and distribution of arciferous Anura, Cope (1866:69) included the Hemiphractidae and Cystignathidae (=Leptodactylidae) in the third of three "groups" of arciferal frogs. The "group" was defined as having cylindrical sacral diapophyses and procoelous vertebrae. The Hemiphractidae was distinguished from the Cystignathidae by the presence of mandibular teeth in the former and their absence in the latter. In Cope's definition of the Hemiphractidae, he concluded (p. 88) that, "It [the Hemiphractidae] is probably intermediate between the Hylidae and Cystignathidae." Cope (1868:114) described a third species of *Hemiphractus*, *H. divaricatus*, collected by Professor James Orton from "Peru, Napo and Marañon rivers."

Jiménez de la Espada (1871) reported on his extensive collections from South America, including an account of *Hemiphractus scutatus* and the description of a new genus, *Cerathyla*. He distinguished (pp. 62 and 63) *Cerathyla* from *Hemiphractus* in a general way, noting that *Hemiphractus* was "toad-like," whereas *Cerathyla* was "hylid-like." The latter conclusion probably was based on the larger size of *H. scutatus* and the reduction of its digital discs as contrasted with the smaller specimens with ex-

panded digital discs allocated to *Cerathyla*. Both genera were placed in the family Hemiphractidae, and the family within a "section" entitled Hemiphractina (Opisthoglossa Platydactyla: Batrachia Salientia: Amphibia). In this paper (p. 64), four new species were described and placed in the genus *Cerathyla*. These are: 1) *C. proboscidea* from Sumaco, Ecuador, 2) *C. bubalus* from Archidona, Ecuador, 3) *C. palmarum* from San José de Moti, Ecuador, and 4) *C. braconnieri* from Archidona, Ecuador.

Brocchi (1877) published a detailed osteological study of *Hemiphractus scutatus*. His osteological illustrations (Pl. 16) are plentiful and accurate. Although Brocchi correctly stated that *H. scutatus* possesses odontoids on the mandible instead of true teeth, he erroneously described the vertebrae as being opisthocoelous. Boulenger (1882:451-455) maintained *scutatus* and *divaricatus* in the genus *Hemiphractus*, and in an obvious error, cited *Cerathyla* as *Ceratohyla*. He distinguished the two genera on the basis of dilated (*Ceratohyla*) versus non-dilated (*Hemiphractus*) digital discs. Boulenger included *braconnieri*, *palmarum*, *bubalus*, *proboscidea*, and *fasciata* in the genus *Ceratohyla*. The family Hemiphractidae (including three genera—*Hemiphractus*, *Ceratohyla*, and *Amphodus* [=*Phyllodytes*]) was included in Boulenger's Series Arcifera (suborder Phaneroglossa: order Ecaudata: class Batrachia).

Unfortunately the mistakes of Brocchi and Boulenger were perpetuated and compounded by Gadow (1901) who recognized hemiphractines as a subfamily, Hemiphractinae, and allied it with the leptodactylids (p. xi; family Cystignathidae: suborder Phaneroglossa: order Anura: subclass Lissamphibia: class Amphibia). Gadow's Hemiphractinae contained three genera (*Hemiphractus*, *Ceratohyla*, and *Amphodus*) and, among other things, was characterized by 1) teeth on both jaws, the vomers, and palatine bones, or on the palatines and parasphenoids in *Amphodus*, and 2) opisthocoelous vertebrae. He further stated (p. 210) that the skin of the head is involved in cranial ossification in *Hemiphractus*.

Two additional species of *Cerathyla* were described in 1917. The first, *C. panamensis*, was described by Stejneger (1917:31) from Signal Loma on the north coast of Panamá. The second, *C. johnsoni*, was named by Noble (1917:789) from Santa Rita Creek, Departamento Antioquia, Colombia. Miranda-Ribeiro (1926: 118) described *Hemiphractus boulengeri* from the Buckley collection from "Ecuador." Finally, Noble (1926:18-19) synonymized *Cerathyla* with *Hemiphractus*, noting that both genera are characterized by procoelous vertebrae, slightly dilated sacral diapophyses and broad, overlapping coracoid cartilages in the pectoral girdle. Noble (1931) later recognized the subfamily Hemiphractinae (family Hylidae: suborder Procoela: order Salientia) within which he included all hylids in which the females carry eggs on

their backs. This assemblage comprises *Hemiphractus, Cryptobatrachus, Gastrotheca,* and *Amphignathodon;* parenthetically, it should be noted that *Amphignathodon* does possess true mandibular teeth.

The most recent species to have been described in this group is *Ceratohyla cristata* from the Río Pastaza watershed in Ecuador by Andersson (1945:18), who placed the genus in the family Leptodactylidae. Contemporaneously, Myers and Carvalho (1945: 18-19) described a recently acquired individual of *Hemiphractus scutatus.* In comparing the specimen (Museu Nacional No. A842 from the state of Amazonas, Brasil) with Boulenger's (1882:452) description of *scutatus* and that of Miranda-Ribeiro (1926:118) for *Hemiphractus boulengeri,* they implicitly concluded that *boulengeri* was not distinct from *scutatus.* Finally, Myers and Carvalho (pp. 20-21) described a large female *Hemiphractus,* also from Amazonas, Brasil. On the basis of comparison of this specimen with Boulenger's (1882) account of *bubalus* and Noble's (1926) description of *johnsoni,* they erroneously placed *johnsoni* in the synonymy of *bubalus* and designated *Cerathyla bubalus* Jiménez de la Espada as the type species of the genus *Cerathyla.* The description of this specimen (Museu Nacional No. A841) and accompanying photographs (Figs. 17 and 18) clearly indicate that the individual is identified correctly as *Hemiphractus johnsoni* and not *Hemiphractus bubalus.*

Hemiphractus Wagler, 1828

Hemiphractus Wagler, 1828, column 743 [Type species.—*Hemiphractus spixii* Wagler, 1828 (=*Rana scutata* Spix, 1824) by monotypy]. Noble, 1926:19 synonymy of *Cerathyla* with *Hemiphractus.*

Cerathyla Jiménez de la Espada, 1871:63 [Type species.—*Cerathyla bubalus* Jiménez de la Espada, by subsequent designation (Myers and Carvalho, 1945:21)].

Ceratohyla Boulenger, 1882:453 [lapsus for *Cerathyla*].

Diagnostic definition.—1) Skull extensively casqued, characterized by prominent, posterolaterally projecting paraoccipital processes; 2) dermal roofing bones exostosed in a reticulate and/or tuberculate pattern of dermal sculpturing; 3) dermal roofing bones not co-ossified; 4) maxillary, premaxillary, and prevomerine teeth fang-like and curved inward when present; 5) palatine edentate, bearing serrations; 6) mandible bearing odontoid serrations and a pair of enlarged, fang-like odontoids in the area of the mandibular symphysis; 7) cultriform process of parasphenoid overlapped anteriorly by prevomers; 8) arciferal pectoral girdle with minute omosternum, small clavicles, broadly overlapping epicoracoid cartilages, and massive coracoid bones; 9) presacral vertebrae procoelous, with enlarged neural spines which protrude dorsally in living and preserved specimens; 10) ilium bearing distinct dorsal crest;

11) vocal sacs and vocal slits absent; 12) submentalis muscle extremely small and araphic; 13) intermandibularis muscle undifferentiated, incompletely developed anteriorly, and bearing an extensive median aponeurosis; 14) small, fleshy proboscis on terminus of snout; 15) one or more prominent, fleshy tubercles on the eyelid; 16) tympanum large and vertically ovoid with its surface plane oriented at a distinct angle to the longitudinal axis of the body; 17) hands large with well-developed, non-bifid subarticular tubercles, ovoid, elevated thenar palmar tubercle and diffuse, cordiform outer palmar tubercle; 18) fingers basally webbed or lacking webbing, length from shortest to longest 2-1-4-3; 19) nuptial excrescence absent; 20) toes basally to one-half webbed; 21) pupil horizontal; 22) palpebrum clear; 23) eggs carried on back of female where young undergo direct development and are attached to dorsal skin of female by means of gill structures.

Content.—As defined here, the genus *Hemiphractus* contains five known species (Table 1): *H. fasciatus* Peters, *H. bubalus* (Jiménez de la Espada), *H. proboscideus* (Jiménez de la Espada), *H. johnsoni* (Noble), and *H. scutatus* (Spix).

Distribution.—Upper Amazon Basin of Colombia, western Brasil, Ecuador, Perú, and Bolivia ascending the slopes of the Andes to elevations of 1830 m; northern and eastern slopes of the Cordillera Occidental and Cordillera Central of the Andes in northern Colombia; Pacific slopes and lowlands of northwestern Ecuador, Colombia, and eastern Panamá; Caribbean slopes of western Panamá (to elevations of 1600 m).

ANALYSIS OF CHARACTERS

Cranium.—The cranial architecture of *Hemiphractus* is unique and, in its own fashion, as strange as the better known pipids and ceratophryine leptodactylids. The dermal roofing bones are ex-

Table 1.—Alphabetical Synonymy of the Species of *Hemiphractus*.

Trivial Name, Original Generic Name, Author, Date	Current Name
boulengeri, Hemiphractus, Miranda-Ribeiro, 1926	*H. scutatus*
braconnieri, Cerathyla, Jiménez de la Espada, 1871	*H. bubalus*
bubalus, Cerathyla, Jiménez de la Espada, 1871	*H. bubalus*
cristata, Ceratohyla, Andersson, 1945	*H. proboscideus*
divaricatus, Hemiphractus, Cope, 1868	*H. scutatus*
fasciatus, Hemiphractus, Peters, 1862	*H. fasciatus*
johnsoni, Cerathyla, Noble, 1917	*H. johnsoni*
palmarum, Cerathyla, Jiménez de la Espada, 1871	*H. bubalus*
panamensis, Cerathyla, Stejneger, 1917	*H. fasciatus*
proboscidea, Cerathyla, Jiménez de la Espada, 1871	*H. proboscideus*
scutatus, Rana, Spix, 1824	*H. scutatus*
spixii, Hemiphractus, Wagler, 1828	*H. scutatus*

tensively casqued, so that in dorsal aspect the skulls appear to be heavily armored triangular structures characterized by robust, posterolaterally projecting paraoccipital processes (Fig. 2). The latter processes are formed jointly by posterolateral growth of the frontoparietals and otic rami of the squamosals. Although the skulls are casqued and ornately exostosed in a reticulate pattern (Figs. 8, 11, and 14), the dermal bones are not co-ossified with the covering skin. In each species the neurocranium is solidly roofed. The maxillaries are characterized by massive development of the pars facialis both preorbitally and postorbitally (Fig. 2b). An analogous lateral element has arisen from the quadratojugal in the temporal region. The quadratojugal is characterized further by the presence of one or two bony tubercular projections posterolaterally. Dentitionally, most *Hemiphractus* are armed with fang-like, inwardly curved maxillary, premaxillary, and prevomerine teeth (Fig. 2b, c). The premaxillary series is interrupted medially by a slight diastema into which the mandibular odontoids fit when the mouth is closed. When present, the prevomerine dentition is limited to one to three teeth clustered on a low pedicle on the anterior part of the prevomer; *H. johnsoni* lacks prevomerine teeth. The mandible has an exceedingly broad and massive articular surface. The angular and dentary bones have a well-developed, thin bony ridge bearing a series of odontoid serrations (Fig. 2c). Anteromedially, there are paired odontoid structures which are similar in size and configuration to the maxillary teeth and distinctly larger than the other mandibular odontoids. These large mandibular odontoids seem to arise from the anteriormost end of the dentary bone. The dentaries lie closely adjacent to one another; there is no indication of mentomeckelian ossification.

A variety of other interesting osteological features is visible in the ventral aspect of the skull (Figs. 2b, 9, 12, and 15). The prevomers of the genus are attenuate structures which extend from the level of the palatines to the anterior end of the maxillary. In addition to the teeth described above, each prevomer bears a median, serrate ridge which extends from the level of the teeth, posteriorly, to the terminus of the bone. The lateral wings of the prevomers are reduced, forming only the anteromedial margin of the choanae. The palatines are slender structures which are narrowly separated medially and which bear series of irregular odontoid serrations. The parasphenoid has a noticeably long cultriform process which extends anteriorly between the palatines and terminally is overlapped by, or juxtaposed to, the prevomers. The cultriform process is smooth in all species except *johnsoni* (Fig. 15) in which it usually bears an indistinct median keel. The most dominant ventral element is the pterygoid bone. The anterior ramus of this structure articulates with a massive bony process of

the maxillary (herein referred to as the pterygoid process of the maxillary) and extends posteriorly to the otic region of the neurocranium. The medial ramus arises at this level. In ventral view, only the ventral edge of the medial ramus is visible as it articulates with the anterior edge of the parasphenoid ala. The medial ramus consists of a diffuse, vertically oriented sheet of bone which faces the anterior surface of the otic capsule and extends laterally from the otic capsule forming a thin wall of bone. The bone attaches to the expanded ventral ramus of the squamosal, thereby forming a partition between the orbital and otic regions of the skull. The posterior ramus of the pterygoid is notable for its massive articular surface. With the exception of *scutatus,* which bears a series of odontoids along the anterior, lingual margin of the anterior ramus of the pterygoid, the pterygoids of *Hemiphractus* are edentate and smooth.

There are two distinct types of skulls in the genus *Hemiphractus.* One group, composed of *scutatus* (Fig. 1) and *fasciatus* (Figs. 11 and 12), is characterized by especially massive skulls which lack a postorbital fenestra and which are obviously much broader than long (Table 2). Preoccipital and postorbital cranial ridges are absent and the supraoccipital, canthal, zygomatic and maxillary ridges tend to be indistinct, especially in large females. In lateral view, it is evident that the subtemporal fenestra is relatively small; consequently, the lateral elements of the quadratojugal, squamosal, and maxillary are greatly expanded as contrasted to the same elements in *johnsoni* (Fig. 14), *bubalus* (Fig. 8), and *proboscideus* (Fig. 2c). The snout regions of *scutatus* and *fasciatus* are not depressed; the alary processes of the premaxillaries are inclined posteriorly at approximately a 45 degree angle. Ventrally, the pterygoid process of the maxillary can be seen to arise at approximately the midlength of the maxillary arch. *Hemiphractus fasciatus* can be distinguished readily from *H. scutatus* by the presence of pterygoid odontoids in the latter and the obvious difference (Figs. 1 and 11) in the respective orientations of the paraoccipital processes. Moreover, the sphenethmoid is completely obscured dorsally in *scutatus* and *johnsoni,* whereas a small part of this element is visible in *fasciatus.*

The second group, composed of *johnsoni, bubalus,* and *proboscideus,* is characterized by somewhat less extensively casqued skulls which are only slightly longer than broad (Table 2; Figs. 2, 8, 9, 14, and 15). Each of these species has a postorbital indentation. The indentation is smallest in *johnsoni* and rounded; whereas *bubalus* and *proboscideus* are characterized by larger indentations that are noticeably broader than long. All three species have zygomatic, maxillary, canthal, and supraorbital cranial ridges; the ridges are least evident in *johnsoni* and best developed in *bubalus. Hemi-*

TABLE 2.—Comparison of Size and Proportions of Species of *Hemiphractus*. (Means are given in parentheses below observed ranges. SVL=snout-vent length; F^1, F^2, and F^3=lengths of first three digits on hand, respectively; N^1= sample size for snout-vent length; N^2=sample size for computed ratios)

Species	Sex	N^1/N^2	Snout-vent length (mm; N^1)	Tibia length/ SVL (%; N^2)	Foot length[a]/ SVL (%; N^2)	Head length/ SVL (%; N^2)	Head width/ SVL (%; N^2)	F^2/F^1 (%; N^2)	F^3/F^1 (%; N^2)
H. bubalus	♂	22/22	38.2-50.5 (43.8)	53.9-62.4 (58.2)	80.5-91.9 (85.5)	39.9-47.4 (42.3)	44.3-50.1 (46.5)	76.2- 98.5 (89.0)	123.0-151.4 (134.8)
	♀	6/3	43.1-66.3 (57.9)	59.8-61.5 (60.7)	62.7-85.6 (84.8)	41.8-45.7 (43.7)	45.9-47.3 (46.5)	82.6- 95.7 (89.9)	126.7-133.3 (129.6)
H. fasciatus	♂	14/11	39.6-55.7 (49.6)	52.0-60.0 (54.8)	73.0-82.6 (77.2)	40.9-50.3 (43.6)	46.7-51.5 (48.8)	78.0-108.6 (89.5)	118.4-156.5 (131.6)
	♀	13/10	33.7-68.7 (57.3)	46.9-56.1 (52.6)	71.6-81.0 (75.8)	43.2-48.9 (45.1)	45.6-56.0 (50.5)	82.6- 96.6 (89.0)	112.8-141.9 (128.2)
H. johnsoni	♂	2/2	43.5-52.9 (48.2)	49.9-57.9 (53.9)	74.7-80.0 (77.4)	41.0-48.9 (45.0)	46.9-50.8 (48.9)	95.1[b] ---	148.4[b] ---
	♀	5/2	60.7-77.2 (68.2)	55.7-60.0 (55.8)	77.7-78.6 (78.1)	43.3-43.4 (43.35)	49.6-52.9 (51.2)	89.5- 91.0 (90.2)	124.5-125.8 (125.1)
H. proboscideus	♂	15/14	42.8-49.7 (46.3)	57.0-66.1 (61.3)	77.8-87.4 (83.0)	39.9-44.1 (42.3)	43.4-49.1 (46.6)	83.2-111.5 (91.2)	122.9-150.4 (131.6)
	♀	25/24	44.4-67.1 (56.1)	45.4-66.4 (61.3)	78.8-90.1 (84.5)	40.4-46.4 (43.2)	44.2-49.8 (47.3)	72.1- 94.9 (87.3)	108.6-149.6 (126.9)
H. scutatus	♂	8/7	36.9-57.4 (50.7)	42.3-48.0 (45.3)	64.3-72.2 (68.4)	47.6-52.3 (50.4)	56.6-65.5 (61.4)	81.3- 98.2 (90.0)	107.9-135.3 (125.4)
	♀	15/14	60.4-80.5 (70.4)	39.3-47.6 (43.9)	62.6-79.0 (69.7)	42.7-53.3 (48.3)	57.1-65.7 (59.6)	76.1- 95.5 (89.6)	120.4-138.1 (127.7)

[a] Including tarsus

[b] $N^2=1$

phractus bubalus has a well-developed preoccipital ridge which is absent in *proboscideus* and incompletely developed in *johnsoni*. The postorbital ridge is present only in *bubalus*. The subtemporal fenestra is proportionately much larger in this group than in either *scutatus* or *fasciatus*. The snout regions of *proboscideus* and *bubalus* are elongated and depressed, the alary processes of the premaxillaries being posteriorly inclined at approximately a 25 degree angle. The snout of *johnsoni* is intermediate in character between that typical of *scutatus* and *fasciatus* and that characterizing *bubalus* and *proboscideus*. Ventrally, the pterygoid process of the maxillary lies posterior to the midlength of the maxillary arch. *Hemiphractus johnsoni* is distinguished from all other members of the genus by the presence of an indistinct mid-ventral parasphenoid keel in some individuals and the absence of prevomerine teeth.

Pectoral girdle.—The pectoral girdle is arciferal but characterized by a number of unusual features (Fig. 3). A cartilaginous omosternum is present but minute in size. The epicoracoid cartilages are extensive and the precoracoid bridge exceedingly narrow. The sternum consists of a large, flat cartilaginous plate with no evidence of ossification or calcification. The coracoid bones are massive; these elements are expanded medially and broadly overlapping. The clavicles of *bubalus, proboscideus* (Fig. 3c), and *johnsoni* (Fig. 3d) are moderately well-developed elements. Those of *fasciatus* (Fig. 3b) are less robust in comparison, and those of *scutatus* (Fig. 3a) are reduced to very slender elements. The clavicles are straight and oriented more nearly perpendicular to

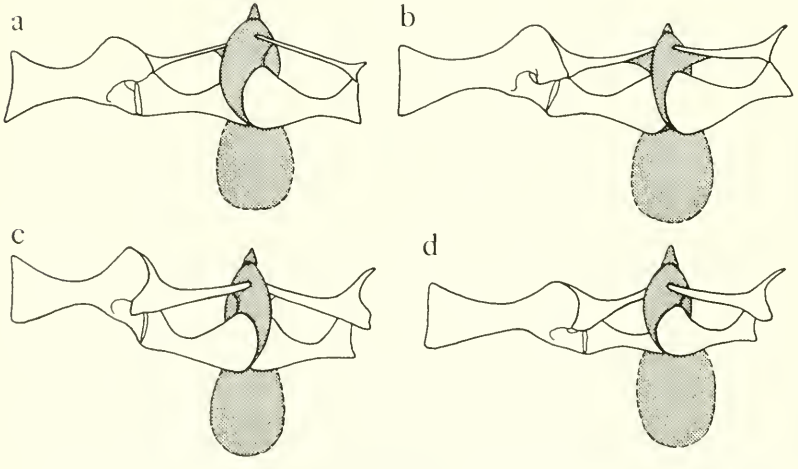

FIG. 3. Pectoral girdles of *Hemiphractus* in ventral view. Suprascapulae and left scapulae not shown. Stippled areas represent cartilaginous or secondarily ossified portions of girdle. a) *H. scutatus;* b) *H. fasciatus;* c) *H. proboscideus;* d) *H. johnsoni.*

the midline of the body than is typical of most hylids. The scapulae are robust, bicapitate elements. The suprascapulae are well ossified in the area of the cleithrum; however, ossification is limited to this leading edge and a diffuse proliferation of bone along the basal, articular margin of the element.

Vertebral column.—The vertebral columns of *Hemiphractus* are uniformly procoelous and have non-imbricate neural arches. The transverse processes of presacral vertebrae III through VIII tend to be wide (*i.e.*, nearly as broad as, or broader than, the sacrum) and uniform in length (Table 3; Fig. 4a). This tendency is most evident in *scutatus* and *proboscideus* and least evident in *johnsoni*, *bubalus* and *fasciatus*. The cervical cotyles have a moderately wide medial separation; however, they are more closely associated to one another than is characteristic of other hylids. The cotyles are quite distinctly stalked or notched in *scutatus* and *fasciatus* (Fig. 4c) in contrast to the remaining three species (Fig. 4f). Although there is no fusion between the cervical and second presacral vertebrae, the cervical bears a neural spine which articulates with the neural spine of the second presacral (Fig. 4b). Perhaps the most striking vertebral character of this genus is the series of enlarged neural spines (Fig. 4b). Although each presacral bears a well-developed neural spine, one or two of these spines are noticeably enlarged. In *scutatus* the third neural spine is larger, whereas in *fasciatus* it is the sixth, and in *johnsoni* the seventh. The fourth neural spine is enlarged in *bubalus;* in *proboscideus* the fourth and fifth are about equal in size and distinctly larger than the other neural spines.

There is a tendency for the skin to adhere to the neural spines in all species. In *fasciatus* and *scutatus* the skin is only loosely connected to the tops of the posterior two to four neural spines. The skin of the remaining three species is applied firmly to the entire neural spine; thus, in both preserved and living specimens, the neural spines appear to protrude dorsally through the skin although they do not actually do so. In *johnsoni* the posterior five or six neural spines distinctly protrude, whereas in *proboscideus* and *bubalus* six or seven neural spines are evident. In each of these species, the skin tends to be more loosely applied to the posteromost neural spine.

The sacrum is posterolaterally oriented in each species and only moderately expanded. In all species, except *scutatus* (Table 3), the width of the sacral diapophyses is less than that of the transverse processes of the eighth presacral vertebra. The urostyle bears a bicondylar articulation with the sacrum and a well-developed dorsal crest (Fig. 4b; Table 3). The ventral shaft of the urostyle bears a slight lateral expansion in all species except *bubalus*. Proportionately, the urostyle is shortest in *scutatus* (Table 3).

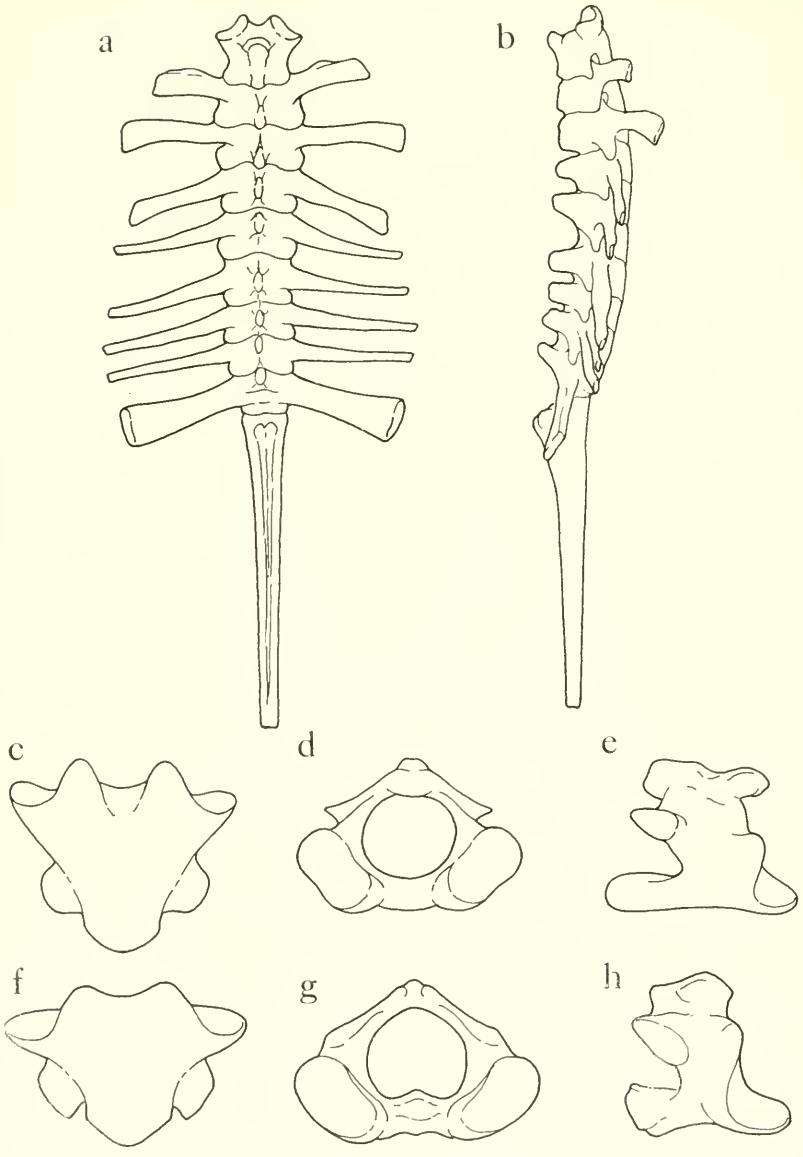

Fig. 4. Vertebral column structure of *Hemiphractus*. a) Dorsal view of vertebral column of *H. fasciatus;* b) Lateral view of vertebral column of *H. fasciatus;* c-e) Cervical vertebra of *H. fasciatus* (c, ventral view; d, anterior view; e, right lateral view); f-h) Cervical vertebra of *H. proboscideus* (f, ventral view; g, anterior view; h, right lateral view).

TABLE 3.—Axial dimensions of *Hemiphractus*. Values expressed as percentages. Abbreviations: TPW, ratio of width of transverse processes of presacral vertebrae to sacral diapophyses width; UHD, ratio of diameter of urostyle shaft to urostyle length; UHP, ratio of greatest height of urostyle (at proximal end of crest) to urostyle length; UL, ratio of urostyle length to average snout-vent length of adult of same sex as measured.

Character	*scutatus* KU 129752, ♀	*fasciatus* KU 93509, ♀	*johnsoni* KU 153436, ♂	*bubalus* KU 124140, ♀	*proboscideus* KU 124139, ♀
TPW II	73.7	76.7	78.0	72.3	81.2
TPW III	100.8	102.8	99.2	89.9	103.4
TPW IV	105.9	92.6	92.4	81.5	91.5
TPW V	96.6	99.4	93.2	92.4	93.2
TPW VI	95.8	108.0	101.7	99.2	97.4
TPW VII	99.2	111.9	105.1	105.0	103.4
TPW VIII	99.6	110.8	107.6	110.9	108.5
UL	28.0	35.1	32.2	31.1	31.7
UHP	22.8	16.9	18.1	13.3	13.5
UHD	4.6	4.5	4.5	2.8	3.4

Pelvic girdle.—The pelvic girdle is characterized by a well-ossified ilium and ischium, and a cartilaginous or secondarily calcified pubis (Fig. 5). The ilium bears a distinct crest in each species; it is least well developed in *scutatus* (Fig. 5a). The ilial crest tends to have a slightly irregular dorsal margin in *fasciatus* (Fig. 5c) and *johnsoni* (Fig. 5e), whereas the dorsal margin is distinctly serrate in *proboscideus* and *bubalus* (Fig. 5b, d). The ilial crest terminates posteriorly in a prominent, rounded ilial protuberance in *scutatus*

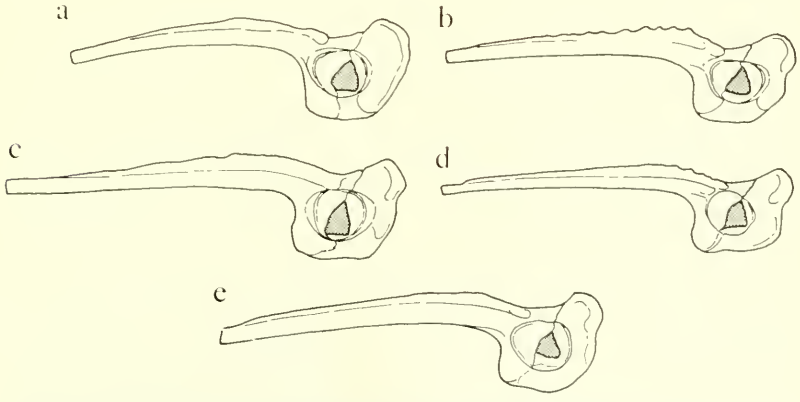

FIG. 5. Pelvic girdles of *Hemiphractus* in left lateral view. Stippled areas represent acetabular cavity. a) *H. scutatus;* b) *H. proboscideus;* c) *H. fasciatus;* d) *H. bubalus;* e) *H. johnsoni.*

and *fasciatus;* although present, the protuberance is much less distinct in *bubalus, proboscideus,* and *johnsoni.*

Hand and foot.—Although the phalangeal formula of *Hemiphractus* is the same as most other hylids (*i.e.,* 2-2-3-3; exclusive of intercalary cartilages), the relative lengths of the digits is unusual. In the majority of hylids the length of the digits from shortest to longest is 1-2-4-3. However, in *Hemiphractus* the first metacarpal is relatively longer and the second shorter; thus, the pattern is 2-1-4-3. This configuration is typical of some leptodactylid groups, and only a few other hylids. The prepollex is small. The terminal phalanges are blunt, claw-like structures. Intercalary cartilages are uniformly present.

The phalangeal formula of the foot is the expected 2-2-3-4-3 (exclusive of intercalary cartilages). Intercalary cartilages are present, and the terminal phalanges are like those of the hand. The prehallux is only moderately developed in each species except *scutatus,* in which it is very well developed. In the latter species this element is anvil-shaped and is composed of three bony elements.

Skin.—*Hemiphractus* is characterized by a number of striking dermal modifications. Chief among these is the presence of a fleshy proboscis on the tip of the snout in each species. The proboscis is small, triangular and dorsoventrally flattened in all species except *proboscideus,* in which the structure is proportionately much larger and laterally compressed (Fig. 6). The upper eyelids are coarsely granular and bear one or more enlarged, fleshy tubercles (Fig. 7). In *Hemiphractus johnsoni* and *scutatus* the eyelids are coarsely granular with one or two slightly enlarged conical tubercles. *Hemiphractus fasciatus* has a single enlarged tubercle and scattered, smaller tubercles on an otherwise granular eyelid. In *proboscideus* and *bubalus* there is a central, enlarged conical tubercle which is

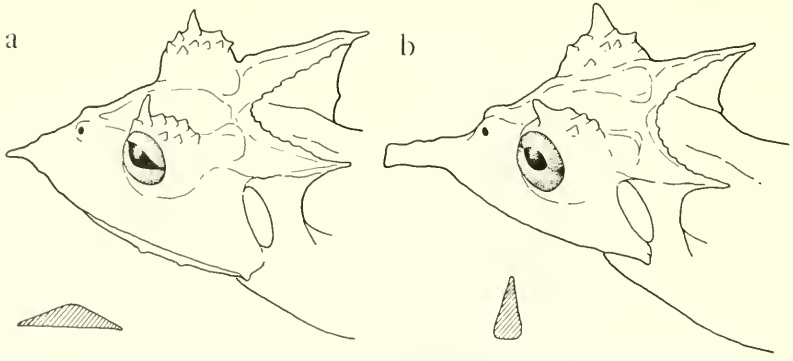

FIG. 6. Heads of two species of *Hemiphractus* showing the two types of proboscises characteristic of the genus. Hatched drawings at lower left represent cross-sectional views of proboscises of a) *H. bubalus* and b) *H. proboscideus.* (Both heads *ca.* × 1.5).

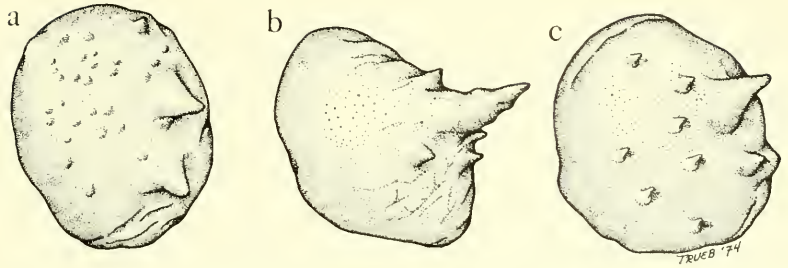

FIG. 7. Tuberculation of eyelids in *Hemiphractus.* a) *H. johnsoni;* b) *H. fasciatus;* c) *H. bubalus.*

flanked by several slightly smaller tubercles. All species bear one to three tubercular projections at the angle of the jaw; these, however, are bony projections of the quadratojugal and not fleshy tubercles. Typically, the dorsal surfaces of the forearms are tuberculate. Tubercles are scattered in *johnsoni* and *fasciatus,* whereas they are oriented in transverse or oblique rows corresponding to forearm marks in the remaining species. Tuberculation of the dorsal and outer surfaces of the hind limbs corresponds to that of the forearm except in *fasciatus* and *johnsoni.* In *fasciatus* tubercles are indistinct and aligned in transverse rows, and in *johnsoni* tubercles are absent or poorly developed. Each species bears three or four slightly enlarged tubercles at the knee. These are best developed in *scutatus* and least developed in *johnsoni.* Well-developed calcars are present on the heels of *proboscideus* and *bubalus.* The calcar is poorly developed in *fasciatus* and *johnsoni,* and absent in *scutatus.*

The skin of the back is shagreened. A few small, scattered tubercles are variably present on the back; these are most evident in *scutatus.* The posterior surfaces of the thighs are moderately granular in all species except *proboscideus* in which they are nearly smooth. The flanks and ventral surfaces are smooth in *johnsoni.* There are scattered, low subconical tubercles on these surfaces in *fasciatus,* whereas the flanks and venters of *bubalus* and *proboscideus* are finely granular. The flanks and venter, especially the abdomen and ventral surfaces of the thighs, are coarsely granular in *scutatus.*

External characters of hands and feet.—Hands of *Hemiphractus* are characterized by reduced webbing, well-developed subarticular tubercles, and low supernumerary tubercles. The fingers of *johnsoni, bubalus,* and *proboscideus* are unwebbed. In *fasciatus* webbing may be absent or basal, and in *scutatus* the digits are about one-fourth webbed. All species have well-developed adhesive discs except *scutatus.* In the latter species, the tips of the digits are either scarcely expanded or not expanded at all; the poorly-developed

adhesive discs are visible ventrally. The subarticular tubercles are round and non-bifid. The thenar tubercle is elliptical and elevated, whereas the outer palmar tubercle is a flat, diffuse structure tending to have a cordiform shape. There are no nuptial pads or excrescences present in males.

The feet, like the hands, have reduced webbing, well-developed, non-bifid subarticular tubercles, and relatively few supernumerary plantar tubercles. Webbing is basal in *bubalus, fasciatus,* and *johnsoni;* whereas the toes of *proboscideus* are about one-fourth webbed and those of *scutatus* one-half webbed. *Hemiphractus scutatus* has only small, poorly-developed adhesive discs on the toes; in all other species the adhesive discs of the toes are slightly smaller than those of the fingers. The inner metatarsal tubercle is elliptical and elevated in all species; it is best developed in *scutatus.* The outer metatarsal tubercle is indistinct or absent in all species except *fasciatus,* in which the structure is present as a small, subconical tubercle.

Coloration in preservative.—Based on examination of preserved specimens, the coloration and markings of *Hemiphractus* are highly variable within each species. Generally, the ground color varies from a dark reddish brown to a pale grayish tan with dark brown markings. Two species, *fasciatus* and *bubalus,* have a characteristic dorsal pattern. *Hemiphractus bubalus* has a dark brown dorsal ground color; the presacral region of the back bears two sets of paravertebrally nested chevrons. The chevrons (two per set) are irregular cream marks oriented in such a way that the points of the medial chevrons lie medially adjacent on either side of the vertebral column. Posteriorly, on the sacral region of the back, there are two additional pale colored chevrons. These are posteriorly directed with the bases of the chevrons lying on the vetrebral column. Large females of *fasciatus* tend to have a uniform gray or red-brown dorsum which may be indistinctly or boldly mottled; however, in smaller individuals and males there is a distinct pattern. The presacral region of the back bears a pale colored chevron on either side of the vertebral column; the chevrons are directed laterally as in *bubalus.* A large, irregularly shaped pale spot is located posteromedially on the back. The backs of *johnsoni* and *proboscideus* are uniform in color or irregularly mottled; no distinct pattern is visible. *Hemiphractus scutatus* may be uniformly dark brown to pale tan dorsally; in some specimens an irregular dark mottling is superimposed on the ground color. Frequently, individuals are marked with two dark, irregularly shaped vertebral spots; the posterior spot lies above the sacrum and the other spot lies anterior to the first.

The interorbital and paraoccipital regions of the heads of *Hemiphractus* are not marked in *proboscideus* and *johnsoni.* Oc-

casionally, a narrow interorbital bar and scattered spots occur in *scutatus*. The heads of both *bubalus* and *fasciatus* may be either uniform in color or indistinctly marked; infrequently, they are boldly patterned. The labial and temporal markings of *Hemiphractus* are distinctive. All species tend to have a pattern of labial stripes or bars radiating from the suborbital margin to the lip margin, except *scutatus*. The latter lacks labial bars and is characterized, instead, by a bold suborbital dark mark which borders the lower margin of the eye and expands posteroventrally from the posteroventral corner of the orbit. This mark usually extends about one-half the distance to the maxillary and frequently is fragmented into a series of spots. Usually a dark mark extends from the anterodorsal corner of the orbit posteriorly across the margin of the eyelid and along the lateral margin of the paraoccipital process. Frequently, there are scattered dark spots in the pre- and posttympanic areas. The pattern of radiating labial bars is most distinct and uniform in *bubalus* which is characterized by wide dark bars with narrow, light interspaces. The pattern is present but variable in its distinctness in *proboscideus* and *johnsoni*. The latter species bears a distinctive, horizontal post-ocular light bar. In *H. fasciatus* the labial-temporal pattern varies from one of well-defined radial bars to one of indistinct bars anteriorly with the posterior and suborbital bars fragmented in a pattern reminiscent of that of *scutatus*.

The gular patterns of *Hemiphractus* run the gamut of variation. Two species, *johnsoni* and *fasciatus*, have mandibular (or peripheral gular) bars which correspond to the labial bars. *Hemiphractus scutatus* and *johnsoni* frequently bear a pale mid-ventral stripe which terminates in the pectoral region. This feature is occasionally present in *fasciatus*, although the line may be interrupted. Mid-ventral stripes are absent in *bubalus* and *proboscideus;* however, a pale pectoral spot or light colored pectoral tubercle is almost always present. Aside from the aforementioned features, the gular region varies from uniform to spotted in *scutatus*, uniform with an occasional proliferation of small, pale spots in *johnsoni*, and uniform to heavily mottled or marbled in *fasciatus*, *proboscideus*, and *bubalus*.

The bellies of all species tend to be uniformly dark or heavily mottled anteriorly, becoming less heavily pigmented posteriorly and peripherally. The flanks are spotted in *johnsoni*. In the remaining species the flanks tend to be more heavily mottled or marbled. Heavy marbling is especially characteristic of *bubalus*. *Hemiphractus scutatus* is distinguished by an extensive, finely venate pigment pattern which covers the anterior flanks in the postocular area above the forelimb.

The forelimbs of *Hemiphractus* may be uniformly dark. More frequently, the ground color of the forearm is sufficiently pale that

transverse dark bands are visible. The three or four bands are indistinct, diagonally oriented, and extend onto the dorsal surface of the hand in *scutatus*. Similar bands, transversely oriented, are present in *bubalus* and *johnsoni*. Both *proboscideus* and *fasciatus* are characterized by a single, wide wrist band. In all species, the outer digits (usually the third and fourth fingers) are noticeably darker in color than the inner digits. *Hemiphractus proboscideus* is uniquely characterized by its white or cream colored discs on the first and second fingers.

In most *Hemiphractus* the entire dorsal or exposed surface of the hind limb bears transverse bands. These are best developed in *bubalus* in which the dorsum of the thigh is marked by a series of wide bars with paler interspaces containing a shorter, narrower bar. The bars are less distinctly developed and the interspaces plain in *johnsoni* and *fasciatus*. In *scutatus* and *proboscideus* the leg bands frequently are fragmented into series of spots or diffuse areas of mottling. The anterior surfaces of the thighs tend to be lightly pigmented ventrally. Posteriorly, the inguinal area is pigmented heavily in all species. *Hemiphractus fasciatus* differs from the other species in having a diffuse pale marking bordering the dorsal margin of a dark inguinal marking and extending dorsal to the cloaca to form an indistinct cloacal stripe. The ventral surfaces of the tarsi and feet of all species are uniformly dark and sharply delimited from the less uniform dorsal pattern. Like the fingers, the outer three toes are more heavily pigmented than the inner two toes. The first and second toepads of *proboscideus* are white or cream dorsally.

Color notes on living individuals are recorded separately in the individual species accounts.

KEY TO THE SPECIES OF *HEMIPHRACTUS*

1. Adhesive discs on digits minute, tips of digits slender with no evidence of discs visible in dorsal view; canthal ridge absent, canthus rounded in section; anterior ramus of pterygoid bearing denticulate serrations on lingual margin; prehallux well developed, anvil-shaped ..... *H. scutatus*

   Adhesive discs on digits expanded; canthal ridge present, canthus rounded or angular in section; pterygoid edentate; prehallux only moderately to poorly developed, not anvil-shaped 2

2. Postorbital indentation absent, orbit with complete bony margin; otic margin of paraoccipital process approximately parallel to longitudinal axis of body; supraorbital ridges absent ..... *H. fasciatus*

   Postorbital indentation present, orbit without complete bony margin; otic margin of paraoccipital process not parallel to longi-

tudinal axis of body; supraorbital ridges present 3

3. Transverse preoccipital ridge present, uniting posterior ends of supraorbital ridges; postorbital ridge present; ventral shaft of urostyle not laterally expanded ..... *H. bubalus*

   Preoccipital ridge absent; postorbital ridge absent; ventral shaft of urostyle laterally expanded 4

4. Canthal ridge anterolaterally concave; snout not depressed in lateral profile; proboscis short, triangular, dorsoventrally depressed; postorbital indentation small; subtemporal fenestra minute; prevomerine teeth absent ..... *H. johnsoni*

   Canthal ridge straight; snout depressed in lateral profile; proboscis long, triangular, laterally compressed; postorbital indentation large; subtemporal fenestra large; prevomerine teeth present ..... *H. proboscideus*

ACCOUNTS OF SPECIES

Hemiphractus bubalus (Jiménez de la Espada)
New combination

Cerathyla bubalus Jiménez de la Espada, 1871:64 [Holotype.—MNCN 176 from Archidona, Provincia Pastaza, Ecuador; Jiménez de la Espada collector].

Cerathyla braconnieri Jiménez de la Espada, 1871:64 [Holotype.—MNCN 174 from "Zarajioto, Orillas del Napo," Provincia Napo, Ecuador; Jiménez de la Espada collector]. New synonym.

Cerathyla palmarum Jimenéz de la Espada, 1871:64 [Holotype.—MNCN 175 from San José de Moti, Provincia Napo, Ecuador; Jiménez de la Espada collector]. New synonym.

Ceratohyla bubalus—Boulenger, 1882:453.

Ceratohyla palmarum—Boulenger, 1882:455.

Ceratohyla braconnieri—Boulenger, 1882:455.

Justification of synonymy.—I have examined the holotypes of *Cerathyla bubalus*, *C. braconnieri*, and *C. palmarum* housed in the collections of the Museo Nacional de Ciéncias Naturales in Madrid. Each species is represented by a single specimen and each is a female, poorly preserved, soft and faded so as to obscure any color pattern which may have been present. The measurements of the specimens (Table 4) are similar to one another and well within the range of variation for the specimens of *bubalus* I examined (Table 2). Jiménez de la Espada (1871:64) distinguished the three specimens (MNCN 174, 175, and 176) on the bases of tongue shape and small variations in cranial structure. I found each specimen to have an ovoid tongue and basically the same skull structure. The only obvious variation in these frogs involves the fleshy proboscis at the tip of the snout; the proboscis is easily lost or damaged. In MNCN 176 (*C. bubalus*) the proboscis is absent, whereas in MNCN

174 (*C. braconnieri*) it is minute and blunt; and in MNCN 175 (*C. palmarum*) it is small and laterally compressed. Because of the similarity of these three specimens with respect to cranial structure, size and proportions, and site of origin (all from Amazonian Ecuador), I herewith place the names *braconnieri* and *palmarum* as junior synonyms of *bubalus*, which has line priority.

Diagnosis.—1) Size moderate, sexual dimorphism evident; maximum observed snout-vent length in males 50.5 mm ($\bar{x}$=43.8), in females 66.3 mm ($\bar{x}$=57.9); 2) postorbital indentation large, not rounded, about twice as wide as long; 3) posterior projection of paraoccipital process relatively greater in males (18.4% head length, N=22) than in females (4% head length, N=3); width between distal tips of processes relatively greater in males (96.6% head width) than in females (83.0% head width); 4) otic margin of paraoccipital process approximately parallel to maxillary arch in dorsal view and characterized by distinct, well-developed ridge (Figs. 8 and 9); 5) canthal ridge distinct and anterolaterally concave; canthus angular in section; 6) supraorbital ridges well developed, converging posteromedially and merging with preoccipital ridge; 7) preoccipital ridge present; 8) postorbital ridge well developed along posterior margin of postorbital indentation; 9) zygomatic ridge well developed, extending diagonally downward from rear margin of ventral arm of squamosal along posterolateral margin of orbit to terminate suborbitally; 10) subtemporal fenestra large; 11) pterygoid edentate; 12) cultriform process of parasphenoid not keeled; 13) snout depressed in lateral profile; 14) clavicles moderately well

TABLE 4.—Comparison of Morphological Measurements (mm) of Holotypes of *Cerathyla bubalus, C. bracounieri* and *C. palmarum*. (SVL=snout-vent length; HW=head width)

Character	*C. bubalus*, ♀ (MNCN 176)	*C. braconnieri*, ♀ (MNCN 174)	*C. palmarum*, ♀ (MNCN 175)
Snout-vent length	60.7	66.3	61.0
Tibia length	33.7	34.3	33.5
(%SVL)	(55.5)	(51.7)	(54.9)
Foot length[a]	27.5	33.3	31.4
(%SVL)	(45.3)	(50.2)	(51.5)
Head length	25.5	27.4	25.6
(%SVL)	(42.0)	(41.3)	(42.0)
Head width	27.0	29.6	28.1
(%SVL)	(44.5)	(44.6)	(46.1)
Interorbital width	7.6	7.8	7.0
(%HW)	(28.1)	(26.4)	(24.9)
Internarial distance	2.4	2.9	3.0
Eye diameter	6.8	6.9	6.4
Tympanum width	3.2	3.4	4.2
Tympanum height	6.6	6.0	6.4

[a] Excluding tarsus

developed; 15) neural spines of presacrals IV-VIII and sacrum enlarged, with that of the fourth presacral being largest; 16) width of sacral diapophyses less than width of transverse processes of presacral VIII and greater than width of presacral III; 17) ventral shaft of urostyle not laterally expanded; 18) prehallux poorly developed; 19) proboscis small, triangular and dorsoventrally depressed; 20) eyelid with central, enlarged conical tubercle flanked by several slightly smaller tubercles; 21) tubercles on dorsal surface of forearm arranged in oblique rows corresponding to dark bars; 22) tubercles on dorsal surfaces of hind limb aligned in oblique rows corresponding to dark bars; 23) small, distinct calcar present on heel; 24) skin of flanks and venter finely granular; 25) fingers not webbed; 26) toes basally webbed; 27) adhesive discs present; those of toes slightly smaller than those of fingers.

Hemiphractus bubalus differs from all other members of the genus by having a distinct transverse preoccipital ridge which, in conjunction with the other cranial ridges, forms a unique pentagonal configuration on the top of the head (Fig. 8).

Distribution.—All specimens have been collected from the upper Amazon Basin in the provinces of Napo and Pastaza in Ecuador (Fig. 10). The species occurs between elevations of 300 and 1740 m on the Amazonian slopes of the Andes.

Remarks.—Available field notes indicate that *bubalus* is an inhabitant of dense cloud forest and favors perches 1-2.5 m above the ground on branches of bushes and small trees. Save for one individual found on the forest floor by day, all specimens were collected at night. One adult female (KU 124140, 48.0 mm snout-vent length) contained a lizard, *Alopoglossus buckleyi*, in her stomach. Several individuals (adult males and females) displayed what is described most appropriately as "gaping behavior"; when disturbed, these frogs typically open their mouths to their fullest extent exhibiting 1) the inordinately large size of the buccal cavity, 2) a bright yellow or orange tongue, and 3) an impressive pair of mandibular odontoids (Fig. 9). Presumably such behavior is a defense posture common to the genus (see accounts of *fasciatus* and *proboscideus*).

At night these frogs typically are pale yellowish tan with dark brown markings; the venter is white with pale gray or brown markings and the iris is cream colored. By day, most individuals become darker brown dorsally and exhibit yellow-tan markings. The venters darken substantially, becoming dark brown with gray mottling, and the iris changes from cream to brown with a ring of gray around the pupil.

Unfortunately, nothing is known about the breeding habits of this species. Presumably *bubalus*, like all the other members of the genus, carries eggs that undergo direct development on its back;

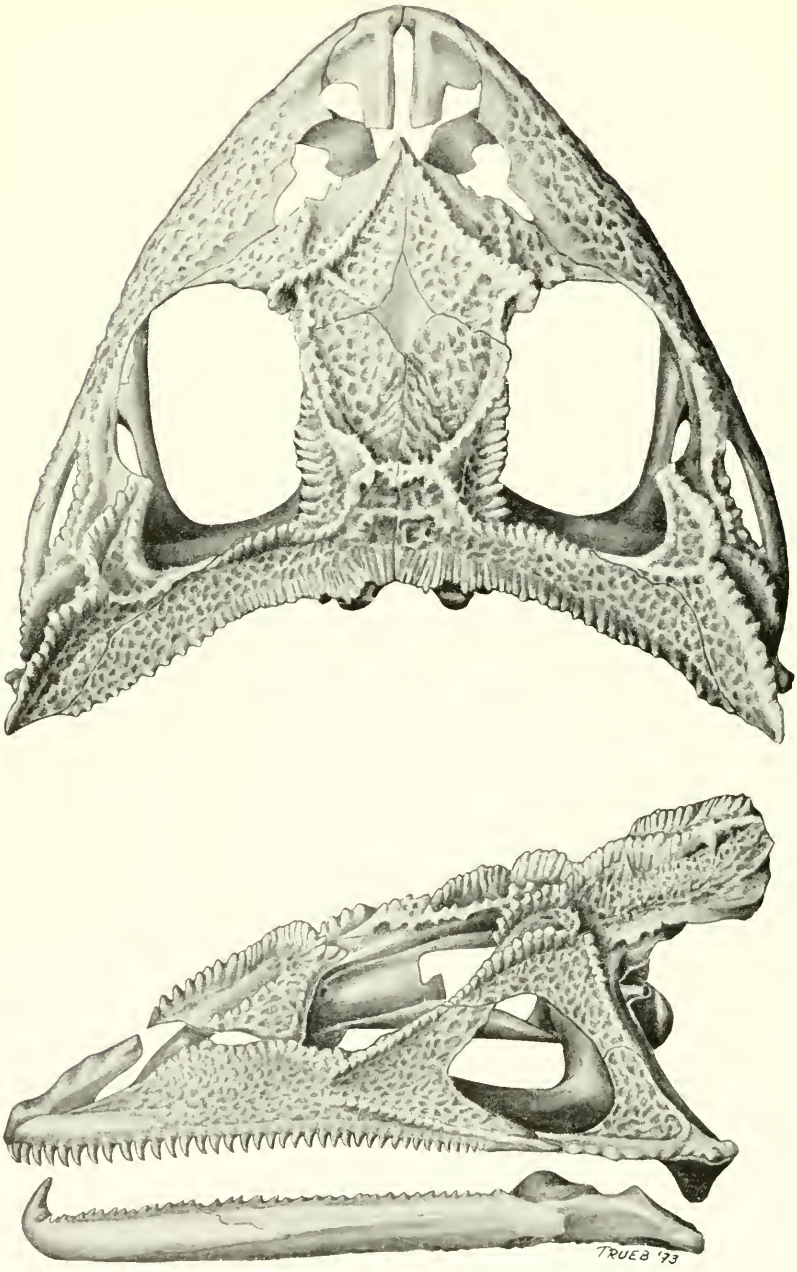

FIG. 8. Skull of *Hemiphractus bubalus* (KU 124140, ♀; *ca.* ×4). Top: Dorsal view. Bottom: Lateral view of skull and mandible.

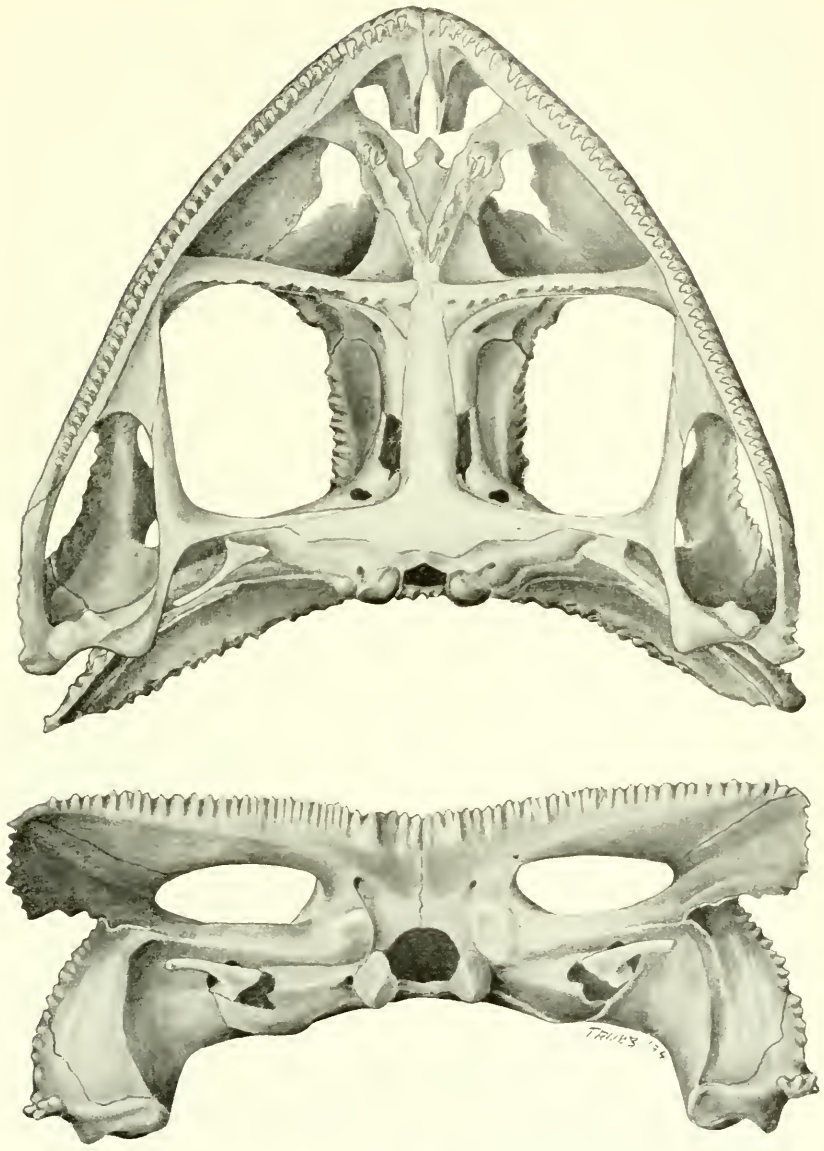

FIG. 9. Skull of *Hemiphractus bubalus* (KU 124140, ♀; *ca.* × 4). Top: Ventral view. Bottom: Posterior view.

however, there is no direct evidence of this. Specimens have been collected in January, March, June, August, and October. Females (2) with large to moderate-sized ovarian eggs were obtained in August as were most mature males (4 of 5). In contrast, October

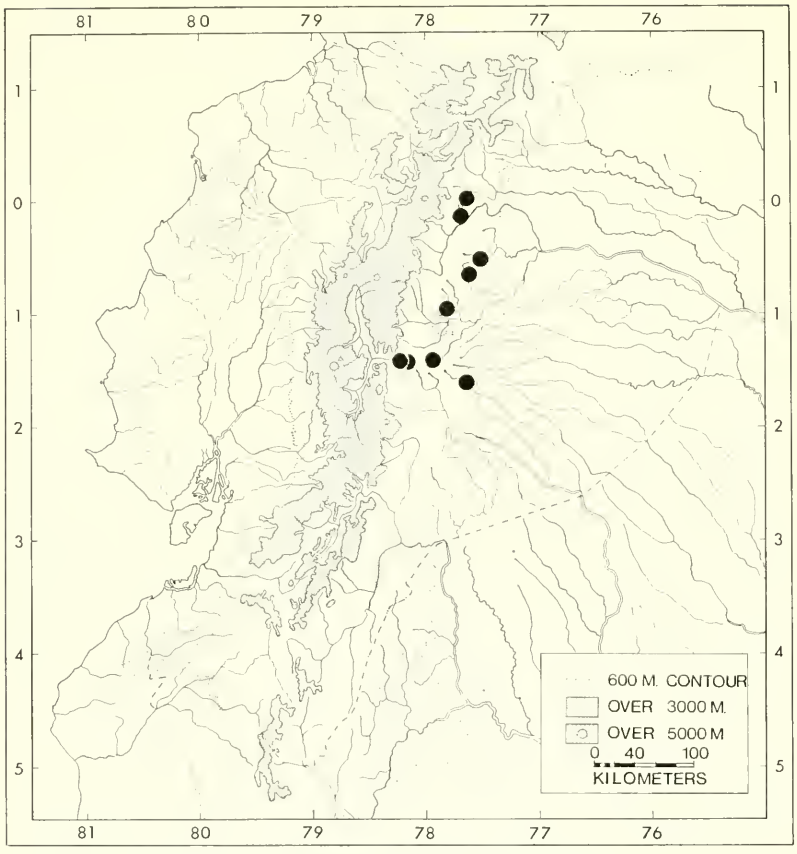

FIG. 10. Distribution of *Hemiphractus bubalus* in Ecuador.

collections resulted in acquisition of 14 juveniles and one subadult female and no adults; juveniles also were collected in June (3) and August (2).

Hemiphractus fasciatus Peters

Hemiphractus fasciatus Peters, 1862:149 [Holotype.—ZSM 36/0 from "Pastaza Valley, Ecuador" (in error); Moritz Wagner collector].
Ceratohyla fasciata—Boulenger, 1882:454.
Cerathyla panamensis Stejneger, 1917:31 [Holotype.—USNM 55320 from Signal Loma, 5 km south of Santa Isabel, Provincia Colón, Panamá; Mr. Charles Gordon Holland collector]. New synonym.
Hemiphractus panamensis—Duellman, 1970:140.

Justification of synonymy.—Examination of the holotypes of *Cerathyla panamensis* and *Hemiphractus fasciatus* has shown that these two frogs are extremely similar. Stejneger's specimen of *panamensis* is a large female, whereas Peters' specimen of *fasciatus*

is a much smaller female; both individuals fall well within the range of observed variation of snout-vent length, and head length, head width, and tibia length relative to snout-vent length (compare Tables 2 and 5). Although *panamensis* was described from Panamá and *fasciatus* from Amazonian Ecuador (a type locality which must be in error, because no other specimen of *fasciatus* has been collected from the Amazonian side of the Andes south of northwestern Colombia), the specimens are nearly identical in all diagnostic features—1) the crania are the same; 2) the tongues are ovoid; 3) the skin is finely granular; 4) although Stejneger's specimen is faded, his color notes generally concur with those of Peters; and 5) both specimens have a small, dorsoventrally depressed proboscis. Because of these obvious similarities, I herein place the name *panamensis* as a junior synonym of *fasciatus* which has priority.

TABLE 5.—Comparison of Morphological Measurements (mm) of Holotypes of *Hemiphractus fasciatus* and *Cerathyla panamensis*. (SVL=snout-vent length; HW=head width; HL=head length)

	H. fasciatus, ♀ (ZSM 36/0)		*C. panamensis*, ♀ (USNM 55320)	
Character	Original description; Peters, 1862	Measurements by Trueb	Original description; Stejneger, 1917	Measurements by Trueb
Snout-vent length	46.0	46.5	60.0[a]	59.1[a]
Head length, medial	18.0	----	----	23.1
Head length	----	21.0	----	28.7
(%SVL)	----	(45.2)	----	(48.6)
Head length, tip of snout to paraoccipital horn	23.0	----	----	33.0
Head width	21.7	21.4	32.0	33.1
(%SVL)	(47.2)	(46.0)	(53.3)	(56.0)
Interorbital distance	----	8.3	12.0	11.2
(%HW)	----	(38.8)	(37.5)	(33.8)
Internarial distance	----	2.7	----	3.5
Nostril to orbit distance	----	5.5	7.0	7.0
(%HL)	----	(26.2)	----	(24.4)
Nostril to snout distance	----	4.9	6.0[a]	4.0[a]
Tibia length	----	24.5	31.5	33.0
(%SVL)	----	(52.7)	(52.5)	(55.8)
Forelimb length	34.0	----	40.0	----
Hind limb length	80.0	----	99.0	----

[a] Stejneger measured lengths involving the head from the tip of the fleshy proboscis, whereas I did not; hence, his values are greater than mine.

Diagnosis.—1) Size moderate, sexual dimorphism evident; maximum observed snout-vent length in males 55.7 mm ($\bar{x}$=49.6), in females 68.7 mm ($\bar{x}$=57.3); 2) postorbital indentation absent; 3) posterior projection of paraoccipital process relatively greater in males (11.7% head length, N=11) than in females (4.0% head length, N=10); width between distal tips of processes about the same in males (87.9% head width) as in females (85.5% head width); 4) otic margin of paraoccipital process not parallel to maxillary arch in dorsal view; instead, approximately parallel to longitudinal axis of body, slightly concave laterally, and characterized by low but distinct ridge (Fig. 11); 5) canthal ridge indistinct, anterolaterally concave; canthus angular in section; 6) supraorbital ridges absent; 7) preoccipital ridge absent; 8) postorbital ridge absent; 9) zygomatic ridge indistinct and poorly developed, extending diagonally downward from rear margin of ventral arm of squamosal to posteroventral margin of orbit; 10) subtemporal fenestra small, relatively smaller in females than in males; 11) pterygoid edentate; 12) cultriform process of parasphenoid not keeled (Fig. 12); 13) snout not depressed in lateral profile; 14) clavicles not well developed; 15) neural spines of presacrals III-VIII and sacrum enlarged, with that of the fifth presacral being the largest; 16) width of sacral diapophyses less than width of transverse processes of presacral VIII and approximately equal to width of presacral III; 17) ventral shaft of urostyle laterally expanded; 18) prehallux moderately developed; 19) proboscis small, triangular and dorsoventrally depressed; 20) eyelid granular with a single enlarged tubercle amid several smaller, scattered tubercles; 21) tubercles on dorsal surface of hind limb indistinct and aligned in transverse rows; 23) small, poorly developed calcar present on heel; 24) skin of flanks and venter with scattered, low subconical tubercles; 25) fingers not webbed, or only basally webbed; 26) toes basally webbed; 27) adhesive discs present; those of the toes slightly smaller than those of the fingers.

Hemiphractus fasciatus can be distinguished from other members of the genus by the combination of its lack of a postorbital indentation (Fig. 11) and the presence of well-developed adhesive discs on the digits. It is distinguished further by having a diffuse pale mark bordering the dorsal margin of a dark inguinal mark; the pale mark extends dorsal to the cloaca to form an indistinct cloacal stripe.

Distribution.—This species is widespread throughout Panamá, northern Colombia, and the Pacific slopes of Colombia and northwestern Ecuador between elevations of 300 and 1600 m (Fig. 13).

Remarks.—This species is perhaps the best known of the genus. It has an extensive range and a wide altitudinal distribution; moreover, its habits, habitat preferences, coloration, and behavior are well documented in the copious field notes of Charles W. Myers,

who collected many individuals in the course of three years' field work in Panamá. He reported (1966) some initial observations on the distribution and behavior of *fasciatus*, and included a photograph of its defense or "gaping" posture and a report of a release call (one of two such reports, the other being for *proboscideus*). It seems appropriate here to note that Myers reported (field notes of 18 January 1966) that the Panamanian natives refer to *fasciatus* as "rana brava," and to supplement this statement with an anecdote excerpted from Myers' field notes of 13 December 1964: "I made the mistake of sticking a finger in the gaping mouth to see if it [the frog] would bite. It did and held on like a vise. The two fangs in the lower jaw (which I was unaware of, else would not have been so stupid) made two puncture marks (like a small snake bite) which bled real blood." Benefiting from Myers' experience, those of us who have had the opportunity to collect *Hemiphractus* on subsequent occasions find that it is safer and wiser to grasp the species by the tips of the paraoccipital horns from the rear.

This species, like other members of the genus, is a denizen of the forest; however, because of its relatively wide altitudinal distribution, it inhabits lowland tropical rainforests, lower montane forests and cloud forests. By day it is found amidst leaf litter on the forest floor, whereas by night, it favors perches above the ground. Most individuals have been found sitting on sticks or low vegetation 0.3-0.6 m above the ground. Occasionally, larger individuals perch 1-2 m above the ground on tree trunks, branches, and in the bases of arboreal bromeliads. There is evidence that the species preys upon a variety of animals; one specimen, a large female (KU 93503) had an unidentified gastropod, a lizard (*Ptychoglossus*), and a dendrobatid frog (*Colostethus*) in her stomach.

Coloration in living *fasciatus* is highly variable. Generally, the dorsal ground color varies from dull olive green or yellowish tan to dark brown; darker dorsal markings (usually brown) are nearly always present. The flanks, and anterior and posterior surfaces of the thighs are lighter than the dorsum, usually a pale tan or flesh color with brown mottling; in at least one individual, the posterior surfaces of the thighs were dark brown. The venter varies from dark brown to gray; some mottling, varying between light brown, yellow and white is present. In some individuals, the gular and pectoral regions are darkest and grade to a perceptibly paler abdominal color. Nearly all individuals have a distinct, pale gular spot. The iris is almost invariably pale, its tone varying from pale yellow or pale orange-gold to light brown. The color may be uniform, save for the horizontal brown stripe bisecting the iris through the pupil, or the iris may be two-toned. In the latter case, the lower part of the iris is darker than the upper portion and varies

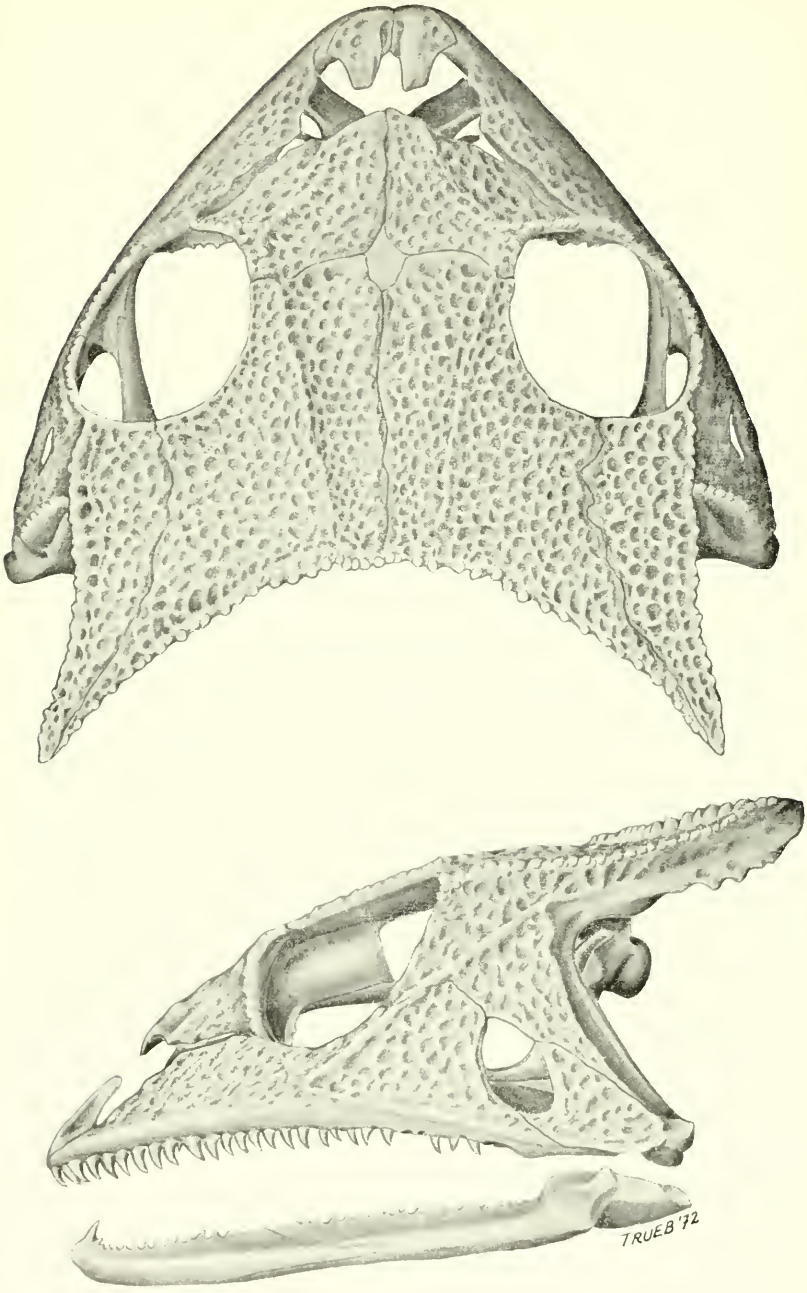

FIG. 11. Skull of *Hemiphractus fasciatus* (KU 93510, ♂; *ca.* × 4.5). Top: Dorsal view. Bottom: Lateral view of skull and mandible.

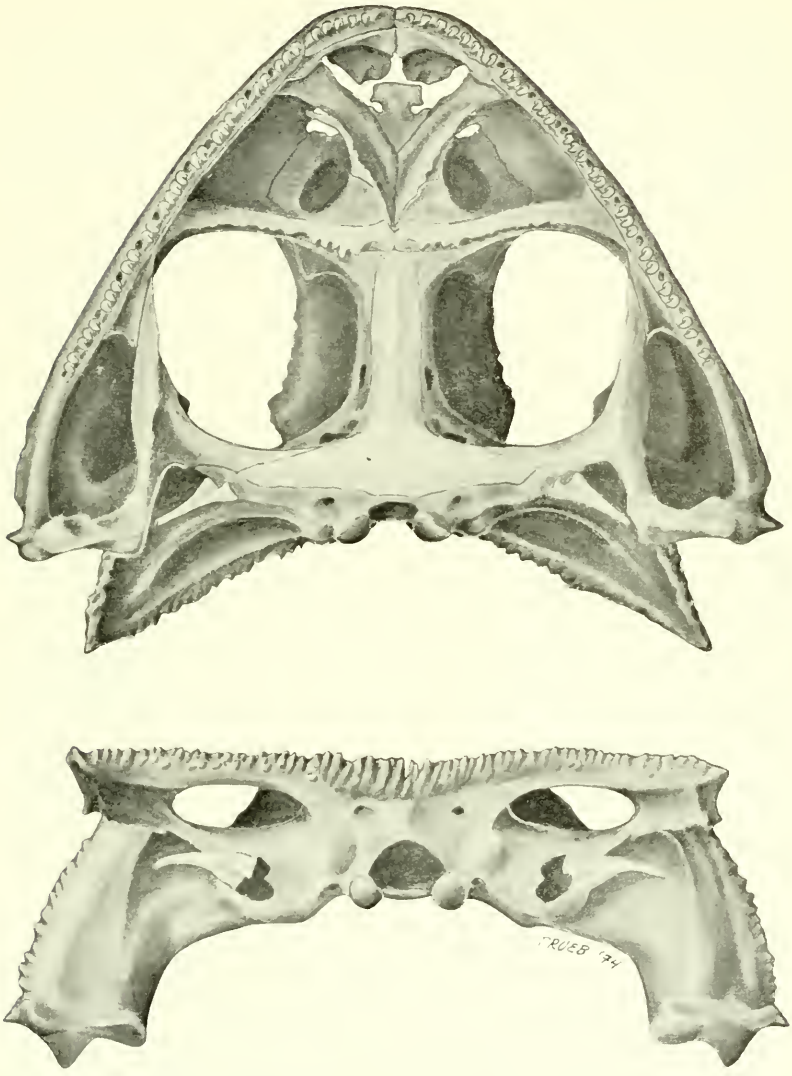

FIG. 12. Skull of *Hemiphractus fasciatus* (KU 93510, ♂; *ca.* × 4.5). Top: Ventral view. Bottom: Posterior view.

from gray-gold to reddish gray. The irises of some individuals are characterized by fine red or black reticulations.

Hemiphractus fasciatus has been collected in all months except March, April, August, and October. The one female with associated young (BYU 19142, see Duellman, 1970:143 and Pl. 7 for a detailed discussion of this specimen) was collected in September. Females with large (*ca.* 5-6 mm diameter) eggs were obtained in November

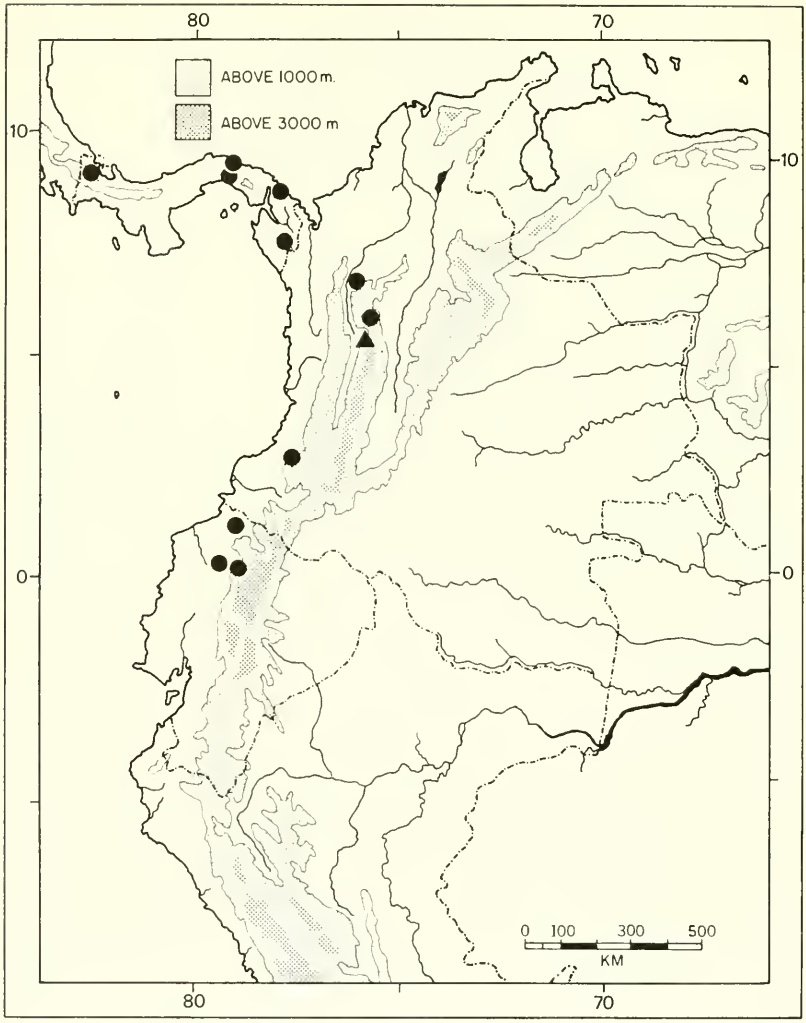

FIG. 13. Distribution of *Hemiphractus fasciatus* (circles) and the type locality of *Hemiphractus johnsoni* (triangle) in lower Central America and northwestern South America. See figure 17 for distribution map of *H. johnsoni*.

(1), December (1), and May (1); females with moderate to small-sized ovarian eggs were obtained in January (4) and May (2). Mature males were collected in January (10) and May (1); subadult males and females were obtained at the same times, and juveniles in the months of February, May through July, and September.

While examining specimens at the Natural History Museum in Stockholm, I encountered a specimen of *Hemiphractus* with a manu-

script name of *Cerathyla minima* applied to it by Andersson. The specimen (NHRM 1981 from El Tambo, La Costa, Departamento Cauca, Colombia, collected on 16 June 1936 by K. von Sneidern) is a juvenile male (25.8 mm snout-vent length). It is pale tan in color with no evident markings. The configuration of the skull confirms its identification as *Hemiphractus fasciatus*.

Hemiphractus johnsoni (Noble) new combination

Cerathyla johnsoni Noble, 1917:798 [Holotype.—AMNH 1341 from Santa Rita Creek, 14 miles north of Mesopotamia, Departamento Antioquia, Colombia; R. D. O. Johnson collector].
Cerathyla bubalus—Myers and Carvalho, 1945:21 [in part].

Diagnosis.—1) Size moderately large, sexual dimorphism evident; maximum observed snout-vent length in males 52.9 mm ($\bar{x}$=48.2), in females 77.2 mm ($\bar{x}$=68.2); 2) postorbital indentation moderately small, rounded (Fig. 14); 3) posterior projection of paraoccipital process relatively less in males (19.5% head length, N=2) than in females (27.3% head length, N=2); width between distal tips of processes relatively less in males (82.1% head width) than in females (90.1% head width); 4) otic margin of paraoccipital process more nearly parallel to maxillary arch than to longitudinal axis of body in dorsal view; 5) canthal ridge distinct, anterolaterally concave; canthus angular in section; 6) supraorbital ridges moderately developed, slightly convergent posteriorly, terminating just anterior to occipital flange; 7) preoccipital ridge absent; 8) postorbital ridge absent; 9) zygomatic ridge indistinct, extending from rear margin of ventral arm of squamosal to posterolateral margin of orbit, parallel and ventral to zygomatic arm of squamosal; 10) subtemporal fenestra minute; 11) pterygoid edentate (Fig. 15); 12) cultriform process of parasphenoid usually with indistinct keel; 13) snout not depressed in lateral profile; 14) clavicles moderately well developed; 15) neural spines of presacrals IV-VIII enlarged, with none being distinctly larger than any other; 16) width of sacral diapophyses less than width of transverse processes of presacral VIII and greater than width of presacral III; 17) ventral shaft of urostyle laterally expanded; 18) prehallux poorly developed; 19) proboscis small, triangular and dorsoventrally depressed; 20) eyelid coarsely granular with one slightly enlarged, conical tubercle; 21) tubercles on dorsal surface of forearm scattered; 22) tubercles on dorsal surface of hind limb absent or poorly developed; 23) small, poorly-developed calcar present on heel; 24) skin of flanks and venter smooth; 25) fingers not webbed; 26) toes basally webbed; 27) adhesive discs present; those of toes slightly smaller than those of fingers.

Hemiphractus johnsoni differs from other members of the genus by the presence of a small, round postorbital depression. Further-

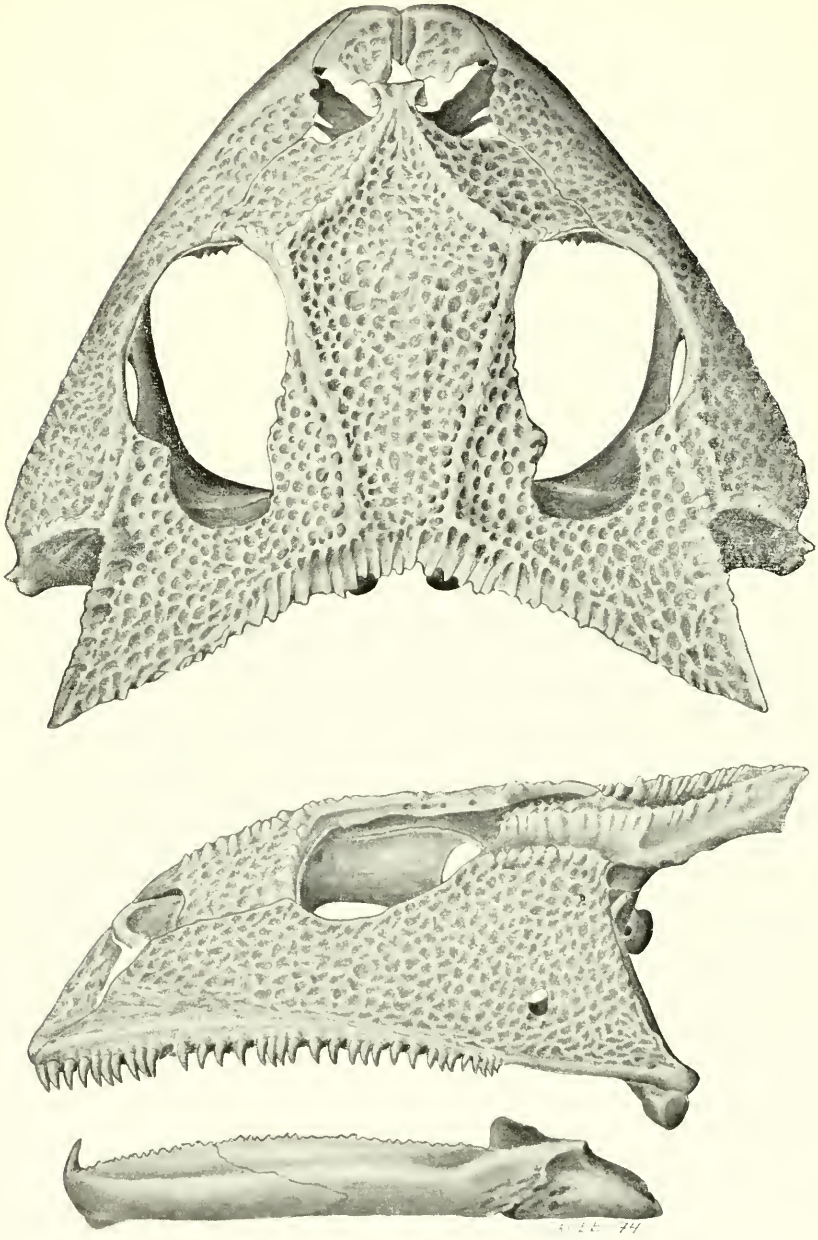

FIG. 14. Skull of *Hemiphractus johnsoni* (KU 153436, ♂; *ca.* × 4). Top: Dorsal view. Bottom: Lateral view of skull and mandible.

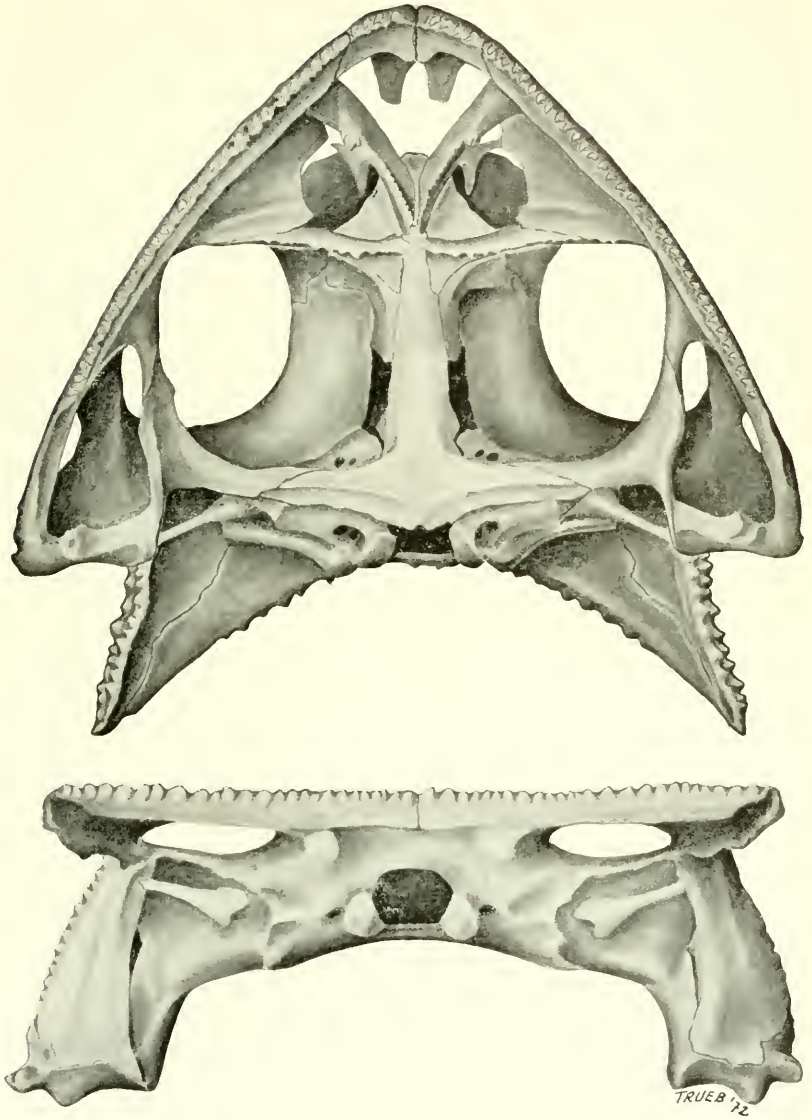

FIG. 15. Skull of *Hemiphractus johnsoni* (KU 153436, ♂; *ca.* × 4). Top: Ventral view. Bottom: Posterior view.

more, it lacks the bold dorsal markings characteristic of *bubalus*, and has a small proboscis which distinguishes it from *proboscideus*.

Distribution.—This species is known from 11 specimens representing an extraordinary distribution that ranges from the northern Andean slopes of Colombia and the upper Amazon Basin and lower Amazonian slopes of the Andes from Ecuador to northern Bolivia

(Figs. 13 and 17). It occurs between elevations of 300 and 1910 m.

Remarks.—On the basis of available museum specimens, *H. johnsoni* is the rarest member of the genus. There are 11 known specimens exclusive of young associated with an adult female. The only notes on habitat (Noble, 1917:801) and the localities from which specimens have been collected indicate that this species inhabits dense forests. One specimen (AMNH 58631) is a female from Perú with 18 young attached to her back; another female collected by David B. Wake and Richard Etheridge in Perú in July had 17 eggs on her back. Available field notes indicate that *johnsoni* perches on low branches (0.3-0.7 m above ground) at night. In life, this frog is tan-brown dorsally with reddish mottling and darker brown spots. The venter is grayish white and the iris gold above and orange below with a horizontal brown streak. For notes on the location of the type locality, see Trueb (1971:28). It should be noted that Myers and Carvalho's (1945:19-21; Figs. 17 and 18) discussion of *Cerathyla bubalus* is referrable to *Hemiphractus johnsoni.*

Hemiphractus proboscideus (Jiménez de la Espada)

New combination

Cerathyla proboscidea Jiménez de la Espada, 1871:64 [Holotype.—MNCN 173 from Sumaco, Provincia Napo, Ecuador; Jiménez de la Espada collector].
Ceratohyla proboscidea—Boulenger, 1882:453.
Ceratohyla cristata Andersson, 1945:18 [Holotype.—NHRM 1911 from Río Pastaza watershed, Ecuador; William Clarke-MacIntyre collector]. New synonym.

Justification of synonymy.—Types of both *proboscidea* and *cristata* are from Amazonian Ecuador. The snout-vent lengths of each and their head widths, head lengths and tibial lengths relative to the snout-vent lengths fall within or near the range of observed variation for the individual's respective sex (compare Tables 2 and 6). The holotype of *proboscidea* is a small male which is poorly preserved and completely faded, making comparison with the larger female type of *cristata* difficult. Nonetheless, the cranial characteristics of both specimens are the same and unique among hemipractines. Furthermore, both have ovoid tongues, a small dermal protuberance on each eyelid, and a long, fleshy proboscis with an irregular dorsal edge. Because of these distinct resemblances, I herein place the name *cristata* as a junior synonym of *proboscideus.*

Diagnosis.—1) Size moderate, sexual dimorphism evident; maximum observed snout-vent length in males 49.7 mm ($\bar{x}$=46.3), in females 67.1 mm ($\bar{x}$=56.1); 2) postorbital indentation large, rounded, and about twice as wide as long (Fig. 2); 3) posterior projection of paraoccipital process relatively greater in males (24.5%

TABLE 6.—Comparison of Morphological Measurements (mm) of Holotypes of *Cerathyla proboscidea* and *Ceratohyla cristata*. (SVL=snout-vent length; HW=head width)

Character	*Cerathyla proboscidea*, ♂ (MNCN 173)	*Ceratohyla cristata*, ♀ (NHRM 1911)	
	Measurements by Trueb	Original description; Andersson, 1945	Measurements by Trueb
Snout-vent length	42.8	62.0	62.0
Head length	19.0	—	28.3
(%SVL)	(44.4)	—	(45.6)
Head width	20.5	30.0	29.6
(%SVL)	(47.9)	(48.4)	(47.7)
Interorbital distance	6.0	10.0	9.0
(%HW)	(29.3)	(33.3)	(30.4)
Internarial distance	1.9	2.5	2.6
Width of upper eyelid	3.2	6.0	5.5
Nostril to snout distance	4.3	6.0	6.9
Tibia length	26.3	36.5	36.2
(%SVL)	(61.4)	(58.9)	(58.4)
Foot length[a]	20.3	28.9	—
(%SVL)	(47.4)	(46.6)	—

[a] Excluding tarsus

head length, N=14) than in females (19.8% head length, N=24); width between distal tips of processes relatively greater in males (105.1% head width) than in females (97.7% head width); 4) otic margin of paraoccipital process approximately parallel to maxillary arch in dorsal view, characterized by a distinct, well-developed ridge; 5) canthal ridge distinct and straight; canthus angular in section; 6) supraorbital ridges distinct, slightly convergent posteromedially, terminating just anterior to occipital flange; 7) preoccipital ridge absent; 8) postorbital ridge absent; 9) zygomatic ridge well developed, extending diagonally downward from rear margin of ventral arm of squamosal along posterolateral margin of orbit to merge inconspicuously with suborbital margin; 10) subtemporal fenestra large; 11) pterygoid edtentate; 12) cultriform process of parasphenoid not keeled; 13) snout depressed in lateral profile; 14) clavicles moderately well developed; 15) neural spines of presacrals IV-VIII and sacrum enlarged, with those of presacrals IV-VIII being distinctly larger than that of sacrum; 16) width of sacral diapophyses slightly less than width of transverse processes of presacral VIII and slightly greater than width of presacral III; 17) ventral shaft of urostyle laterally expanded; 18) prehallux poorly developed; 19) proboscis large, laterally compressed and characterized by an irregular dorsal edge; 20) eyelid with central, enlarged conical tubercle flanked by several slightly smaller tubercles;

21) tubercles on dorsal surface of forearm arranged in oblique rows; 22) tubercles on hind limb aligned in oblique rows; 23) small, distinct calcar present on heel; 24) skin of flanks and venter finely granular; 25) fingers not webbed; 26) toes one-fourth webbed; 27) adhesive discs present; those of toes slightly smaller than those of fingers.

Hemiphractus proboscideus can be distinguished from other members of the genus by its long, compressed proboscis, large postorbital indentation, and characteristic white or cream colored (in preservative) discs on the inner two fingers.

Distribution.—This species is known only from the upper Amazon Basin in Ecuador, where it occurs between elevations of 300 and 720 m along the Andean slopes (Fig. 16).

Remarks.—Of the 72 preserved specimens of *proboscideus,* 46 are from Santa Cecilia, Ecuador, and have been collected during a period of five years. Although intensive field work has been

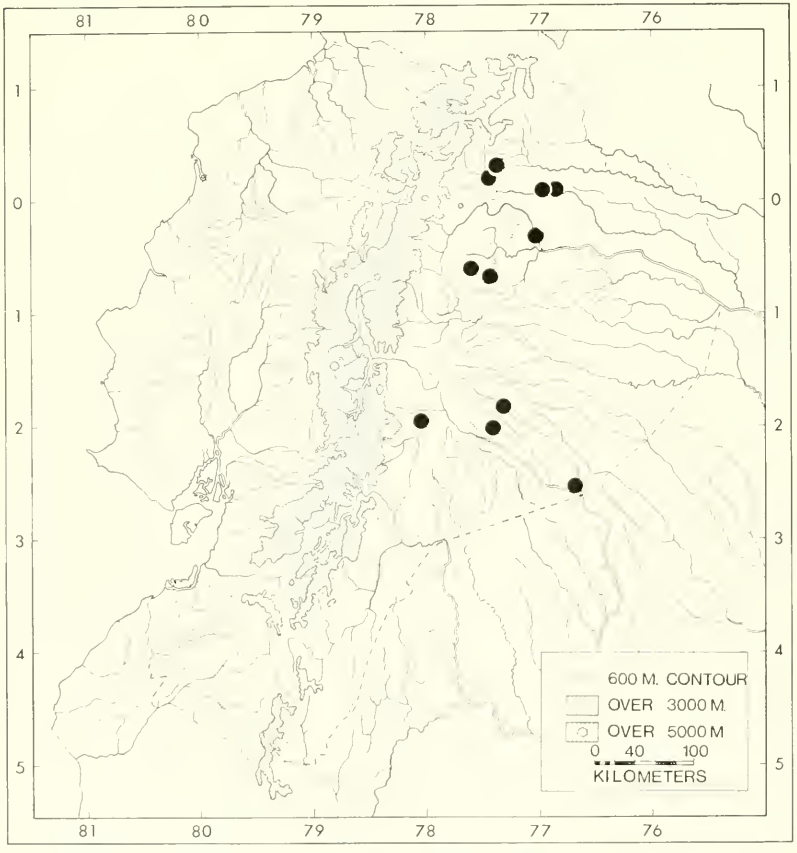

Fig. 16. Distribution of *Hemiphractus proboscideus* in Ecuador.

carried out at this locality throughout the year, no *proboscideus* have been obtained in February, September, or December. The majority of specimens (juveniles, adult males, and females with moderate or small-sized ovarian eggs; total of 34 frogs) was collected in June and July. In addition, juveniles and adult males were found from March through May and in August. Juveniles were collected also in October, and females in January, March, May through August and October and November. The temporal distribution of juveniles suggests that breeding must occur throughout the year, but it is disheartening to note that none of the KU females has large ovarian eggs, eggs on the back or any evidence of having recently had young on the back. One female (UMMZ 92110, 61.3 mm snout-vent length) has depressions on her back, thereby documenting the reproductive mode in this species. Based on examination of the Santa Cecilia collection, it is obvious that *proboscideus* has a diverse appetite; among the stomach contents were a variety of beetles and orthopterans in nearly all specimens. Other food items found were an unidentifiable frog (genus *Hyla*), a juvenile lizard (*Anolis chrysolepis*), two adult frogs (*Eleutherodactylus conspicillatus* and *Osteocephalus leprieurii*), and a variety of unidentified eggs and an annelid.

Hemiphractus proboscideus seems to be restricted to lower montane forest and lowland rainforest, where it occasionally is found amidst leaf litter by day, but most often is found perched on low vegetation (below 1.5 m above the ground) at night. Typically, the species is found on palm fronds, vines, leaves of low herbs, bushes and trees.

The irises of *proboscideus* vary between pale pink and pale gray with indistinct, diffuse gray triangles anterior and posterior to the pupil (apices are located at the margin of the pupil). The tongue and buccal cavity are bright yellow. Otherwise coloration in this species is highly variable individually, and within individuals from day to night. By night, the dorsal areas of most individuals are yellowish tan with darker tan or brown markings; occasionally, individuals are found which are gray with brown reticulations. By day, the typical dorsal coloration is transformed to a dark brown with darker brown markings. The venter, which is pale colored or white at night, changes dramatically to a deep brown or reddish brown by day. This dark ventral ground color is variously punctuated by orange or yellowish tan abdominal blotches and yellow to white spots in the gular area. The flanks tend to be pale flesh color and the thighs vary from yellowish tan with reddish brown bands to a dark gray posteriorly. According to field notes, the adhesive discs are orange in life.

On at least two occasions this species has been observed to assume the "gaping" defense posture (discussed in the Remarks

section of the account of *fasciatus*) when disturbed, exposing the bright yellow buccal cavity and tongue. Both individuals are males (48.2 and 43.1 mm snout-vent length), and neither one could be induced to bite. The larger of the two frogs emitted a "grunting" sound when collected.

Hemiphractus scutatus (Spix)

Rana scutata Spix, 1824:28 [Holotype.—formerly in Zoologisches Sammlung München; no number and now destroyed or lost].
[*Stombus*] *scutata*—Gravenhorst, 1825:920.
Hemiphractus spixii Wagler, 1828:743 [Substitute name for *Rana scutata*].
Hemiphractus scutatus—Peters, 1862:146.
Hemiphractus divaricatus Cope, 1868:114 [Holotype.—ANSP 4132 from "Peru, Napo, and Marañon rivers"; Prof. James Orton collector]. New synonym.
Hemiphractus boulengeri Miranda-Ribeiro, 1926:118 [Holotype.—BMNH 1880.12.5.153 from "Ecuador"; Mr. Buckley collector]. Synonymy *fide* Myers and Carvalho (1945:19).

Justification of synonymy.—Having examined the type of *divaricatus* and compared it and Cope's description with the descriptions of *scutatus* by Peters (1862) and Brocchi (1877), I find no grounds on which to recognize *divaricatus* as distinct from *scutatus;* accordingly, I place the name *divaricatus* as a junior synonym of *scutatus.* The differences described by Cope (1868) are minor variations in certain cranial features which he discerned by comparison of his specimen with Peters' description. Examination of table 7 shows that morphometrically, the types of *divaricatus* and *boulengeri* compare favorably with the measurements reported by Peters for *scutatus* and those reflecting variation within the sample I examined (Table 2).

Diagnosis.—1) Size large, sexual dimorphism evident; maximum observed snout-vent length in males 57.4 mm ($\bar{x}$=50.7), in females 80.5 mm ($\bar{x}$=70.4); 2) postorbital indentation absent (Fig. 1); 3) posterior projection of paraoccipital process approximately the same in males (18.0% head length, N=7), as in females (17.9% head length, N=14); width between distal tips of processes about the same in males (93.8% head width) as in females (92.7% head width); 4) otic margin of paraoccipital process approximately parallel to maxillary arch in dorsal view (Fig. 1) and characterized by a low but distinct ridge; 5) canthal ridge absent; canthus rounded in section; 6) supraorbital ridges absent; 7) preoccipital ridge absent; 8) postorbital ridge absent; 9) zygomatic ridge scarcely evident, extending diagonally upward from the posterolateral margin of the orbit about half the distance to rear margin of ventral arm of squamosal; 10) subtemporal fenestra small; 11) anterior ramus of pterygoid bearing denticulate serrations on lingual margin; 12) cultriform process of parasphenoid not keeled; 13) snout slightly depressed in lateral profile; 14) clavicles poorly

TABLE 7.—Comparison of Morphological Measurements (mm) of Holotypes of *Hemiphractus scutatus, H. divaricatus,* and *H. boulengeri.* (SVL=snout-vent length; HW=head width)

Character	*H. scutatus*, sex?	*H. divaricatus*, sex?, (ANSP 4132)	*H. boulengeri*, ♂ BMNH 1880.12.5.153
	Description by Peters, 1862	Original description; Cope, 1868	Measurements by Trueb
Snout-vent length	60.0	55.0	57.6
Head length, medial	23.0	22.2	—
Head length, tip of snout to paraoccipital horn	31.0	28.0	—
Head length	—	—	29.1
(%SVL)	—	—	(50.5)
Head width	32.0	33.9	33.8
(%SVL)	(53.3)	(61.6)	(58.7)
Forelimb length	37.0	31.8	—
Hind limb length	75.0	75.1	—
Foot length[a]	—	34.9	35.0
(%SVL)	—	(63.5)	(60.8)
Interorbital distance	—	10.6	12.7
(%HW)	—	(31.3)	(37.6)
Internarial distance	—	3.2	3.5

[a] Including tarsus

developed; 15) neural spines of presacrals I-VIII and sacrum enlarged, with that of the third presacral being the largest; 16) width of sacral diapophyses greater than width of transverse processes of presacral VIII and about equal to width of presacral III; 17) ventral shaft of urostyle laterally expanded; 18) prehallux well developed, anvil-shaped; 19) proboscis small, triangular and dorsoventrally depressed; 20) eyelid coarsely granular with one slightly enlarged conical tubercle; 21) tubercles on dorsal surface of forearm arranged in oblique rows corresponding to dark bars; 22) tubercles on dorsal surfaces of hind limb aligned in oblique rows; 23) calcar absent on heel; 24) skin of flanks an venter coarsely granular; 25) fingers about one-fourth webbed; 26) toes basally webbed; 27) adhesive discs on fingers and toes vestigial, not visible in dorsal view.

Hemiphractus scutatus differs from all other members of the genus by its lack (vestigial presence) of visible adhesive discs. It is distinguished further by its large size, and lack of 1) a postorbital indentation, 2) a canthal ridge, and 3) a pattern of labial stripes radiating from the suborbital margin to the edge of the lip.

Distribution.—This species occurs in the upper Amazon Basin in Ecuador, Perú, and western Brasil between elevations of 250 and 1830 m (Fig. 17).

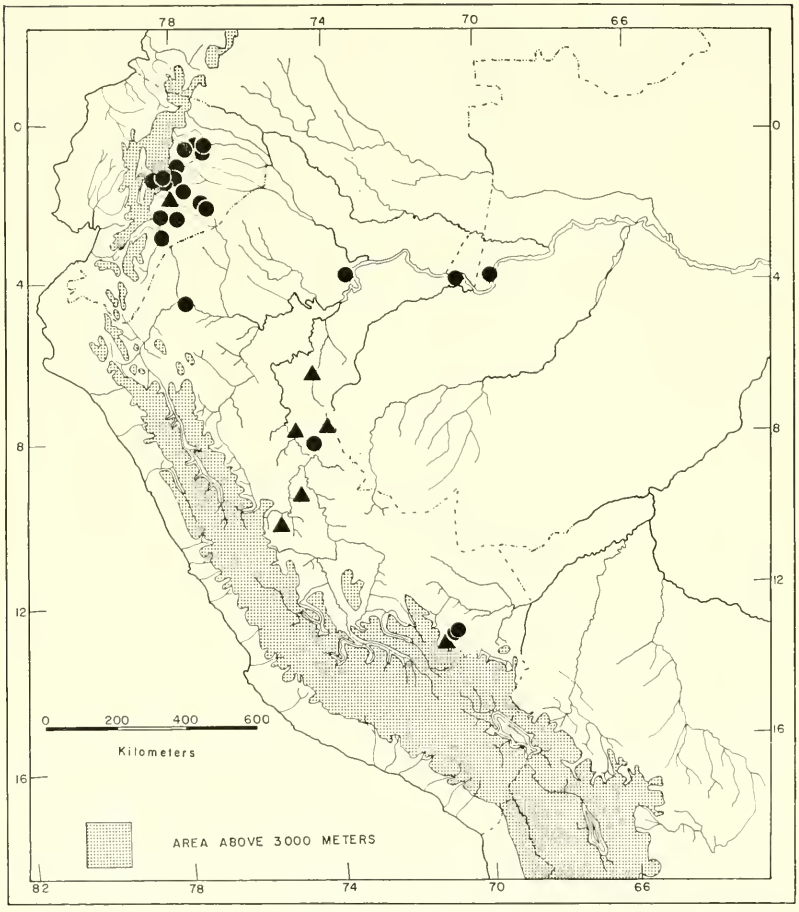

FIG. 17. Distribution of *Hemiphractus scutatus* (circles) and *Hemiphractus johnsoni* (triangles) in Ecuador, Perú, and Brasil. See figure 13 for location of type locality of *H. johnsoni* in Colombia.

Remarks.—Until the recent acquisition of two specimens of *scutatus* from cloud forest at elevations of 1400 and 1830 m, this species was thought to be an inhabitant of lower montane and lowland rainforest exclusively. It differs in one respect from its congeners in that available field notes indicate that *scutatus* is always found on the forest floor—a habit to be expected in view of its loss of functional toe pads. Color notes are rare (see Myers and Carvalho, 1945, for a résumé); the most recent notes reported that an adult *scutatus* was pale tan above marked with darker brown. The specimen had black marks on the upper lip and a black border around the eye; the iris was bronze.

There are three preserved females with associated embryos (eggs). One of these (KU 129751, 72.3 mm snout-vent length) was collected in November and carried five eggs, each of which is about 9 mm in diameter. The oviducts of this specimen were empty and greatly distended. A second female (UMMZ 92106, 80.5 mm snout-vent length), for which there is no date of collection, has four depressions on her back; the associated embryos are 10 mm in diameter and the oviducts are empty. The third female (FMNH 121855, 67.3 mm snout-vent length) was collected in September; only two embryos are associated with this individual. The balance of the specimens for which data are available are females with moderate (*ca.* 6 mm) to small-sized ovarian eggs obtained in January, February, May and November. An adult male was collected in December and a juvenile in February.

There are no records of a call for this species, no documentation of the color of the buccal cavity, and no account of its assuming the "gaping" defense posture typical of other members of the genus.

INTRAGENERIC RELATIONSHIPS

In order to hypothesize on intrageneric relationships within *Hemiphractus,* it is necessary to establish the probable evolutionary patterns or directions of those character states that will be utilized in the subsequent analysis. Recently, there has been considerable commentary on the kinds of characters useful in anuran classification and the nature of their change through time (see various papers in Vial, 1973). In working with *Hemiphractus,* I am confronted with two basic problems. The evolutionary status of most anuran characters has been discussed at broader taxonomic levels than that of the genus. Secondly, *Hemiphractus* is extremely specialized and probably a highly derived group; thus, my conclusions cannot be expected to be necessarily comparable or parallel to those determined for other Neotropical genera (*e.g.*, see Trueb and Duellman, 1971; Trueb, 1971). Nonetheless, in the discussions that follow, the criteria for the various states of primitiveness, derivation, advancement, specialization and generalization are the same as those discussed in an earlier paper (Trueb, 1973:65-66).

Most of the characters to be considered are osteological; these, as a suite, clearly establish the advanced and derived status of *Hemiphractus* (see Trueb, 1973). Given this conclusion, I will attempt to delineate the evolutionary trends within the genus and their phylogenetic and, if possible, adaptive significance. It has been shown that casque-headedness is a derived state (Trueb, 1970; 1973), and that in casque-headed frogs, the degree of casquing is usually greater in the more derived species. Following this line of reasoning, *fasciatus* and *scutatus* should be considered more advanced than their congeners that possess less extensively ossified

skulls by reason of the presence of postorbital indentations, dorsally exposed sphenethmoids, and moderate to large subtemporal fenestrae. However, it has been demonstrated also that there is an obligate ontogenetic sequence of ossification in which casquing always precedes exostosis—the appositional growth of dermal bone to form sculptured surfaces and, subsequently, ridges and flanges (Trueb, 1973). Because *proboscideus* and *bubalus* possess complexly exostosed crania (Figs. 2 and 8), I suggest that the reduced amount of casquing in these species as contrasted to *scutatus* and *fasciatus* (Fig. 11) is the result of secondary reduction of ossification of a more extensively casqued skull which may have been similar to that of *johnsoni* (Fig. 14). Although not as extensively casqued as *fasciatus* and *scutatus* and less ornamented than *proboscideus* and *bubalus*, the skull of *johnsoni* has developed dermal sculpturing to a degree that nearly all dermal cranial sutures are obscured; because of the sculpturing, it is impossible to ascertain externally whether or not the sphenethmoid is exposed dorsally.

Two members of the genus exhibit species-specific specializations; these are the parasphenoid keel of *johnsoni* (Fig. 15) and the pterygoid odontoids of *scutatus*. With respect to the skull shape, *fasciatus* is the only species in which the otic margin of the paraoccipital process is about parallel to the longitudinal axis of the body. This feature results from a slight difference in the configuration of the process (compare Figs. 1, 2, 8, 11, and 14) as contrasted with the remaining species in which the margin of the flange lies approximately parallel to the maxillary arch. *Hemiphractus scutatus* and *fasciatus* are similar in having a more rounded canthus as contrasted with their congeners; furthermore, these two species have robust, short snouts in lateral view (Figs. 1 and 11) as contrasted with the long, depressed snouts of *proboscideus* (Fig. 2c) and *bubalus* (Fig. 8). *Hemiphractus johnsoni* (Fig. 14) has a snout shape which is intermediate between these two groups. With the exception of some minor specializations (*viz.*, the parasphenoid keel, absence of prevomerine teeth, small postorbital indentation, and highly developed dermal sculpturing), it appears that on the basis of cranial structure, *johnsoni* is most similar to the ancestral condition and intermediate between two distinct hemiphractine lines—one (*scutatus* and *fasciatus*) committed to increased armorment of the cranium, and a second (*proboscideus* and *bubalus*) in which armorment (and consequently weight) has been decreased and ornamentation markedly incremented.

The results of critical analysis of cranial characters largely are corroborated by data derived from study of the postcranial skeleton. The general configuration of the vertebral column (Table 3; Fig. 4a) is one adapted to terrestrial situations (Trueb, 1973) and derived from an advanced group. The length and general uniformity of the

lengths of the transverse processes, especially those of the posterior presacrals and the relatively narrow expansion of the sacral diapophyses represent terrestrial and perhaps semi-arboreal adaptations; the procoelous, non-imbricate nature of individual vertebrae suggests relatively recent derivation from an advanced group. As on the basis of cranial architecture, *Hemiphractus* is divisible into two groups by the nature of the cervical vertebrae. The *scutatus-fasciatus* line is characterized by a distinct notch between the cervical cotyles (Fig. 4c-e), whereas the *johnsoni-proboscideus-bubalus* group lacks such a notch (Fig. 4f-g). With respect to the relative widths of the transverse processes, *scutatus* is the most divergent, having a relatively narrow sacrum with respect to the widths of the presacral transverse processes. Inspection of table 3 shows that *fasciatus* and *johnsoni* are more similar to one another than either is to *bubalus* or *proboscideus*. The adaptive significance of the relatively great heights of the neural spines is an enigma; there are no muscle attachments to these spines. Each species has its own distinctive profile with regard to the relative heights of the neural spines; those of *bubalus* and *proboscideus* are more similar to one another than are any of the others to one another. *Hemiphractus fasciatus* and *scutatus* differ from the remaining three species in that the overlying skin is loosely applied to the protruding vertebrae.

The proportions of the urostyle and ilia are inextricably related. Examination of table 3 and figure 5 clearly illustrates that *scutatus* has, proportionately, the shortest urostyle and ilia, and *fasciatus* the longest. Proportional shortness of these elements normally is associated with a trend towards a walking or hopping gait (Trueb, 1973), whereas increase in length usually reflects a trend towards more efficient jumping or leaping. The ilium bears only an indistinct crest in *scutatus* as contrasted to the remaining species, especially *fasciatus*. The proportional lengths of the urostyles and ilia of *johnsoni, bubalus,* and *proboscideus* lie between the extremes of *scutatus* and *fasciatus,* suggesting that these species are more generalized in their pelvic structure than either of the other two. Like *fasciatus,* each of these species bears a distinct ilial crest; however, in none is it as well developed as in *fasciatus*. Among the three, the crest is least developed in *johnsoni* and best developed in *proboscideus;* this may suggest a trend from generalized to more specific arboreality within these three frogs.

Although the pectoral girdle structure varies considerably in *Hemiphractus* (Fig. 3), the interpretation of this variation is as questionable as it is among anurans in general. *Hemiphractus scutatus* is most distinctive by virtue of its greatly reduced clavicles and obviously short scapulae (Fig. 3a). The clavicles are somewhat better developed in *fasciatus* (Fig. 3b), but still moderate in comparison with those of *bubalus, proboscideus* (Fig. 3c) and *john-*

soni (Fig. 3d); the scapulae of the latter three species are intermediate in length between those of *scutatus* and *fasciatus*. *Hemiphractus johnsoni* is distinguished by less massive coracoids than in the other species. As with consideration of the crania, and axial and vertebral morphology, a basic dichotomy is evinced in pectoral morphology. *Hemiphractus scutatus* and *fasciatus* seem to represent one evolutionary sequence and *proboscideus* and *bubalus* a second, and *johnsoni* emerges as the least specialized of the species.

With respect to foot morphology there is only one character worth mentioning, and that is the presence of a well-developed prehallux in *scutatus*. The presence of this structure suggests that *scutatus* digs with its hind feet, a habit not unexpected in a forest floor dweller.

In general, the distribution of soft morphological features closely parallels those evident osteologically. For example, the fingers and toes of *bubalus, proboscideus, johnsoni,* and *fasciatus* tend to have reduced webbing, whereas those of *scutatus* are distinctly webbed. *Hemphractus scutatus* differs from its congeners in having vestigial toe pads, the remnants of which are visible only on careful examination of the ventral digital tips. A number of dermal characteristics tend to support the alliances suggested above. All hemiphractines are characterized by the presence of a proboscis; however, that of *proboscideus* is proportionately larger and distinctly different in shape (Fig. 6) than those of the other species. *Hemiphractus johnsoni* and *scutatus* have a similar dermal configuration of the eyelids. Likewise, the eyelids of *proboscideus* and *bubalus* are the same, but distinct from those of *johnsoni* and *scutatus* and those characteristic of *fasciatus* (Fig. 7). Apparently there has been an evolutionary trend towards development of calcars on the heels within the *proboscideus-bubalus* lineage. They are well developed in the two latter arboreal species, whereas calcars are poorly developed in *johnsoni* and *fasciatus*, and absent in *scutatus*. This seems to indicate a counter trend involving the loss of the calcar in the more terrestrial, ground-dwelling species. In contrast to the smooth ventral skin of *johnsoni*, the venters of *proboscideus* and *bubalus* are finely granular. The venter of *fasciatus* bears scattered, low tubercles and that of *scutatus* is coarsely granular.

Available ecological data concerning favored microhabitat haunts of the various *Hemiphractus* confirm expectations based on observed morphological features. *Hemiphractus proboscideus* and *bubalus* are characterized by relatively light weight skulls, generalized axial and pelvic osteology, robust pectoral girdles, extensive dermal ornamentation and disruptive color patterns. These two species most frequently perch between 1.0 and 2.5 meters above the ground on small branches and twigs amidst dense vegetation (see figure 18); clearly, they are arboreal species. On the other hand, *johnsoni*

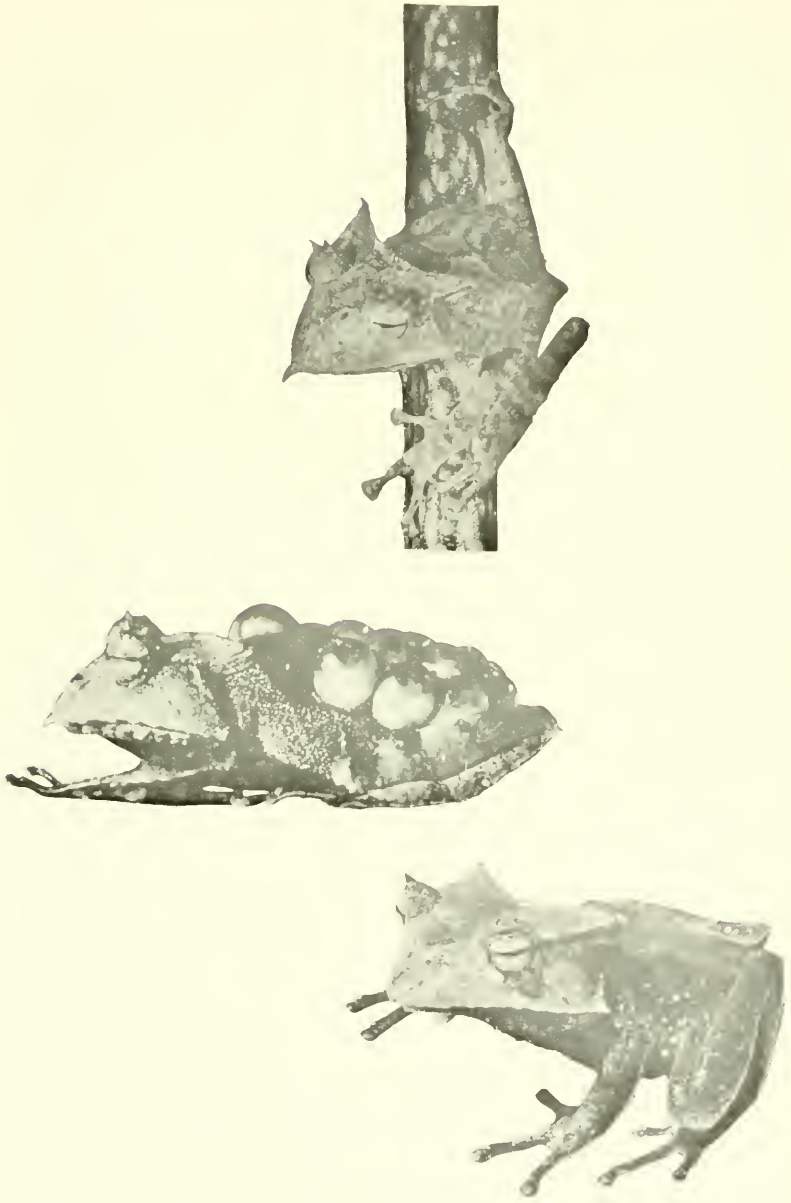

FIG. 18. Three species of *Hemiphractus*. Top: *H. bubalus*. Middle: *H. johnsoni* female carrying eggs (photograph by David B. Wake). Bottom: *H. fasciatus*. All approximately 1.0-1.5 times natural size.

and *fasciatus* are found less than 0.7 meters above the ground and sometimes on logs or the forest floor itself. *Hemiphractus scutatus* is exclusively a forest floor, leaf-litter dweller. The latter three species are characterized by a predominantly reddish or grayish brown color scheme with irregular, darker dorsal mottling which cryptically conceals them. Of the three, *johnsoni* (Fig. 18) is the most generalized morphologically, save for a few minor features of the skull, and is at least semi-arboreal. Both *fasciatus* (Fig. 18) and *scutatus* seem to have adapted for a terrestrial life style in the lower strata of the forest by retaining and/or incrementing a heavily armored skull and apparently developing distinctly different modes of locomotion. The attenuate, crested ilia of *fasciatus* suggest that it is more adept at leaping than any other member of the genus, especially *scutatus*. Because it has a moderately well-developed pectoral girdle and large adhesive discs, *fasciatus* obviously is arboreal, although less specialized for this mode of existence than either *proboscideus* or *bubalus*. The short, low-crested ilia, massive skull, well-developed prehallux and effective loss of adhesive discs in *scutatus* seem to represent an adaptive adjustment to the hopping and walking gait and burrowing habits usually associated with inhabitants of the leaf litter of the forest floor.

In summary, I suggest that *johnsoni* is the most generalized member of the genus and probably most closely resembles in appearance and habit the common ancestor of the five species. It is noteworthy that *johnsoni* is the widest ranging species of the group both latitudinally and altitudinally; it occurs over an elevational range of 1610 meters, from Colombia to Bolivia. From a South American *johnsoni*-like ancestor, I propose that two lineages arose—one giving rise to *proboscideus* and *bubalus*, which adopted an arboreal mode of existence, and a second giving rise to *fasciatus* and *scutatus*, which successfully exploited a terrestrial, semi-arboreal life style in one case and a completely terrestrial existence in the other. I am not prepared to comment on the relative degrees of specialization of *bubalus* and *proboscideus* on the basis of the present data. Both inhabit the upper Amazonian slopes of the Ecuadorian Andes. They are not known to occur sympatrically, and on the basis of the most reliable locality records, it seems that *proboscideus* is primarily an inhabitant of lower montane and lowland rainforests, whereas *bubalus* is found most frequently in cloud forests. Both *scutatus* and *fasciatus* have wide distributions, the ranges of which are separated by the Andes, with *scutatus* being Amazonian and *fasciatus* being Pacific. Given that they had a common ancestor not unlike *johnsoni*, it seems reasonable that a more generalized prototype may have specialized for their respective modes of existence as a result of isolation and concomitant competition with the myriad of other anurans which have evolved on and inhabit the South American landmass.

INTERGENERIC RELATIONSHIPS

On the basis of the literature surveyed throughout this report, it is evident that the familial allocation of *Hemiphractus* has been uncertain. To those familiar with the Leptodactylidae (see Lynch, 1971, for a review of this family), the hemiphractines seem similar in superficial appearance, certain aspects of cranial and axial architecture, and habit to some of the ceratophryine leptodactylids. However, *Hemiphractus* differs by the combination of the following three characters from all known leptodactylids: 1) claw-shaped terminal phalanges, 2) intercalary cartilages, and 3) a reproductive mode unknown among leptodactylids. The possession of these three characters allies *Hemiphractus* with a second, widespread Neotropical family, the Hylidae.

In the most recent and comprehensive treatment of Neotropical hylids, Duellman (1970:18-19) divided the New World Hylidae into four subfamilies—the Hylinae, Phyllomedusinae, Amphignathodontinae, and Hemiphractinae. The hemiphractines and amphignathodontines are distinguished from the hylines and phyllomedusines (which together include the majority of known genera) by their extensively ossified skulls, "brooding" mode of reproduction, and unique larval gill structure. This mode of reproduction, in which the eggs and larvae are transported on the dorsum of the female, and the modified larval gill structure were described first by Boulenger (1898) in *Gastrotheca cornuta*. A more complete analysis and survey of these characters were presented by Noble (1927). He proposed that those hylids in which 1) larvae are transported on the back of the female, 2) the dorsal epidermis of the female is attenuated and vasculated, and 3) the larvae have specialized "bell-shaped" gills constitute a natural phylogenetic unit. Noble considered this unit to be distinct from other hylids which exhibit a variety of reproductive modes exclusive of the "brooding" habit. Several questions now arise. Do the so-called "brooding" hylids actually represent a single phyletic unit? If so, what are the evolutionary patterns within this line and the interrelationships of the nine genera currently included in the group?

It is difficult for me to conceive of an evolutionary course in which the combination of the terrestrial brooding habit and the specialized gill structure (both of which are unique among anurans) could have arisen independently more than one time from a group of advanced frogs. Therefore, without evidence to the contrary, it is most parsimonious to conclude that these anurans (*i.e.*, Amphignathodontinae and Hemiphractinae) do represent a single phyletic line which has diversified considerably. Duellman (1970) included eight genera in the subfamily Amphignathodontinae; these are: *Anotheca, Nyctimantis, Fritziana, Flectonotus, Gastrotheca, Amphignathodon, Cryptobatrachus* and *Stefania*. The inclusion of *Ano-*

theca and *Nyctimantis* is problematic. The first genus, *Anotheca* (from southern México, Costa Rica, and Panamá), does not brood its young. Eggs are known to be deposited in bromeliads and water-filled tree cavities where the larvae undergo development; furthermore, the larvae lack specialized gills. The reproductive mode of the second genus, *Nyctimantis* (known only from Ecuador), is unknown. Females do not possess a brood pouch, and neither eggs nor larvae have been associated with *Nyctimantis;* however, my colleagues and I have heard and collected males calling from water-filled cavities in bamboo. Perhaps the reproductive mode of this frog is the same as that of *Anotheca.* Morphologically, both of these montypic genera share a great many features with *Gastrotheca;* thus, despite the apparently more generalized reproductive mode and larval gill structure, Duellman (1970) elected to include them in the Amphignathodontinae. The placement of *Anotheca* and *Nyctimantis* in the Amphignathodontinae obviously is debatable. Without further study of the entire subfamily, I prefer not to rearrange Duellman's classification; furthermore, the subfamilial allocation of these two genera is not especially pertinent to the intergeneric relationships of *Hemiphractus.*

In the third genus, *Fritziana* (from the mountains of southeastern Brasil), a single, shallow basin forms on the backs of females. In this basin a cluster of unprotected eggs develops. The larvae are characterized by bell-shaped gills. *Flectonotus* (from the mountains of southeastern Brasil and the coastal cordillera of northern Venezuela and the continental islands of Trinidad and Tobago) affords more protection for the developing young. The females of this genus are characterized by a brood pouch with a medial, slit-like opening. The larvae undergo direct development in this pouch. The way in which eggs are placed on the back of the female is unknown in both of these genera. In both *Fritziana* and *Flectonotus* the first finger is either equal in length to the second, or the second is shorter than the first.

Gastrotheca is a genus represented by at least 34 species which, as a group, are widespread; it occurs in southeastern Brasil, moderate to high elevations from northern Argentina to Colombia and Venezuela, and low to moderate elevations in northwestern South America and Panamá. All female *Gastrotheca* possess a dorsal brood pouch with a posterior opening, and all known larvae have specialized gill structures. Mertens (1957) discussed the passive introduction (by gravity) of eggs into the pouch of *Gastrotheca ovifera,* and Hoogmoed (1967) described the way in which a male and female cooperate during amplexus to maneuver fertilized eggs into the female's pouch in *Gastrotheca riobambae.* The larvae of some *Gastrotheca* undergo partial development in the pouch and subsequently are expelled from the pouch to complete develop-

ment in an aquatic medium. In other species, the eggs undergo direct development into small frogs without an intermediate aquatic larval stage. In some members of the genus, the second finger is shorter than the first. Like *Gastrotheca*, *Amphignathodon* (known only from Ecuador) is characterized by larvae with specialized gills and the presence of a brood pouch in females. Osteologically, *Amphignathodon* is similar to certain of the casque-headed *Gastrotheca;* it is distinguished from the latter and all other known anurans by the presence of true teeth in the lower jaw.

The remaining two genera, *Cryptobatrachus* and *Stefania*, have relatively limited distributions and a number of peculiar characters in common. Neither has a brood pouch, but each has larvae with specialized gills which undergo direct development on the back of the female. In both *Cryptobatrachus* (from the Andes and Sierra Santa Marta of Colombia) and *Stefania* (from the Guyana Highlands), the eggs reside within individual shallow depressions on the backs of females. The way in which eggs are positioned on the backs of the females is unknown, although in one species, *Stefania scalae*, Rivero (1970:463-464) provided some indication of the manner in which they adhere to the back once in place. He presented evidence suggesting that the female secretes a porous membrane, or otherwise modifies the epidermis of her back; thus, the skin surface may serve as a "template" for the secretion of a substance by individual embryos that ensures their secure adherence to the dorsum of the female. *Cryptobatrachus* and *Stefania*, like *Flectonotus*, *Fritziana*, and some *Gastrotheca*, are characterized by having the first and second fingers equal in length or the second distinctly shorter than the first. The significance of this modification is unknown, but Rivero (1970:465) pointed out that this characteristic may in some way relate to the egg-carrying capacity of these frogs.

The Hemiphractinae, as defined by Duellman (1970) contains only one genus, *Hemiphractus*. Relative to the eight genera discussed above, it shares the most reproductive characters with *Cryptobatrachus* and *Stefania*. The large-yolked eggs reside in individual shallow depressions on the back of the female, and there undergo direct development. Furthermore, the second finger is invariably shorter than the first in both sexes of each species. Because of the suite of unique osteological features distinguishing *Hemiphractus* from the other eight genera, it has been placed in a separate subfamily.

Noble (1927) assumed that *Cryptobatrachus* and *Hemiphractus* were primitive among the hylids that brood their young, because the eggs are carried fully exposed on the backs of females. By logical association, we now would have to include *Stefania* and *Fritziana* in this group also. Noble further stated that among those species

having larvae with expanded gills, those in which the gills are composed of four separate sheets of tissue were more primitive than those in which either the posterior pair of gill sheets are lost (in at least one species of *Cryptobatrachus*) or fusion of the gill sheets had taken place. *Hemiphractus* is an example of the latter condition. Each pair of gill sheets has fused, forming "bells" of vascular tissue laterally; together these bells enclose the ventral half of the embryo (Noble, 1927). Noble considered those frogs which brood their young within protective pouches to be the most advanced. This group includes *Flectonotus, Gastrotheca*, and *Amphignathodon.* The gills of embryonic *Gastrotheca* are like those of *Hemiphractus;* the details of the larval gill structure of *Flectonotus* and *Amphignathodon* are unknown.

It is evident that much remains to be learned about the breeding biology in general, and the specific aspects of reproduction and development of all of these frogs. Furthermore, detailed systematic studies of each of the genera should be executed before the status of their phylogenetic relationships can be assessed with any confidence. On the basis of the available information, it would seem that *Anotheca* and *Nyctimantis* might represent early derivatives of a hylid line committed towards evolution of behavioral and morphological traits associated with parental care of the young. Thus, although *Anotheca* and *Nyctimantis* are not adapted morphologically to keep their young with them, they may have elected an alternative solution, that is, to deposit eggs in places affording them some protection such as bromeliads and tree-cavities. A more advanced derivative of this general hylid line might be represented by *Fritziana* in which larvae having specialized gills are carried in a shallow depression on the dorsum of the female. An anuran like *Fritziana* well may represent a reproductive and morphological prototype from which at least two, more specialized evolutionary lines could have been derived. The first and more primitive of these probably is represented today by *Cryptobatrachus, Stefania,* and *Hemiphractus.* Members of this lineage failed to develop a maternal brood pouch, but did develop a means of affording individual embryos an intimate and discrete attachment with the female. Hypothetically, a second, derived lineage may be represented by *Flectonotus, Gastrotheca* and *Amphignathodon.* The simplest form of a maternal brood pouch seems to be that of *Flectonotus* in which the dorsal skin of the female forms lateral flaps which occlude medially. The pouches of *Gastrotheca* and *Amphignathodon* are complete, having only a posterior opening and affording the developing larvae the most protection of any of these hylids.

SUMMARY

Between 1824 and 1945 twelve nominal hemiphractine species were described. Of these twelve, five are recognized in this paper as comprising the genus *Hemiphractus;* these are: *Hemiphractus bubalus* (Jiménez de la Espada), *H. fasciatus* Peters, *H. johnsoni* (Noble), *H. proboscideus* (Jiménez de la Espada), and *H. scutatus* (Spix). The species are readily distinguished on the basis of cranial characters in addition to prevailing differences in sizes, proportions, tuberculation, and coloration. The genus is widespread, occurring in the upper Amazon Basin of Colombia, western Brasil, Ecuador, Perú and Bolivia, the Andes of northern Colombia, the Pacific slopes of northwestern Ecuador, Colombia and eastern Panamá, and the Caribbean slopes of western Panamá. *Hemiphractus* occurs between elevations of 250 and 1830 meters, and is an inhabitant of the lower strata of lowland rainforests and lower montane and cloud forests.

Hemiphractus is allied with the Hylidae by possession of claw-shaped, terminal phalanges, intercalary cartilages, and a reproductive mode which involves direct development of larvae with specialized gills on the dorsum of the female. Osteologically, members of this genus differ from all other known hylids by the unique configuration of cranial casquing, the presence of pterygoid odontoids (in one species), the shape of the prevomers, the presence of an enlarged pair of mandibular odontoids and tooth-like mandibular serrations. They differ further by the presence of greatly enlarged neural spines. Because of this combination of characteristics, this genus is retained in a separate subfamily, the Hemiphractinae.

Despite the unique suite of morphological characters ascribed to the Hemiphractinae, this hylid subfamily seems to be closely related to the Amphignathodontinae on the basis of their common reproductive mode. Both subfamilies differ from the two remaining New World hylid subfamilies (the Hylinae and Phyllomedusinae) in that the amphignathodontines and hemiphractines demonstrate ethological and morphological evolutionary trends towards parental care of the young. In the simplest stage of this progression, eggs are deposited in protected environmental situations (*e.g.,* water-filled cavities in trees). A significant advance is shown by those genera in which embryos are carried about exposed, on the backs of females. The embryos undergo direct development and are equipped with specialized, "bell-shaped" gills which serve as an interface between the developing larvae and the maternal epidermis. In the most derived form of parental care, eggs are carried within a brood pouch on the dorsum of the female and, thus, are afforded maximal protection during their development; these larvae also are equipped with specialized gills. These data suggest that

the Amphignathodontinae and Hemiphractinae represent a single phyletic line distinct from their Neotropical relatives, the Hylinae and Phyllomedusinae.

RESUMEN

Doce especies nominales de ranas hemiphractines se describieron entre 1824 y 1945. Cinco de ellas se reconocen en el presente trabajo en el género *Hemiphractus;* éstas son: *Hemiphractus bubalus* (Jiménez de la Espada), *H. fasciatus* Peters, *H. johnsoni* (Noble), *H. proboscideus* (Jiménez de la Espada), y *H. scutatus* (Spix). Las especies se pueden distinguir fácilmente en base a las características craneales, además de las diferencias en tamaños, proporciones, tubérculos de la piel y coloración. El género está ampliamente distribuido, pues ocurre en la depresión alta amazónica de Colombia, occidente de Brasil, Ecuador, Perú, y Bolivia, los Andes al norte de Colombia, las faldas montañosas nor-occidentales de Ecuador, Colombia, y este de Panamá. El género *Hemiphractus* se distribuye a elevaciones que oscilan entre 250 y 1830 metros e igualmente se encuentra en los bosques lluviosos, montaños y nublados.

Hemiphractus está emparentado con la familia Hylidae, ya que posée falanges terminales en forma de uña cartílagos intercalares, y un modo reproductivo caracterizado por desarrollo directo de la larva, con branquias especializadas, en el dorso de la hembra. Osteologicamente, los miembros de este género se diferencian de otros hílidos conocidos por tener una configuración única del casquete craneal, presencia de odontoides pterigoideos (en una especie), forma de los prevómeres, presencia de un par agrandado de odontoides mandibulares, y endentaduras mandibulares en forma de dientes. Además, ellos se diferencian por poseer espinas neurales muy dilatadas. Tomando en cuenta esta combinacion de características, el género se mantiene en una subfamilia separada, la Hemiphractinae.

A pesar del grupo de características que permiten distinguir a Hemiphractinae, esta subfamilia de hílidos parece estar muy emparentada con Amphignathodontinae, en base a su modo reproductivo común que poseen. Ambas subfamilias difieren de las otras dos subfamilias de hílidos del Nuevo Mundo (Hylinae y Phyllomedusinae) en que elllas tienen tendencias evolutivas etológicas y morfológicas hacia el cuidado parental de las crías. El primer paso hacia esta tendencia lo muestran aquellas especies que depositan sus heuvos en habitáculos protegidos (*i.e.,* cavidades con agua en los troncos de los árboles). Un avance significativo lo muestran aquellos géneros cuyas hembras cargan los embriones en la espalda, pero carecen de bolsa o marsupio. Los embriones tienen desarrollo directo y están en contacto con la epidermis materna mediante branquias campaniformes especiales. En la forma más

derivada de cuidado parental, hembras llevan los huevos dentro de bolsas o marsupios dorsales, de tal manera que hay una protección máxima de los huevos durante el desarrollo; estas larvas tabien están equipadas con branquias especiales. Estos datos sugieren que Amphignathodontinae y Hemiphractinae representan a una sola línea filética distinta de sus relativas neotropicales, Hylinae y Phyllomedusinae.

SPECIMENS EXAMINED

Locality data for each specimen examined are listed in the following paragraphs. The data are arranged as follow: alphabetically by country, state (department or province), and locality; alphabetically by the first letter in the abbreviations for the museums, and numerically after each museum abbreviation. Specimens lacking precise locality data are listed in the first most restricted political unit possible. Unless otherwise noted, all specimens are preserved in alcohol.

Hemiphractus bubalus

ECUADOR: *Napo:* Archidona, MNCN 176; Río Azuela, 1740 m, BMNH 1973.2850, KU 143107-17; San José de Moti, MNCN 175; SE slopes Cerro Sumaco, CAS 122207-08; S slope Cordillera del Dué above Río Coca, 1150 m, KU 123160-68, 124140 (skeleton); "Zarajioto, Orillas del Napo," MNCN 174. *Pastaza:* Canelos, 300 m, MCZ 17937; headwaters of Río Arajuno, CAS 87364; headwaters of Río Arajuno, about 10 km NE Puyo, CAS 122213; Mera, 1000 m, UMMZ 92109; Río Alpayacu, 1 km E Mera, 1100 m, KU 120763; Río Sandalia, tributary of Río Puyo, USNM 193287.

Hemiphractus fasciatus

COLOMBIA: *Antioquia:* Alto de la Honda, near San Rafael, LACM 47147; 8 km S Valdivia, 1450 m, FMNH 63850. *Cauca:* La Costa, El Tambo, NHRM 1981.

ECUADOR: *Esmeraldas:* near the lower Río Blanco [0° 02-03′ N, 79° 10-15′ W], CAS 122206; near the upper Cachabí [0° 56-58′ N, 78° 35-38′ W], CAS 122205. *Pastaza:* "Pastaza Valley," ZSM 36/0; Mindo, UMMZ 55523.

PANAMÁ: *Bocas del Toro:* 18.6 km W Almirante, upper Río Changena camp, CAS 93836, CAS-SU 21772; north slope Cerro Pando, 1450 m, KU 107426; Río Changena, 650 m, KU 128077 (cleared and stained). *Colón:* Signal Loma (Loma Peak), 5 km S San Isabel, USNM 55320-21. *Darién:* north ridge Cerro Cituro, Serranía de Pirre, 900-1320 m, KU 107408-422, 107425; southeast slope Cerro Pirre, 1440-1450 m, KU 93504-508, 93509-10 (skeletons). *Panamá:* Altos de Pacora, 800 m, KU 77107, 93503. *San Blas:* Camp Summit, 300-400 m, KU 116353-5.

Hemiphractus johnsoni

BOLIVIA: "Linimbane," 1000 m, BMNH 1901.8.2.51.

COLOMBIA: *Antioquia:* Santa Rita Creek, 22.5 km N Mesopotamia, 1890-1910 m, AMNH 1341-42, 1343 (skeleton).

ECUADOR: *Pastaza:* Canelos, 300 m, BMNH 1880.2.5.192.

PERÚ: *No specific locality:* "Eastern Perú," BMNH 1902.5.29.204. *Cuzco:* Marcapata Valley, KU 153436 (skeleton). *Huánuco:* S slope Serranía de Sira, 690 m, KU 154671-72. *Loreto:* Río Tapiche, Monte Alegre, AMNH 42862;

Río Ucayali, Cashiboya, AMNH 43452; Tangarana Hills, Alto Utoquinia, AMNH 58631 (adult female with series of 18 young). *Pasco:* Chontilla, Iscozazin Valley, USC-CRE 716, 717 (partial egg clutch).

Hemiphractus proboscideus

ECUADOR: *No specific locality:* "Eastern Ecuador," AMNH 52931; "Río Pastaza watershed," NHRM 1911. *Morona-Santiago:* Chiguaza, CAS 122211. *Napo:* Bermejo No. 4, 720 m, 15 km ENE Umbaqui [77° 22′ W, 00° 11′ N], KU 123149-54, 124139 (skeleton); Lago Agrio, KU 126326; Loreto, CAS 122212; Puerto Libre, Río Aguarico, 570 m, KU 123155-59; Río Coca, 300 m, UMMZ 92108; Río Napo, 300 m, UMMZ 92110; Santa Cecilia, 340 m, AUM 8046-51, BMNH 1973.2851, KU 104774-77, 106970, 109336-38, 111627-28, 123134-47, 124135-38 (skeletons), 126325, 146265-70, 150616-19; slopes of Cerro Sumaco, USNM 193288; Sumaco, MNCN 173. *Pastaza:* Copataza, a tributary of the Río Pastaza, CAS 122209-10; Río Pastaza, Andoas, AMNH 52929; Sarayacu, CAS-SU 11433.

Hemiphractus scutatus

BRASIL: *Amazonas:* Igarapé Belém, near Río Solinoes, *ca.* 70 km E Leticia, AMNH 85375-76.

ECUADOR. *Morona-Santiago:* Macuma, KU 129751, 129752 (skeleton), UIMNH 59616-17; Río Piuntza, KU 147117-18; Taisha, Macas, USNM 193577. *Napo:* ? Archidona, USNM 193582; Armenia, 250 m, UMMZ 92105; Boca, Río Coca, 300 m, UMMZ 92104; Loreto, CAS-SU 11434, USNM 193578, 193584; San José de Moti, MNCN 192 (lot of two preserved specimens and one skeleton); SE slope Cerro Sumaco, CAS 87365, 87366 (skeleton), CAS-SU 11435, USNM 193583; top of Cerro Sumaco, San José Abajo, AMNH 22210. *Pastaza:* Abitagua, UMMZ 92106; Alpayacu, 300 m, UMMZ 92103; between Abitagua and Río Pastaza Valley, UMMZ 92107; Río Arajuno, headwaters, USNM 193580; Río Bufeo, tributary of Baja Río Bobonaza, USNM 193576; Río Rutuno, tributary of Río Bobonaza, USNM 193580; Río Talin, headwaters of Río Bobonaza, USNM 193579. *Tungurahua:* Mirador, AMNH 38527; Palmera, Pastaza River Valley, 1333 m, AMNH 39488.

PERÚ: *Cuzco:* Quince Mil, Boca Río Marcapata, FMNH 121855. *Loreto:* Caballococha, AMNH 43044; Cadena de Manseriche, AMNH 43403; Iquitos, AMNH 42768; middle Río Utoquinia, CAS-SU 9332.

NO DATA: UMMZ s-1015 (skeleton).

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