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A SYNOPSIS OF NEOTROPICAL HYLID FROGS, GENUS *OSTEOCEPHALUS*

By

LINDA TRUEB[1] AND WILLIAM E. DUELLMAN[2]

When we initiated a study of the herpetofauna at Santa Cecilia in Amazonian Ecuador in 1966, we were immediately confronted with many kinds of animals that we could not identify with the existing literature. Comparisons of our specimens with those preserved in other museums resolved some of the problems, but many identifications could be made only after study of type specimens; even then some determinations remained questionable. We now find that in order to prepare a meaningful account of the herpetofauna of Santa Cecilia, we must complete several taxonomic studies, the limits of which extend far beyond eastern Ecuador. Because of our interests in hylids we have begun our studies on these frogs.

One of us (Trueb, 1970a) studied the cranial osteology of casque-headed hylid frogs and redefined the genus *Osteocephalus* but did not determine the number of species in the genus. Our work in Amazonian Ecuador resulted in the discovery of the sympatric occurrence of three species at each of two localities; one of these species was found with a fourth species at another locality. Study of museum specimens confirmed the recognition of these four species in the Amazon Basin and lower Amazonian slopes of the Andes. A fifth species from Bolivia and Perú also is included in the genus. Examination of museum specimens has provided data on the geo-

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[1] Research Associate, Division of Herpetology, Museum of Natural History, University of Kansas.

[2] Curator, Division of Herpetology, Museum of Natural History, University of Kansas.

graphic variation in, and distribution of, the five species. However, our conclusions pertaining to some populations need substantiation, because we have been hampered by inadequate material from areas beyond Ecuador. More than half of the 905 specimens of *Osteocephalus* are from Ecuador, a relatively small part of the total range of the genus.

In this paper we are presenting a taxonomic review of the genus *Osteocephalus;* of necessity our study has been at the alpha level. We have utilized all of the usual external characters, as well as osteological features in our definitions of the species. Tadpoles and mating calls are available for only one species, *O. verrucigerus* (Trueb and Duellman, 1970); these and other important systematic characters, such as karyotypes, are not available for the group at this time. Our tendency has been to take a conservative view of species; thus it is doubtful that any subsequent worker will recognize fewer species in the genus. Our observations on these frogs in Amazonian Ecuador are presented in a final section of this paper.

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sincere thanks to all of these persons for their contributions to our endeavors.

MATERIALS AND METHODS

We have examined 893 preserved frogs, including the type specimens of all included nominal taxa, 8 skeletons, 1 lot of eggs, and 3 lots of tadpoles that we refer to the genus *Osteocephalus;* in addition skulls were removed from five preserved specimens, and radiographs were made of 12 other preserved specimens. We have been fortunate in seeing living individuals of all species, except *O. pearsoni,* but we have colored photographs of a living specimen of that species. Figures 1 and 2 were drawn from projected colored transparencies of living frogs. Terminology follows that of Duellman (1970b). On the distribution maps solid symbols indicate localities from which we have examined specimens ;open symbols represent additional locality records based on the literature. Throughout the text specimens are listed 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
ASU	Arizona State University
AUM	Auburn University Museum
BMNH	British Museum (Natural History)
CAS	California Academy of Sciences
CAS-SU	Stanford University Collection (In California Academy of Sciences)
CM	Carnegie Museum
FMNH	Field Museum of Natural History
KU	University of Kansas Museum of Natural History
MCZ	Museum of Comparative Zoology, Harvard University
MIZS	Museo ed Istituto di Zoologi Sistematico, Università di Torino
MJP	Museo Javier Prado, Lima
MNHN	Muséum National d'Histoire Naturelle, Paris
MPEG	Museu Paraense Emiliano Goeldi, Belém
MVZ	Museum of Vertebrate Zoology, University of California, Berkeley
MZUSP	Museu de Zoología, Universidade da São Paulo
NHMG	Naturhistoriska Museet Göteborg
NHMW	Naturhistorisches Museum, Wien
NHRM	Naturhistoriska Riksmuseet, Stockholm
RMNH	Rijksmuseum van Natuurlijke Histoire, Leiden
SMF	Senckenbergische Museum, Frankfurt
UIMNH	University of Illinois, Museum of Natural History
UMMZ	University of Michigan Museum of Zoology
UP	Université de Paris
UPR-M	University of Puerto Rico, Mayagüez
UTA	University of Texas, Arlington

USNM	United States National Museum
UZM	Universitets Zoologiske Museum, Copenhagen
WCAB	Werner C. A. Bokermann, São Paulo, Brasil
ZMB	Zoologisches Museum Berlin
ZSM	Zoologisches Sammlung München

HISTORICAL RESUMÉ

Because of the taxonomic confusion that has surrounded the generic name *Osteocephalus* and two of the species (and their synonyms), we present a brief resumé of the taxonomic history of the group.

Among the amphibians sent to the Muséum National d'Histoire Naturelle in Paris by a Monsieur Leprieur in French Guiana was a single female specimen of a moderately large hylid having a well-ossified skull and smooth dorsal skin. This specimen escaped from the covetous eyes of Johann Tschudi, who prematurely named several species on the basis of specimens in Paris, and survived without an epithet until Duméril and Bibron (1841) proposed for it the name *Hyla leprieurii.* The description of the species is fairly detailed, but the specimen was not illustrated. This is the earliest trivial name now associated with *Osteocephalus.*

Fitzinger (1843) in his generic synopsis of amphibians and reptiles proposed the generic name *Osteocephalus* but did not associate a specific name with the genus. Consequently, *Osteocephalus* Fitzinger, 1843, is a *nomen nudum.* Franz Steindachner followed Leopoldo Fitzinger at the Naturhistorisches Museum in Vienna, where he had access to Fitzinger's notes and, of course, the important collections housed in that museum. Steindachner (1862) named two species of *Osteocephalus* on the basis of Brasilian specimens collected by Johann Natterer. Both species were named in the same publication; *O. taurinus* appeared on page 77, and *O. flavolineatus,* on p. 80. This is the earliest association of the generic name *Osteocephalus* with a specific name and a description, both of which satisfy the Code of Zoological Nomenclature for generic availability. Therefore, Steindachner is the authority for the generic name *Osteocephalus,* which has *O. taurinus* as the type species by original designation. It is not possible to determine whether or not Steindachner's usage of *Osteocephalus* was the same as that intended by Fitzinger 19 years earlier.

Steindachner (1862) gave reasonably good descriptions of his two new species and provided excellent illustrations of the two specimens, both large females. Apparently impressed by the similarities between *Trachycephalus nigromaculatus* Tschudi, 1838, and

Osteocephalus taurinus, Steindachner (1867) used the combination *Trachycephalus (Osteocephalus) taurinus.* This ambiguous usage for the 1860's precludes our determining if Steindachner was in effect synonymizing *Osteocephalus* with *Trachycephalus* or whether he was placing *Osteocephalus* in a subgeneric status. Steindachner (1867) did not mention *O. flavolineatus;* perhaps by that time he had concluded that *flavolineatus* was only a color morph of *taurinus.*

Cope (1867) placed *Hyla leprieurii* in the genus *Hypsiboas* Wagler, 1830. Cope (1874) named *Osteocephalus planiceps* from Nauta, Perú. The single specimen was among the collections made by the Orton Expedition to the upper Amazon Basin and was deposited in the Academy of Natural Sciences in Philadelphia.

Boulenger (1882) placed both *Osteocephalus* and *Trachycephalus* is the synonymy of *Hyla;* he recognized *Hyla taurina* (with *O. flavolineatus* as a synonym), *H. leprieurii,* and *H. planiceps.* In the same publication Boulenger named *Hyla buckleyi* on the basis of 10 specimens in the British Museum from Ecuador; in the description he stated that *buckleyi* was like *leprieurii* and *taurinus* in having paired lateral vocal sacs. Boulenger held a lasting influence on taxonomic herpetology, and his generic synonymy of *Osteocephalus* was unchallenged until only a decade ago.

Goin (1961) presented a generic synopsis of the genera of hylid frogs, in which he recognized *Osteocephalus* and stated: "There are perhaps eight or ten species of this genus in South America. Certainly *taurinus, britti, leprieuri, buckleyi* and *pearsoni* belong here. *O. planiceps* is surely a synonym of *leprieuri* and I believe that *garbei* is as well. The status of such forms as *macrotis, riopastazae,* and *depressa* has not yet been settled." Goin defined *Osteocephalus* as follows: "Males with paired vocal pouches, one at each angle of the jaw; derm of head not co-ossified with skull but roof of skull exostosed." Trueb (1970a) elaborated on Goin's definition and assuredly included only *O. taurinus* and *O. leprieurii* in the genus.

Goin's inclusion of *buckley, britti,* and *pearsoni* in *Osteocephalus* was the first association of any of these names with that genus. Duellman (1970a) demonstrated that *Garbeana garbei* Miranda-Ribeiro, 1926, was a member of the *Hyla rubra* group. *Hyla macrotis* Andersson, 1945, is a *Phrynohyas.* Trueb and Duellman (1970) determined that *Hyla verrucigera* Werner, 1901, is the earliest name for an *Osteocephalus* displaying striking sexual dimorphism in coloration and texture of the dorsal skin; *Hyla riopastazae* Andersson, 1945 (female holotype), and *Hyla orcesi*

Funkhouser, 1956 (male holotype), were placed in the synonymy of *Osteocephalus verrucigerus.*

Hyla pearsoni Gaige, 1929, is a small species of *Osteocephalus.* Our findings substantiate Goin's suggestions relative to two other taxa. *Hyla leprieurii britti* Melin, 1941, from the Rio Uaupés, Brasil, and *Hyla depressa* Andersson, 1945, from the Río Pastaza watershed, Ecuador, are members of the genus *Osteocephalus,* but both are synonyms of earlier names—*leprieurii* and *taurinus,* respectively. Another name proposed by Melin (1941), *Hyla (Trachycephalus) vilarsi* from Taracuá, Brasil, also is placed in the synonymy of *O. taurinus.*

Cochran and Goin (1970) were unaware of the identities of *Hyla verrucigera* and *riopastazae;* they used the later name *Osteocephalus orcesi* for Colombian frogs that are correctly referred to *O. verrucigerus.* Although Goin (1961) placed *Hyla buckleyi* and *H. pearsoni* in *Osteocephalus,* Cochran and Goin (1970) recognized a "*buckleyi* group" in *Hyla* that included these two species plus a new species, *Hyla cabrerai* from Amazonian Colombia and Brasil (total of three specimens). Also, these authors named *Hyla carri* from a single Colombian specimen. Study of the types of *Hyla cabrerai, H. carri,* and *H. festae* Peracca, 1904, from Ecuador, reveal that all of these names are synonyms of *Osteocephalus buckleyi.*

Much of the taxonomic confusion and multiplicity of trivial names is due to the great amount of color variation in *taurinus* and to the sexual dimorphism in the texture of the dorsal skin in all of the species. The details of variation in these and other characters and our justifications for the synonymies are given in the accounts of the species. All of the trivial names that apply to species herein recognized as members of the genus *Osteocephalus* are listed in table 1.

Osteocephalus Steindachner, 1862

Osteocephalus Steindachner, 1862:77 [Type species.—*Osteocephalus taurinus* Steindachner, 1862, by original designation]. Not *Osteocephalus* Fitzinger, 1843:50 *(nomen nudum).*

Diagnostic Definition.—1) Skull broader than long; 2) dermal roofing bones of skull well ossified, exostosed, and/or co-ossified in some species; 3) prenasal and internasal bones absent; 4) parasphenoid alae posterolaterally oriented; 5) dentigerous processes of prevomers angular (/¯ ¯\); 6) vocal sacs paired, posterior, and when inflated protruding posteroventral or posterolateral to angles of jaws; 7) submentalis muscle moderate in size and araphic; 8) intermandibularis muscle undifferentiated and bearing an elongate

TABLE 1.—Alphabetical Synonymy of the Species of *Osteocephalus*.

Trivial Name, Original Generic Name, Author, Date	Current Name
britti (Hyla leprieurii) Melin, 1941	*O. leprieurii*
buckleyi (Hyla) Boulenger, 1882	*O. buckleyi*
cabrerai (Hyla) Cochran and Goin, 1970	*O. buckleyi*
carri (Hyla) Cochran and Goin, 1970	*O. buckleyi*
depressa (Hyla) Andersson, 1945	*O. taurinus*
festae (Hyla) Peracca, 1904	*O. buckleyi*
flavolineatus (Osteocephalus) Steindachner, 1862	*O. taurinus*
leprieurii (Hyla) Duméril and Bibron, 1841	*O. leprieurii*
orcesi (Hyla) Funkhouser, 1956	*O. verrucigerus*
pearsoni (Hyla) Gaige, 1929	*O. pearsoni*
planiceps (Osteocephalus) Cope, 1874	*O. taurinus*
riopastazae (Hyla) Andersson, 1945	*O. verrucigerus*
taurinus (Osteocephalus) Steindachner, 1862	*O. taurinus*
verrucigera (Hyla) Werner, 1901	*O. verrucigerus*
vilarsi (Hyla) Melin, 1941	*O. taurinus*

median aponeurosis; 9) parotoid glands absent or poorly developed, skin not producing viscous secretion characteristic of *Phrynohyas;* 10) skin on dorsum tuberculate in males, smooth in females; 11) tympanum large, 60 percent or more of diameter of eye; 12) fingers about one-third, toes more than three-fourths webbed; 13) discs large, round; 14) nuptial excrescences present in breeding males; 15) inner metatarsal tubercle not modified for digging; 16) outer metatarsal tubercle absent; 17) tarsal fold weak or absent; 18) pupil horizontal; 19) palpebrum clear; 20) known tadpoles having two upper and five lower rows of teeth.

Content.—As defined here, the genus contains five known species: *O. buckleyi* (Boulenger), *O. leprieurii* (Duméril and Bibron), *O. pearsoni* (Gaige), *O. taurinus* Steindachner, and *O. verrucigerus* (Werner).

Distribution.—The Guianas and Amazon Basin; also in the upper Orinoco and Magdalena drainages. Most localities are at elevations below 500 m, but the genus ascends the Amazonian slopes of the Andes to elevations of about 1800 m.

ANALYSIS OF CHARACTERS

Size and Proportions.—Frogs of the genus *Osteocephalus* are moderate to large hylids. The largest species is *taurinus,* attaining a snout-vent length of 103.1 mm; the smallest is *pearsoni,* which attains a length of 54.7 mm. Considerable intraspecific geographic variation occurs in adult size, especially in *taurinus.* Females of all species attain a noticeably larger size than males, but no significant differences are apparent in proportions (Table 2).

TABLE 2.—Comparison of Size and Proportions in the Species of *Osteocephalus*.
(Means are given in parentheses below observed ranges)

Species		*N*	Snout-vent Length	Tibia Length/ S-V L	Foot Length/ S-V L	Head Length/ S-V L	Head Width/ S-V L	Tympanum/ Eye
O. buckleyi	♂	30	37.9-48.1	0.478-0.580	0.375-0.444	0.319-0.357	0.329-0.368	0.608-0.820
			(43.3)	(0.520)	(0.408)	(0.343)	(0.351)	(0.711)
	♀	31	48.6-75.1	0.476-0.599	0.363-0.469	0.310-0.358	0.318-0.367	0.574-0.905
			(61.7)	(0.553)	(0.428)	(0.333)	(0.348)	(0.734)
O. leprieurii	♂	21	41.2-48.4	0.514-0.571	0.383-0.430	0.308-0.357	0.326-0.368	0.652-0.884
			(44.7)	(0.538)	(0.408)	(0.335)	(0.348)	(0.777)
	♀	21	46.6-61.5	0.516-0.592	0.382-0.453	0.314-0.343	0.328-0.363	0.698-0.909
			(57.1)	(0.539)	(0.404)	(0.329)	(0.349)	(0.785)
O. pearsoni	♂	2	45.3-46.2	0.481-0.504	0.404-0.437	0.322-0.335	0.327-0.342	0.660-0.673
			(45.8)	(0.493)	(0.421)	(0.329)	(0.335)	(0.666)
	♀	1	54.7	0.521	0.405	0.318	0.346	0.862
O. taurinus	♂	59	40.3-84.6	0.512-0.576	0.387-0.445	0.296-0.345	0.301-0.355	0.638-0.896
			(66.3)	(0.541)	(0.416)	(0.318)	(0.324)	(0.752)
	♀	45	45.1-103.1	0.520-0.577	0.391-0.448	0.306-0.334	0.308-0.347	0.640-0.817
			(75.8)	(0.542)	(0.420)	(0.321)	(0.327)	(0.758)
O. verrucigerus	♂	11	50.4-54.3	0.494-0.552	0.409-0.442	0.322-0.346	0.328-0.344	0.623-0.804
			(53.0)	(0.519)	(0.427)	(0.333)	(0.337)	(0.730)
	♀	3	63.1-65.8	0.532-0.561	0.435-0.463	0.345-0.347	0.348-0.379	0.692-0.808
			(64.5)	(0.545)	(0.448)	(0.346)	(0.358)	(0.731)

Coloration.—All *Osteocephalus* are predominantly brown frogs usually with some darker dorsal markings (Figs. 1 and 2). *Osteocephalus verrucigerus* has a nearly uniform dark brown dorsum and no distinct transverse bars on the limbs, whereas all of the other species have distinct bars on the limbs. The dorsal markings on the body consist of irregular blotches in *buckleyi, pearsoni,* and *taurinus* but are narrow transverse marks in *leprieurii.* A narrow middorsal cream or yellow stripe is present in some individuals of *buckleyi* and *taurinus* but absent in all individuals of the other species. The flanks are uniform pale tan in *leprieurii* and uniform reddish brown in *verrucigerus;* in the other species the flanks are cream to brown with dark brown or black spots (also dark diagonal marks in some *buckleyi*). A creamy white anal stripe is present in some specimens of *leprieurii* but absent in all individuals of other species.

The postocular region, encompassing the tympanum, is dark brown in most specimens. In adults of *pearsoni* and *taurinus* the upper lips are dark brown. A pale cream or tan suborbital spot is present in *pearsoni* and in some *taurinus;* in some specimens of *taurinus* the suborbital spot is expanded posteriorly forming a labial stripe on the posterior part of the lip. The labial markings of *verrucigerus* are similar to the latter pattern, except that in females a distinct, light labial stripe extends the length of the lip. *Osteocephalus leprieurii* has a distinct, broad, pale labial stripe. The lips are barred cream and dark brown in *buckleyi.*

The venter is uniform creamy white or pale tan in *leprieurii,* uniform white in some *buckleyi* (most males), and uniform tan in some *taurinus.* The other species and some individuals of *taurinus* and *buckleyi* (most females) have dark ventral markings. These markings are most distinctive in *verrucigerus,* in which the venter is white with bold black mottling and spots (Fig. 3c). Those individuals of *taurinus* having ventral markings usually have indistinct, diffuse brown spots on the throat and chest (Fig. 3b). *Osteocephalus pearsoni* is characterized by a fine brown reticulation on the venter and on the anterior and posterior surfaces of the thighs in adults (Fig. 3a). Individuals of *buckleyi* that have ventral markings vary between the patterns illustrated for *pearsoni* and *taurinus* (Figs. 3b and c).

Ontogenetic change in coloration is slight or non-existent in *buckleyi, pearsoni,* and *taurinus,* except that juveniles lack ventral markings. A dark blotch on the back and distinct transverse bars on the limbs are evident in juveniles of *verrucigerus;* these markings are obscured in the adults. Juveniles of *leprieurii* are olive-brown

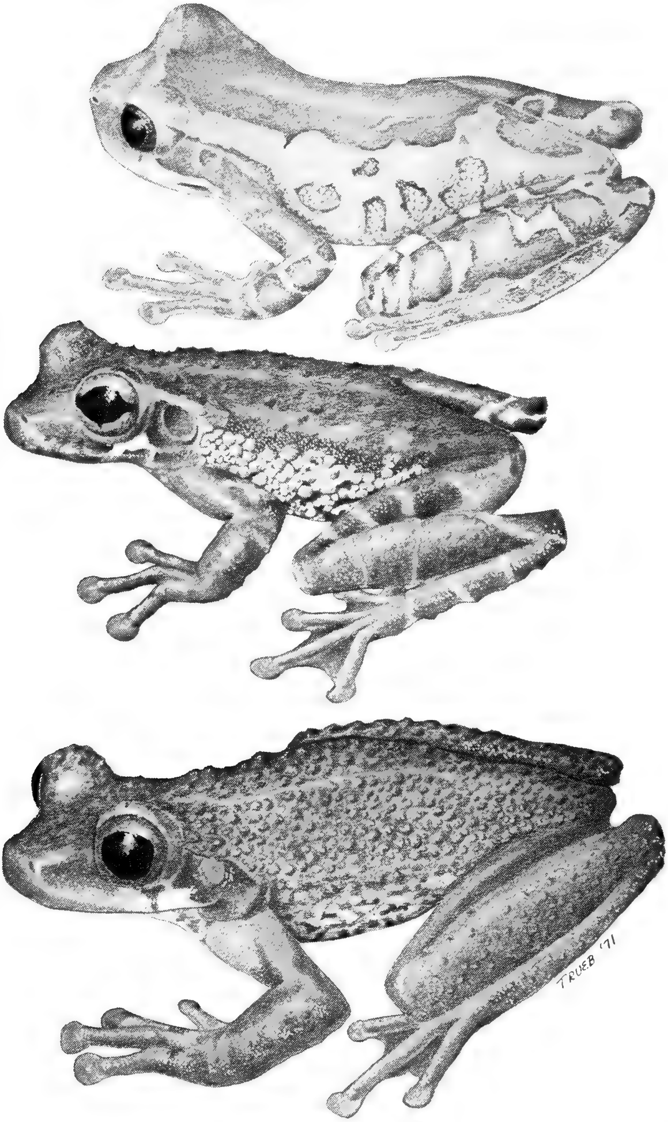

FIG. 1. Species of *Osteocephalus:* Top. *O. pearsoni,* KU 136312, ♂; Middle. *O. buckleyi,* KU 123172, ♂; Bottom. *O. verrucigerus,* KU 123177, ♂. ×1.5.

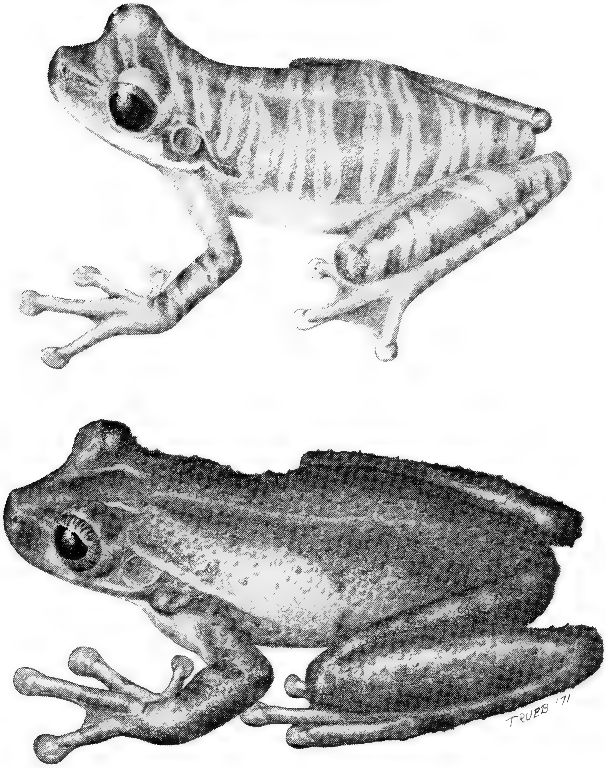

Fig. 2. Species of *Osteocephalus:* Top. *O. leprieurii,* KU 126611, ♀; Bottom. *O. taurinus,* KU 126648, ♂. ×1.

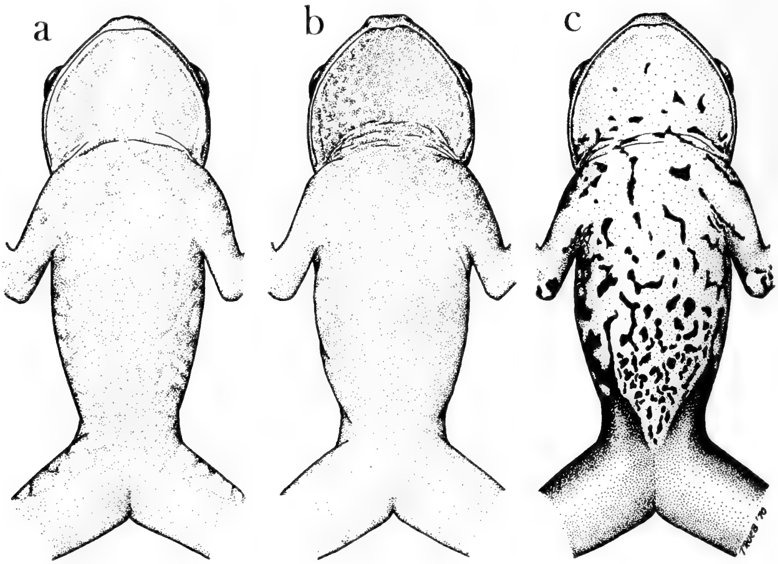

FIG. 3. Diagrammatic views of ventral color patterns in *Osteocephalus:* a. *O. pearsoni,* UMMZ 57533, ♂; b. *O. taurinus,* USNM 166037, ♂; c. *O. verrucigerus,* KU 123185, ♀.

with yellow dorsolateral stripes; the transverse dark marks, characteristic of the adults, appear before the stripes are lost.

Skin.—The dorsal skin of all males of *Osteocephalus* is tuberculate to varying degrees, whereas the dorsal skin of females is smooth, or nearly so (Fig. 4). *Osteocephalus verrucigerus* differs from other members of the genus by the presence of numerous, large tubercles bearing keratinized tips. The tubercles of *leprieurii* are numerous and spinous but much smaller than those of *verrucigerus;* those of *taurinus* are spinous but less numerous than in *leprieurii. Osteocephalus buckleyi* has a mixture of large and small, non-spinous tubercles, and *pearsoni* has only a few, small, scattered, non-spinous tubercles. Fleshy tubercles occur on the eyelids and supratympanic fold in females of *buckleyi;* a few small tubercles are present on the back of females of *pearsoni,* whereas the dorsal skin in females of the other species is smooth. The skin on the flanks of both sexes of *buckleyi* is weakly areolate; in the other species the flanks are smooth. The skin on the top of the head in *taurinus* is rugose as a consequence of co-ossification. In all species the anal opening is directed posteriorly at the upper level of the thighs.

Hands and Feet.—The feet of *Osteocephalus* are fully webbed or

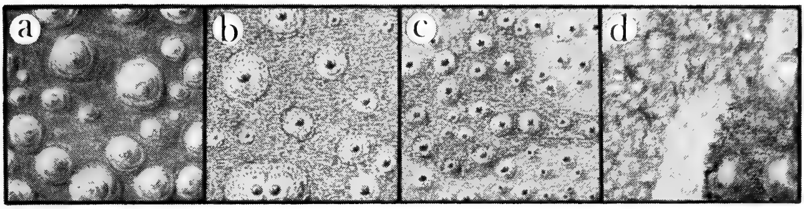

FIG. 4. Segments of dorsal skin of males of *Osteocephalus* showing size and arrangement of tubercles: a. *O. verrucigerus*, KU 123183; b. *O. taurinus*, USNM 166033; c. *O. leprieurii*, KU 126616; d. *O. buckleyi*, USNM 165999. Each square = 1 sq. cm.

nearly so. Webbing between fingers one and two is basal in all species. Webbing between fingers two, three, and four is most extensive in *taurinus*, in which the three fingers are about one-half webbed (Fig. 5). *Osteocephalus buckleyi*, *pearsoni*, and *verrucigerus* have reduced webbing between fingers two and three, and *leprieurii* has reduced webbing between fingers two, three, and four. All members of the genus have well-developed subconical subarticular tubercles on the fingers and toes; there is a tendency for the distal tubercle on the fourth finger to be weakly bifid. Palmar and plantar supernumerary tubercles are well developed in *taurinus*, moderately developed in *buckleyi*, *leprieurii*, and *pearsoni*, and barely evident in *verrucigerus*. All of the species have a noticeable fold on the wrist and enlarged prepollices, bearing horny nuptial excrescences in breeding males. The prepollex is least enlarged in *buckleyi*. Outer metatarsal tubercles are absent. The inner metatarsal tubercle is moderately well developed and ovoid in *leprieurii* and *pearsoni*; it is elliptical and flat in the other species. Tarsal folds are absent in all species except *verrucigerus*, in which the folds are barely evident.

Cranium.—As a genus, the cranial structure is remarkably uniform and quite generalized when viewed in the context of the family Hylidae. The skulls are broad and relatively flat, each being only slightly more broad than long and about one-third as high as long. In dorsal aspect the snouts are broadly rounded; the snout of *buckleyi* is somewhat less rounded and appears to be slightly longer than the snouts of other species. This subtle difference relates to the relative narrowness of the premaxillaries in *buckleyi*.

The genus is characterized by well-developed dermal roofing bones and an unusually large exposure of the sphenethmoid dorsally (Fig. 6). The conformation of the sphenethmoid exposed dorsally is determined by the marginal positions of the adjacent, overlapping

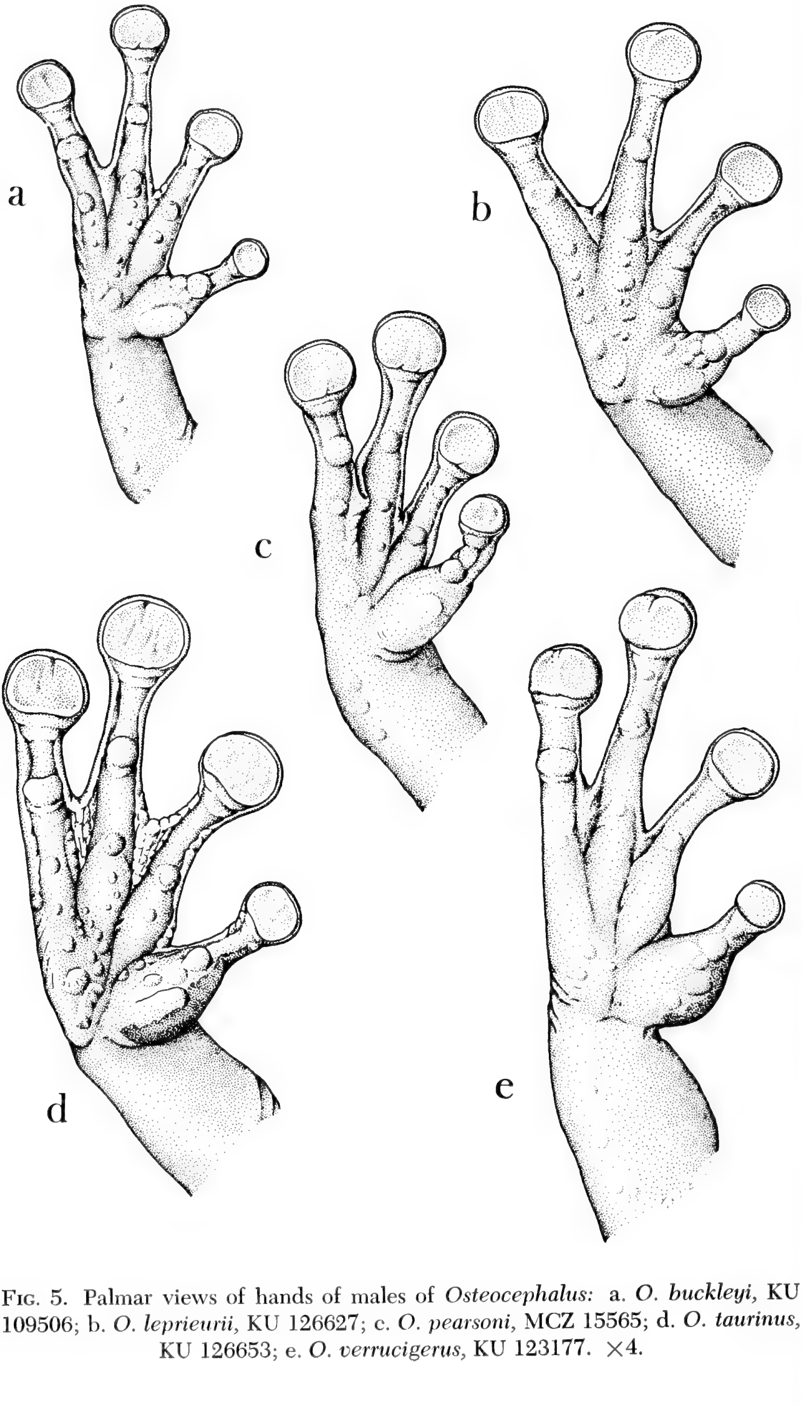

FIG. 5. Palmar views of hands of males of *Osteocephalus:* a. *O. buckleyi,* KU 109506; b. *O. leprieurii,* KU 126627; c. *O. pearsoni,* MCZ 15565; d. *O. taurinus,* KU 126653; e. *O. verrucigerus,* KU 123177. ×4.

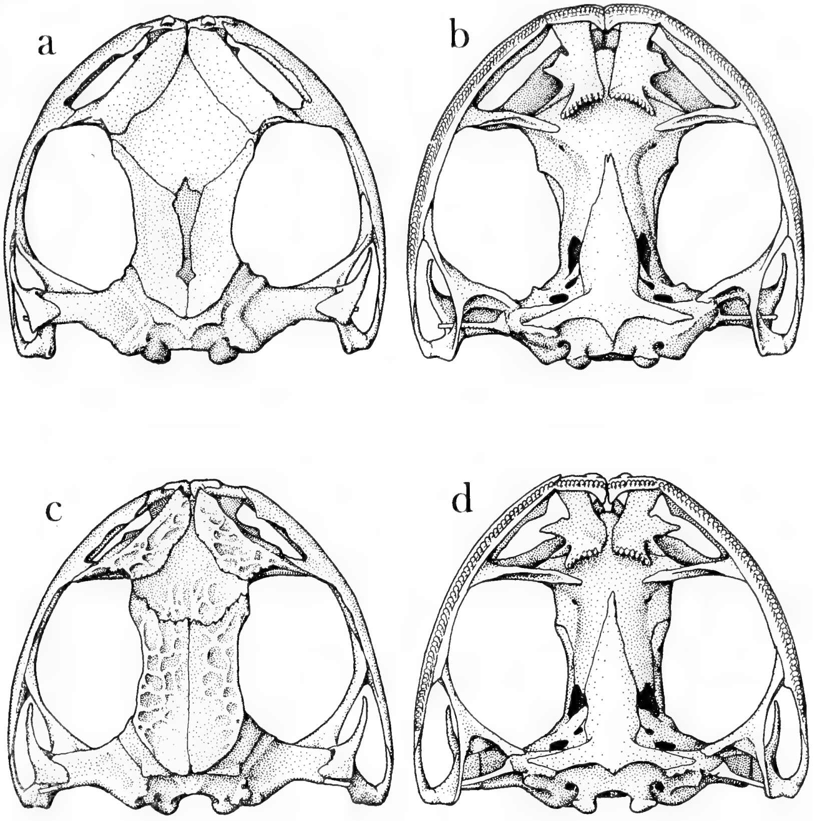

FIG. 6. Skulls of two species of *Osteocephalus:* a and b. *O. leprieurii,* KU 125961; c and d. *O. pearsoni,* UMMZ 67465. ×3.

elements—the nasals and frontoparietals. Medially the nasals overlap the lateral margins of the sphenethmoid. Anteromedially, the nasals converge in *leprieurii* and *taurinus,* are narrowly separated in *buckleyi* and *pearsoni,* or are more widely separated in *verrucigerus.* In all species the nasals terminate at the anterodorsal corner of the orbit. The frontoparietals of *buckleyi, leprieurii,* and *taurinus* have an anterolateral extension, which marginally overlaps the dorsolateral edge of the sphenethmoid and articulates with the posterodorsal corner of the nasal in *buckleyi* and *taurinus;* the bones are narrowly separated in *leprieurii.* The frontoparietals of *pearsoni* and *verrucigerus* have more extensive median ossification and less extensive anterolateral ossification. Thus, in those species the posteromedian portion of the sphenethmoid is obscured, and the lateral margins are partly exposed. The frontoparietal fontanelle is completely covered in all species, except *buckleyi* and *leprieurii,* in which an irregular, median separation of the frontoparietals exposes a small portion of the fontanelle. The posterolateral margins of the frontoparietals lie medial to the epiotic eminences.

Dermal ornamentation, involving the nasals, frontoparietals, and sphenethmoid, occurs in *taurinus* and, to a limited extent, in *pearsoni.* In the latter species marginal portions of the frontoparietals, the dorsal surfaces of the nasals, and the posteromedial part of the exposed sphenethmoid are slightly exostosed, resulting in an open, reticulate pattern of dermal sculpturing of exceedingly low relief (Fig. 6c). *Osteocephalus taurinus* is characterized by casquing, co-ossification, and a rather intricate pattern of dermal sculpturing, which was described in detail and illustrated by Trueb (1970a).

The squamosals of all species are moderately large structures having otic plates that overlie the lateral portion of the cristae paroticae. The posterior rami are short; the zygomatic rami of all species, except *taurinus,* extend slightly more than one-half of the distance to the maxillary. In *taurinus* the zygomatic ramus extends nearly to, or articulates with, the maxillary.

The maxillary arches are complete and relatively robust. The alary processes of the premaxillaries are vertically oriented in *leprieurii, pearsoni,* and *taurinus* and very slightly inclined posteriorly in *buckleyi* and *verrucigerus.* The maxillaries are uniformly characterized by the absence of postorbital processes and by the presence of preorbital processes that articulate with the maxillary processes of the nasals. The partes facialae of the maxillaries are moderately developed in all species, except *taurinus,* in which the pars fascialis tends to articulate with the lateral margin of the nasal in well-ossified individuals. The partes palatinae are poorly developed in all species, except *buckleyi,* in which the pars palatina of the premaxillary is moderately robust.

The pterygoids are uniformly tri-radiate structures. The anterior rami terminate at about the mid-level of the orbit, and the medial rami articulate firmly with the anterolateral corner of the otic capsule. The palatines are well-developed elements bearing ventral ridges; the ridges are somewhat irregular in *buckleyi, taurinus,* and *verrucigerus* but smooth in *leprieurii* and *pearsoni.* The parasphenoids are large elements characterized by acuminate cultriform processes and posterolaterally inclined alary processes. The basal areas of the cultriform processes bear small odontoid protuberances in *buckleyi, taurinus,* and *verrucigerus,* whereas they are smooth in

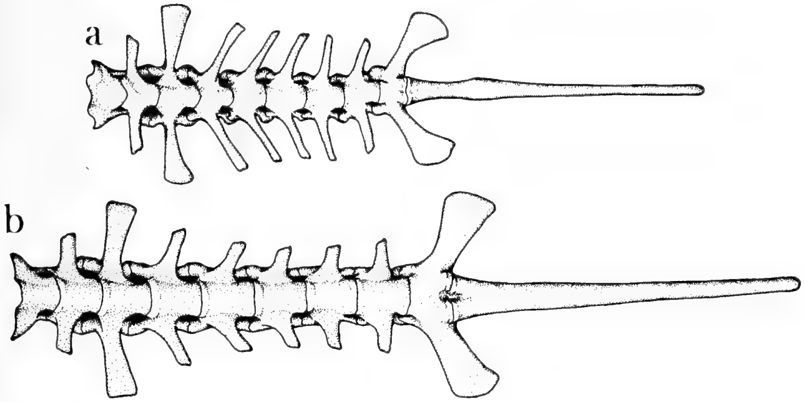

FIG. 7. Dorsal views of vertebral columns of two species of *Osteocephalus:* a. *O. leprieurii,* KU 125962, ♀; b. *O. buckleyi,* USNM 165997, ♀. ×2.

leprieurii and *pearsoni.* The prevomers are remarkably uniform, moderately well-developed structures. In each species the anterior ramus lies adjacent to the premaxillary, and the lateral wings form the anterior, medial, and posteromedial margins of the internal nares. The dentigerous processes are characteristically large and angular and bear numerous teeth. The sphenethmoid and otoccipitals are well ossified; a dermal sphenethmoid is present only in *taurinus.*

Vertebral Column.—The cervical cotyles are uniformly widely displaced. The neural arches are low and non-imbricate. The transverse processes of the third presacral vertebrae are approximately equal in width to the sacral diapophyses in all species, except *buckleyi,* in which the processes of the third presacral are slightly narrower than the diapophyses. *Osteocephalus buckleyi* is further distinguished by the presence of narrow transverse processes on presacrals five through eight (Fig. 7b); males have narrower processes than do females. The processes are moderately wide but subequal in width in *pearsoni, taurinus,* and *verrucigerus,* whereas they are nearly equivalent in width to one another and to the sacral diapophyses in *leprieurii* (Fig. 7a). The scaral diapophyses of all species are moderately dilated and posterolaterally inclined. The coccyx bears a distinct dorsal ridge and has a bicondylar articulation with the sacrum.

Pectoral Girdle.—The pectoral girdles are fully arciferal and bear small, cartilaginous omosterna and moderately large cartilaginous sterna. The coracoids are robust, and the clavicles are strongly arched. Procoracoid cartilage seems to be absent. The scapulae are large, longer than the clavicles, and bicapitate proximally. The suprascapulae are moderately large and well ossified in *leprieurii* and *taurinus.* The suprascapula of *verrucigerus* is poorly ossified, and that of *buckleyi* is not ossified.

Pelvic Girdle.—The ilia of *buckleyi, taurinus,* and *verrucigerus* lack any indication of a crest on the shaft, whereas *leprieurii* has a low crest. The dorsal acetabular expansion of the ilia is moderately low in *taurinus* and *verrucigerus,* but distinctly lower in *buckleyi* and *leprieurii.* The ilia of all species bear low dorsal protuberances. The ischia of *leprieurii, taurinus,* and *verrucigerus* are moderately expanded; that of *buckleyi* is somewhat less expanded dorsally. The pubis of *leprieurii, taurinus,* and *verrucigerus* are calcified, whereas that of *buckleyi* remains cartilaginous.

Throat Musculature and Vocal Sac Structure.—Tyler (1971) described the throat myology of *Osteocephalus.* The genus is characterized by a moderate-sized araphic submentalis muscle and an undifferentiated intermandibularis having an elongate median aponeurosis. The intermandibularis and submentalis are completely independent in *buckleyi,* whereas in the other species there is a small attachment between these muscles.

According to Tyler (pers. com.), *Osteocephalus* has three distinctive types of vocal sac structure which result from differences in the development of the interhyoideus muscle and the overlying skin. In *leprieurii* and *verrucigerus* the supramandibular portions of the interhyoideus form a simple tubular, posterolateral extension; there is no modification of the associated skin. *Osteocephalus buckleyi* and *pearsoni* have more extensive development of the supramandibular portions of the interhyoideus; furthermore, the associated skin forms a broad, loose fold extending from the ventromedial surface of the throat dorsolaterally to the base of the supratympanic fold. Like *buckleyi* and *pearsoni,* the supramandibular portion of the interhyoideus is much expanded in *taurinus.* The vocal sac structure of *taurinus* differs from that of other members of the genus in that the skin of *taurinus* forms an everted pouch, which dangles loosely beneath the supratympanic fold.

KEY TO THE SPECIES OF *Osteocephalus*

1. Inner edge of third finger webbed to mid-length of antepenultimate phalange; dorsum brown with dark brown spots or median blotch; skull in adults casqued and co-ossified with prominent supraorbital flanges .... *O. taurinus*

Inner edge of third finger webbed to base of antepenultimate phalange; dorsum plain or marked with dark blotches or transverse bars; skull in adults smooth or slightly exostosed, lacking supraorbital flanges 2

2. Skin on flanks areolate; dorsum in males bearing a mixture of large and small non-spinous tubercles; lips distinctly barred .... *O. buckleyi*

Skin on flanks smooth; dorsum in males bearing tubercles of uniform size; lips not barred 3

3. Dorsal pattern consisting of narrow transverse dark bars; dorsum in males bearing numerous small spinous tubercles .. *O. leprieurii*

Dorsal pattern not consisting of transverse bars; dorsal tubercles large or few in number 4

4. Dorsum uniformly dark brown; venter heavily mottled with black, especially in females; dorsum in males bearing large, keratinized tubercles .... *O. verrucigerus*

Dorsum tan with irregular dark brown blotches; venter cream with fine brown reticulations; dorsum in males bearing few, small non-spinous tubercles .... *O. pearsoni*

ACCOUNTS OF SPECIES

Osteocephalus buckleyi (Boulenger)

Hyla buckleyi Boulenger, 1882:362 [Syntypes.—BMNH 1947.2.13.36-39 from Sarayacu, Provincia Pastaza, Ecuador; BMNH 1947.2.13.40-41, 1947.2.13.43-45 from Canelos, Provincia Pastaza, Ecuador; BMNH 1947.2.13.46 from "Paitanga" (= Pallatanga), Provincia Chimborazo, Ecuador (in error); Mr. Buckley collector; BMNH 1947.2.13.44 here designated as lectotype].

Hyla festae Peracca, 1904:39 [Holotype.—MIZS 2950 from "Valle de Santiago" (= lower Río Zamora), Provincia Morona-Santiago, Ecuador; Enrico Festa collector]. New synonymy.

Osteocephalus buckleyi—Goin, 1961:13.

Hyla carri Cochran and Goin, 1970:211 [Holotype.—FMNH 69702 from Acevedo, Río Suaza, Departamento Huila, Colombia; Philip Hershkovitz collector]. New synonymy.

Hyla cabrerai Cochran and Goin, 1970:215 [Holotype.—USNM 152759 from Caño Guacayá, tributary of lower Río Apoporis, Comisaria Amazonas, Colombia; Isadore Cabrera collector]. New synonymy.

Justification of Synonymy.—Boulenger (1882:362) listed 11 specimens in his description of *Hyla buckleyi.* We have examined all of these and conclude that one (BMNH 1947.2.13.42) is *O. leprieurii.* Cochran and Goin (1970:213) restricted the type locality to Canelos, Provicia Pastaza, Ecuador; we here select BMNH 1947.2.13.44 from that locality as the lectotype. This specimen is a male having a snout-vent length of 37.9 mm; the diameter of the tympanum is 3.5 mm, 81.4 percent of the diameter of the eye. The type series, exclusive of BMNH 1947.2.13.42 (= *O. leprieurii*) consists of six males having snout-vent lengths of 37.9-44.6 (mean 40.4) mm, and four females having snout-vent lengths of 50.0-53.9 (mean 51.5) mm. The dorsum in the males bears a mixture of large and small tubercles, whereas the dorsum in females is nearly smooth. The skin on the flanks, especially the axilla, is areolate. The coloration consists of a creamy tan ground color with irregular reddish brown markings on the back and broad transverse bars on the limbs. The dorsal markings are narrowly bordered by creamy white; those on the back consist of an interorbital bar and a pair of longitudinal marks beginning in the scapular region and usually diverging posteriorly in the sacral region or converging into a broad median blotch. One specimen has a middorsal creamy white stripe from the tip of the snout to the vent. In all of the types large dark brown spots are present on the flanks and posterior surfaces of the thighs. The ventral surfaces are pale creamy tan with or without diffuse brown spots on the throat and chest.

The holotype of *Hyla festae* is a female having a snout-vent length of 75.0 mm; the diameter of the tympanum is 3.9 mm, 57.4 percent of the diameter of the eye. The skin is smooth on the dorsum and areolate on the anterior part of the flanks. The dorsum is pale brown with a large median longitudinal dark brown blotch on the back and broad transverse bars, narrowly outlined by cream, on the limbs. Dark brown spots are present on the flanks; the posterior surfaces of the thighs are dark brown. The throat and belly are grayish white with irregular dark brown spots.

The holotype of *Hyla carri* is a female having a snout-vent length of 66.1 mm; the diameter of the tympanum is 4.7 mm, 81.0 percent of the diameter of the eye. The skin on the dorsum is smooth with scattered small tubercles and areolate on the anterior part of the flanks. The dorsum is tan with irregular dark brown blotches on the back and transverse bars on the limbs; all dorsal markings are narrowly outlined by creamy white. Dark brown spots are present on the flanks; the venter and posterior surfaces of the thighs are tan without dark spots.

The holotype of *Hyla cabrerai* is a female having a snout-vent length of 52.7 mm; the diameter of the tympanum is 4.0 mm, 76.9 percent of the diameter of the eye. The skin on the dorsum is weakly tuberculate and that on the anterior part of the flanks is areolate. The dorsum is creamy tan with dark brown markings (interorbital bar, reticulations on occiput, three longitudinal streaks on back, and broad transverse bars on limbs). Irregular dark brown spots are present on the flanks. The venter is pinkish tan with small reddish brown spots on the throat and darker brown spots on the chest and belly.

In their description of *Hyla cabrerai,* Cochran and Goin (1970: 217) stated: "This species, together with *buckleyi* and *pearsoni* certainly make a closely knit group. . . . Both *buckleyi* and *cabrerai* have long hind legs, with the extended heel reaching to the tip of the snout, while in *pearsoni* the extended heel reaches only to the eye. *H. buckleyi* has the belly dusky, while it is heavily spotted in *cabrerai* and is reticulated in *pearsoni. H. cabrerai* seems to have the heaviest hands with the most webbing between the fingers; the other two species have the webbing reduced between the fingers." The description of *Hyla cabrerai* was based on three specimens. We have examined the holotype and one paratype (WCAB 13284 from Territorio do Amapá, Brasil). Another paratype in the private collection of C. J. Goin from Caño Tuí, between Mitú and Raudal de Yurupari, Comisaria de Vaupés, Colombia, was not examined.

Cochran and Goin (1970:211) based their description of *Hyla carri* on one gravid female and stated: "A large *Hyla* with the vomerine teeth in two ∧∧ shaped patches between the somewhat squarish choanae; reduced webs between the fingers; and a pattern of dorsal dark blotches bordered by light margins. The species is not similar to any other species known in Colombia. It is perhaps most closely related to *Hyla claresignata* of Brazil, from which it can be differentiated by its more heavily spotted dorsum, larger tympanum, and lack of dark anal spots."

Except for the inclusion of the name in checklists, *Hyla festae* has not been mentioned in the literature since the original description.

The wholesale synonymization of names, which, on the bases of their published diagnoses, seem to apply to distinctly different species, is possible with the application of uniform criteria to the types and series of other specimens. In measurements and proportions the type specimens of the nominal taxa all fall within the range of variation exhibited by a series of 18 males and 15 females from Provincia Pastaza, Ecuador, except the ratio of the diameter of the tympanum to that of the eye in the female holotype of *Hyla festae.* In that specimen the ratio is 0.574, whereas the ratio in the 15 females from Provincia Pastaza is 0.587-0.905 (mean 0.736).

Ventral coloration is the most variable character among the types. The venter in the type of *Hyla festae* is boldly spotted; it is distinctly spotted in *cabrerai,* uniform tan in *carri,* and tan, flecked, or spotted in the type series of *buckleyi.* The ventral coloration in series of specimens from Amazonian Ecuador encompasses that observed in all of the types, except that of *festae,* which has more ventral spotting than any other individual.

The webbing on the hand usually excludes the penultimate phalanges of the fingers, but in some specimens from Amazonian Ecuador the webbing encompasses the proximal parts of the penultimate phalanges of the fingers. In a few of these specimens, the holotype of *festae,* and one paratype of *cabrerai* the webbing extends to the middle of the penultimate phalanges of the third and fourth fingers. In the holotype of *cabrerai* the webbing extends to the middle of the penultimate phalanges of the third and fourth fingers and to the base of the disc of the second finger.

The types of the nominal taxa and series of specimens from Guyana and Amazonian Ecuador display noticeable variation in dorsal coloration. The variety of dorsal patterns of all of the types is included in the variation displayed by the other specimens. All specimens have some amount of dark spotting on the flanks; all have vertically barred lips, on which a pale subocular spot usually is evident. Probably the most unifying physical characteristic of all of the specimens is the nature of the skin on the anterior part of the flank. The skin is elevated amidst an irregular network of depressions. This areolate dermal condition is present in all specimens and does not occur in other species of *Osteocephalus.* The degree of tubercularity of the skin on the dorsum is variable and sexually dimorphic. All males are tubercular, whereas small females are smooth or have only a few scattered tubercles. Large females usually have pronounced tubercles on the eyelids and supratympanic fold.

In their description of *Hyla carri,* Cochran and Goin (1970:211) misrepresented the nature of the dentigerous processes of the prevomers, which are angular, not ʌ-shaped. Their suggestion that the Colombian *Hyla carri* is related to *Hyla claresignata* in southeastern Brasil is unfounded. The latter species is smaller (40 mm), has a yellow dorsum and venter, dark brown spots dorsolaterally, oblique dentigerous processes of the prevomers, small tympanum, and smooth skin dorsally.

The ventral coloration of the type of *Hyla festae* resembles that of *Osteocephalus verrucigerus,* but the type differs from *verrucigerus* by having areolate skin on the flanks and distinct dark markings on the dorsum. In *verrucigerus* the skin on the flanks is smooth, and the dorsum is uniform dark brown, except for a tan snout in females.

Comparisons of the types of the nominal species with series of specimens from Guyana, Colombia, Ecuador, and Perú suggest strongly that the types are representative of one taxon, the oldest name for which is *Hyla buckleyi* Boulenger, 1882. Consequently, we place *Hyla festae* Peracca, 1904, *Hyla carri* Cochran and Goin, 1970, and *Hyla cabrerai* Cochran and Goin, 1970, as junior synonyms of *Hyla buckleyi* Boulenger, 1882.

Diagnosis.—1) Size moderate, sexual dimorphism extreme; maximum observed snout-vent length in males 48.1 mm, in females 75.1 mm; 2) skin on dorsum in males bearing a mixture of large and small non-spinous tubercles; 3) skin on flanks, especially anteriorly, areolate; 4) web usually extending only to base of antepenultimate phalange on inner edge of third finger; 5) dorsum pale tan or green with irregular, longitudinal, dark brown blotches, usually narrowly outlined with cream; 6) venter cream or tan, suffused with brown or marked with brown spots in some specimens; 7) lips marked with vertical brown and cream bars; 8) flanks creamy tan with irregular brown spots and/or diagonal marks; 9) dermal roofing bones of skull lacking exostosis; 10) dermal sphenethmoid absent; 11) nasals widely separated medially; 12) anteromedial margin of frontoparietal at mid-level of orbit; 13) frontoparietal fontanelle partially exposed; 14) palatine serrate; 15) parasphenoid bearing odontoids; 16) zygomatic ramus of squamosal extending approximately one-half of distance to maxillary arch; 17) transverse processes of third presacral vertebra narrower than sacral diapophyses; transverse processes of presacral vertebrae 3-8 subequal in width and narrower in males than in females; 18) intermandibularis and submentalis muscles independent; 19) supramandibular portion of interhyoideus extensively developed; associated skin forming broad loose fold.

Osteocephalus buckleyi can be distinguished readily from all other species in the genus by the presence of areolate skin anteriorly on the flanks and by the rather boldly contrasting dorsal pattern. Furthermore, females are distinctive in having tubercles on the eyelids and supratympanic folds.

Distribution.—The periphery of the Amazon Basin, in the Guianas and Territorio do Amapá in northeastern Brasil; the upper Amazon Basin from southern Colombia to east-central Bolivia; one locality (Acevedo) in upper Río Magdalena drainage in Colombia (Fig. 8). All localities are at elevations of less than 700 m. Records

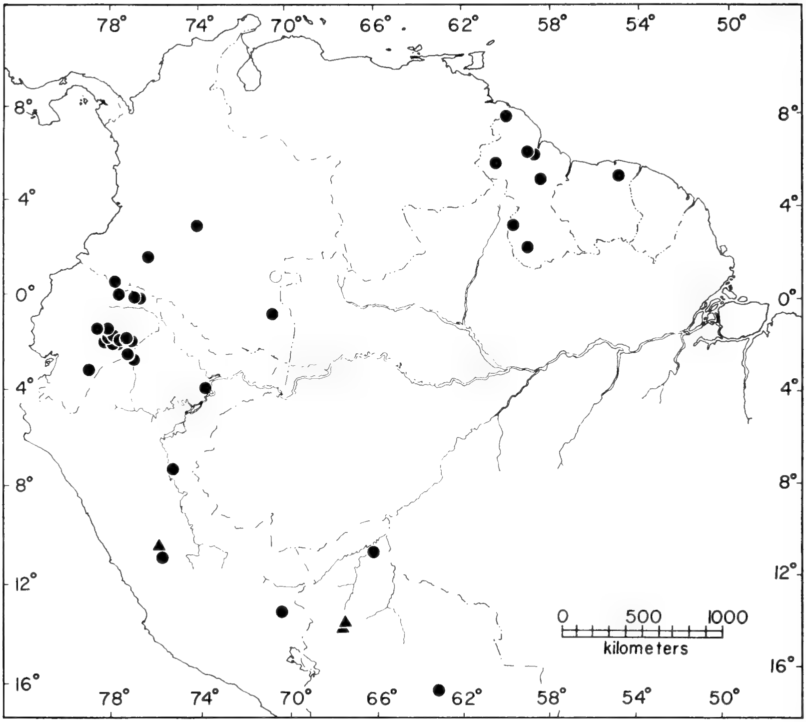

FIG. 8. Distribution of *Osteocephalus buckleyi* (circles) and *O. pearsoni* (triangles).

for Pallatanga and Santiago in Provincia Chimborazo, Ecuador (high on the Pacific slopes of the Andes), are considered to be erroneous. 78 specimens from 40 localities.

Remarks.—In life the dorsum is green with dark markings. A male (KU 123171) from Santa Cecilia, Ecuador, was: "Dorsum green with dark brown blotches. Anterior and posterior surfaces of thighs dull blue. Venter brown, flecked with white. Iris greenish bronze with brown horizontal triangles and ventromedian brown line." (W. E. Duellman, field notes, 16 June 1968.) A female (KU 126646) from Lago Agrio, Ecuador, was: "Dorsum pale green with darker green blotches and creamy yellow middorsal stripe. Lateral blotches bronze-tan. Flanks tan with black blotches. Anterior surfaces of thighs dark brown. Dorsal and posterior surfaces of thighs and shanks tan with dark brown blotches. Webbing brown. Suborbital spot green. Postorbital bar black. Belly grayish brown in appearance—tips of granules white; intergranular spaces brown. Iris golden bronze with black flecks peripherally and median, horizontal, reddish brown streak." (W. E. Duellman, field notes, 12 May 1969.)

No ontogenetic change in coloration has been noted.

Osteocephalus leprieurii (Duméril and Bibron)

Hyla leprieurii Duméril and Bibron, 1841:553 [Holotype.—MNHN 4629 from "Cayenne"; Mons. Leprieur collector].

Hypsiboas leprieurii—Cope, 1867:200.

Hyla leprieurii britti Melin, 1941:42 [Holotype.—NHMG 489 from the Rio Uaupés, north of the Rio Japu, Territorio do Amazonas, Brasil; Douglas Melin collector]. New synonymy.

Hyla leprieurii leprieurii—Melin, 1941:42.

Osteocephalus britti—Goin, 1961:13.

Osteocephalus leprieurii—Goin, 1961:13.

Justification of Synonymy.—The holotype of *Hyla leprieurii* is a female having a snout-vent length of 46.6 mm. The diameter of the tympanum is 3.7 mm, 69.8 percent of the diameter of the eye. The dorsal roofing bones are smooth, and the skin on the dorsum is smooth. The penultimate phalanges of the fingers are not included in the webbing. When we examined the specimen on 2 July 1969, it was slightly soft and somewhat faded to a peculiar grayish green color with faint darker transverse bars on the limbs. Duméril and Bibron (1841:554) described the coloration, as follows: "The loreal region in black. A stripe of the same color extends from the posterior border of the orbit to the corner of the mouth, passing through the tympanum. All of the dorsal parts are grayish white with large transverse brown bands, which are more expanded and less regularly outlined on the back than on the limbs. There is one of these on the occiput that is in a triangular shape. All of the venter is white." (Free translation from French.)

The holotype of *Hyla leprieurii britti* is a male having a snout-vent length of 48.1 mm. The diameter of the tympanum is 3.6 mm, 65.5 percent of the diameter of the eye. The skin on the dorsum is tubercular; the tubercles are small on head and on the dorsal surfaces of the limbs and slightly larger on the back. The penultimate phalanges of the fingers are not included in the webbing. Melin (1941:43) stated: "Above blackish brown with a very indistinct band between the eyes; iris with mottle of metalic lustre; hinder parts of upper jaw whitish; sides of body mottled with blackish brown; hind limbs (especially tibiae and tarsi) with narrow, diffuse cross bars; beneath whitish with slight brown mottle along jaw." We examined the type on 17 February 1969; at that time it was dull brown above with faint, narrow, dark brown, transverse bars on the back and dorsal surfaces of the limbs. A cream subocular spot was evident, and the venter was creamy white.

Melin (1941:42) stated that the holotype of *Hyla leprieurii britti* ". . . resembles a good deal *H. leprieurii* Dum. & Bibr. As, however, it differs from the latter species by its very concave loreal region, small tympanum, and almost uniformly brownish colour, it may at least form a subspecies of *leprieurii* . . ." The pattern of narrow transverse bars on the backs of the holotypes of *H. leprieurii* and *H. britti* is a condition shared only by these two nominal taxa that are placed in *Osteocephalus*. Melin noted that *britti* differed from *leprieurii* in the depth of the loreal concavity and in the size of the tympanum. Neither of these differences is noteworthy in comparison with series of specimens. The depth of the loreal concavity is a highly subjective character, and we note no differences between the types. The ratio of the diameter of the tympanum to the diameter of the eye is relatively smaller in both holotypes (0.698 in *leprieurii*—♀; 0.655 in *britti*—♂) than in series of fresh specimens from Lago Agrio, Ecuador (0.652-0.884, mean 0.785 in 17 males; 0.700-0.909, mean 0.790 in 20 females). The smaller proportions in the types may be due to geographic variation or to shrinkage as a result of many years in preservative (130+ years for *leprieurii;* 45 for *britti*).

Comparisons of the holotypes with series of specimens from Ecuador, Guyana, and Surinam indicate that one morphological species occurs throughout the upper Amazon Basin and the Guianas and that both type specimens are representatives of one species. Consequently, we consider *Hyla leprieurii* Duméril and Bibron, 1841, to be a monotypic species with *Hyla leprieurii britti* Melin, 1941, as a junior synonym.

In their account of *Osteocephalus leprieurii,* Cochran and Goin (1970:323) stated: "The specimen described and illustrated (MCZ 28042) has been directly compared with the types of *leprieurii, planiceps,* and *vilarsi* by the junior author and there seems to be no doubt that all are conspecific. Another specimen (CNHM 69716) has been directly compared with the types of *planiceps* and *vilarsi* and these, likewise, are considered conspecific." With this justification Cochran and Goin (1970:322) included *Osteocephalus planiceps* Cope, 1874, and *Hyla vilarsi* Melin, 1941, in the synonymy of *Osteocephalus leprieurii.*

We do not concur with Cochran and Goin's synonymy and contend that *planiceps* and *vilarsi* are synonyms of *Osteocephalus taurinus;* we give our reasons in the account of that species. We have examined the specimens listed as *O. leprieurii* by Cochran and

Goin; several of them, including CNHM (= FMNH) 69716, are *taurinus.* Thus, due to Cochran and Goin's confusion of two taxa, their comparisons of certain specimens with types has little meaning.

Cochran and Goin did not include *Hyla leprieurii britti* in their synonymy of *Osteocephalus leprieurii* but did discuss the name in their account of *Osteocephalus orcesi (= O. verrucigerus),* as follows (1970:319): "When we first examined one of the specimens we felt sure that we had Melin's *Hyla britti* at hand, but on direct comparison with the type of *britti* the two proved to be different. After studying the type of *orcesi* (SUNHM 13150) we have no doubt that the specimens at hand are *orcesi* and that *britti* is a different, probably valid species."

Diagnosis.—1) Size moderate, sexual dimorphism evident; maximum observed snout-vent length in males 48.4 mm, in females, 61.5 mm; 2) skin on dorsum in males bearing numerous, minute, spinous tubercles; 3) skin on flanks smooth; 4) web extending to base of antepenultimate phalange on inner edge of third finger; 5) dorsum tan or olive-brown with transverse brown or olive bars; 6) venter creamy white or pale tan without markings; 7) lips marked with creamy tan labial stripe and suborbital spot; 8) flanks pale tan with no markings; 9) dermal roofing bones of skull lacking exostosis; 10) dermal sphenethmoid absent; 11) nasals juxtaposed medially; 12) anteromedial margin of frontoparietal between mid- and anterior levels of orbit; 13) frontoparietal fontanelle partially exposed; 14) palatine not serrate; 15) parasphenoid lacking odontoids; 16) zygomatic ramus of squamosal extending about one-half of distance to maxillary arch; 17) transverse processes of presacral vertebrae 3-8 about equal in width to one another and to sacral diapophyses; 18) intermandibularis and submentalis muscles connected; 19) supramandibular portion of interhyoideus forming simple tubular posterolateral extension; associated skin unmodified.

Osteocephalus leprieurii differs from all other members of the genus by having transverse dark bars on the back. Two other hylids *(Hyla lanciformis* and *multifasciata)* in the Amazon Basin have transverse dark marks on the dorsum. Both of these differ from *leprieurii* by having pointed snouts, much longer hind limbs, and smooth skin dorsally.

Distribution.—The periphery of the Amazon Basin, in the Guianas and the upper part of the basin in southern Colombia, Ecuador, Perú, and extreme western Brasil (Fig. 9). Most localities are at elevations of less than 500 m, but the species ascends the lower

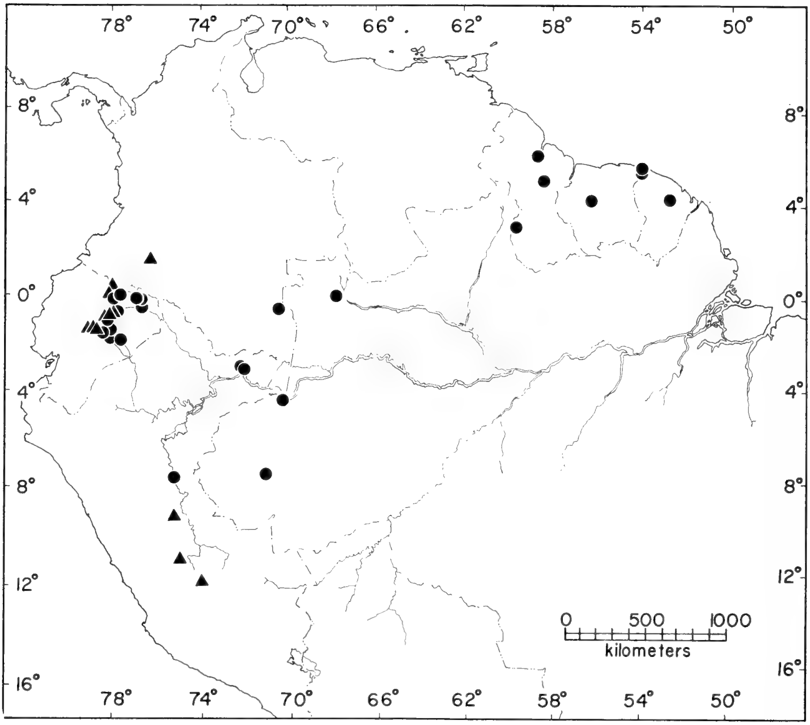

FIG. 9. Distribution of *Osteocephalus leprieurii* (circles) and *O. verrucigerus* (triangles).

Andean slopes to elevations of 1100 m. 265 specimens from 31 localities.

Remarks.—Most adults of *leprieurii* have distinct transverse markings on the back; these are variable in width, extent, and arrangement. In some specimens, such as USNM 166557, some of the transverse bars are fragmented into spots; in a few specimens the dorsal pattern consists solely of small dark spots arranged in transverse rows. Such specimens have a dorsal pattern resembling that of some *taurinus*. The transverse nature of the dorsal markings is further modified in some specimens, such as USNM 166555, in which the dark bars are fragmented and oblique.

Extreme ontogenetic change in color pattern is exhibited by this species (Fig. 10). Juveniles having snout-vent lengths of less than 28 mm have an olive-brown dorsum with a pale cream stripe across the head and broad, cream, dorsolateral stripes; transverse dark bars are absent on the body and limbs. Individuals having snout-vent lengths of 30-35 mm have dark brown transverse bars on

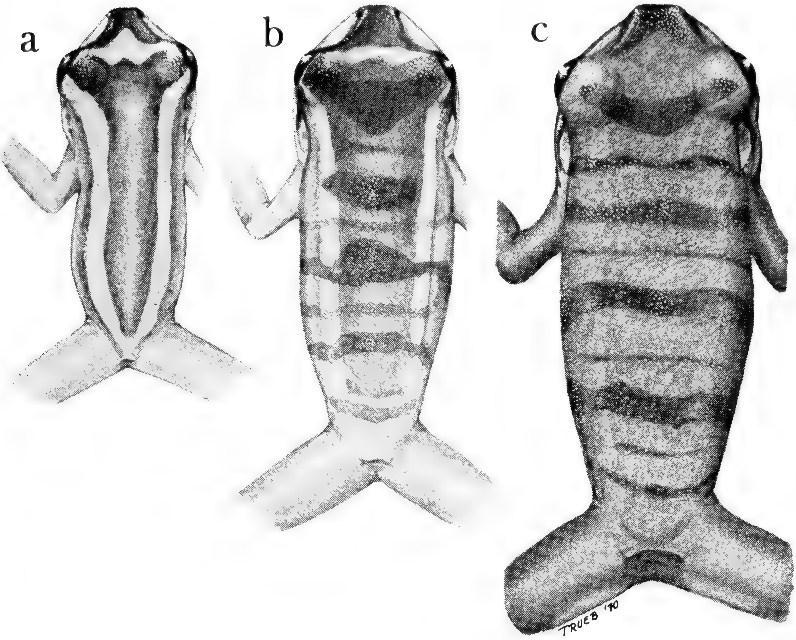

FIG. 10. Ontogenetic change in color pattern in *Osteocephalus leprieurii:* a. KU 126644; b. KU 126640; c. KU 126625. ×2.

the back and limbs but still retain the light dorsolateral stripes, whereas the stripes are lost in larger individuals.

Coloration in life of specimens from Lago Agrio, Ecuador: "In males the dorsal ground color varies from dark brown to ochre-tan; dorsal markings uniformly dark brown. Most specimens have dark brown and cream anal stripes; labial area cream-colored. Flanks vary from tan to white. Ventral coloration varies from salmon to tan to white. The iris is bronze with a greenish cast and black reticulations. In females the dorsal coloration is the same as in males, except that dark marks tend to be outlined with cream; venter tannish salmon." (W. E. Duellman, field notes, 12 May 1969).

Osteocephalus pearsoni (Gaige)

Hyla pearsoni Gaige, 1929:3 [Holotype.—UMMZ 57548 from the upper Río Beni, below mouth of Río Mapiri, Departamento El Beni, Bolivia; N. E. Pearson collector].
Osteocephalus pearsoni—Goin, 1961:13.

Justification of Synonymy.—Goin (1961:13) suggested that *Hyla pearsoni* Gaige was an *Osteocephalus,* but Cochran and Goin (1970:

217) considered *pearsoni* to be a *Hyla.* The presence of exostosed dermal roofing bones, angulate prevomerine dentigerous processes, and the structure of the vocal sacs are characters which place the species in *Osteocephalus.*

Diagnosis.—1) Size moderate, sexual dimorphism evident; maximum observed snout-vent length in males 46.2 mm, in females 54.7 mm; 2) skin on dorsum in males bearing a few, small, scattered nonspinous tubercles; 3) skin on flanks smooth; 4) web extending to base of antepenultimate phalange on inner edge of third finger; 5) dorsum tan with irregular brown blotches; 6) venter cream with fine brown reticulations; 7) lips dark with pale vertical bar below eye; 8) flanks pale tan with round, brown spots; 9) dermal roofing bones of skull slightly exostosed; 10) dermal sphenethmoid absent; 11) nasals narrowly separated medially; 12) anteromedial margin of frontoparietal between mid- and anterior levels of orbit; 13) frontoparietal fontanelle covered; 14) palatine not serrate; 15) parasphenoid lacking odontoids; 16) zygomatic ramus of squamosal extending about one-half distance to maxillary arch; 17) transverse processes of third presacral vertebra approximately equal in width to sacral diapophyses; transverse processes of presacral vertebrae 3-8 subequal in width; 18) intermandibularis and submentalis muscles connected; 19) supramandibular portion of interhyoideus extensively developed; associated skin forming broad loose fold.

Osteocephalus pearsoni can be distinguished most readily from other members of the genus by the brown reticulate pattern on the venter, round brown spots on the flanks, and smooth skin on the flanks. Also, it is the least tuberculate species in the genus.

Distribution.—Upper Amazon Basin and Amazonian slopes of the Andes in central Perú (1620 m in Río Ucayali drainage) and northern Bolivia (less than 500 m in Río Beni drainage) (Fig. 8). 6 specimens from 3 localities.

Remarks.—The specimen from Yaupi, Perú (KU 136312) is a subadult female having a snout-vent length of 39.8 mm. In life the coloration was: "Dorsum light pinkish brown with large rich chocolate brown blotch from eyes to anterior tips of ilia; numerous small chocolate blotches on flanks; dorsal surfaces of thighs and shanks, canthus, and supraorbital region to insertion of forearm chocolate brown; supralabial border and short bar from eye to lip bronze-white; venter bronze-white with numerous tiny chocolate brown flecks [tending to form reticulations on throat and chest]; anterior and posterior surfaces of thighs light olive-brown; iris largely black with gold flecks." (Thomas H. Fritts, field notes, 23

March 1970.) On the basis of this one subadult, it seems likely that reticulations on the venter develop with age.

Osteocephalus taurinus Steindachner

Osteocephalus taurinus Steindachner, 1862:77 [Holotype.—NHMW 16492 from Barra do Río Negro, Manáus, Territorio do Amazonas, Brasil; Johann Natterer collector].

Osteocephalus flavolineatus Steindachner, 1862:80 [Holotype.—NHMW 16495 from Cucuí, Territorio do Amazonas, Brasil; Johann Natterer collector].

Trachycephalus (Osteocephalus) taurinus Steindachner, 1867:64.

Osteocephalus planiceps Cope. 1874:122 [Holotype.—ANSP 11399 from Nauta, Departamento de Loreto, Perú; James Orton collector]. New synonymy.

Hyla taurina—Boulenger, 1882:363 [synonymized *Osteocephalus flavolineatus* Steindachner, 1862, with *O. taurinus* Steindachner, 1862].

Hyla planiceps—Boulenger, 1882:364.

Hyla (Trachycephalus) vilarsi Melin, 1941:40 [Holotype.—NHMG 488 from Taracuá, Rio Uaupés, Territorio do Amazonas, Brasil; Douglas Melin collector]. (*fide* Bokermann, 1966:64.)

Hyla depressa Andersson, 1945:73 [Holotype.—NHRM 1966 from the Río Pastaza watershed (? Provincia Pastaza), Ecuador; William Clarke-MacIntyre collector]. New synonymy.

Justification of Synonymy.—The holotype of *Osteocephalus taurinus* is a female having a snout-vent length of 103.9 mm. The diameter of the tympanum is 6.8 mm, 77.3 percent of the diameter of the eye. The skull is strongly exostosed, and the lateral edges of the frontoparietals are elevated so as to form distinct ridges. The skin on the dorsum is smooth. When we examined the type on 5 August 1969, the specimen was soft and badly faded to a pale creamy tan with pale brown transverse bars on the hind limbs and spots on the flanks. Steindachner (1862:79) described the coloration of the type: "In the preserved specimen the dorsum of the entire body, including fore and hind limbs, is a light yellow-brown color, which becomes lighter towards the venter. The belly is whitish, as are the undersides of the arms and legs. The throat is indistinctly marbled with brown. Roundish dark brown flecks are randomly distributed in a considerable number along the side of the body up to the eye; the tympanum is more or less fully surrounded by brown. A few discrete spots, always more or less drawn out in length, on the sides of the body, are also found on the posterior part of the back. The dorsal surfaces of the fore and hind feet are marked with somewhat obliquely arranged brown transverse bands, which are more intensively colored near the margin than in the middle of the band." (free translation from German.)

The holotype of *Osteocephalus flavolineatus* is a female having a snout-vent length of 81.8 mm. The diameter of the tympanum is 6.0 mm, 71.4 percent of the diameter of the eye. The skull is strongly exostosed, and the lateral edges of the frontoparietals are elevated so as to form a ridge on each side. The skin on the dorsum is very weakly tuberculate. We examined the type on 9 August 1969 and found it to be in excellent condition. The color pattern is unchanged from that described by Steindachner (1862:81). The dorsum is tan with irregular brown blotches on the back, spots on the flanks, and transverse bars on the limbs. A narrow creamy white, middorsal stripe extends from the snout to the vent. The subocular area is creamy tan, and the venter is tan. Boulenger (1882:363) questionably synonymized *flavolineatus* with *taurinus*. We have observed that a middorsal cream stripe occurs in about 10 percent of the specimens of *taurinus* and in some specimens of *buckleyi*. This is a common color morph in many species of *Eleutherodactylus*. In the absence of distinguishing morphological characteristics we can only conclude that the middorsal stripe is a pattern variant and that Boulenger was correct in synonymizing *flavolineatus* with *taurinus*.

The holotype of *Osteocephalus planiceps* is a male having a snout-vent length of 58.5 mm. The diameter of the tympanum is 4.9 mm, 77.8 percent of the diameter of the eye. The skull is moderately exostosed, and the lateral edges of the frontoparietals are distinctly elevated. The skin on the dorsum is tuberculate. Cope (1874:122) described the coloration of the type as follows: "Color above uniform dark brown, concealed surfaces on the limbs similar and without any markings. Sides a little varied with the white of the belt. A light border to the upper lip, and lighter line from the orbit to the angle of the mouth; dermal scapular fold pale edged. Femur and tibia with dark crossbands on the exposed surfaces." We examined the holotype on 25 September 1969, and found it to be soft and rubbed. The coloration remains much the same as described by Cope, who provided no means of distinguishing *planiceps* from *taurinus*. The coloration and morphometric and structural characters of the type of *planiceps* all fall within the range of variation displayed by series of *O. taurinus* from the upper Amazon Basin.

The type of *Hyla vilarsi* is a gravid female having a snout-vent length of 62.7 mm. The diameter of the tympanum is 4.8 mm, 73.8 percent of the diameter of the eye. The dorsal roofing bones of the skull are moderately exostosed, and the lateral edges of the frontoparietals are distinctly elevated. The skin on the dorsum is smooth.

Melin (1941:42) described the coloration of the holotype as follows: "Above uniform reddish brown; upper eyelids and sides of head darkish brown; below the rostral edge a narrow dark band, continuing as a broader light-edged one through the eye and tympanum towards the base of the forelimb and then farther on continuing along the sides as a line of black spots; sides of upper jaw whitish with traces of dark cross bars (one distinct under the eye); sides of body darkish with black spots and marble, often on a whitish ground; thighs, tibiae, and tarsi each with two broad light-edged, dark cross bars on a brownish ground (less distinct on thighs); sides of thighs finely mottled with brown; beneath whitish with small, sparse spots along jaw, on the chest and sides." We examined the type on 17 February 1969, at which time the specimen was somewhat desiccated, especially the hands and feet. The coloration remains much the same as described by Melin, except that he failed to note the presence of four elongate spots on the back.

The status of the names *Osteocephalus planiceps* Cope and *Hyla vilarsi* Melin was confused by Cochran and Goin (1970:322), who assigned these names to the synonymy of *O. leprieurii.* Bokermann (1966:64) placed *Hyla vilarsi* in the synonymy of *Osteocephalus taurinus* without justification. The type specimens of both *planiceps* and *vilarsi* have moderately exostosed dermal roofing bones and distinct cranial ridges. The type of *planiceps* has moderately large tubercles on the dorsum, and the type of *vilarsi* has spots on the throat, chest, and flanks and longitudinal markings on the back. All of these features are characteristic of *taurinus* and not of *leprieurii,* which lacks exostosis and cranial ridges and has transverse markings on the back, no spots on the throat, chest, and flanks, and in males has small dorsal tubercles.

The type of *Hyla depressa* is a male having a snout-vent length of 69.8 mm. The diameter of the tympanum is 5.2 mm, 77.6 percent of the diameter of the eye. The dorsal roofing bones of the skull are moderately exostosed, and the lateral edges of the frontoparietals are elevated. The skin on the dorsum is tuberculate. The dorsum is dull brown with a broad darker brown longitudinal mark having indistinct lateral edges from the snout to the post-sacral area. A narrow cream middorsal line extends from the snout to the vent. The side of the head is dark brown, palest posteroventral to the orbit. The posterior surfaces of the thighs are dull brown; the flanks are pale brown, and the ventral surfaces are pale creamy tan. Dark brown transverse bars are present on the limbs. When we examined the type on 3 January 1969, it was in excellent condition.

Andersson (1945:75) contrasted the type of *Hyla depressa* with *leprieurii* and *buckleyi*, but he did not compare his specimen with *taurinus*, from which it exhibits no distinguishing features.

Osteocephalus taurinus is a widespread and variable species, and it has received several specific names. We are convinced that *Osteocephalus taurinus* Steindachner, 1862, is the oldest available name for this large Amazonian species. The following names are junior synonyms: *Osteocephalus flavolineatus* Steindachner, 1862; *Osteocephalus planiceps* Cope, 1874; *Hyla (Trachycephalus) vilarsi* Melin, 1941; *Hyla depressa* Andersson, 1945.

Diagnosis.—1) Size large; sexual dimorphism evident; maximum observed snout-vent length in males 84.6 mm, in females 104 mm; 2) skin on dorsum in males bearing many moderately large, spinous tubercles; 3) skin on flanks smooth; 4) web extending to middle of antepenultimate phalange on inner edge of third finger; 5) dorsum brown usually with a large medial dark brown blotch or, less frequently, several dark spots; narrow middorsal yellow line present in some; 6) venter cream or tan with or without small, irregular brown flecks; 7) lips brown with vertical cream bar below eye in some, expanded into pale labial stripe posteriorly in some females; 8) flanks tan or cream with or without small, irregular brown spots; 9) dermal roofing bones of skull exostosed, casqued, and co-ossified (in large adults); 10) dermal sphenethmoid present; 11) nasals juxtaposed medially; 12) anteromedial margin of frontoparietals at mid-level of orbit; 13) frontoparietal fontanelle covered; 14) palatine serrate; 15) parasphenoid bearing odontoids; 16) zygomatic ramus of squamosal usually articulating with maxillary arch; 17) transverse processes of third presacral vertebra approximately equal in width to sacral diapophyses; transverse processes of presacral vertebrae 3-8 subequal in width; 18) intermandibularis and submentalis muscles connected; 19) supramandibular portion of interhyoideus extensively developed; associated skin forming everted pouch.

The moderately rugose dorsum (in males), large size, extensive webbing on the hand, and frontoparietal flanges in adults serve to distinguish *taurinus* from other members of the genus.

Distribution.—The Amazon Basin, the upper Orinoco Basin, and the Guianas. Most localities are below 500 m, but the species ascends the lower Amazonian slopes of the Andes to elevations of about 1000 m (Fig. 11). A record from Caracas, Venezuela, and those from Provincia Carchi and Provincia Esmeraldas, Ecuador, are considered to be erroneous. The latter specimens were included

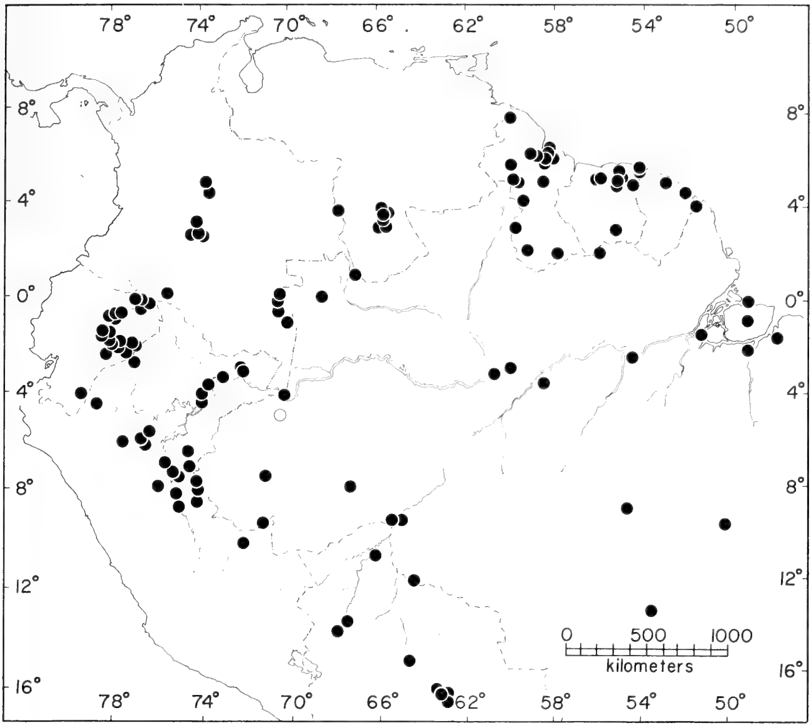

FIG. 11. Distribution of *Osteocephalus taurinus.*

in a collection sold to the University of Illinois; contained in the collection are many common Amazonian species unknown from the Pacific lowlands. 516 specimens from 151 localities.

Remarks.—This widespread species is highly variable in size and coloration. Striking differences in snout-vent length are evident in series from various parts of the range. The smallest calling males (CAS-SU 12351-6 from Rio Tapirapé, Brasil) have snout-vent lengths of 46.5-60.3 (mean 53.3) mm, whereas the largest (FMNH 140254, KU 92243-6, WCAB 9997, 10001, 10003-4 from Igarapé Marmelo, Brasil) have snout-vent lengths of 71.5-84.6 (mean 77.6) mm. Mean values of snout-vent lengths of males from other localities are: Río Pastaza drainage, Ecuador 73.8 mm, Surinam 67.7 mm, Río Ucayali drainage, Perú 57.6 mm, and Guyana 55.5 mm. Although the difference between the smallest and largest adults is highly significant, populations bridging the gap do exist. Furthermore, the geographic arrangement of small versus large frogs is a confusing mosaic. We have entertained the thought that we have included more than one species in *taurinus,* but on the basis of preserved specimens we are unable to detect consistent differences distinguishing two or more taxa.

The coloration and pattern of *taurinus* are so variable that no one series of statements can describe samples drawn from the entire range of species. We have been unable to determine geographic trends in color pattern; instead the variation within a given sample can encompass the variety known in most other samples. Two minor exceptions do exist. A narrow middorsal light stripe is present in some individuals from throughout the range, but striped specimens are most common in the upper Amazon Basin. The absence of dorsal markings is uncommon in the entire species, but it is most frequent in individuals from the Guianas. A few individuals, such as KU 105230, have scattered white spots on the dorsum.

The coloration of four males in life from Lago Agrio, Ecuador (KU 126652-5) was: "Dorsal ground color tan to dark brown with darker brown markings. Flanks creamy tan to yellow with brown or black flecks or mottling. Venter uniform creamy yellow or yellow with brown spots or reticulations. Iris greenish yellow with radiating black streaks and a median, horizontal reddish brown streak." (W. E. Duellman, field notes, 12 May 1969.) A female from Santa Cecilia, Ecuador (KU 123173), was: "Dorsum mottled olive-green and tan. Flanks tan with brown spots. Belly and throat creamy white, becoming tan posteriorly. Edge of upper jaw olive-green." (W. E. Duellman, field notes, 16 June 1968.) Another female from Santa Cecilia (KU 123175), was: "Brown dorsally with cream-colored mottling. Transverse bars on legs darker brown with cream-colored edges. Margin of upper lip creamy yellow. Anterior and posterior surfaces of thighs tan. Flanks white with brown spots. Venter creamy white. Iris greenish bronze with heavy radiating reticulations of black." (W. E. Duellman, field notes, 22 July 1968.)

The tendency for females to have a labial stripe posteriorly and the absence of dorsal tubercles in females has resulted in the identification of many such specimens as *O. leprieurii.*

Ontogenetic change in coloration is slight in *taurinus.* Most juveniles (less than 40 mm in snout-vent length) can be identified readily. There is a tendency for the dorsal markings of juveniles to consist of several small spots. Apparently with growth the spots usually coalesce, forming a large median blotch, but some adults retain the juvenile pattern. Cochran and Goin (1970:251) erroneously identified several juveniles from Colombia as *Hyla palpebrogranulata* Andersson.

Osteocephalus verrucigerus (Werner)

Hyla verrucigera Werner, 1901:601 [Holotype.—ZMB 16589 from "Ecuador"; Richard Haensch collector].

Hyla riopastazae Andersson, 1945:72 [Holotype.—NHRM 1960 from Baños, Río Pastaza, Provincia Tungurahua, Ecuador; William Clarke-MacIntyre collector].

Hyla orcesi Funkhouser, 1956:78 [Holotype.—CAS-SU 13150 from Río Pacayacu, tributary of Río Cotapino, Provincia Napo, Ecuador; collector unknown].

Osteocephalus orcesi—Cochran and Goin, 1970:317.

Osteocephalus verrucigerus—Trueb and Duellman, 1970:601 [Synonymized *Hyla riopastazae* Andersson, 1945, and *Hyla orcesi* Funkhouser, 1956, with *Hyla verrucigera* Werner, 1901].

Justification of Synonymy.—Trueb and Duellman (1970:605) discussed the assignment of the names in the synonymy of *O. verrucigerus;* only a brief resumé is given here.

The extant type of *Hyla verrucigera* is a juvenile male having a snout-vent length of 32.0 mm. The dorsum is smooth except for tubercles on the eyelids; the skin is loose, and the body is soft. The specimen is faded to a pale brown; indistinct dark spots are present on the back, and transverse bars are evident on the limbs.

The holotype of *Hyla riopastazae* is a gravid female having a snout-vent length of 64.7 mm. The dorsum is smooth. The dorsal ground color is pale brown with indistinct brown transverse bars on the limbs. The throat, chest, and belly are cream with brown spots and mottling.

The holotype of *Hyla orcesi* is an adult male having a snout-vent length of 52.6 mm. The dorsum is heavily tuberculate. The dorsum is dark brown with faint transverse bars on the forearms and feet; the ventral surfaces are creamy brown.

Trueb and Duellman (1970) provided conclusive evidence that the types of *H. verrucigera, riopastazae,* and *orcesi* are a juvenile, adult female, and adult male, respectively, of one species, the earliest available name for which is *Hyla verrucigera* Werner, 1901.

Diagnosis.—1) Size moderate, sexual dimorphism evident; maximum observed snout-vent length in males 54.3 mm, in females 65.8 mm; 2) skin on dorsum in males bearing large, keratinized tubercles; 3) skin on flanks smooth; 4) web extending to base of antepenultimate phalange on inner edge of third finger; 5) dorsum uniformly dark brown or black, with tan snout in females; 6) venter creamy white, heavily mottled with black or dark brown, especially in females; 7) lips marked with pale tan labial stripe and suborbital bar; 8) flanks dull reddish brown; 9) dermal roofing bones of skull lacking exostosis; 10) dermal sphenethmoid absent; 11) nasals widely separated medially; 12) anteromedial margin of frontoparietals at anterior border of orbit; 13) frontoparietal fontanelle covered; 14) palatine serrate; 15) parasphenoid bearing odontoids; 16) zygomatic ramus of squamosal extending approximately one-half of distance to maxillary arch; 17) transverse processes of third presacral vertebra approximately equal in width to sacral diapophyses; transverse processes of presacral vertebrae 3-8 subequal in width; 18) intermandibularis and submentalis muscles connected; 19) supramandibular portion of interhyoideus forming simple, tubular, posterolateral extension; associated skin unmodified.

Osteocephalus verrucigerus can be distinguished from other members of the genus by its uniformly dark dorsum, heavily mottled venter, and large, spinous tubercles on the dorsum in males.

Distribution.—Lower Amazonian slopes (500-1840 m) of the Andes and on the western fringe of the Amazon Basin in Ecuador and Perú; one locality (Acevedo) in upper Río Magdalena drainage in Colombia (Fig. 9). 40 specimens from 13 localities.

Remarks.—In life the dorsum in males is dull olive-green; the groin, anterior and posterior surfaces of the thighs, inner surfaces of limbs, and upper arms are dark brown. The ventral surfaces of the limbs are pinkish tan; the other ventral surfaces are pale creamy tan with reddish brown spots. The suborbital spot is pale greenish tan, and the iris is deep reddish brown. In females the dorsum is dull olive-brown; the anterior part of the head is tan, and the suborbital spot is yellowish tan. The groin and hidden surfaces of the limbs are dark reddish brown. The ventral surfaces of the limbs are brown; the throat and chest are creamy white, and the belly is reddish tan, both with dark brown mottling.

Considerable ontogenetic change occurs in coloration. Juveniles are pale above with a dark median dorsal blotch and dark transverse bars on the limbs. The venter is white. The change consists principally of an increase in dark pigment and subsequent obliteration of the juvenile pattern.

Tadpoles of this species have moderately long tails with low fins, robust bodies, two rows of labial papillae with median part of the upper lip bare, and two upper and five lower rows of teeth. Trueb and Duellman (1970) described the eggs, tadpoles, mating call, and variation in the adults.

GENERIC RELATIONSHIPS

Among the 33 genera currently recognized in the family Hylidae, there are two basic types of vocal sac structure (Duellman, 1970b), namely the subgular type and the lateral type. Only four hylid genera, all Neotropical lowland groups, are known to possess paired lateral vocal sacs; these are *Osteocephalus, Argenteohyla, Phrynohyas,* and *Trachycephalus.* The geographical distributions and morphological characteristics of these four genera suggest that they are more closely related to one another than with any other hylid genera.

Of the four genera, *Osteocephalus* is the most generalized in morphology, and, like *Phrynohyas,* has no specialized habits. *Osteocephalus* and *Argenteohyla* are similarly distinguished from *Phrynohyas* and *Trachycephalus* on the basis of vocal sac structure. The vocal sacs of *Osteocephalus* and *Argenteohyla* are posterior and protrude posterolateral to the angles of the jaws when they are inflated, whereas those of *Phrynohyas* and *Trachycephalus* are more lateral and protrude posterior to the angles of the jaws when inflated.

Although *Osteocephalus* and *Argenteohyla* have similar vocal sac structure, they are obviously distinct. The monotypic *Argenteohyla* is a rather specialized, semifossorial frog (Trueb, 1970b), characterized by smooth skin, moderate-sized digital discs, and a large inner metatarsal tubercle. The general architecture of the skull is not unlike that of *Osteocephalus;* the skulls of both are well roofed, broader than long, and characterized by posterolaterally oriented parasphenoid alae. *Argenteohyla* bears small, slightly curved prevomerine dentigerous processes in contrast to the large, angular processes of *Osteocephalus.* The skull of *Argenteohyla* shows specializations, apparently adaptations to its semifossorial mode of existence, which further distinguish the genus from *Osteocephalus.* In comparison with *Osteocephalus,* the cranium of *Argenteohyla* is slightly depressed anteriorly, the roofing bones extensively casqued, and the palatines robust.

Osteologically, *Osteocephalus* more closely resembles *Phrynohyas* than either of the other two genera, but *Osteocephalus* and *Phrynohyas* are clearly distinct on the basis of their respective vocal sac structure. Like *Osteocephalus,* skulls of the members of the genus *Phrynohyas* are broader than long, have extensive dermal roofing bones, and have posterolaterally oriented parasphenoid alae. In contrast to *Osteocephalus,* the dentigerous processes of the prevomers are curved, rather than angular in *Phrynohyas.* Furthermore, the latter genus is singularly distinguished from *Osteocephalus, Argenteohyla,* and *Trachycephalus* by having extensively developed parotoid glands that produce a viscous, milky volatile secretion.

Trachycephalus is the most readily identifiable of the four genera under discussion. Members of this genus are large frogs with heavily casqued and co-ossified skulls (Trueb, 1970a). The dermal roofing bones bear ornate and characteristic patterns of sculpturing. The medial ramus of the pterygoid does not articulate with the otic capsule, and the parasphenoid alae are laterally, rather than posterolaterally, oriented. A dermal sphenethmoid is present, and the parasphenoid bears odontoids. The basic structure of the skull has many characters in common with both *Osteocephalus* and *Phrynohyas.* The obvious modifications of dermal roofing bones and of palatal and suspensory elements seem to be specializations adapting members of the genus *Trachycephalus* to their peculiar phragmotic habits. The vocal sac structure of *Trachycephalus* is like that of *Phrynohyas* and therefore further distinguishes it from *Osteocephalus.*

Morphologically, *Osteocephalus* seems to be sufficiently diverse and generalized so as to represent a modern derivative of an ancestral type which might have given rise to *Phrynohyas, Trachycephalus,* and *Argenteohyla.* The specialized vocal sac structure in *Phrynohyas* and *Trachycephalus* suggests that these two genera may be rather closely allied and represent a single phyletic line from an ancestral stock similar to *Osteocephalus. Argenteohyla* is quite distinct from *Phrynohyas* and *Trachycephalus* and apparently represents a distinct phyletic line from the ancestral stock.

OCCURRENCE OF *OSTEOCEPHALUS* IN AMAZONIAN ECUADOR

All of our observations on members of this genus have been made at four localities: 1) Santa Cecilia at an elevation of 340 meters on the Río Aguarico, a tributary of the Río Napo, 2) Lago Agrio, 330 meters, about 14 kilometers east of Santa Cecilia, 3) Puerto Libre, 570 meters, on the Río Aguarico just east of its formation by the confluence of the Río Cofanes and Río Chingua, and 4) south slope of the Cordillera del Dué, above the Río Coca, 1150 meters. *Osteocephalus leprieurii* was found at all four localities, and *buckleyi* was found at all but the last; *taurinus* was found at Santa Cecilia and Lago Agrio, and *verrucigerus* was found only in the Cordillera del Dué. Our data are based on collections of 113 frogs and three lots of tadpoles, as well as observations on calling sites and young. The observations are summarized by species, as follows:

Osteocephalus buckleyi.—No breeding activity was observed. Males were found only at night in March, June, and July. One was perched on a *Heliconia* leaf in a swamp at Puerto Libre, and two were on bushes in the forest at Santa Cecilia. A gravid female was found on a recently felled tree at Lago Agrio on the night of 12 May 1969.

Osteocephalus leprieurii.—Males were heard calling sporadically at Puerto Libre in July 1968, and at Santa Cecilia in May 1969. A small chorus was found on the night of 12 May 1969 at Lago Agrio, where the frogs were perched on branches of fallen trees over a temporary pool. The call is a soft rattling chuckle. In late April and May many gravid females and males with well-developed nuptial excrescences were obtained from trees as they were felled at Lago Agrio. The reproductive condition of the frogs indicates that they probably breed in May. One individual called nearly every night from a large tree at Puerto Libre between 4-17 July 1968. The tree was felled on the latter date, but no frog was found. Two nights later apparently the same individual called from a bromeiad at a height of about 10 m on a large bamboo adjacent to the felled tree; the frog was collected when the bamboo was cut down.

Throughout the rainy months that we have worked in Ecuador (April-August) we have found occasional individuals perched on bushes or low trees at night. Large numbers of adults were observed only during a clearing operation which resulted in the felling of many large trees. Thus, it seems likely that *leprieurii* is a tree-top inhabitant. A partially digested adult male was removed from the stomach of a *Hemiphractus proboscideus*.

At Santa Cecilia many recently metamorphosed young and juveniles were found in June and July 1968. Most of these were on low bushes or herbs in swamp forest at night; some were found in unfolded *Heliconia* leaves by day, and one was observed on the forest floor by day. Snout-vent lengths of 18 specimens are 12.3-17.0 (mean 15.1) mm. The smaller frogs were recently metamorphosed as evidenced by the melanophore deposits above the vent. The coloration of the young is strikingly different from that of the adults (see account of *O. leprieurii*), so the association of the young and adults was not made until individuals with intermediate patterns were obtained at Lago Agrio in May 1969. Probably juveniles obtained in June and July are the offspring of an April or May breeding. We have been unable to associate tadpoles with this species.

Osteocephalus taurinus.—A small chorus occurred at Lago Agrio on 12 May 1969. Males were calling from the ground adjacent to a small pool amidst recently felled trees. The males were very wary and, when approached, jumped onto limbs and ran up branches; this behavior was noted by Bokermann (1964). The call consists of a series of low-pitched, short notes—like a slow trill—four to six notes per call group. Call groups are repeated two, three, or four times followed by a lapse of several minutes. Although no amplectant pairs were found, several gravid females were collected at Lago Agrio in May, so it can be safely assumed that the species breeds in May. From April through July occasional individuals were observed on bushes and trees at night. During clearing operations at Lago Agrio several individuals were obtained from the tops of trees as they were felled.

Osteocephalus verrucigerus.—Observations were made in a broad, shallow ravine, in which there was a small stream. On 2-4 August 1968, males were observed calling from low bushes and rocks at the edge of a quiet pool in the stream. The call consists of a series of well-pulsed, low-pitched, guttural notes produced at the rate of 5-10 per minute. One amplectant pair was found at the base of a bush adjacent to the pool on 3 August. Another female was found on a branch of a tree 2 m above the ground and 10 m from the stream. Tadpoles of this species were found in the quiet silt-bottomed pool.

SPECIMENS EXAMINED

The localities for each of the specimens examined are given in the following paragraphs. The arrangement of the data is as follows: 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 first in the most restricted political unit possible; localities which have not been found on maps or the positions of which are not known to us are given in quotation marks. Where more than one specimen is included under one museum number, the number of specimens is given in parentheses after the museum number. Unless noted otherwise, all specimens are alcoholics.

Osteocephalus buckleyi

BOLIVIA: *El Beni:* Ivón, BMNH 1967.2070-1. *Santa Cruz:* Buenavista, CM 4333, 4339, UMMZ 66563-5.

BRASIL: *Amapá:* No specific locality, WCAB 13284.

COLOMBIA: *Amazonas:* Río Guacaya, USNM 152759. *Huila:* Acevedo, Río Suaza, FMNH 69702. *Nariño:* Rumiyacu, FMNH 54756. *Meta:* Río Guejar, Campamento La Macarena, USNM 152199.

ECUADOR: No specific locality, NHMW 6209, WCAB 35499. *Chimborazo:* Pallatanga, BMNH 1947.2.13.46; Santiago, FMNH 42529. *Morona-Santiago:* "Río Santiago" (= Río Zamora), MIZS 2950. *Napo:* Lago Agrio, KU 126646; Puerto Libre, Río Aguarico, KU 123172; Santa Cecilia, AUM 8138, KU 105208-9, 109506, 123171. *Pastaza:* Alpayacu, BMNH 1912.11.1.64; Canelos, BMNH 1947.2.13.40-1, 1947.2.13.43-5; Colonia Mena, Río Conambo, ZSM 33/1962; Don Tomás, USNM 166014; Guaché, Río Pastaza, AMNH 79986; Río Bobonaza, USNM 166005; Río Capahuari, USNM 166554; Río Conambo at Río Shiona-yacu, USNM 166018; Río Copataza, upper Río Pastaza, USNM 166007-13; Río Pastaza, NHRM 1946; Río Pucyacu, USNM 165997 (skeleton), 165998-6001; Río Rutuno, USNM 166006; Río Villano, USNM 166002-4; Sarayacu, BMNH 1947.2.13.36-9, MCZ 26090, ZMB 10166.

GUYANA: *Mazaruni-Potaro:* Kartabo, AMNH 70971; Membaru River, upper Mazaruni River, UMMZ 85168; Oko Mountains, FMNH 26722-3. *North West:* Amakura River, Haulover, UMMZ 83558-9. *Rupununi:* Marudi River, AMNH 46233; Shudi-kar-wau, AMNH 49252. *West Demerara:* Dunoon, UMMZ 52449, 52508.

PERÚ: *Junín:* Chanchamayo, BMNH 1911.12.13.79-80. *Loreto:* Andoas, AMNH 79984-5; Cashiboya, AMNH 43454; San Antonio, Río Itaya, AMNH 43218. *Puno:* Yahuaramayo, BMNH 1913.2.25.7.

SURINAM: *Suriname:* Powakka, CM 44217.

SOUTH AMERICA: No specific locality, NHMW 6208.

Osteocephalus leprieurii

BRASIL: *Acre:* Tarauacá, FMNH 83247. *Amazonas:* Rio Javari, Benjamin Constant, CAS-SU 12620; Río Uaupés, north of Rio Japú, NHMG 489.

COLOMBIA: *Amazonas:* Gino-goje, lower Río Apoporis, MCZ 28038, 28040-2, 28044, USNM 152136-8.

ECUADOR: No specific locality, WCAB 35452-3; "Napo-Pastaza," USNM 166571. *Napo:* Avila, UMMZ 92093; south slope Cordillera del Dué, KU 123170; Lago Agrio, KU 125961-2 (skeletons), 126611-44, UMMZ 129326 (2); Limón Cocha, Río Napo, KU 99210-6, UIMNH 63087-9, 63098, 63106-9, 63118-9, 64802-4, 64858, 87998-9, 88001-30, 88437-8, 88580, 88604-5, 89852-97, 89999-90000; Loreto, CAS-SU 11439, WCAB 36526; Puerto Libre, Río Aguarico, KU 123190-1; Puerto Napo, UIMNH 55818-20; Río Cotapino, UMMZ 92094; Río Napo, UMMZ 92078; Santa Cecilia, AUM 8099, 8102, 8113-5, 8127-9, 8131, 8137, 8139-46, 8148, KU 105210-20, 109509-11, 111971, 122964-87, 123169, 126645. *Pastaza:* Canelos, BMNH 1947.2.13.42, KU 120915; Río Alpayacu, UMMZ 92079; Río Arajuno, USNM 166560-2, WCAB 40176; Río Oglán, USNM 16655203, 166558; Río Rutuno, USNM 166559; Río Shilcayacu, below Puyo, USNM 166557; Río Villano, USNM 166551.

FRENCH GUIANA: No specific locality, MNHN 4629. *Inini:* Lunier River, MNHN 98/217.

GUYANA: *Mazaruni-Potaro:* Kartabo, AMNH 70967-8, 70972, 70976. *Rupununi:* Shudi-kar-wau, AMNH 49255. *West Demerara:* Demerara Falls, BMNH 72.10.16.23, 72.10.16.37-8.

PERÚ: *Loreto:* Estirón, Río Ampiyacu, MZUSP 31033-4; Pebas, CAS-SU 3158, 3160; Roaboya, AMNH 43064.

SURINAM: No specific locality, MCZ 2036, RMNH 11468. *Marowijne:* Camp 3, RMNH 13045-6; Wane Creek North, RMNH 11469-70. *Saramacca:* Right Coppename River, RMNH 11467.

Osteocephalus pearsoni

BOLIVIA: *El Beni:* upper Río Beni, below mouth of Río Mapiri, MCZ 15565, UMMZ 57548, 67464-5; Rurrenbaque, UMMZ 57533.

PERÚ: *Pasco:* Yaupi, KU 136312.

Osteocephalus taurinus

BOLIVIA: *El Beni:* Ivón, BMNH 1967.2040; Reyes, UMMZ 57532. *La Paz:* San Ernesto, Mapiri District, BMNH 1901.8.2.54. *Santa Cruz:* Buenavista, AMNH 33951-2, 33958, BMNH 1927.8.1.19, 1927.8.1.118, FMNH 27091, UMMZ 63319-21, 63959(2), 63961(2), 66566(2), 66567, 66568(2), 66569 (2), 66570, 66571(2), 66575-6, 68196; Río Mamore, 2 km N Boca Chaparé, AMNH 79324; Sara, CM 3840-1; Surutu, CM 3814-5.

BRASIL: No specific locality: "Interior," BMNH 74.7.16.8-9. *Acre:* Plácido de Castro, MZUSP 6518; Tarauacá, WCAB 2496. *Amazonas:* Cucuí, NHMW 16495; Manacapurú, ZMB 28492, ZSM 278/1925; Manáus, MCZ 56281, NHMW 16492; Maués, AMNH 69623, 76177; Taracuá, NHMG 488, WCAB 18463-4. *Mato Grosso:* Mabuca, MZUSP 4272; Posto Coluene, Rio Xingú, WCAB 812; "Puerto Cabello," AMNH 3154; Tapirapé, AMNH 73647-62, CAS-SU 12351-6, MNHN 46/324. *Pará:* No specific locality, MPEG 623-6; Belém, KU 129866; Cachimbo, FMNH 175876, UIMNH 42149, WCAB 813; Cametá, NHMW 15892; Gurupá, BMNH 96.6.29.13; Ilha de Marajó, BMNH 1923.11.9.20-4; Ilha Mexicana, ZSM 111/1911, 112/1912; "Ponto Dois Indios," BMNH 1939.1.5.5; Santarém, BMNH 75.10.22.1-4, MCZ 354. *Rondonia:* Abuná, CAS 49773-4, FMNH 64239; Forte Principe da Beira, WCAB 10230; Igarapé Marmelo, FMNH 140254, KU 84725 (skeleton), 92243-6, 92247-8 (skeletons), WCAB 9997, 10001, 10003-4; Porto Velho, MZUSP 16343.

COLOMBIA: *Amazonas:* Gino-goje, lower Río Apoporis, USNM 152139; Leticia, USNM 152010-1; Raudal de la Playa, lower Río Apoporis, MCZ 28050; Río Apoporis, MCZ 28060. *Boyacá:* Sutatenza, USNM 152054-6. *Cundinamarca:* Medina, MCZ 16269-71, USNM 152089-90, 152092-7, 152757. *Meta:* El Mico, Río Guejar, USNM 152203; Río Duda, Sierra de Macarena, AMNH 79914; Río Guapaya, Sierra de Macarena, FMNH 81332; Río Guaviari, Casa de Piedra, UTA No number. *Putumayo:* Río Mecaya, FMNH 69711-4, 69716. *Vaupés:* Gomogoje, lower Río Apoporis, MCZ 28048.

ECUADOR: No specific locality, WCAB 35451, 35785; "Oriente," UMMZ 90418. *Carchí:* below Salinas, USNM 166059. *Esmeraldas:* Carondelet, UIMNH 53560-9; Lagartera, Río Caoni, UIMNH 53441, 53458-79. *Morona-Santiago:* Macuma, UIMNH 63142-3, 63145, 63147, 63151, 63154, 63157, USNM 166060. *Napo:* Avila, UMMZ 92077; Cuyabeno, UIMNH 63158, 90111; Lago Agrio, KU 126647-55; Limón Cocha, Río Napo, AUM 8132-4, KU 99207-8, 99421-3, 99424 (skeleton), 99425, UIMNH 64801, 87798, 87800, 88032-5, 88576, 90066, 90082, 90102, 90104, 90314, 90984; Loreto, WCAB 35352; Río Cotapino, UMMZ 92080; Río Napo, UMMZ 84120; San José Abajo, AMNH 1295, 1449, 22180, 79990; Santa Cecilia, AUM 8117, 8150, KU 105230-3; south slope Volcán Sumaco, USNM 166570. *Pastaza:* No specific locality, ZSM 31/1956; Arajuno, USNM 165995; Bufeo, lower Río Bobonaza, USNM 166046-8; Canelos, BMNH 80.12.5.179, 1947.2.13.48, UMMZ 89066;

Don Tomás, Río Bobonaza, USNM 166049-50; Montalvo, CAS-SU 10320, USNM 165987-9, 166058, 166566; 2.5 km SE Puyo, USNM 166051; Río Arajuno, USNM 166043-5; Río Arajuno (headwaters), USNM 166053; Río Bobonaza, WCAB 3613-4, 35504; Río Capahuari, USNM 165990, 166555-6; Río Capahuari (headwaters), USNM 166057; Río Conambo, USNM 166569, ZSM 28/1962, 35/1962; Río Conambo at Río Ollaguanga, USNM 166568; Río Conambo at Río Shiona-yacu, USNM 166019, 166563-5; Río Corrientes, USNM 195994, 166020-38, WCAB 3841-2; Río Huiyo-yacu, Pico de Conambo, USNM 166052; Río Pastaza, MCZ 19697; Río Pastaza (drainage), NHRM 1966, USNM 165996; Río Pindo, USNM 166039-41; Río Pindo at Río Tigre (village), USNM 165992-3, 166042; Río Pucayacu, USNM 166054, 166056; Río Rutuno, USNM 166055; Río Solis, upper Río Bobonaza, WCAB 39914; Río Villano, USNM 165991, 166567; Sarayacu, BMNH 80.12.5.213, 80.12.5.239-40, MZUSP 323; Shell Mera, KU 99420. *Zamora-Chinchipe:* "Yani-Inzari," AMNH 43259, 43394; Zamora, AMNH 78928.

FRENCH GUIANA: *Cayenne:* Crique Grégoire, UP 40; Maripa, Oyapok River, UP 72; Oyapok River, UZM 1473. *Inini:* Crique Gabrielle, UP 118-20.

GUYANA: No specific locality: RMNH 1873(3), ZMB 3102(2). *East Demerara:* Atkinson Field, ASU 11622. *Mazaruni-Potaro:* Chinapora River, upper Potaro River, BMNH 1905.11.1.20-1; Kamakusa, AMNH 21416, 21418-9, 21422; Kartabo, AMNH 11689, 11691, 11697-9, 11703, 11706-8, 23107, 39730, 70966, 70969-70, 70973-5, USNM 118057; Moraballi Creek, Essequibo River, BMNH 1930.10.10.47-51; Oko Mountains, FMNH 26692-705; upper Potaro River, Tung District, BMNH 1905.11.1.40; Rockstone, FMNH 26591. *North West:* Amakura River, Haulover, UMMZ 83735. *Rupununi:* north of Acaray River, west of New River, KU 69747-8; Kuyuwini Landing, AMNH 46283; Pakaraima Mountains, BMNH 1933.6.19.49; Shudi-kar-wau, AMNH 10665, 39637, 49256(2). *West Demerara:* Demerara, CAS 54773-4; Demerara Falls, BMNH 72.10.16.16-22, 72.10.16.25-32; Dunoon, MCZ 4834, UMMZ 46736, 52493-4, 52502, 52504-5, 57271; Vryheid, BMNH 78.12.13.18.

PERÚ: *Amazonas:* Río Cenepa, AMNH 43400. *Huanuco:* Monte Alegre, Río Pachitea, AMNH 43014, 43019. *Loreto:* Achinamisa, Río Huallaga, AMNH 42178, 42502; Andoas, Río Pastaza, AMNH 79991; Cashiboya, AMNH 43388, 43453; Estirón, Río Ampiyacu, CAS 93264-74, 93276, 93278-9, 93281, 93283-6, 93289, 93311, 93327; Igarapé Champuia, upper Río Curiuja, MZUSP 10339; Iquitos, AMNH 42204, 42442, 43468, NHMW 6118; Lago de Miraño, mouth of Río Napo, AMNH 42712, 43186; Nauta, ANSP 11399; Ollanta, AMNH 42865; Pampa Hermosa, Río Cushabatay, AMNH 43124, 43146; Pebas, CAS-SU 6375; Pucallpa, MJP 101(2), 140(3); Punga, Río Tapiche, AMNH 43194; "Rancho de Indiana, Iquitos District," MVZ 16890; upper Río Abujao, AMNH 42908; Río Itaya, AMNH 42755; upper Río Pisqui, AMNH 43536; Río Tapiche at Río Contaya, AMNH 42983; Río Utoquinia at Brasilian frontier, AMNH 43137; Sobral, Río Tamaya, AMNH 43242; Yurimaguas, BMNH 84.2.18.50. *San Martín:* Cainarachi, AMNH 42763; Moyobamba, ZSM 19/1914.

SURINAM: No specific locality, BMNH 70.3.10.67, NHMW 18433.3. *Brokopondo:* Afobaka, RMNH 16536; Brownsweg, RMNH 16537; Railway km. 121, RMNH 16534. *Marowijne:* Djai Creek, RMNH 16513-4; Maroni River, ZMB 8240, 8531; Nassaugebergte, RMNH 16517-33; Paloemeu, USNM 159025; Swamp Camp, RMNH 16515. *Nickerie:* Sipaliwini, RMNH 16538. *Saramacca:* Left Coppename River, RMNH 16535; Tibiti, RMNH 16516.

Suriname: Berlijn, RMNH 15064; Powakka, CM 44226; Zanderij, CM 50568.

VENEZUELA: *Amazonas:* Cerro Duida, UPR-M 2875; Cerro Marahuaca, UPR-M 114-5; Esmeralda, AMNH 23174; Iniridi, SMF 2640; La Culebra, MCZ 28572, UPR-M 117; Laguna, between Tama Tama and Esmeralda, UPR-M 2760; Río Pescado, AMNH 23177; Tapara, UPR-M 113. *Distrito Federal:* Caracas, BMNH 51.7.17.182.

Osteocephalus verrucigerus

COLOMBIA: *Huila:* Acevedo, Río Suaza, FMNH 69709-10.

ECUADOR: No specific locality, ZMB 16589. *Napo:* Avila, UMMZ 90413; south slope Cordillera del Dué, KU 123176-88, 123189 (skeleton), 124208 (eggs), 124209-11 (tadpoles); L'Alegria, USNM 167472-3; Río Pacayacu, tributary of Río Cotapino, CAS-SU 13150; southeast slope Volcán Sumaco, CAS-SU 11442. *Pastaza:* Abitagua, CAS-SU 5067, FMNH 25791, 27619, UMMZ 90414, 92092; Alpayaca, Río Pastaza, BMNH 1912.11.1.64; Mera, UMMZ 90412(4). *Tungurahua:* Baños, NHRM 1960.

PERÚ: *Ayacucho:* La Mar, Sivia, Río Apurimac, FMNH 39853. *Huanuco:* Río Pachitea, midway between Puerto Victoria and Puerto Inca, CAS-SU 17745. *Junín:* Satipo, MJP 38.

LITERATURE CITED

ANDERSSON, L. G.

1945. Batrachians from east Ecuador collected 1937, 1938 by Wm. Clarke-MacIntyre and Rolf Blomberg. Arkiv Zool., 37A(2):1-88.

BOKERMANN, W. C. A.

1964. Field observations on the hylid frog *Osteocephalus taurinus* Fitz. Herpetologica, 20:252-255.

1966. Lista anotada das localidades tipo de anfíbios Brasileiros. São Paulo, 183 pp.

BOULENGER, G. A.

1882. Catalogue of the Batrachia Salientia s. Ecaudata in the collection of the British Museum, ed. 2, London, xvi+503 pp.

COCHRAN, D. M. and C. J. GOIN

1970. Frogs of Colombia. Bull. U.S. Natl. Mus., 288:xii+655 pp.

COPE, E. D.

1867. On the families of the raniform Anura. Jour. Acad. Nat. Sci. Philadelphia, 2:189-206.

1874. On some Batrachia and Nematognathi brought from the upper Amazon by Prof. Orton. Proc. Acad. Nat. Sci. Philadelphia, 25:120-137.

DUELLMAN, W. E.

1970a. Identity of the South American hylid frog *Garbeana garbei.* Copeia, (3):534-538.

1970b. The hylid frogs of Middle America. Monog. Mus. Nat. Hist., Univ. Kansas, 1:xi+753 pp.

DUMÉRIL, A. M. C. and G. BIBRON

1841. Erpétologie générale ou histoire naturelle compléte des reptiles, vol. 8. Paris, 792 pp.

FITZINGER, L.

1843. Systema reptilium. Vienna, ix+106 pp.

FUNKHOUSER, J.
1956. New frogs from Ecuador and southwestern Colombia. Zoologica, 91:73-80.

GAIGE, H. T.
1929. Three new tree-frogs from Panama and Bolivia. Occas. Papers Mus. Zool. Univ. Michigan, 207:1-6.

GOIN, C. J.
1961. Synopsis of the genera of hylid frogs. Ann. Carnegie Mus., 36:5-18.

MELIN, D.
1941. Contribution to the knowledge of Amphibia of South America. Göteborgs Kungl. Vetensk.-och Vitterh.-Sam. Handl., Ser. B, 1(4):1-71.

PERACCA, M. G.
1904. Viaggio del Dr. Enrico Festa nell' Ecuador e regioni vicine. Reptile ed amfibii. Boll. Mus. Zool. Anat. Comp., Univ. Torino, 19:1-41.

STEINDACHNER, F.
1862. Über zwei noch unbeschriebene Batrachier. Arch. Zool. Anat. Fisiol., 2:77-82.
1867. Amphibien. Novara Expedition. Zool. Theil, 1, Vienna, 70 pp.

TRUEB, L.
1970a. The evolutionary relationships of casque-headed treefrogs with co-ossified skulls (family Hylidae). Univ. Kansas Publ. Mus. Nat. Hist., 18:547-716.
1970b. The generic status of *Hyla siemersi* Mertens. Herpetologica, 26:254-267.

TRUEB, L. and W. E. DUELLMAN
1970. The systematic status and life history of *Hyla verrucigera* Werner. Copeia (4):601-610.

TYLER, M.
1971. The phylogenetic significance of vocal sac structure in hylid frogs. Univ. Kansas Publ. Mus. Nat. Hist., 19:319-360.

WERNER, F.
1901. Ueber Reptilien und Batrachier aus Ecuador und Neu-Guinea. Verh. Zool.-Bot. Gesell. Wien, 50:593-614.

UNIVERSITY OF KANSAS PUBLICATIONS

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NOTEWORTHY RECORDS OF BATS FROM NICARAGUA, WITH A CHECKLIST OF THE CHIROPTERAN FAUNA OF THE COUNTRY

By

J. Knox Jones, Jr.,[1] James Dale Smith,[2]
Ronald W. Turner[3]

Nicaragua occupies a strategic position in Central America with respect to mammalian distributional patterns, but relatively little has been published concerning the fauna of the country and its zoogeographic relationships. The present paper records information on distribution, variation, and natural history of 40 species of bats from Nicaragua, 14 of which are here recorded for the first time from the country. Appended is a checklist of the chiropteran fauna of Nicaragua in which only primary literature with actual reference to specimens from the republic is cited.

The specimens upon which this report is based are, with few exceptions, in the collections of the Museum of Natural History of The University of Kansas. Some of our material was obtained in 1956 by J. R. and A. A. Alcorn, field representatives of the Museum and sponsored by the Kansas University Endowment Association; most of the specimens, however, were obtained by field parties of which we were members that worked in Nicaragua in 1964, 1966, 1967, and 1968 under the aegis of a contract (DA-49-193-MD-2215)

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[1] Curator, Division of Mammals, Museum of Natural History, University of Kansas.

[2] Assistant Professor, Department of Biology, California State College, Fullerton, California.

[3] Assistant Professor, Department of Biology, St. Benedicts College, Atchison, Kansas.

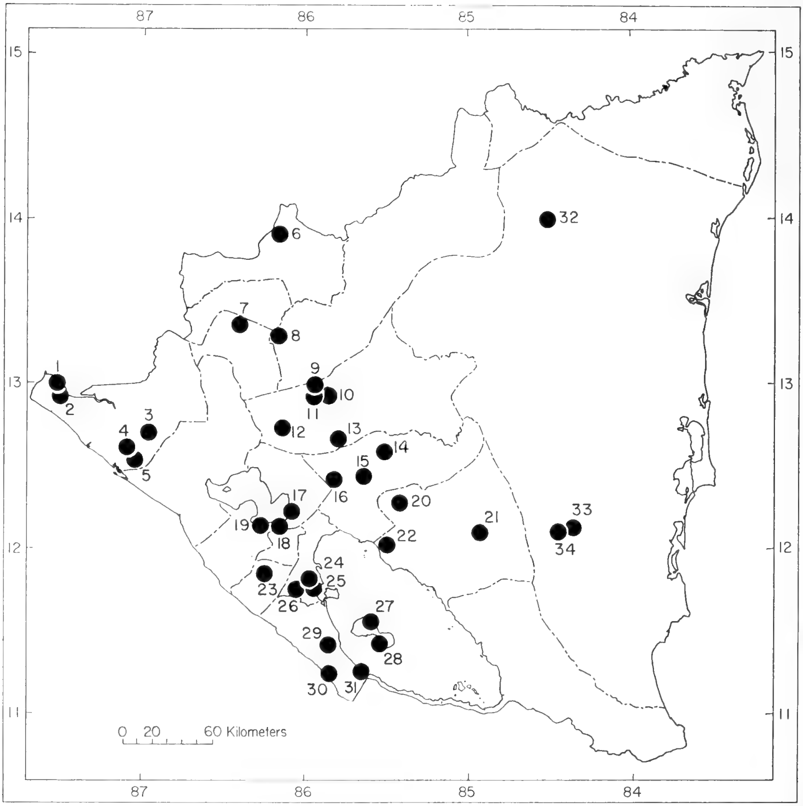

Fig. 1.—Map of Nicaragua showing location of place-names associated with specimens reported in this paper. Localities, identified by number, are as follows: 1, Potosí; 2, Cosigüina; 3, Hda. Bellavista, Volcán Casita; 4, Chinandega; 5, San Antonio; 6, Jalapa; 7, Condega; 8, Yalí; 9, Santa María de Ostuma; 10, San Ramón; 11, Matagalpa; 12, Darío; 13, Esquipulas; 14, Santa Rosa; 15, Boaco; 16, Teustepe; 17, Tipitapa; 18, Sabana Grande; 19, Managua; 20, Cuapa; 21, Villa Somoza; 22, Hato Grande; 23, Diriamba; 24, Guanacaste; 25, Mecatepe; 26, Nandaime; 27, Alta Gracia, Isla de Ometepe; 28, Mérida, Isla de Ometepe; 29, Rivas; 30, San Juan del Sur; 31, Sapoá; 32, Bonanza; 33, El Recreo; 34, Cara de Mono.

between the U.S. Army Medical Research and Development Command and The University of Kansas. Place-names associated with localities mentioned in the text from which specimens at Kansas were collected are plotted on Fig. 1.

In the accounts that follow, departments in Nicaragua are listed alphabetically, but localities within each department are arranged from north to south; elevations are given in meters or feet, depending on which was used on specimen labels. All specimens are in the Museum of Natural History of The University of Kansas unless noted otherwise. We are indebted to Drs. Charles O. Handley, Jr., and Ronald Pine of the U.S. National Museum (USNM) for lending us certain critical specimens.

ACCOUNTS OF SPECIES

Saccopteryx leptura (Schreber, 1774)

Two specimens from El Paraíso, 1 km N Cosigüina, 20 m, Chinandega, on the Cosigüina Peninsula, provide the fourth locality of record for this white-lined bat in Nicaragua. Jones (1964a:506) and Davis *et al.* (1964:375) earlier reported a total of eight specimens from the departments of Managua and Zelaya. The species is known as far north in Middle America as Chiapas (Carter *et al.*, 1966:489).

Our two bats, both females, were shot on the evening of 1 March 1968 as they foraged around a yard light. One carried an embryo that measured 8 mm (crown-rump), whereas the other was reproductively inactive.

Peropteryx macrotis macrotis (Wagner, 1843)

Four females (one young and three adult) captured 5 km N and 9 km E Condega, 800 m, in Madriz, on 23 June 1964, provide the first record of this small sac-winged species from Nicaragua. The bats were shot from daytime roosts in small, well-lighted, cave-like spaces formed among immense blocks of granite in a small patch of tropical deciduous forest surrounded by extensive pine-oak woodland. None of the adult females was reproductively active. *Glossophaga soricina, Diphylla ecaudata,* and a large nursery colony of *Desmodus rotundus* were found in association with the *Peropteryx.* Measurements of our specimens agree closely with those reported for material from El Salvador (Felten, 1955:284) and Costa Rica (Starrett and Casebeer, 1968:3-4).

Noctilio labialis labialis (Kerr, 1792)

Specimens.—Boaco: 4 km W Teustepe, 140 m, 9. *Chontales:* Hato Grande, 13 km S, 8 km W Juigalpa, 60 m, 49. *Rivas:* 4 km S, 1.5 km E Alta Gracia, 40 m, Isla de Ometepe, 1; Finca Amayo, 13 km S, 14 km E Rivas, 40 m, 4. *Zelaya:* S side Río Mico, El Recreo, 25 m, 1; Cara de Mono, 50 m, 2.

This species has been reported previously from Nicaragua by several authors. All our specimens were netted over small streams or shot as they foraged; parts of scarabids and lepidopterans were found in the mouths of several individuals shot at Finca Amayo. Twenty-six of 31 autopsied females taken in April were pregnant, each containing a single embryo—average crown-rump length 16.7 (5-26) mm. Testes of 15 males collected in April had an average length of 4.6 (2-7) mm, those of four taken in June, 5.2 (4-6) mm.

We follow Cabrera (1958:55), Husson (1962:63), and Handley (1966b:758) in use of the subspecific name *labialis*, the type locality of which is the "Mosquito shore" of Nicaragua, rather than Perú as suggested by Hershkovitz (1949:433-434).

Noctilio leporinus mexicanus Goldman, 1915

Specimens.—Chinandega: Potosí, 5 m, 2. *Chontales:* Hato Grande, 13 km S, 8 km W Juigalpa, 60 m, 4. *Rivas:* 4 km S, 1.5 km E Alta Gracia, 40 m, Isla de Ometepe, 4; Mérida, 40 m, Isla de Ometepe, 2; Finca Amayo, 13 km S, 14 km E Rivas, 40 m, 1.

This fish-eating species, first reported from Nicaragua by Davis *et al.* (1964:376), apparently occurs throughout Middle America, although known from the region by comparatively few records. We have 13 additional Nicaraguan specimens as listed above.

The two individuals (both females, one pregnant with an embryo that measured 20 mm) from Potosí were caught on 6 March in a mist net set over a large pool in a shallow estuarine stream; the mouth of the stream opened into the Gulf of Fonseca approximately 200 yards below our netting site. Other individuals of this species were observed as they foraged over large pools formed at high tide near the mouth of the stream. Our other specimens were caught in mist nets set over fresh water streams near Lake Nicaragua or along the shores of the lake. A female from near Alta Gracia, caught on 27 March, carried a single embryo that measured 41 mm, whereas one from Finca Amayo was lactating on 25 June. Four males taken on Isla de Ometepe in late March and early April had a mean testicular length of 9.5 (8-10) mm.

Pteronotus davyi fulvus (Thomas, 1892)

Specimens.—Chontales: Cuapa, 4. *Matagalpa:* 3 mi E San Ramón, 126.

This small naked-backed bat has not been reported previously from Nicaragua. Autopsy of seven females collected on 9 May near San Ramón revealed that four were pregnant, each with a single embryo—average crown-rump length 25.0 (21-29) mm.

The distribution of *P. davyi* is poorly known in much of Central America. The species was reported only recently from Costa Rica (Starrett and Casebeer, 1968:8) and is unknown from Panamá. We assign our specimens tentatively to the subspecies *fulvus* on geographic grounds.

Pteronotus parnellii fuscus (J. A. Allen, 1911)

Specimens.—Boaco: Santa Rosa, 17 km N, 15 km E Boaco, 300 m, 1; Los Cocos, 14 km S Boaco, 220 m, 1. *Chinandega:* 6.5 km N, 1 km E Cosigüina, 10 m, 1. *Zelaya:* Bonanza, 850 ft, 1; 2 mi SW Bonanza, 600 ft, 1; S side Río Mico, El Recreo, 25 m, 1; Cara de Mono, 50 m, 4.

Although this species is widespread in Middle America, it has been known previously from Nicaragua only by a specimen from "Chontales" (Miller, 1902:402). All of our specimens were captured in mist nets. Two adult females (one taken on 28 February and the other on 8 March) each carried a single embryo (13 and 18 mm in crown-rump length, respectively); a female taken in April was lactating and had a flaccid uterus suggesting relatively recent parturition. Adult females captured in the months of June, July, and August evidenced no sign of reproductive activity. Two of these were in dark, fresh pelage, but one captured on 24 June and another on 28 July were molting. In both individuals, active molt evidently had slowed or subsided and remnants of the old pelage (rich ochraceous orange) were confined to a narrow strip at the lateral edges of the body.

We tentatively apply the subspecies name *fuscus* to our Nicaraguan bats on geographic grounds; one of us (Smith) currently is investigating geographic variation in the genus *Pteronotus.*

Pteronotus suapurensis (J. A. Allen, 1904)

Specimens.—Chontales: Cuapa, 1. *Matagalpa:* 3 mi E San Ramón, 24. *Zelaya:* Cara de Mono, 25 m, 4.

This relatively poorly known monotypic species occurs from southern Veracruz to the Amazon Basin. It has been reported from several localities in Central America including one in Nicaragua (Goodwin, 1942a:88). Three pregnant females from near San Ramón (9 May) carried embryos that had crown-rump lengths of 27, 27, and 28 mm, and two netted on 24 April at Cara de Mono each had an embryo that measured 22 mm. All of our specimens are in bright pelage that is fulvous red in color.

Micronycteris megalotis mexicana Miller, 1898

Specimens.—Carazo: 3 km N, 4 km W Diriamba, 600 m, 5. *Granada:* Hda. Mecatepe [2 km N, 11.5 km E Nandaime], 5. *Managua:* 5 mi NW Managua, 1. *Matagalpa:* Río Viejo, 7 mi WNW Darío, 4; 11 mi SE Darío, 1. *Zelaya:* S end Isla del Maíz Grande, 9.

The individuals from Isla de Maíz Grande were shot on 30 June as they flew from small caves and crevices in rocky outcrops on the south end of the island. Of the three adult females obtained at

TABLE 1.—Selected measurements of adults of two subspecies of *Micronycteris megalotis* from Nicaragua. Superscript numbers indicate fewer specimens averaged than indicated in left-hand column.

Number of specimens averaged or catalogue number, and sex	Length of forearm	Greatest length of skull	Zygomatic breadth	Breadth of braincase	Length of maxillary toothrow
Micronycteris megalotis mexicana, west-central Nicaragua[a]					
Average 8 (3♂, 5♀)	35.4	19.5^6	9.5	8.0^7	7.5
Minimum	33.0	18.8	9.1	7.7	7.3
Maximum	38.1	20.3	9.8	8.2	7.7
Isla del Maíz Grande, Nicaragua					
Average 6 (3♂, 3♀)	35.6	19.4	9.2	7.8	7.4
Minimum	34.5	19.1	9.0	7.7	7.3
Maximum	37.0	19.8	9.3	7.9	7.5
Micronycteris megalotis microtis, Greytown, Nicaragua (holotype)					
USNM 16366/23364, ♂	31.5	18.2	8.8	7.6	6.9
Río Coco, Nicaragua (AMNH)					
Average 6 (3♂, 3♀)	33.6	18.9^3	—	7.5^3	7.1^3
Minimum	32.7	18.8	—	7.4	7.0
Maximum	34.2	19.0	—	7.6	7.2
Bonanza, Nicaragua					
KU 96251, ♂	32.3	18.4	8.8	7.6	7.0

[a] Specimens labeled with reference to Darío, Diriamba, and Managua.

that time, two were lactating; each was accompanied by a young, the forearms of which measured 19.7 (male) and 21.3 mm (female). Two adult males from Isla del Maíz Grande had testes 2 mm in length.

Four of the five specimens taken northwest of Diriamba were shot from a daytime retreat in a culvert; the fifth was caught by hand as it attempted to fly out of a hollow, fallen tree. Two adult females captured on 31 March were pregnant, each carrying a single embryo (13 and 14 mm in crown-rump length), whereas two obtained on 14 August showed no sign of reproductive activity. An adult male, also taken on 14 August, had testes 2 mm in length. Of three additional adult females, one captured on 3 June was pregnant (embryo 21 mm in crown-rump length), whereas two obtained on 14 April evinced no gross reproductive activity.

The subspecies *mexicana* has not been reported previously from Nicaragua, although Gardner *et al.* (1970:715) recently extended its known distribution southward from Honduras (Goodwin, 1942c: 124) and El Salvador (Felten, 1956:180) to west-central Costa Rica. In Nicaragua, as apparently in Costa Rica, *mexicana* occupies the Pacific versant, the Caribbean lowlands being inhabited by the smaller race, *Micronycteris megalotis microtis* Miller, 1898 (type locality, Greytown, Nicaragua—reported also from "Río Coco," Nicaragua, by J. A. Allen, 1910:110). Nicaraguan examples of *M. m. mexicana* are, on the average, considerably larger in cranial dimensions and length of forearm than are specimens of *M. m. microtis* (see Table 1). The series of *microtis* from "Río Coco," probably from the headwaters of that stream in the vicinity of San Juan de Río Coco and thus near the divide between Caribbean and Pacific drainages, is intermediate in size between the two subspecies and suggests intergradation between them. As noted also by Gardner *et al.* (1970:715), we find no differences in length of ear between *microtis* and *mexicana* (contrary to Miller's claim, in the original description, that *microtis* had noticeably smaller ears), nor do we note any consistent differences in color between the two races on the basis of the specimens at hand.

Our specimens from Isla del Maíz Grande inexplicably agree rather closely in size (average but slightly smaller) with specimens of *M. m. mexicana* from western Nicaragua and elsewhere within the range of the subspecies, and are tentatively, therefore, referred to *mexicana*. Four specimens earlier reported (G. M. Allen, 1929: 130) from the same island also are relatively large (forearm 35 mm). Further commentary on this insular population must await a time when additional material is available from Central America.

Tonatia nicaraguae Goodwin, 1942

Specimens.—Boaco: Santa Rosa, 17 km N, 15 km E Boaco, 300 m, 1. *Chontales:* Hato Grande, 13 km S, 8 km W Juigalpa, 60 m, 1.

Only four specimens of this seemingly rare species have been recorded previously from Nicaragua—one (the holotype) from Kanawa Creek, near Cukra, north of Bluefields, 100 ft, Zelaya (Goodwin, 1942b:205), another from 12.5 mi. S and 13 mi. E Rivas, 125 ft, Rivas (Davis and Carter, 1962:67-68), and two from 6 km N Tuma, 500 m, Matagalpa (Valdez and LaVal, 1971:248). Our specimens were caught in mist nets placed over small, quiet streams that were fringed with tall, gallery forest. The surrounding areas were savanna-like with small stands of secondary forest. An adult male taken on 21 April had testes that measured 5 mm in length, whereas those of another (9 August) were 3 mm.

Handley (1966b:761) synonymized *T. nicaraguae* with *Tonatia minuta* Goodwin, 1942, a conclusion with which we agree. However, the name *nicaraguae* (Goodwin, 1942b:205) has page priority over *minuta* Goodwin (*op. cit.*:206) and is the valid name for the species rather than *minuta* as used by Handley (see also LaVal, 1969:820; Gardner *et al.*, 1970:716; Valdez and LaVal, 1971:248).

Measurements of the two males (that from Hato Grande listed first) are as follows: total length, 63, 60 mm; length of tail, 5, 6 mm; length of hind foot, 10, 9 mm; length of ear, 23, 23 mm; length of forearm, 34.5, 35.6 mm; weight, 11.4, 8.8 gms; greatest length of skull, 20.2, 20.5 mm; zygomatic breadth, 9.5, 9.5 mm; breadth of braincase, 8.5, 8.2 mm; postorbital breadth, 3.1, 2.9 mm; length of maxillary toothrow, 7.0, 7.1 mm; breadth across upper molars, 6.3, 6.5 mm. We have not compared our specimens directly with others from Middle America. On the basis of available measurements, they resemble material reported from Honduras (LaVal, 1969:820), averaging larger than other specimens for which measurements have been published (see especially Goodwin, 1942b:206; Davis and Carter, 1962:68; Davis *et al.*, 1964:379; Gardner *et al.*, 1970: 716-717).

Phyllostomus hastatus panamensis J. A. Allen, 1904

Specimens.—Carazo: 3 km N, 4 km W Diriamba, 600 m, 1. *Madriz:* Darailí, 5 km N, 14 km E Condega, 940 m, 4. *Managua:* 3 km SW Tipitapa, 40 m, 1; 3 km N Sabana Grande, 50 m, 2; 2 km N Sabana Grande, 40 m, 1; 5 mi S Managua, 2. *Matagalpa:* La Danta, 1 km N, 5 km E Esquipulas, 760 m, 1. *Nueva Segovia:* 4.5 km N, 2 km E Jalapa, 630 m, 2; 1.5 km N, 1 km E Jalapa, 660 m, 1. *Zelaya:* Bonanza, 850 ft, 2; El Recreo, 25 m, 8.

This large spear-nosed species has been reported previously from Nicaragua only from Matagalpa (Goodwin, 1942c:126). *Phyllostomus hastatus* evidently occurs throughout the country and is relatively common in some places.

Two females taken 5 mi S Managua on 13 March each carried a single embryo (crown-rump length 27 and 32 mm). Lactating females were captured in June, July, and August.

Trachops cirrhosus coffini Goldman, 1925

A male fringe-lipped bat netted over a small stream at Cara de Mono, 50 m, Zelaya, in the Caribbean lowlands, on 24 April, 1968, constitutes the second known occurrence of this species in Nicaragua. Carter *et al.* (1966:491) earlier reported two males from Río Coco, 64 mi NNE Jinotega, 1000 ft, Jinotega. The testes of our specimen were 4 mm long.

Davis and Carter (1962:69), Carter *et al.* *(loc. cit.)*, and Starrett and Casebeer (1968:11) did not apply a trinomen to bats of this species and noted overlap of measurements between *T. c. cirrhosus* (Spix) and *T. c. coffini* Goldman. However, until detailed comparisons can be made, we follow Jones (1966:452) in retaining the subspecific name *coffini.*

Chrotopterus auritus auritus (Peters, 1856)

An adult male captured in a mist net set in a forest clearing at Santa María de Ostuma, 1250 m, Matagalpa, represents the first record of this bat from Nicaragua. The testes of our individual, taken on 1 July 1966, were 6 mm in length. Externally and cranially our Nicaraguan example closely resembles specimens of *C. auritus* from Veracruz and the Yucatán Peninsula. Handley (1966b:762) and Starrett and Casebeer (1968:12) expressed doubt as to the validity of the currently used subspecific names in this species. Comparisons of cranial and external measurements of the material at hand with those given in various published accounts—Burt and Stirton (1961), Starrett and Casebeer (1968), and Thomas (1905), for example—reveal little variation. Until additional information is available (especially as concerns the South American races), however, we tentatively apply the subspecific name *C. a. auritus* to Middle American populations.

Anoura geoffroyi lasiopyga (Peters, 1868)

Four specimens of this species, netted on 24 and 25 July 1967 in a banana grove 1.5 km N and 1 km E Jalapa, 660 m, Nueva Segovia, provide the first record of this glossophagine from Nicaragua. Two males each had testes 6 mm in length; one female evidenced no reproduction activity, whereas another carried an embryo 4 mm in crown-rump length. In addition to our material, there is a specimen in the British Museum (BM 8.6.22.4) from Cafetal "Concordia," 4000 ft, Jinotega.

It may be noteworthy that the two localities at which this bat is known both are in the highlands of the northern part of Nicaragua, and that we failed to take additional specimens in many hundreds of hours of netting in other places in the country.

Choeroniscus godmani (Thomas, 1903)

Godman's bat was reported from Nicaragua by Handley (1966a: 86), who used the locality designation "El Realejo" for the three specimens available to him. Actually, the three are from the nearby Hda. San Isidro, 10 km S Chinandega. We have taken three additional specimens as follows: Santa Rosa, 17 km N and 15 km E Boaco, 300 m, Boaco (an adult female taken on 21 March, which was pregnant with an embryo measuring 16 mm in crown-rump length); 2 km E Yalí, 900 m, Jinotega (an adult male netted on 3

August, testes 4 mm in length); and Santa María de Ostuma, 1250 m, Matagalpa (a nonpregnant, adult female captured on 11 April). Bats of this species have been taken as far north as the western Mexican state of Sinaloa (Jones, 1964b:510).

Lichonycteris obscura Thomas, 1895

Managua is the type locality of this rare long-nosed species and a specimen was reported from 6 mi W Rama, 50 ft, Zelaya, by Davis *et al.* (1964:380). Our collection contains three males, one from Jalapa, 660 m, Nueva Segovia, captured on the night of 27 July 1967 as it flew around a lighted room in a house, and two from the south side of the Río Mico, El Recreo, 25 m, Zelaya, taken on 26 and 27 July 1966 (one was netted and the other caught by hand in the lighted room of a building at night).

Selected measurements of the three males are, respectively: total length, 55, 58, 57 mm; length of tail, 7, 10, 9 mm; length of hind foot, 7, 9, 9 mm; length of ear, 10, 11, 11 mm; length of forearm, 30.9, 31.0, 30.8 mm; weight, 6.8, 6.8, 6.2 gms; length of testes, 1, 2, 2 mm; greatest length of skull, 18.5, 18.0, 17.9 mm; breadth of braincase, 8.1, 8.4, 8.3 mm; length of maxillary toothrow, 5.7, 5.5, 5.7 mm.

Carollia castanea H. Allen, 1890

Specimens.—Boaco: Santa Rosa, 17 km N, 15 km E Boaco, 300 m, 7. *Chontales:* 1 km N, 2.5 km W Villa Somoza, 330 m, 4. *Matagalpa:* 1 km NE Esquipulas, 420 m, 1. *Nueva Segovia:* 7 km N, 4 km E Jalapa, 660 m, 4. *Zelaya:* S side Río Mico, El Recreo, 25 m, 6; Cara de Mono, 50 m, 15.

Bats of this species apparently are common in the Caribbean lowlands of Nicaragua; the highest altitude at which we have taken specimens is 660 meters. The only previous report of *C. castanea* from Nicaragua evidently is that of Davis *et al.* (1964:379), who mentioned it in passing (from Cacao, Zelaya) in an account of *Macrophyllum macrophyllum.* Two adult females each carried an embryo having crown-rump lengths of 20 (21 March) and 10 mm (27 July). Adult females evincing no gross reproductive activity were taken in February (one), March (one), April (four), June (three), July (two), and August (two). Four adult males netted on 24 April had testes with an average length of 7.0 (5-9) mm, whereas those of four other adult males taken in late June had an average of 4.0 (2-6) mm.

In our collections from Nicaragua, we find at least three kinds of *Carollia* and we follow Handley (1966b:764-765) in tentatively assigning these to *C. castanea, C. subrufa,* and *C. perspicillata.* The systematics of this genus is currently under study by Ronald H. Pine. In Nicaragua, *castanea* differs from *subrufa* (with which it has been confused in the past) in being smaller, both externally and cranially, and much darker in color as well as in the additional characters mentioned by Handley *(loc. cit.)*.

Sturnira ludovici ludovici Anthony, 1924

An adult male (testes 6 mm) yellow-shouldered bat from Darailí, 5 km N and 14 km E Condega, 940 m, in Madriz, provides the only specimen thus far reported from Nicaragua. *Sturnira ludovici* evidently is relatively rare in Nicaragua and may be confined to the highlands in the north, whereas the smaller *S. lilium* is abundant throughout the country and is the only other species of *Sturnira* represented in our collections.

We provisionally refer our specimen to *S. l. ludovici* pending Luis de la Torre's forthcoming review of the genus. Selected measurements are: total length, 77 mm; length of hind foot, 15 mm; length of ear, 19 mm; length of forearm, 44.8 mm; weight, 26.8 gms; greatest length of skull, 24.2 mm; zygomatic breadth, 14.2 mm; postorbital breadth, 6.3 mm; breadth of braincase, 10.5 mm; length of maxillary toothrow, 6.8 mm.

Uroderma magnirostrum Davis, 1968

In the original description of *U. magnirostrum,* Davis (1968: 680) reported one specimen from Nicaragua—a female in our collection from 3 km N and 4 km W Sapoá, 40 m, Rivas. We have two additional specimens, both from the relatively dry northwestern Departamento de Chinandega. On 8 July 1966, a male (testes 2 mm) was netted under trees along a small stream at San Antonio, 35 m, and a female (one embryo 28 mm in crown-rump length) was netted on 4 March 1968 over a warm spring at a place 4.5 km N Cosigüina, 15 m. Judging from published records, this species is limited in Middle America to the Pacific versant.

Selected measurements of the three Nicaraguan specimens are, respectively: total length, 65, 64, 67 mm; length of hind foot, 12, 11, 14 mm; length of ear, 16.5, 16, 18 mm; length of forearm, 42.2, 41.7, 45.2 mm; weight, 16.2, 13.8, 21.4 (pregnant) gms; greatest length of skull, 22.7, 23.4, 23.8 mm; zygomatic breadth, 12.4, 12.9, 13.1 mm; postorbital breadth, 5.8, 5.5, 5.9 mm; mastoid breadth, 10.9, 11.1, 11.1 mm; length of maxillary toothrow, 7.9, 8.1, 8.6 mm.

Vampyrops helleri Peters, 1866

Specimens.—Boaco: Santa Rosa, 17 km N, 15 km E Boaco, 300 m, 3. *Carazo:* 3 km N, 4 km W Diriamba, 600 m, 2. *Chinandega:* Potosí, 5 m, 1;

6.5 km N, 1 km E Cosigüina, 10 m, 1; 4.5 km N Cosigüina, 15 m, 3; Hda. Bellavista, 720 m, Volcán Casita, 13. *Chontales:* 1 km N, 2.5 km W Villa Somoza, 330 m, 4. *Granada:* Finca Santa Cecilia, 6.5 km SE Guanacaste, 660 m, 4. *Matagalpa:* Finca Tepeyac, 10.5 km N, 9 km E Matagalpa, 960 m, 1. *Nueva Segovia:* 4.5 km N, 2 km E Jalapa, 680 m, 2; 1.5 km N, 1 km E Jalapa, 660 m, 2. *Rivas:* 2 km N, 3 km E Mérida, 200 m, Isla de Ometepe, 4; 4 km N, 4 km W Sapoá, 40 m, 1. *Zelaya:* S side Río Mico, El Recreo, 25 m, 3.

Only two specimens of this small white-lined species have been reported previously from Nicaragua—one from 1 km NW La Gatiada, 1300 ft, Chontales (Davis *et al.*, 1964:383), and the other from 3 mi NNW Diriamba, Carazo (Jones, 1964a:507). This bat was relatively rare in collections until the last decade or so. Handley (1966b:766) reported *V. helleri* as abundant in the lowland areas of Panamá, and we found the same to be true in Nicaragua. We suspect that future investigations in Middle America will reveal this species to be a common member of lowland tropical communities. It is known as far north as southern Veracruz (Carter *et al.*, 1966:494).

Most of our specimens were captured in mist nets set over small streams bordered by gallery forest, or in banana groves. The range of ecological conditions in which this species was taken is represented by the semiarid environment of the Cosigüina Peninsula in northwestern Nicaragua and the humid tropical forest (secondary growth) in the vicinity of El Recreo in the Caribbean lowlands. Pregnant females were captured in March, April, June, July, and August, indicating that this species probably breeds throughout much of the year.

Vampyrodes major G. M. Allen, 1908

Specimens.—Boaco: Santa Rosa, 17 km N, 15 km E Boaco, 300 m, 8. *Chontales:* 1 km N, 2.5 km W Villa Somoza, 330 m, 2. *Zelaya:* S side Río Mico, 25 m, 6.

This large white-lined stenodermine was known previously from Nicaragua by a single specimen from an unknown locality (J. A. Allen, 1910:112). All of our specimens were caught in mist nets, which were set over streams at Santa Rosa and near Villa Somoza, and in a banana grove at El Recreo. Two pregnant females, captured on 11 and 13 July at Santa Rosa, each carried an embryo (4 and 27 mm in crown-rump length, respectively); one of two other adult females captured there on 9 August also had an embryo (35 mm in length) but the other evidently was reproductively quiescent. Testes of adult males varied in length from 3 to 10 mm on the following dates (testicular lengths in parentheses): 25 February

(10 mm); 21 March (8, 8 mm); 17 June (3, 4 mm); 13 July (6 mm); 27-28 July (4, 4 mm); 3 August (4 mm); 5 August (3 mm); 9 August (4 mm).

We follow Starrett and Casebeer (1968:12) in the use of the specific name *major*, rather than *caraccioli* as suggested by Cabrera (1958), Goodwin and Greenhall (1961), and Handley (1966b).

Vampyressa nymphaea Thomas, 1909

A pregnant female (crown-rump length of embryo 5 mm) was captured in a mist net set in a small banana grove on the south side of the Río Mico, El Recreo, 25 m, in the Caribbean lowlands, on 27 February 1968. This specimen provides the first record of the big yellow-eared bat from Nicaragua. The species was recently reported for the first time from Costa Rica (Gardner *et al.*, 1970: 721); it was characterized as uncommon in Panamá by Handley (1966b:767). The one Costa Rican locality of record also is in the Caribbean versant.

Selected external and cranial measurements of our female are: total length, 58 mm; length of hind foot, 11 mm; length of ear, 16 mm; length of forearm, 36.2 mm; weight, 12.3 gms; greatest length of skull, 21.1 mm; condylobasal length, 18.4 mm; zygomatic breadth, 12.3 mm; mastoid breadth, 10.5 mm; breadth across canines, 4.6 mm; breadth of braincase, 9.4 mm; length of maxillary toothrow, 7.2 mm; length of mandibular c-m3, 7.8 mm.

Vampyressa pusilla thyone Thomas, 1909

Specimens.—Boaco: Santa Rosa, 17 km N, 15 km E Boaco, 300 m, 5. *Chontales:* 1 km N, 2.5 km W Villa Somoza, 330 m, 1. *Managua:* Hda. San José, 2. *Matagalpa:* 2 km N, 6 km E Esquipulas, 960 m, 2.

The only previous record of occurrence for the small yellow-eared bat from Nicaragua is based on an adult female from Hda. La Cumplida, 670 m, Matagalpa (Starrett and de la Torre, 1964:60).

Two individuals taken near Esquipulas in mid-March, a pregnant female (crown-rump length of embryo 16 mm) and a male (testes 4 mm), were captured in nets set across trails cut through secondary forest. The wind was quite strong in this area at the time of our visit and only a few other species of bats—*Glossophaga soricina, Artibeus jamaicensis, A. toltecus, A. phaeotis, Uroderma bilobatum, Sturnira lilium, Centurio senex,* and *Diphylla ecaudata* —were taken in the same nets. The specimens from Boaco and Chontales were captured over small streams bordered by gallery forest. Four females collected at Santa Rosa on 21 March were pregnant; each carried a single embryo that measured 5, 18, 21, and

30 mm in crown-rump length; a male taken on the same date had testes that measured 3 mm.

Selected external and cranial measurements of two males, followed by the average (extremes in parentheses) of six females are: length of forearm, 31.1, 30.8, 30.8 (30.0-31.4) mm; greatest length of skull, 18.9, 18.9, 18.5 (18.1-18.8) mm; zygomatic breadth, 11.0, 11.0, 10.6 (10.4-10.9) mm; mastoid breadth, 9.5, 9.2, 9.2 (9.0-9.3) mm; length of maxillary toothrow, 6.1, 5.9, 5.9 (5.7-6.1) mm.

Chiroderma villosum jesupi J. A. Allen, 1900

Specimens.—Chinandega: 6.5 km N, 1 km E Cosigüina, 10 m, 2; 4.5 km N Cosigüina, 15 m, 7; Hda. Bellavista, 720 m, Volcán Casita, 5; San Antonio, 35 m, 2. *Rivas:* 2 km N, 3 km E Mérida, 200 m, Isla de Ometepe, 1.

This species has been reported in Middle America from as far north as southern México. It evidently is uncommon in Costa Rica (see Gardner *et al.*, 1970:722) and Panamá (Handley, 1966b:767). Our material, all collected from mist nets and consisting of 16 specimens from the northwestern department of Chinandega and one from Isla de Ometepe in Lago de Nicaragua, constitutes the first report of this bat from Nicaragua.

Four of five females taken in early March were pregnant; embryos averaged 26.0 (25-29) mm in crown-rump length. Four females taken in July carried embryos 14, 20, 23, and 25 mm in length. Testes of five adult males captured in March and April had an average length of 4.4 (3-7) mm, whereas those of two taken in July were 3 mm in length.

Artibeus toltecus hesperus Davis, 1969

When Davis (1969) named *A. t. hesperus,* he assigned specimens only from as far south as El Salvador to the new subspecies, referring the three Nicaraguan examples of the species at his disposal to the nominal race. On the night of 6-7 April 1968, one of us (Smith) netted bats on the south part of Isla de Ometepe at a place 2 km N and 3 km E Mérida, 200 meters in elevation. One net was set across, and another parallel to, a small, boulder-strewn stream; the surrounding area was planted to coffee and had a good canopy of tall deciduous trees. Among the bats captured at this location were 10 *A. toltecus* that are referable to the subspecies *hesperus,* judging by their small size (Table 2).

Six of our specimens are females and each carried an embryo (range in crown-rump length 20-28 mm). Three adult males had testes 5, 6, and 7 mm in length. External measurements (extremes in parentheses) of our series are: total length, 55.9 (51-60) mm;

TABLE 2.—Selected measurements of two subspecies of *Artibeus toltecus* from Nicaragua.

Number of specimens averaged and sex	Length of forearm	Greatest length of skull	Zygomatic breadth	Mastoid breadth	Length of maxillary toothrow
Artibeus toltecus toltecus, Departamento de Matagalpa					
Average 6 (3♂, 3♀)	40.3	20.3	12.1	10.7	6.6
Minimum	38.8	19.8	11.8	10.5	6.5
Maximum	41.5	20.5	12.5	10.9	6.8
Artibeus toltecus hesperus, Isla de Ometepe, Rivas					
Average 10 (4♂, 6♀)	38.0	19.4	11.5	10.2	6.3
Minimum	37.0	18.8	11.2	9.8	6.1
Maximum	39.7	19.8	11.8	10.5	6.5

length of hind foot, 10.7 (10-12) mm; length of ear, 14.8 (14-16) mm; weight of four males, 9.9 (8.8-11.5) gms; weight of six pregnant females, 14.9 (12.7-16.9) gms.

Artibeus toltecus toltecus (Saussure, 1860)

Specimens.—Matagalpa: Santa María de Ostuma, 1250 m, 5; 2 km N, 6 km E Esquipulas, 960 m, 1.

This bat has been reported from Nicaragua previously by Andersen (1908:300) and Davis (1969:28), based on a total of four specimens. We netted this species at Santa María de Ostuma in patches of cloud forest at a cafetal. The specimen from near Esquipulas was taken in a net placed across a trail in second growth forest. Two females collected on 11 April and one taken on 30 June were pregnant (embryos 21, 26, and 12 mm, respectively, in crown-rump length). Testes of a male netted on 14 March were 7 mm in length, whereas those of two obtained on 11 April measured 4 and 7 mm. Selected measurements of our six specimens are given in Table 2.

Artibeus watsoni Thomas, 1901

Specimens.—Chontales: 1 km N, 1.5 km W Villa Somoza, 330 m, 3. *Nueva Segovia:* 7 km N, 4 km E Jalapa, 600 m, 1. *Zelaya:* Bonanza, 850 ft, 6; S side Río Mico, El Recreo, 25 m, 6; Cara de Mono, 50 m, 1.

Davis (1970a:393-394) recently reviewed the systematic status of this small fruit-eating bat and recorded specimens from southeastern Nicaragua; the species was first reported from the country by Andersen (1908:290), based on a specimen from the Escondido River. Our additional material reveals that *A. watsoni* occurs throughout eastern Nicaragua, the specimen from Nueva Segovia extending the known range as mapped by Davis *(loc. cit.).*

A female from Bonanza (23 February) carried an embryo 14 mm in crown-rump length, whereas one from El Recreo (26 February) was not reproductively active; one of two females netted near Villa Somoza in early August was pregnant (embryo 21 mm in crown-rump length). Seven adult males collected in late February and early March had an average testicular length of 5.9 (5-7) mm; testes of two adults taken in late June and one captured in early August all measured 5 mm. The testes of young males (grayish pelage, partially unfused phalangeal epiphyses) were 2 or 3 mm in length.

Centurio senex senex Gray, 1842

Specimens.—Chinandega: 4.5 km N Cosigüina, 15 m, 1; San Antonio, 35 m, 5. *Matagalpa:* 2 km N, 6 km E Esquipulas, 960 m, 3. *Nueva Segovia:* 7 km N, 4 km E Jalapa, 660 m, 1. *Zelaya:* S side Río Mico, El Recreo, 25 m, 1.

Paradiso (1967) reviewed geographic variation in this unique bat, the type locality of which was restricted to Realejo, Chinandega, Nicaragua, by Goodwin (1946:327). Because additional material had not been reported from Nicaragua, Paradiso (*op. cit.*:598) felt it was "premature to restrict the type locality to a specific area in that country" (the holotype was obtained on the voyage of the H.M.S. Sulphur, which called at Realejo), and preferred the more general designation "west coast of Mexico or Central America." In view of the fact that we now have specimens from but a few miles distant from Realejo (at San Antonio), we see no reason to contest Goodwin's restriction of the type locality to that place.

Specimens from San Antonio were collected along a small stream, bordered by a bilevel gallery forest, in an area otherwise planted mostly to cane. Many trees of the lower level were covered by an extremely thick network of vines, which were interwoven with branches and supported fallen leaves and debris from the upper level. This situation led to formation of small "rooms" or "cubicles" under some shorter trees; the bats were shot as they hung from small branches under one such tree, which was in fruit. All of our other specimens were captured in mist nets.

Pregnant females were taken on the following dates (crown-rump length of embryo in parentheses): 25 February (12 mm), 2 March (17 mm), 15 March (14 mm); a nonpregnant female also was taken on 15 March. Five males captured at San Antonio on 9 and 10 March had an average testicular length of 5.6 (5-6) mm. A male taken in July had testes 4 mm in length, whereas those of one obtained on 14 March were 5 mm long.

Selected measurements (average, with extremes in parentheses) of 11 adults (seven males and four females) are as follows: length of forearm, 42.5 (41.5-43.7) mm; condylobasal length (10 specimens only), 14.8 (14.5-15.0) mm; zygomatic breadth, 14.8 (14.4-15.1) mm; interorbital breadth, 5.0 (4.7-5.2) mm; breadth across upper molars, 10.6 (10.5-11.0) mm; length of maxillary toothrow, 5.0 (4.8-5.3) mm. These measurements generally agree with those given by Paradiso (1967:600) for 20 individuals from Panamá. Females in our series average slightly larger than do males in external and cranial measurements. Six males weighed an average of 22.9 (20.7-25.1) gms; one nonpregnant female weighed 17.1 gms.

Diphylla ecaudata Spix, 1823

Specimens.—Boaco: Los Cocos, 14 km S Boaco, 220 m, 5. *Madriz:* 5 km N, 9 km E Condega, 800 m, 1. *Matagalpa:* 2 km N, 6 km E Esquipulas, 960 m, 1.

Our specimens constitute the first report of this species from Nicaragua. We follow Burt and Stirton (1961:37) in regarding *D. ecaudata* as monotypic.

Specimens from Los Cocos (three males and two females) were captured in a mist net stretched across a large, quiet pool in a small stream. The banks supported well-developed gallery forest, the understory of which had been cleared for human habitation; grassland (grazed) and small stands of secondary forest obtained beyond the riparian habitat. Domestic ducks, a possible source of food, were observed sleeping along the bank of this stream and on top of large boulders situated in the stream. Males from this locality taken on 20 February, 4 April, and 18 July had testicular lengths of 5, 6, and 6.5 mm, respectively. Two adult females collected there on 4 April were reproductively inactive. An adult male (testes 6 mm) from near Condega was captured on 23 June in a daytime roost in a small, cave-like crevice (see account of *Peropteryx marcotis*), and one from northeast of Esquipulas (testes 5 mm) was netted on 14 March along a forest trail (see account of *Vampyressa pusilla*).

Natalus stramineus saturatus Dalquest and Hall, 1949

Specimens.—Granada: 6 km S Nandaime, 5. *Zelaya:* S side Río Mico, El Recreo, 25 m, 2.

This funnel-eared species occupies an extensive geographic range (northern México to Brazil) but appears to be relatively rare in Middle America to the south of Guatemala. Our specimens represent the first of this species to be reported from Nicaragua.

Both specimens from El Recreo, adult males, were caught by hand at night after they flew through an open door into a small room, possibly seeking insects that were swarming around a light bulb. Those from near Nandaime (three males, two females) were caught in a mist net set over the mouth of a well in which they were roosting; the well was approximately 2 m in diameter, and the water level was about 5 m below the rim. The females were not reproductively active (6 August).

We have compared our Nicaraguan material with a number of Mexicans specimens, including the holotype of *N. s. saturatus* and topotypes of *N. s. mexicanus.* We concur with Goodwin (1959) that in México there are two rather distinct subspecies, between which a broad zone of intergradation obtains. Our Nicaraguan specimens agree most closely with *N. s. saturatus,* and, until additional comparative material is available from Middle America, we tentatively refer them to that race. Handley (1966b:770) and Starrett and Casebeer (1968:15), however, regarded *mexicanus* as the appropriate name for specimens from Panamá and Costa Rica.

Selected measurements of two males from El Recreo are: length of forearm, 41.2, 39.0 mm; greatest length of skull, 17.1, 16.5 mm; zygomatic breadth, 8.4, 8.5 mm; mastoid breadth, 7.7, 7.6 mm; breadth of braincase, 8.2, 8.1 mm; interorbital constriction, 3.2, 3.2 mm; length of maxillary toothrow, 7.3, 7.1 mm.

Myotis albescens (É. Geoffroy St.-Hilaire, 1806)

This handsome *Myotis* has been reported previously from Nicaragua only from the Caribbean lowlands—from the Escondido and Prinzapolka rivers (Miller and Allen, 1928:203). We netted two specimens, both males, at Santa Rosa, 17 km N and 15 km E Boaco, 300 m, Boaco, in central Nicaragua on 13 July and 9 August 1967, under the same conditions described in the account of *Myotis elegans.* Testes of our specimens were 7 and 6 mm, respectively, in length. External and cranial measurements are as follows: total length, 84, 83 mm; length of tail, 31, 33 mm; length of hind foot, 9, 9 mm; length of ear, 15, 15 mm; length of forearm, 32.9, 35.1 mm; weight, 6.4, 6.2 gms; greatest length of skull, 13.9, 14.4 mm; zygomatic breadth, 8.9, 9.0 mm; postorbital breadth, 3.8, 3.9 mm; breadth of braincase, 7.2, 7.3 mm; mastoid breadth, 7.4, 7.6 mm; breadth across upper molars, 5.6, 5.5 mm; length of maxillary toothrow, 5.3, 5.3 mm.

Myotis elegans Hall, 1962

The first specimen on record of this rare *Myotis* from Central America, a nonpregnant female, was taken on 11 July 1967 at Santa Rosa, 17 km N and 15 km E Boaco, 300 m, Boaco. It was captured in a mist net as it foraged over a small stream that supported relatively well-developed gallery forest along the bank. The surrounding area was grassland (grazed), with small patches of tropical forest located on the sides of hills. Twenty other species of bats were taken at this same locality including *Myotis argentatus* and *Myotis nigricans nigricans.*

External and cranial measurements of our specimen, followed in parentheses by those of the female holotype from Veracruz, are: total length, 71 (79) mm; length of tail, 32 (34) mm; length of hind foot, 7 (7.5) mm; length of ear, 11 (12) mm; length of forearm, 32.9 (33.0) mm; greatest length of skull, 12.5 (12.4) mm; condylobasal length, 11.6 (11.9) mm; zygomatic breadth, 8.2 mm; breadth of braincase, 5.8 (6.1) mm; postorbital breadth, 3.2 (3.2) mm; length of maxillary toothrow, 4.7 (4.6) mm. Our female weighed 3.2 gms.

Myotis nigricans nigricans (Schinz, 1821)

Specimens.—Boaco: Santa Rosa, 17 km N, 15 km E Boaco, 300 m, 2. *Chinandega:* 6.5 km N, 1 km E Cosigüina, 10 m, 1; San Antonio, 35 m, 1. *Chontales:* 1 km N, 2.5 km W Villa Somoza, 330 m, 1. *Madriz:* Darailí, 5 km N, 14 km E Condega, 940 m, 1. *Nueva Segovia:* 4.5 km N, 2 km E Jalapa, 680 m, 1. *Rivas:* 1 km NW Sapoá, 40 m, 1.

This small Neotropical *Myotis* has been reported from Nicaragua only from the Caribbean lowlands of Zelaya (Davis *et al.*, 1964: 379). Our records indicate that it is widely distributed in the republic but evidently nowhere common. Females taken on 5 March and 6 August each carried a single embryo (7 and 13 mm in crown-rump length, respectively), whereas one obtained on 21 July evidenced no reproductive activity. Richard K. LaVal currently is studying the *Myotis nigricans* complex; pending his revision our specimens are tentatively assigned to *M. n. nigricans.*

Myotis simus riparius Handley, 1960

A male (USNM 52800) from the Escondido River above Bluefields, originally reported by Miller and Allen (1928:203) as one of two *M. albescens* from that locality, provides the first record of the species from Nicaragua and the northernmost from Middle America. The cranial dimensions of this specimen, which compare well with those listed by Handley (1960:467) for the Panamanian holotype and paratype, are: greatest length of skull, 13.8 mm; zygomatic breadth, 8.9 mm; postorbital constriction, 3.5 mm; breadth of braincase, 6.7 mm; mastoid breadth, 7.4 mm; breadth across upper molars, 5.5 mm; length of maxillary toothrow, 5.2 mm.

From Nicaraguan specimens of *albescens*, the skull of the specimen of *simus* examined (skin not seen) differs most conspicuously in having a less inflated braincase, narrower postorbital region, and a distinct sagittal crest.

Eptesicus furinalis gaumeri (J. A. Allen, 1897)

Specimens.—Carazo: 3 km N, 4 km W Diriamba, 600 m, 7. *Chinandega:* Potosí, 5 m, 1; 6.5 km N, 1 km E Cosigüina, 10 m, 1; San Antonio, 35 m, 1. *Chontales:* 1 km N, 2.5 km W Villa Somoza, 330 m, 1; Hato Grande, 13 km S, 8 km W Juigalpa, 60 m, 3.

Davis (1965:234) reported two specimens of this species from Nicaragua, one from Carazo (listed above) and the other from 1 mi SE Yalagüina, 2600 ft, Madriz. The only other specimen on record from Nicaragua is from Greytown (Miller, 1897:100). Except for two individuals that were shot as they foraged in early evening, our specimens were captured in mist nets stretched over water or as described below.

Some of the bats captured northwest of Diriamba were taken in a net placed across the center of a water-filled, concrete cistern that was located in a large, open space used for drying coffee beans. Open at the top, the cistern was approximately 12 m in diameter, and the water level was approximately 3 m below the rim. Several *Artibeus jamaicensis*, *A. lituratus*, and *Molossus pretiosus* were caught in the same net. Aside from bats removed from the net, a few *Eptesicus* and *Molossus* were retrieved from the water where they fell, apparently stunned, after colliding with the wall of the cistern. The fact that a number of decomposed bats of these two species were observed floating in the water indicated that such entrapment was not caused by the placement of our net.

A female pregnant with two embryos (crown-rump length 15 mm) was captured on 22 April, whereas one taken on 5 July was lactating. Adult males taken in March (two) and April (two) had testes 5, 7, 9, and 10 mm long, respectively.

Rhogeessa tumida tumida H. Allen, 1866

Specimens.—Boaco: Santa Rosa, 17 km N, 15 km E Boaco, 300 m, 2. *Carazo:* 3 km N, 4 km W Diriamba, 600 m, 2. *Chinandega:* 6 km N, 1 km E Cosigüina, 10 m, 3; Hda. Bellavista, 720 m, Volcán Casita, 1. *Matagalpa:* 1 km NE Esquipulas, 420 m, 1.

This small vespertilionid occurs throughout much of Central America, but the available material still is insufficient to permit an accurate assessment of geographic variation in that region. All but one of our specimens were trapped in mist nets. Those captured near Diriamba were taken in a net stretched across a trail bordered by high cut-banks, whereas those from other localities were netted over small streams. The one bat from Bellavista was shot as it foraged in the evening along trees bordering the hacienda yard.

Two females taken on 5 March each had swollen uteri and may have been in an early stage of pregnancy. Others taken on 13 July, 9 August, and 15 August were reproductively inactive. Males had testes that measured 2.5 (March), 3 (July), and 2 (August) mm.

We have compared our material with representative specimens from México of *R. parvula* and *R. tumida,* as defined by Goodwin (1958); we are not wholly convinced that these are valid species (rather than variable geographic races of the same species). Certainly there is need for additional investigation of the problem. Our Nicaraguan specimens most closely resemble *R. t. tumida* (see Goodwin, *op. cit.*:3), to which they are tentatively referred.

Selected measurements of two females from Boaco and a male from Matagalpa, followed by the average (and extremes) of three males and three females from western Nicaragua (Carazo and Chinandega), are, respectively: length of forearm, 30.4, 28.5, 28.3, 28.2 (27.5-29.0) mm; greatest length of skull, 12.8, 12.7, 12.8, 12.1 (11.8-12.5) mm; zygomatic breadth, 8.1, 8.4, 8.6, 8.1 (7.8-8.6) mm; mastoid breadth, 7.1, 7.2, 7.2, 6.8 (6.6-7.1) mm; breadth of braincase, 6.0, 5.7, 6.0, 5.6 (5.3-6.1) mm; postorbital constriction, 3.3, 3.0, 3.3, 3.0 (2.9-3.2) mm; length of maxillary toothrow, 4.7, 4.7, 4.5, 4.3 (4.2-4.6) mm; weight, 4.4, 4.3, 3.8, 3.5 (3.1-3.9) gms.

Tadarida laticaudata yucatanica (Miller, 1902)

One adult male (testes 5 mm) of this free-tailed bat from Potosí, 5 m, Chinandega, on the Cosigüina Peninsula, provides the only record of the genus *Tadarida* from Nicaragua. This specimen was netted after dark over a small stream that flowed into the Bay of Fonseca approximately 200 yards below our nets (see account of *Noctilio leporinus*). Other species taken in the same net included *Carollia subrufa, Sturnira lilium, Eptesicus furinalis, Molossus ater,* and *Molossus molossus.*

Selected measurements of the male are: total length, 92 mm; length of tail, 31 mm; length of hind foot, 10 mm; length of ear, 15 mm; length of forearm, 39.2 mm; weight, 10.3 gms; greatest length of skull, 17.2 mm; zygomatic breadth, 10.6 mm; postorbital constriction, 4.0 mm; breadth of braincase, 8.6 mm; length of maxillary toothrow, 6.5 mm.

Eumops auripendulus (Shaw, 1800)

A broken skull (USNM 339917) of a female of this species from Hda. Mecatepe [2 km N, 11.5 km E Nandaime, *ca.* 40 m], Granada, represents the only known specimen of the genus *Eumops* from Nicaragua. This bat was obtained by M. K. Clark on 25 August 1964, but the conditions under which it was captured are not known. Available cranial measurements are: zygomatic breadth, 12.6 mm; breadth of braincase, 10.7 mm; postorbital breadth, 4.3 mm; rostral breadth, 7.4 mm; length of maxillary toothrow, 9.1 mm; length of mandibular c-m3, 10.0 mm.

Molossus ater nigricans Miller, 1902

Specimens.—Chinandega: Potosí, 5 m, 21; 4.5 km N Cosigüina, 15 m, 2; El Paraíso, 1 km N Cosigüina, 20 m, 17; Hda. Bellavista, 720 m, Volcán Casita, 4; Hda. San Isidro, 10 km S Chinandega, 20 m, 2; San Antonio, 35 m, 2. *Nueva Segovia:* Corozo, 15 km NNE Jalapa, 660 m, 1; 3.5 km S, 2 km W Jalapa, 660 m, 4.

Only one specimen of this large molossid (from Volcán de Chinandega—J. A. Allen, 1908:670) has been reported from Nicaragua. All of our specimens are from the northern or northwestern part of the country. Many were shot in early evening as they followed a straight, direct flight pattern (presumably from day-roosts toward foraging or watering areas); the series from Potosí was netted over a small stream as described in the account of *Noctilio leporinus.* We confidently refer our material to the species currently known as *ater,* although assignment to the subspecies *nigricans* is tentative.

Of 21 females autopsied in the first week of March on the Cosigüina Peninsula, seven were pregnant, each with a single embryo (7-22 mm in crown-rump length, average 16.7). Ten males taken at the same time had an average testicular length of 5.7 (2-7) mm, whereas the testes of a male obtained on 9 March at San Antonio measured 8 mm. None of five females obtained in late July in Nueva Segovia evidenced reproductive activity, nor did two of three females taken in July and one taken in August from Chinandega; the fourth Chinandegan female, taken on 17 July, carried an embryo that was 36 mm in length. Two males from southern Chinandega (mid-July) had testes 7 and 4 mm long.

Representative measurements of 10 specimens of each sex from Nicaragua are given in table 4.

Molossus molossus aztecus Saussure, 1860

Specimens.—Chinandega: Potosí, 5 m, 1; Hda. San Isidro, 10 km S Chinandega, 20 m, 1 (USNM). *Boaco:* Santa Rosa, 17 km N, 15 km E Boaco, 300 m, 7. *Managua:* 3 mi SW Managua, 8. *Rivas:* Rivas, 60 m, 4.

This small free-tailed species has been reported from Nicaragua by Felten (1957:14), who listed two females from Corinto. Our records indicate that it is widely distributed, but of localized occurrence. Specimens from Potosí and Santa Rosa were captured in mist nets over streams (as described in the accounts of *Noctilio leporinus* and *Myotis elegans,* respectively). The specimen from Hda. San Isidro was shot in flight, whereas those from Rivas were captured in a daytime retreat in a deep crevice in a concrete school building. We have no precise knowledge of the conditions under which bats from 3 mi SW Managua were obtained but suspect they were taken from a building.

Females in our series were reproductively active at all times for which we have information—early March through mid-July—as follows: a female from Potosí (6 March) carried an embryo that measured 5 mm (crown-rump length) as did one from Santa Rosa (21 March, 17 mm in length); two of three females taken 3 mi SW Managua on 28 March were pregnant (embryos 13 and 15 mm), whereas each of two collected there on 3 May were gravid (embryos 27 and 30 mm); one female from Rivas (25 June) carried an embryo (30 mm) and another was lactating and accompanied by a small (forearm, 19.7 mm) hairless juvenile; and, finally, one of six females netted at Santa Rosa on 13 July was pregnant (embryo 23 mm), but the others evinced no reproductive activity. An adult male, taken at Rivas with the females mentioned above, had testes that were 6 mm in length.

Bats of the genus *Molossus* are in need of thorough systematic study. We think most, if not all, mainland populations of small *Molossus* with pale-based hairs pertain to the species *Molossus molossus,* originally described from the Lesser Antilles. Although there is some variation in size and overall color among our Nicaraguan samples, all seem to represent that species. Because specimens from Nicaragua closely resemble examples of *M. m. aztecus* from Jalisco, México (Table 3), in external and cranial proportions, we tentatively refer them to *aztecus.*

In our field experience in both Middle and South America, colonies of *M. molossus* tend to be extremely localized, with individual populations or demes frequently separated by many miles of territory in which the species seemingly does not regularly occur.

TABLE 3.—Selected measurements of adult *Molossus molossus.*

Number of specimens averaged or catalogue number, and sex	Length of forearm	Greatest length of skull	Condylobasal length	Zygomatic breadth	Mastoid breadth	Breadth of braincase	Postorbital constriction	Length of maxillary toothrow	Breadth across upper molars
Western Jalisco, México									
KU 109075, ♂	38.2	18.0	15.3	11.0	10.5	9.1	3.8	6.2	7.9
KU 109076, ♂	37.3	17.8	15.3	11.0	10.5	9.2	3.6	6.3	8.1
KU 120540, ♂	37.7	17.8	15.3	11.0	10.8	8.9	3.9	6.3	8.1
Average 15 (♀)	37.1	17.2	14.8	10.7	10.3	8.9	3.8	6.1	7.9
Minimum	36.0	16.5	14.2	10.4	10.1	8.5	3.7	6.0	7.7
Maximum	38.1	17.7	15.2	11.0	10.5	9.2	3.9	6.2	8.2
Departamento de Chinandega, Nicaragua									
USNM 337552, ♂	39.0±	18.2	15.5	11.0	10.7	9.0	3.7	6.0	8.0
KU 114140, ♀	37.3	16.8	14.7	10.7	9.9	8.7	3.4	5.9	7.4
3 mi SW Managua, Nicaragua									
KU 71009, ♂	39.8	18.7	16.1	11.1	10.9	8.9	3.8	6.3	8.0
KU 71011, ♂	39.4	18.5	16.5	—	11.0	9.2	3.7	6.7	8.0
Average 5 (♀)	38.9	17.5	15.4	10.7	10.3	9.0	3.6	6.1	7.8
Minimum	38.1	17.2	15.1	10.5	10.1	8.9	3.5	5.9	7.6
Maximum	39.7	18.0	15.9	10.9	10.6	9.1	3.7	6.3	8.0
Santa Rosa, Boaco, Nicaragua									
Average 6 (♀)	36.0	17.5	14.7	10.8	10.6	9.1	3.7	6.0	8.0
Minimum	35.5	17.3	14.4	10.6	10.4	9.0	3.6	5.7	7.8
Maximum	36.7	17.8	15.1	11.0	10.8	9.2	3.8	6.2	8.2
Rivas, Nicaragua									
KU 106291, ♂	38.2	18.8	16.1	11.5	10.9	9.4	3.8	6.6	8.3
KU 106290, ♀	39.6	17.4	15.0	11.0	10.5	9.1	3.6	6.0	7.7
KU 106293, ♀	37.2	17.3	14.8	10.7	10.2	9.0	3.5	5.7	7.8

The localized and presumably highly inbred populations may have diverged morphologically, in some cases at least, to a degree that mensural differences can be demonstrated even between samples from the same general geographic area. Localized variation and relatively marked secondary sexual variation (unrecognized by some earlier workers), superimposed on geographic variation, have resulted in application of a relatively large number of names to these small *Molossus.* Felten (1957:13-14), for example, apparently used different specific names for males and females from El Salvador, and Gardner (1966) employed three different specific names for North American specimens. Only when material is available for a detailed study of variation throughout the Neotropics can the perplexing mosaic of characters in these small *Molossus* be assessed adequately.

We have seen no specimens from Nicaragua that are identifiable as *Molossus bondae,* another relatively small species that has been reported from Greytown (Miller, 1913a:89) and from elsewhere in Central America by other authors (Goodwin, 1942c:145; Handley, 1966b:772; Gardner *et al.,* 1970:727). Our examination of the female holotype of *M. bondae* reveals that it is larger than *M. molossus,* corresponding in size to females recently reported from Costa Rica by Gardner *et al. (loc. cit.),* and that *bondae* has dark-based hairs. The two males reported by Goodwin *(loc. cit.)* from Honduras as *bondae,* would seem to be too small for that species, based on the measurements listed; also, these specimens allegedly have white-based hairs and probably represent *M. molossus* as here defined.

Molossus pretiosus pretiosus Miller, 1902

Specimens.—Boaco: Los Cocos, 14 km S Boaco, 220 m, 28; San Francisco, 19 km S, 2 km E Boaco, 200 m, 3. *Carazo:* 3 km N, 4 km W Diriamba, 600 m, 25. *Managua:* 6 mi WSW Managua, 3.

This relatively large mastiff bat has not been reported previously from Nicaragua. Specimens from several localities in Boaco were captured in mist nets over streams; most of those from northwest of Diriamba were shot in the early evening as they foraged high around large trees in a coffee finca, but several were netted over a water-filled concrete tank or found in the water in the tank as detailed in the account of *Eptesicus furinalis.* At Los Cocos, bats that we netted seemed to be emerging from a hollow located high in a tree over the stream.

Selected measurements of *M. p. pretiosus* from Nicaragua, which compare favorably with those of topotypes from Venezuela, are listed in table 4 along with measurements of *M. ater* and *M. sinaloae.* The taxonomic relationships of *M. pretiosus* and *M. ater* are less than clear, and some authors (Handley, 1966b:773, for instance) have suggested that the two may be conspecific. Whatever their ultimate relationships may prove to be, two distinctive taxa seem to be present in Nicaragua; the larger is assignable to *ater* and the smaller to *pretiosus,* as currently understood. Furthermore, the presumed presence of two large *Molossus* with dark-based hairs elsewhere in Central America (Dilford C. Carter, personal communication) and in southeastern México (Goodwin, 1956:4; Goodwin and Greenhall, 1964:20) argues for specific recognition of *pretiosus.*

The species *ater* and *pretiosus* differ mainly in size (Table 4), some measurements clearly separating the two when sexual dimor-

TABLE 4.—Selected measurements of adults of three species of *Molossus* from Nicaragua.

Number of specimens averaged or catalogue number, and sex	Length of forearm	Greatest length of skull	Condylobasal length	Zygomatic breadth	Breadth of braincase	Length of maxillary toothrow	Breadth across upper canines
Molossus ater nigricans, Departamento de Chinandega, Nicaragua							
Average 10 (♂)	49.5	23.2	20.2	14.3	11.0	8.2	6.1
Minimum	48.2	22.8	19.9	14.1	10.5	8.0	6.0
Maximum	50.7	23.5	20.5	14.9	11.2	8.3	6.3
Average 10 (♀)	49.0	22.0	19.2	13.6	10.7	7.8	5.8
Minimum	47.1	21.5	18.8	13.3	10.5	7.6	5.6
Maximum	51.2	22.5	20.0	14.1	11.0	8.2	6.1
Molossus pretiosus pretiosus, Departamento de Boaco, Nicaragua							
Average 8 (♂)	45.1	21.7	18.8	13.4	10.6	7.6	5.9
Minimum	44.1	21.0	18.3	13.1	10.2	7.4	5.6
Maximum	46.1	22.2	19.1	13.7	10.9	7.9	6.1
Average 23 (♀)	43.6	20.2	17.7	12.5	10.1	7.3	5.2
Minimum	41.0	19.5	17.2	12.2	9.5	7.1	5.0
Maximum	44.8	20.7	18.2	13.1	10.4	7.6	5.6
6 mi SW Managua, Nicaragua							
KU 70135, ♂	44.8	21.7	18.6	13.0	10.2	7.7	5.8
KU 70137, ♂	45.1	21.6	19.0	13.2	10.7	7.7	5.8
KU 70136, ♀	43.5	19.9	17.8	12.7	10.3	7.5	5.5
3 km N, 4 km W Diriamba, Nicaragua							
Average 7 (♂)	44.8	21.2	18.5	13.0	10.5	7.4	5.5
Minimum	43.8	20.7	18.3	12.7	10.2	7.2	5.4
Maximum	45.7	21.3	18.8	13.3	10.9	7.6	5.5
Average 9 (♀)	44.0	20.7	18.0	12.6	10.2	7.3	5.3
Minimum	42.0	20.0	17.4	12.0	10.0	7.0	5.0
Maximum	45.5	21.2	18.6	13.0	10.6	7.5	5.5
Molossus sinaloae sinaloae, El Recreo, Nicaragua							
Average 4 (♂)	47.6	21.2	18.6	12.3	9.8	7.7	5.4
Minimum	46.7	20.7	18.3	12.0	9.7	7.6	5.3
Maximum	48.6	21.5	18.9	12.6	10.0	7.9	5.5
Average 10 (♀)	47.5	20.2	17.8	11.8	9.7	7.3	5.1
Minimum	46.2	20.0	17.6	11.5	9.5	7.1	5.0
Maximum	48.3	20.4	18.0	12.0	9.8	7.5	5.5

phism is considered. Also, the average weights of 18 nonpregnant females and four males of *pretiosus* (all adults) collected on 20 February 1968 at Los Cocos, were 20.9 (14.6-23.8) and 27.0 (24.6-31.7) gms, respectively, significantly smaller than corresponding figures for 11 nonpregnant females and nine males of *M. a. nigricans* taken two weeks later on the Cosigüina Peninsula—29.1

(26.1-33.0) and 32.9 (29.3-35.1) gms. It is of note that we have not collected these two large species at the same localities in Nicaragua, and it is possible that one competitively excludes the other in local situations.

Among females from Departamento de Boaco, none of 18 collected on 20 February was pregnant, whereas three of four obtained on 4 April were gravid (embryos 13, 15, and 17 mm in crown-rump length) as was one (embryo 21 mm) taken on 18 July. Among those from northwest of Diriamba, two of three were pregnant on 30-31 March (embryos 7 and 13 mm in length), whereas only three of eight carried embryos (29, 31, and 34 mm) in mid-August at a time when flying young also were collected. Additionally, a female captured 6 mi WSW Managua on 27 March had an embryo that measured 11 mm.

Four adult males collected on 20 February had an average testicular length of 5.7 (4-7) mm, whereas those of seven obtained in late March averaged 5.0 (4-6) mm; testes of two adults taken on 18 July were 6 and 6.5 mm, and those of three taken in the period 12-15 August were 5 mm in length.

Molossus sinaloae sinaloae J. A. Allen, 1906

Specimens.—Boaco: Santa Rosa, 17 km N, 15 km E Boaco, 300 m, 1. *Managua:* 1 km N Sabana Grande, 1; 3 mi SW Managua, 1; 8 km SW Managua, 400 m, 3. *Rivas:* San Juan del Sur, 20 m, 1. *Zelaya:* S side Río Mico, El Recreo, 25 m, 73.

This mastiff bat can be distinguished easily from the other two large species of *Molossus* in Nicaragua in that the hairs of the dorsum are relatively long and are pale, frequently white, basally. The species has been reported twice previously from Nicaragua—from Greytown by Miller (1913a:89) and by Goodwin and Greenhall (1964:13), who listed four individuals from Río Grande.

Most of our specimens were taken from buildings. A large series obtained in a house at El Recreo in late June 1966 consisted only of females and young, many of which were nearly full grown; some females still were lactating and at least two were pregnant (on 23 June—crown-rump length of embryos 12 and 14 mm). A group taken from another house at El Recreo (from cracks in the stone wall and from between rafters and the corrugated metal roof) in late July 1966 consisted of adult males, lactating females, and young. Similarly, an adult male, a pregnant female (embryo 14 mm in crown-rump length), and a hairless juvenile were shot, on 16 February 1964, from a small colony in an attic of a large house southwest of Managua; *Glossophaga soricina* also was taken in this attic. The testes of an adult male captured in June were 6 mm in length; those of four taken in July were 5, 5, 6, and 7 mm, and one obtained in August had testes that measured 3 mm.

Selected measurements of *M. s. sinaloae* from El Recreo are given in table 4.

CHECKLIST OF NICARAGUAN BATS

Following is a checklist of the 68 species of bats thus far reported from Nicaragua. Citations are given only to publications that are primary sources of information on Nicaraguan specimens. In some instances, specimens were reported in the literature under a name different than the one here employed; we have mentioned earlier-used names where it seemed appropriate to do so. Taxa preceded by an asterisk are included in the present paper.

Family EMBALLONURIDAE

Rhynchonycteris naso (Wied-Neuwied, 1820).—J. A. Allen (1908:669, 1910:110), Sanborn (1937:327), Davis *et al.* (1964:375, 379).

Saccopteryx bilineata (Temminck, 1838-1839).—J. A. Allen (1910:110), Sanborn (1937:331), Jones (1964a:506).

**Saccopteryx leptura* (Schreber, 1774).—Davis *et al.* (1964:374), Jones (1964a:506).

Cormura brevirostris (Wagner, 1843).—J. A. Allen (1910:110—specimens listed as *Peropteryx canina* from Peña Blanca, see Sanborn, 1937:348), Miller (1924:38), Sanborn (1937:349), Goodwin (1942c:119).

Peropteryx kappleri kappleri Peters, 1867.—J. A. Allen (1908:669, 1910:110—as *P. canina*), Sanborn (1937:344).

**Peropteryx macrotis macrotis* (Wagner, 1843).

Balantiopteryx plicata plicata Peters, 1867.—Jones *et al.* (1962:152), Davis *et al.* (1964:375), Jones (1964a:506).

Diclidurus virgo Thomas, 1903.—Alston (1879-82:30).

Family NOCTILIONIDAE

**Noctilio labialis labialis* (Kerr, 1792).—Goodwin (1942c:121, 1946:297), Davis *et al.* (1964:376), Kohls *et al.* (1965:344), Wenzel *et al.* (1966:578).

**Noctilio leporinus mexicanus* Goldman, 1915.—Davis *et al.* (1964:376).

Family PHYLLOSTOMATIDAE

**Pteronotus davyi fulvus* (Thomas, 1892).

**Pteronotus parnellii fuscus* J. A. Allen, 1911.—Miller (1902:402), Rehn (1904:203).

**Pteronotus suapurensis* (J. A. Allen, 1904).—Goodwin (1942a:88, 1946:299, 1953:246).

Micronycteris brachyotis (Dobson, 1879).—Goodwin (1946:302—as *M. sylvestris*), Sanborn (1949:224—as *M. platyceps*), Goodwin and Greenhall (1961:231).

Micronycteris hirsuta (Peters, 1869).—Valdez and LaVal (1971:247).

**Micronycteris megalotis mexicana* Miller, 1898.—G. M. Allen (1929:130).

**Micronycteris megalotis microtis* Miller, 1898.—Miller (1898:328, 1900:154), Lyon and Osgood (1909:263), J. A. Allen (1910:110), Poole and Schantz (1942:133).

Micronycteris minuta (Gervais, 1856).—Valdez and LaVal (1971:248).

Micronycteris schmidtorum Sanborn, 1935.—Davis *et al.* (1964:378).

Macrophyllum macrophyllum (Schinz, 1821).—Davis *et al.* (1964:378), Jones (1964a:506).

**Tonatia nicaraguae* Goodwin, 1942.—Goodwin (1942b:205, 1946:305, 1953: 246), Davis and Carter (1962:67), Valdez and LaVal (1971:248).

Phyllostomus discolor verrucosus Elliot, 1905.—Jones (1964a:507), Wenzel *et al.* (1966:598).

**Phyllostomus hastatus panamensis* J. A. Allen, 1904.—Goodwin (1942c:126), Wenzel *et al.* (1966:597).

**Trachops cirrhosus coffini* Goldman, 1925.—Carter *et al.* (1966:491).

**Chrotopterus auritus auritus* (Peters, 1856).

Vampyrum spectrum nelsoni (Goldman, 1917).—Gray (1844:18), Dobson (1878:471), Alston (1879-82:39), J. A. Allen (1910:111), Goldman (1917:116), Goodwin (1946:310).

Glossophaga commissarisi Gardner, 1962.—Davis *et al.* (1964:380), Jones (1964a:507).

Glossophaga soricina leachii (Gray, 1844).—Gray (1844:18), Dobson (1878: 501), Alston (1879-82:44), J. A. Allen (1910:111), Miller (1913b:419), Alvarez (1963:400), Davis *et al.* (1964:380), Starrett and de la Torre (1964:57).

**Anoura geoffroyi lasiopyga* (Peters, 1868).

**Choeroniscus godmani* (Thomas, 1903).—Handley (1966a:86).

**Lichonycteris obscura* Thomas, 1895.—Thomas (1895:57), Davis *et al.* (1964:380).

**Carollia castanea* H. Allen, 1890.—Davis *et al.* (1964:379).

Carollia perspicillata azteca Saussure, 1860.—Hahn (1907:112), J. A. Allen (1908:669, 1910:111), Davis *et al.* (1964:379), Starrett and de la Torre (1964:58).

Carollia subrufa (Hahn, 1905).—Davis and Carter (1962:71), Davis *et al.* (1964:379).

Sturnira lilium parvidens Goldman, 1917.—Davis *et al.* (1964:379), Starrett and de la Torre (1964:59), Jones (1964a:507).

**Sturnira ludovici ludovici* Anthony, 1924.

Uroderma bilobatum convexum Lyon, 1902.—Davis *et al.* (1964:382), Jones (1964a:507), Davis (1968:695).

Uroderma bilobatum molaris Davis, 1968.—Davis *et al.* (1964:382), Davis (1968:697).

**Uroderma magnirostrum* Davis, 1968.—Davis (1968:680).

**Vampyrops helleri* Peters, 1866.—Davis *et al.* (1964:383), Jones (1964a:507), Valdez and LaVal (1971:248).

**Vampyrodes major* G. M. Allen, 1908.—J. A. Allen (1910:112), Goodwin (1946:320).

**Vampyressa nymphaea* Thomas, 1909.

**Vampyressa pusilla thyone* Thomas, 1909.—Starrett and de la Torre (1964: 60).

**Chiroderma villosum jesupi* J. A. Allen, 1900.

Ectophylla alba H. Allen, 1892.—H. Allen (1892:441, 1898:267), Lyon and

Osgood (1909:266), Poole and Schantz (1942:129), Goodwin (1942c: 134, 1946:323), Goodwin and Greenhall (1962:4). Type locality (Río Segovia) placed in Comarca de El Cabo, Nicaragua, by Miller and Kellogg (1955:77).

Artibeus inopinatus Davis and Carter, 1964.—Davis and Carter (1964:120).

Artibeus jamaicensis paulus Davis, 1970.—Andersen (1908:266), Davis (1970b:121).

Artibeus jamaicensis richardsoni J. A. Allen, 1908.—Andersen (1908:267), J. A. Allen (1908:669), Elliot (1917:168), Goodwin (1953:249), Davis and Carter (1964:120), Davis *et al.* (1964:379), Starrett and de la Torre (1964:60), Davis (1970b:116).

Artibeus lituratus palmarum J. A. Allen and Chapman, 1897.—Andersen (1908:279), Davis and Carter (1964:120), Davis *et al.* (1964:379), Starrett and de la Torre (1964:61).

Artibeus phaeotis palatinus Davis, 1970.—Davis (1970a:401).

Artibeus phaeotis phaeotis (Miller, 1902).—Davis *et al.* (1964:379), Davis (1970a:399).

**Artibeus toltecus hesperus* Davis, 1969.

**Artibeus toltecus toltecus* (Saussure, 1860).—Andersen (1908:300), Davis (1969:28).

**Artibeus watsoni* Thomas, 1901.—Andersen (1908:290), Davis and Carter (1962:71), Davis (1970a:393).

**Centurio senex senex* Gray, 1842.—Goodwin (1946:327, restricted type locality to El Realejo, Nicaragua).

Desmodus rotundus murinus Wagner, 1840.—J. A. Allen (1908:670, 1910: 113).

**Diphylla ecaudata* Spix, 1823.

Family NATALIDAE

**Natalus stramineus saturatus* Dalquest and Hall, 1949.

Family THYROPTERIDAE

Thyroptera discifera discifera (Lichtenstein and Peters, 1854).—Miller 1896: 111, 1931:411), Goodwin (1946:330).

Family VESPERTILIONIDAE

**Myotis albescens* (É. Geoffroy St.-Hilaire, 1806).—Miller and G. M. Allen (1928:203).

**Myotis elegans* Hall, 1962.

**Myotis nigricans nigricans* (Schinz, 1821).—Davis *et al.* (1964:379), McDaniel and Coffman (1970:223).

**Myotis simus riparius* Handley, 1960.

**Eptesicus furinalis gaumeri* (J. A. Allen, 1897).—Miller (1897:100), Davis (1965:234).

Lasiurus borealis frantzii (Peters, 1871).—Davis and Carter (1962:73).

**Rhogeessa tumida tumida* H. Allen, 1866.—J. A. Allen (1910:113), Goodwin (1958:3).

Family MOLOSSIDAE

**Tadarida laticaudata yucatanica* (Miller, 1902).

**Eumops auripendulus* (Shaw, 1800).

**Molossus ater nigricans* Miller, 1902.—J. A. Allen (1908:670).
Molossus bondae J. A. Allen, 1904.—Miller (1913a:89).
**Molossus molossus aztecus* Saussure, 1860.—Felten (1957:14).
**Molossus pretiosus pretiosus* Miller, 1902.
**Molossus sinaloae sinaloae* J. A. Allen, 1906.—Miller (1913a:89), Goodwin and Greenhall (1964:13).

LITERATURE CITED

ALLEN, G. M.
1929. Mammals. Pp. 129-130, *in* Vertebrates from the Corn Islands. Bull. Mus. Comp. Zool., 69:127-146.

ALLEN, H.
1892. Description of a new genus of phyllostome bats. Proc. U.S. Nat. Mus., 15:441-442.
1898. The skull and teeth of Ectophylla alba. Trans. Amer. Philos. Soc., 19:267-272.

ALLEN, J. A.
1908. Mammals from Nicaragua. Bull. Amer. Mus. Nat. Hist., 24:647-670.
1910. Additional mammals from Nicaragua. Bull. Amer. Mus. Nat. Hist., 28:87-115.

ALSTON, E. R.
1879-1882. Biologia Centrali-Americana, Mammalia. London, xx+220 (introduction by P. L. Sclater).

ALVAREZ, T.
1963. The Recent mammals of Tamaulipas, México. Univ. Kansas Publ., Mus. Nat. Hist., 14:363-473.

ANDERSEN, K.
1908. A monograph of the chiropteran genera *Uroderma, Enchisthenes,* and *Artibeus.* Proc. Zool. Soc. London, 204-319.

BURT, W. H., and R. A. STIRTON
1961. The mammals of El Salvador. Misc. Publ. Mus. Zool., Univ. Michigan, 117:1-69.

CABRERA, A.
1958. Catalogo de los mamíferos de America del Sur. Rev. Mus. Argentino Cienc. Nat., Buenos Aires, 4:iv+307.

CARTER, D. C., R. H. PINE, and W. B. DAVIS
1966. Notes on Middle American bats. Southwestern Nat., 11:488-499.

DAVIS, W. B.
1965. Review of the *Eptesicus brasiliensis* complex in Middle America with description of a new subspecies from Costa Rica. Jour. Mamm., 46:229-240.
1968. Review of the genus *Uroderma* (Chiroptera). Jour. Mamm., 49: 676-698.
1969. A review of the small fruit bats (genus *Artibeus*) of Middle America. Southwestern Nat., 14:15-29.
1970a. A review of the small fruit bats (genus *Artibeus*) of Middle America. Part II. Southwestern Nat., 14:389-402.

1970b. The large fruit bats (genus *Artibeus*) of Middle America, with a review of the *Artibeus jamaicensis* complex. Jour. Mamm., 51: 105-122.

Davis, W. B., and D. C. Carter
1962. Notes on Central American bats with description of a new subspecies of Mormoops. Southwestern Nat., 7:64-74.
1964. A new species of fruit-eating bat (genus *Artibeus*) from Central America. Proc. Biol. Soc. Washington, 77:119-121.

Davis, W. B., D. C. Carter, and R. H. Pine
1964. Noteworthy records of Mexican and Central American bats. Jour. Mamm., 45:375-378.

Dobson, G. E.
1878. Catalogue of the Chiroptera in the collection of the British Museum. British Museum, London, xlii+567.

Elliot, D. G.
1917. A check-list of mammals of the North American continent. . . . Suppl., edited by J. A. Allen, Amer. Mus. Nat. Hist., iv+192.

Felten, H.
1955. Fledermäuse (Mammalia, Chiroptera) aus El Salvador. Tiel 1. Senckenbergiana Biol., 36:271-285.
1956. Fledermäuse (Mammalia, Chiroptera) aus El Salvador. Tiel 3. Senckenbergiana Biol., 37:179-212.
1957. Fledermäuse (Mammalia, Chiroptera) aus El Salvador. Tiel 5. Senckenbergiana Biol., 38:1-22.

Gardner, A. L.
1966. A new subspecies of the Aztec mastiff bat, *Molossus aztecus* Saussure, from southern Mexico. Contrib. Sci., Los Angeles Co. Mus., 111:1-5.

Gardner, A. L., R. K. LaVal, and D. E. Wilson
1970. The distributional status of some Costa Rican bats. Jour. Mamm., 51:712-729.

Goldman, E. A.
1917. New mammals from North and Middle America. Proc. Biol. Soc. Washington, 30:107-116.

Goodwin, G. G.
1942a. New Pteronotus from Nicaragua. Jour. Mamm., 23:88.
1942b. A summary of recognizable species of Tonatia, with descriptions of two new species. Jour. Mamm., 23:204-209.
1942c. Mammals of Honduras. Bull. Amer. Mus. Nat. Hist., 79:107-195.
1946. Mammals of Costa Rica. Bull. Amer. Mus. Nat. Hist., 87:271-473.
1953. Catalogue of type specimens of Recent mammals in the American Museum of Natural History. Bull. Amer. Mus. Nat. Hist., 102: 211-411.
1956. A preliminary report on the mammals collected by Thomas MacDougall in southeastern Oaxaca, Mexico. Amer. Mus. Novit., 1757: 1-15.
1958. Bats of the genus *Rhogeessa*. Amer. Mus. Novit., 1923:1-17.
1959. Bats of the subgenus *Natalus*. Amer. Mus. Novit., 1977:1-22.

GOODWIN, G. G., and A. M. GREENHALL

1961. A review of the bats of Trinidad and Tobago. Bull. Amer. Mus. Nat. Hist., 122:189-301.

1962. Two new bats from Trinidad, with comments on the status of the genus *Mesophylla*. Amer. Mus. Novit., 2080:1-18.

1964. New records of bats from Trinidad and comments on the status of *Molossus trinitatus* Goodwin. Amer. Mus. Novit., 2195:1-23.

GRAY, J. E.

1844. Zoology of the voyage of H.M.S. Sulphur. . . . Mammalia (parts 1, 2). London [not seen].

HAHN, W. L.

1907. A review of the bats of the genus Hemiderma. Proc. U.S. Nat. Mus., 32:103-118.

HANDLEY, C. O., JR.

1960. Descriptions of new bats from Panama. Proc. U.S. Nat. Mus., 112:459-479.

1966a. Description of new bats *(Choeroniscus* and *Rhinophylla)* from Colombia. Proc. Biol. Soc. Washington, 79:83-88.

1966b. Checklist of the mammals of Panama. Pp. 753-795, *in* Ectoparasites of Panama (R. L. Wenzel and V. J. Tipton, eds.), Field Mus. Nat. Hist., Chicago, xii+861.

HERSHKOVITZ, P.

1949. Mammals of northern Colombia. Preliminary report no. 5: bats (Chiroptera). Proc. U.S. Nat. Mus., 99:429-454.

HUSSON, A. M.

1962. The bats of Suriname. E. J. Brill, Leiden, 282.

JONES, J. K., JR.

1964a. Bats new to the fauna of Nicaragua. Trans. Kansas Acad. Sci., 67:506-508.

1964b. Bats from western and southern Mexico. Trans. Kansas Acad. Sci., 67:509-516.

1966. Bats from Guatemala. Univ. Kansas Publ., Mus. Nat. Hist., 16: 439-472.

JONES, J. K., JR., T. ALVAREZ, and M. R. LEE

1962. Noteworthy mammals from Sinaloa, Mexico. Univ. Kansas Publ., Mus. Nat. Hist., 14:145-159.

KOHLS, G. M., D. E. SONENSHINE, and C. M. CLIFFORD

1965. The systematics of the subfamily Ornithodorinae (Acarina: Argasidae). II. Identification of the larvae of the Western Hemisphere and descriptions of three new species. Ann. Ent. Soc. Amer., 58:331-364.

LAVAL, R. K.

1969. Records of bats from Honduras and El Salvador. Jour. Mamm., 50:819-822.

LYON, M. W., and W. H. OSGOOD

1909. Catalogue of the type-specimens of mammals in the United States National Museum, including the Biological Survey collection. Bull. U.S. Nat. Mus., 62:ix+325.

McDaniel, B., and C. C. Coffman
1970. The labidocarpid bat-mites of the United States (Acarina: Listrophoridea). Proc. Helminthological Soc. Washington, 37:223-229.

Miller, G. S., Jr.
1896. The Central American *Thyroptera.* Proc. Biol. Soc. Washington, 10:109-112.
1897. Revision of the North American bats of the family Vespertilionidae. N. Amer. Fauna, 13:1-135.
1898. Descriptions of five new phyllostome bats. Proc. Acad. Nat. Sci. Philadelphia, 50:326-337.
1900. Note on *Micronycteris brachyotis* (Dobson) and *M. microtis* Miller. Proc. Biol. Soc. Washington, 13:154-155.
1902. Twenty new American bats. Proc. Acad. Nat. Sci. Philadelphia, 54:389-412.
1913a. Notes on the bats of the genus *Molossus.* Proc. U.S. Nat. Mus., 46:85-92.
1913b. Revision of the bats of the genus *Glossophaga.* Proc. U.S. Nat. Mus., 46:413-429.
1924. List of North American Recent mammals 1923. Bull. U.S. Nat. Mus., 128:xvi+673.
1931. Two new South American bats. Jour. Mamm., 12:411-412.

Miller, G. S., Jr., and G. M. Allen
1928. The American bats of the genera Myotis and Pizonyx. Bull. U.S. Nat. Mus., 144:viii+218.

Miller, G. S. Jr., and R. Kellogg
1955. List of North American Recent mammals. Bull. U.S. Nat. Mus., 205:xii+954.

Paradiso, J. L.
1967. A review of the wrinkle-faced bats (*Centurio senex* Gray), with description of a new subspecies. Mammalia, 31:595-604.

Poole, A. J., and V. S. Schantz
1942. Catalog of the type specimens of mammals in the United States National Museum, including the Biological Surveys collection. Bull. U.S. Nat. Mus., 178:xiii+705.

Rehn, J. A. G.
1904. A study of the mammalian genus Chilonycteris. Proc. Acad. Nat. Sci. Philadelphia, 56:181-207.

Sanborn, C. C.
1937. American bats of the subfamily Emballonurinae. Field Mus. Nat. Hist., Zool Ser., 20:321-354.
1949. Bats of the genus Micronycteris and its subgenera. Fieldiana-Zool., 31:215-233.

Starrett, A., and R. S. Casebeer
1968. Records of bats from Costa Rica. Contrib. Sci., Los Angeles Co. Mus., 148:1-21.

Starrett, A., and L. de la Torre
1964. Notes on a collection of bats from Central America, with the third record of *Cyttarops alecto* Thomas. Zoologica, 49:53-63.

THOMAS, O.

1895. On small mammals from Nicaragua and Bogota. Ann. Mag. Nat. Hist., ser. 6, 16:55-60.

1905. New Neotropical *Chrotopterus, Sciurus, Neacomys, Coendou, Proechimys,* and *Marmosa.* Ann. Mag. Nat. Hist., ser. 7, 16: 308-314.

VALDEZ, R., and R. K. LAVAL

1971. Records of bats from Honduras and Nicaragua. Jour. Mamm., 52:247-250.

WENZEL, R. L., V. J. TIPTON, and A. KIEWLICZ

1966. The streblid batflies of Panama. Pp. 405-675, *in* Ectoparasites of Panama (R. L. Wenzel and V. J. Tipton, eds.), Field Mus. Nat. Hist., Chicago, xii+861.

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QUANTITATIVE ANALYSIS OF THE ECOLOGICAL DISTRIBUTION OF A TROPICAL HERPETOFAUNA

By

MARTHA L. CRUMP[1]

INTRODUCTION

Possibly the rainforest environment is not so constant, equitable, and predictable as ecologists have assumed. Lloyd, Inger, and King (1968) suggested this possibility as a result of studies on amphibian and reptile diversity in tropical rainforests of Borneo. The ways in which species utilize environmental resources have long been of interest in ecology; recently some effort has been made to analyze the inherent properties of the rainforests as they relate to amphibians and reptiles. Schoener (1970) studied nonsynchronous spatial overlap of lizards, genus *Anolis,* in patchy habitats in the West Indies. Schoener and Gorman (1968) studied niche differences of three species of *Anolis* from the southern Lesser Antilles; Schoener (1968) also studied resource partitioning among anoles on South Bimini Island. Rand (1964) examined the ecological distribution of anoles in Puerto Rico. Rand and Humphrey (1968) studied ecological distribution and interspecific competition among lizards in the rainforest at Belém, Brasil. Duellman (1967) studied isolating mechanisms and resource partitioning in tree frogs in Costa Rica. Inger and Greenberg (1966) studied the relation between niche overlap and interspecific competition for three species of frogs, genus *Rana,* in Sarawak. As indicated, the majority of studies have been carried out on specific genera; no extensive, quan-

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[1] Graduate Student, Museum of Natural History, University of Kansas.

titative ecological studies have been carried out in the New World tropics on an entire reptilian or amphibian community.

This is a report on the ecological distribution of amphibians and reptiles undertaken at the Guamá Ecological Research Area near Belém, Brasil. Field work was carried out from mid-January through July 1969, in April 1970, and in June and July 1970. Part of the resultant collection was given to the Museu Goeldi in Belém, and part is catalogued in the Museum of Natural History at the University of Kansas.

The objectives of the present study are threefold: 1) to determine the ecological distribution of 62 species of frogs, salamanders, and lizards within the rainforest environment of Belém; 2) to analyze the environmental parameters affecting the distribution of species; and 3) to compare and contrast the major areas with regard to species composition. The ecological distribution of the herpetofauna presented here is based on data obtained in one small area in part of the year. A similar study carried out from August through January or in a different area probably would yield somewhat different results.

Description of the Area

Belém is located about one degree south of the equator, in the lower Amazon Basin, Estado do Pará, Brasil; the elevation at the highest point is 12 m above sea level. The mean annual temperature is 26°C, and the average monthly temperature varies less than 2°C throughout the year. Seasonality is reflected through the temporal distribution of rainfall, yielding wet and dry seasons. The average annual rainfall (44 years) for the wet season, January through June, at Belém is 2028 mm, whereas that for the dry season, July through December, is 830 mm (Belém Virus Laboratory, 1967 Annual Report).

Belém is the headquarters for the Instituto de Pesquisas e Experimentação Agronomicas do Norte (IPEAN). An area of about 310 hectares of IPEAN property has been designated as the Guamá Ecological Research Area (APEG). Most of my study was carried out in two of the APEG reserves. The Aurá Reserve is part capoeira, part terra firme (Fig. 1), and part varzea forest (Fig. 2); some areas are transitional between terra firme and varzea forests. The Catú Reserve is a transect of igapó forest (Fig. 3) 1000×200 m. See figure 4 for spatial relationship of the reserves. The forest types are defined below.

The reserves are divided into a network of 10×10 m quadrats, each marked with a numbered stake. For each observation or in-

FIG. 1. Terra firme forest (Aurá reserve). Well-drained forest on relatively high ground. Photo by Roger Arle.

FIG. 2. Varzea forest (Aurá reserve). Flooded daily by the back-up from the Rio Guamá; predominance of Acai palm trees (*Euterpe oleracea*). Photo by Roger Arle.

FIG. 3. Igapó forest (Catú reserve). Permanently flooded forest. The boardwalk provides easy access.

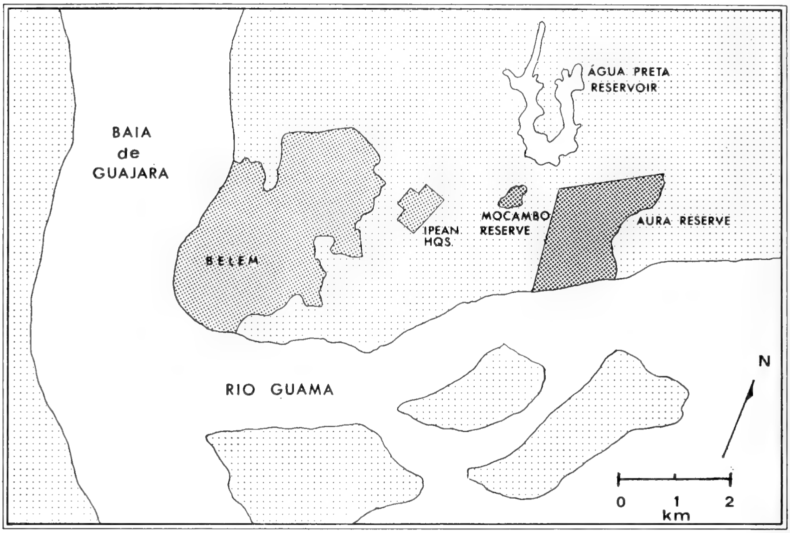


FIG. 4. Map of Mocambo and Aurá Reserves in relation to Belém and the Rio Guamá. The Mocambo Reserve consists of terra firme forest, surrounded by the Catú reserve of igapó forest (not indicated on map); the Aurá Reserve consists of terra firme, capoeira, varzea, and transition forest areas. Some studies were carried out in the vicinity of the IPEAN headquarters and at the Agua Preta Reservoir (Utinga Reserve).

dividual collected, the hectare and quadrat numbers were recorded, thereby assuring that all data were collected in the same spatial frame of reference. The distribution of water was determined and mapped for the capoeira, terra firme, and varzea study areas (Figs. 5-9); species distributions were superimposed on these maps to determine the associations of species with standing water. For the various quantitative analyses, 44 sampling plots, each 20×30 m, from four of the major forest areas were studied. The location of the 4 capoeira-terra firme transition, 19 terra firme-varzea transition, and 9 varzea plots relative to each other and to the distribution of water is shown in figures 10 and 11. The other 12 plots were in the igapó forest. For the purpose of an analysis of ecological distribution, the rainforest at Belém was divided into seven major areas:

Terra firme forest.—Well-drained forest on relatively high ground that is never subject to flooding is called terra firme forest. It is a well-structured, complex, tropical rainforest. One 5.5 hectare area of terra firme forest (Mocambo Reserve) has been studied extensively by botanists. Cain *et al* (1956) found the area to be extremely complex, both in vegetation species richness and in vegetation density; they estimated the density of trees exceeding 10 cm

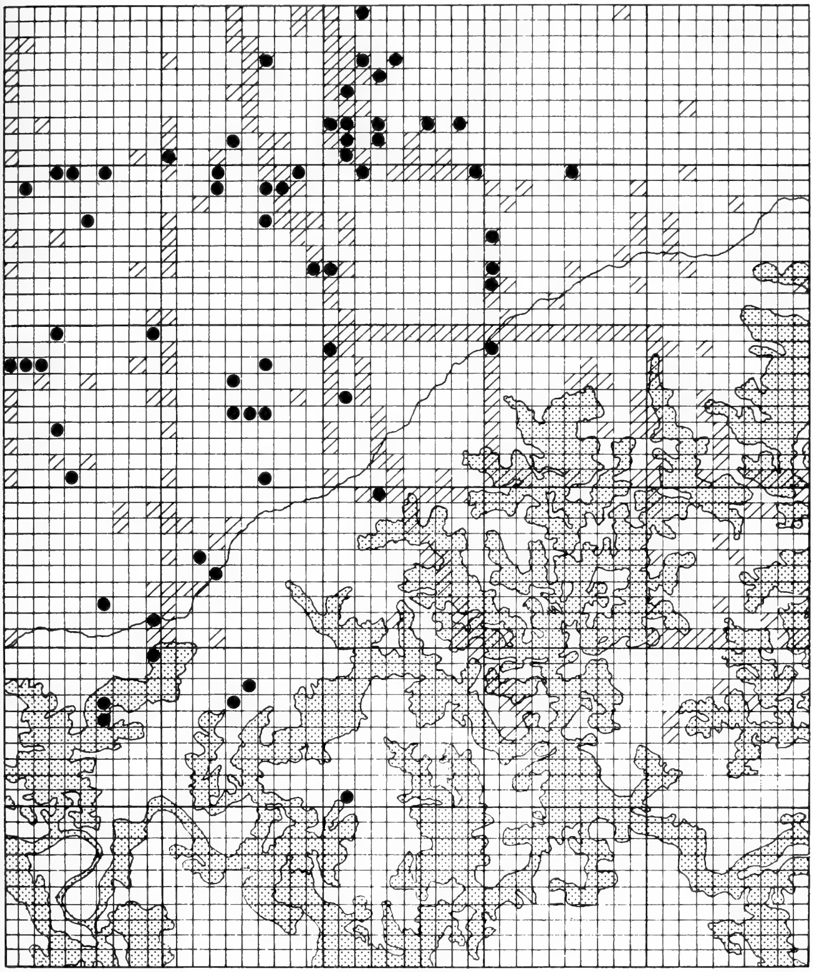


FIG. 5. Distribution of *Bolitoglossa altamazonica* in relation to distribution of water in terra firme, capoeira, and varzea transition forest. Each small square represents a quadrat, 10 x 10 m. Cross-hatched quadrats are those areas in which at least one frog, salamander, or lizard was observed by the author. Stippled areas represent terra firme-varzea transition depressions filled with standing water; non-stippled areas are better drained and usually are located on higher ground. Each dot represents the observation of at least one individual of *Bolitoglossa altamazonica* within the particular quadrat.

in diameter to be 594 trees per hectare. Dr. Murca Pires, a botanist associated with IPEAN, identified 215 species of trees in this area. Hatheway (1967) estimated the canopy to be 80 percent closed, with an average canopy height of about 35 m. He distinguished three strata of vegetation. Beneath the nearly closed canopy is a

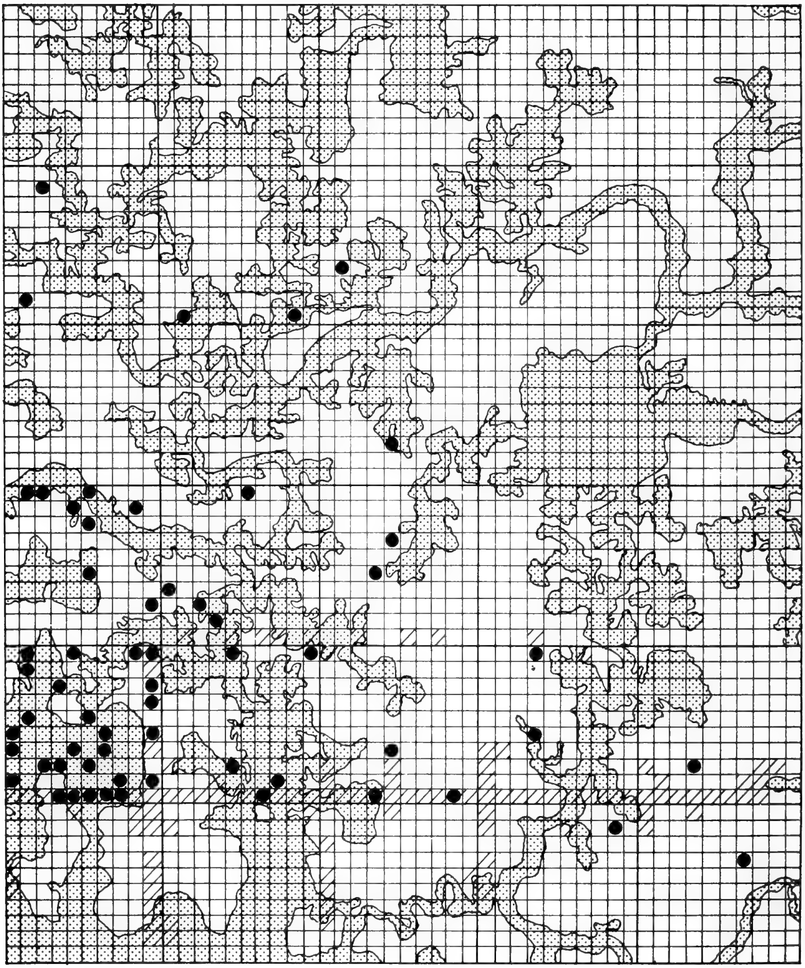


FIG. 6. Distribution of *Bolitoglossa altamazonica* in relation to distribution of water in varzea forest. See figure 5 for explanation; in this figure stippled areas represent varzea depressions filled with standing water.

deep layer of trees up to 20 m in height; the bottom, dense, scrubby layer extends to a height of about 1.5 m from the ground.

Varzea forest.—Swamp forest bordering the rivers is known locally as varzea. This forest is flooded daily by the back-up of the Rio Guamá, due to tidal effect. The degree of flooding varies throughout the year and is correlated with rainfall. All aquatic environments in the immediate vicinity of Belém seem to be freshwater (Humphrey, pers. com.). The "white water," so called because of the presence of sand, silt, and clay particles, yields a con-

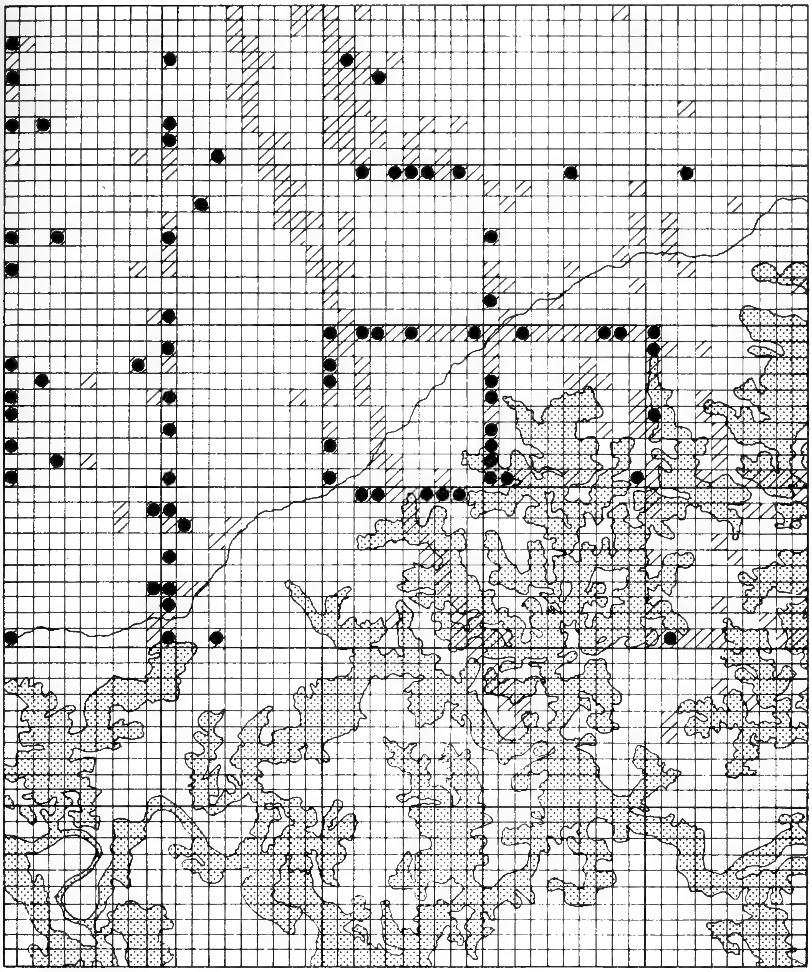


FIG. 7. Distribution of *Leptodactylus marmoratus* in relation to distribution of water in terra firme, capoeira, and varzea transition forest. See figure 5 for explanation of symbols.

tinual deposition of alluvium. The resultant alluvial varzea soil is rich, but has a low permeability. During the rainy season, parts of the varzea are flooded to a depth of 1 m or more. Depressions are present, resulting in differential drainage. Tall woody plants, palms, and giant aquatic herbs exist nearly side by side as a consequence of drainage patterns (Hatheway, 1967). There is a predominance of palms in the varzea forest; the acai palm *(Euterpe oleracea)* is the most common tree. Lianas and epiphytes are common, and moss as thick as 1 cm covers the trunks of trees up to 2 m

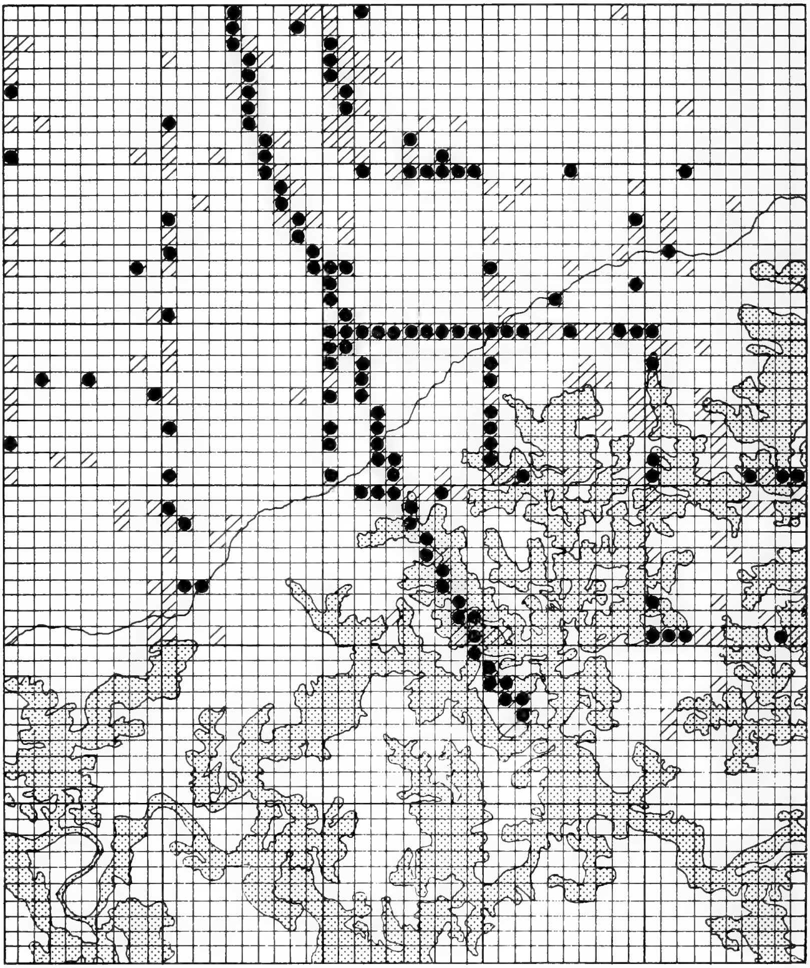


FIG. 8. Distribution of *Gonatodes humeralis* in relation to distribution of water in terra firme, capoeira, and varzea transition forest. See figure 5 for explanation of symbols.

from the ground. Hatheway (1967) proposed that epiphytic mosses likely indicate high humidity in tropical forests. In the varzea, this high humidity probably results from constant evaporation from the moist ground and water. Hatheway estimated that the total density of trees over 10 cm in diameter is probably greater than 600 trees per hectare. The canopy is about 50 percent open, and the canopy trees are 30-35 m in height.

Igapó forest.—This is forest that is permanently flooded with "black water," so called because of organic residues. Hatheway

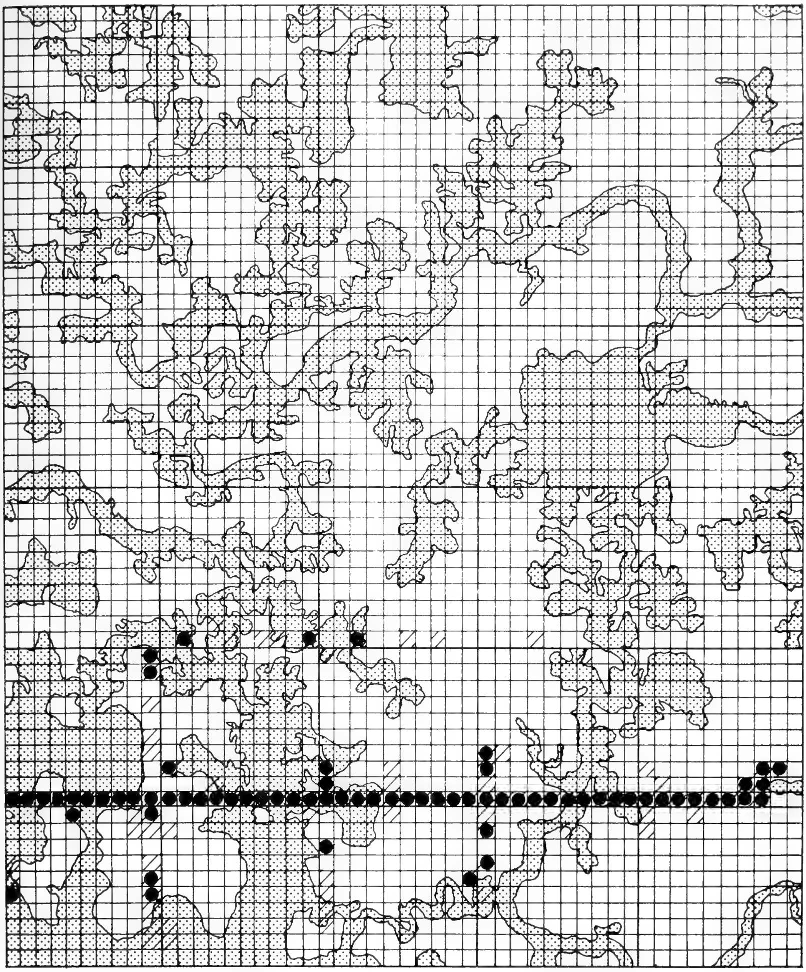


FIG. 9. Distribution of *Gonatodes humeralis* in relation to distribution of water in varzea forest. See figure 6 for explanation of symbols.

(1967) estimated the average depth of water to be 25 cm; beneath the water is another 25 cm of organic, water-logged muck, underneath which is white clay. The area consists of many stagnant, foul-smelling, interconnected pools. Small islands of root masses project from the pools; much of the vegetation in the swamp forest is supported on these islands, although a few trees are rooted in the muck. There is no well-formed canopy, and other distinct vegetational layers are difficult to distinguish. Most trees are small-crowned, slender dicots, rising above the thick mesh of tangled roots elevated to 3 m above the deep mud of the swamp.

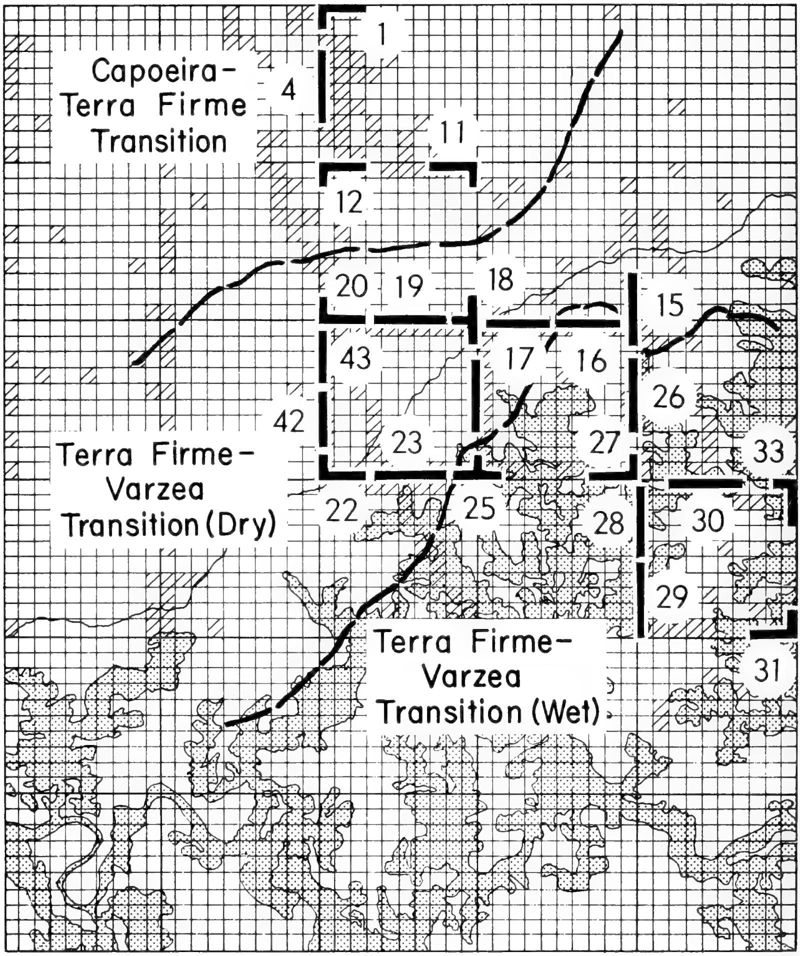


FIG. 10. Distribution of sampling plots in relation to distribution of water in terra firme, capoeira, and varzea transition forest. See figure 5 for explanation of symbols. The numbered plots, each 20 x 30 m, are indicated by heavy, straight lines; data from these plots were used in the contingency table analysis.

Capoeira forest.—This is second growth forest on well-drained ground. The capoeira areas studied had relatively open canopies and fairly dense ground cover. Much of the area is composed of tall grasses and ferns; the forest floor in some sections is covered with brush and fallen logs.

Capoeira-terra firme transition.—Four plots were studied which are intermediate between capoeira and terra firme forest with re-

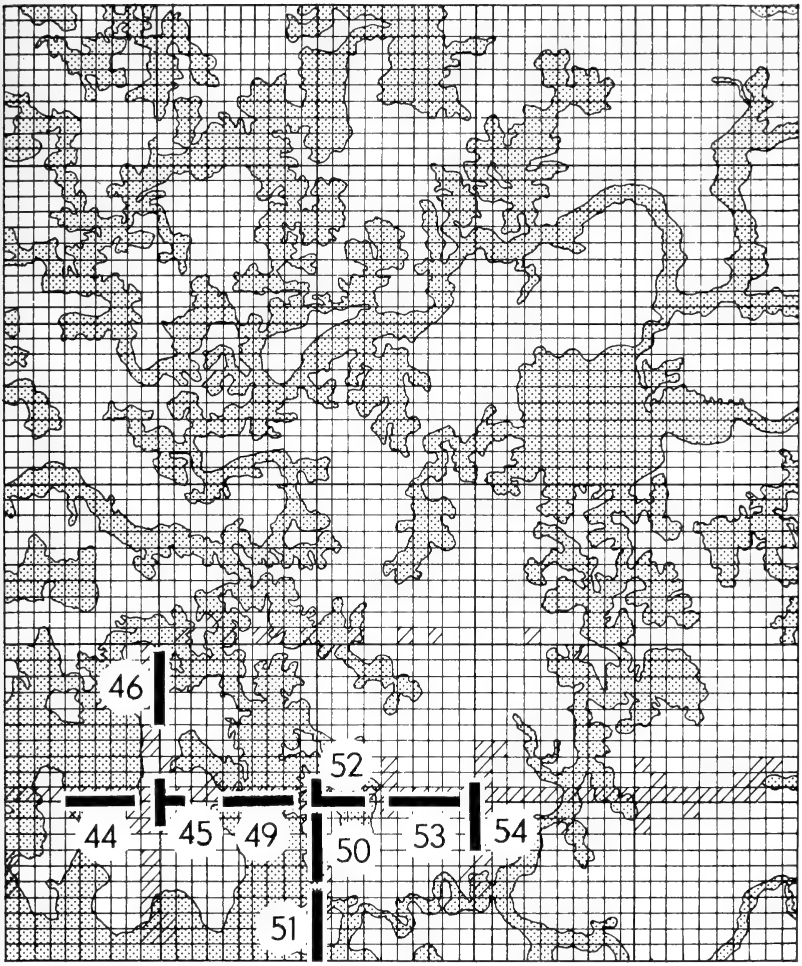


FIG. 11. Distribution of sampling plots in relation to distribution of water in varzea forest. See figures 6 and 10 for explanation.

gard to characteristics of canopy and ground cover. The plots exhibit a greater vegetation density than typical capoeira, but less than typical terra firme forest.

Terra firme-varzea transition.—Plots in one area exhibit some characteristics of both terra firme and varzea forests, but differ noticeably in other ways. For instance, on well-drained ground there is a lower vegetation density than in typical terra firme forest. The flooded portion lacks the predominance of palms, characteristic of typical varzea forest. Corresponding to the varzea and terra firme forests respectively, some of the soil in the transition area is a poorly-drained, silty-clay alluvium, whereas other soil is a well-drained, heavy, yellow laterite.

Open and edge.—All non-forest study sites are grouped in this category. Observations and collections were made in swampy areas in open fields, ponds along forest edges, and in second growth vegetation bordering the IPEAN reserves. During the rainy season, the swamps and ponds contained water to a depth of about 1 m but were usually less than half as full during June and July. Dirt roads and roadside ditches on IPEAN property and sewage swamps within the city were examined weekly.

Composition of the Herpetofauna

Three orders of amphibians: Gymnophiona (caecilians), Caudata (salamanders), and Anura (frogs) and four orders of reptiles: Amphisbaenia (amphisbaenids), Crocodilia (crocodilians), Squamata (lizards and snakes), and Testudines (turtles) are represented in the herpetofauna (116 species) of the Belém area; amphibians represent 35.4 percent of the herpetofauna, and reptiles 64.6 percent. The breakdown of species is as follows: caecilians—3, salamanders—1, frogs—37, amphisbaenids—3, crocodilians—1, lizards—24, snakes—44, and turtles—3. Further field work probably will reveal several additional species of snakes, caecilians, and turtles, as well as species of other groups.

Methods

Most observations and collections in the forests were made along paths and boardwalks constructed several years previously. Therefore, the data are biased to whatever extent the different species are influenced by the narrow, open areas maintained by continuous human activity. Species distributions necessarily reflect my sampling activity (Figs. 5-9).

An approximately equal amount of field work was done by day and by night. Every frog, salamander, and lizard observed was recorded by species, date, and locality (including hectare and quadrat numbers from the labeled study areas). The distribution of each of the 62 species was plotted on quadrat maps. Although snakes, turtles, and caecilians were collected, the few numbers of specimens of these groups precluded their inclusion in the analyses. Environmental gradients affecting the distribution of species within four major forest areas was inferred by use of a contingency table analysis. Resource partitioning was studied by means of field observations and analyzed by niche breadth and niche overlap analyses. Following the analysis of species distributions, the species compositions of the major areas were compared and contrasted by means of the Shannon species diversity formula, an equitability index, and coefficients of communities (see appropriate sections).

Definitions of terms, as I am using them, and a brief discussion of techniques of analysis are given below. The analytical techniques are treated in detail in appropriate subsequent sections of this paper.

Major areas.—The region studied can be divided into several geographical sections referred to as major areas. I have delimited the artificial boundaries in such a way that each area possesses a certain subjective uniformity with regard to physical environmental parameters, such as vegetational physiognomy, light intensity, water, and soil type. The quantitative analyses were carried out on data obtained from four major forest areas: 1) capoeira-terra firme transition; 2) terra firme-varzea transition; 3) varzea; and 4) igapó. Resource partitioning observations were carried out in the following major areas: 1) open and edge; 2) capoeira; 3) terra firme; 4) varzea; and 5) igapó.

Habitat.—This term refers to the structural aspect of a niche; it is that portion of the physical environment in which an organism carries out its life processes. The physical environment supports species in three major ways: 1) vertical zonation; 2) horizontal distribution; and 3) temporal spacing.

Community.—A community consists of interacting populations of animals. Each of the major areas included in this analysis has a herpetofaunal community different from every other area. The interaction and organization of each community is expressed in terms of resource partitioning with regard to differential utilization of the environment in space and time, species diversity including both species richness and equitability components, and species composition and relative abundance.

Resource partitioning.—This term refers to the differential utilization of the physical environment in space and time by different species. The result of resource partitioning is highly efficient utilization of environmental resources.

Niche.—This is an abstract concept referring to the habitat and biotic relationships of an animal. A niche can be thought of as a hypervolume, consisting of numerous dimensions (Hutchinson, 1957); the dimensions are physical factors and biotic relationships required by a species for survival. The physical factors of the environment making up the structural component (habitat) of the niche exist independent of the species, but the entire niche, inclusive of the position (biotic relationship) of the animal, does not exist independent of the species. Therefore, the niche is a function of the species. Formation of a particular niche is ultimately dependent on the structural adaptations, physiological requirements and capabilities, and correlated behavioral patterns of the species. No two species have identical physical and biotic requirements, coupled with identical structural, physiological, and behavioral attributes, and therefore no two species have the same niche.

Niche breadth.—This term is used to describe the spectrum of any given dimension of the niche hypervolume. For instance, one can speak of the food preference niche breadth of species A and B. If species A eats 10 different kinds of insects and species B eats only 2 kinds of insects, species A is said to have a broad food preference niche breadth and species B a narrow food preference niche breadth relative to each other. Niche breadth as used in this paper refers to the habitat niche breadth.

Niche overlap.—This term refers to the situation in which two or more species have similar requirements with respect to some dimension of the niche hypervolume. Niche overlap is a measure of the association of two or more species. The measurements in this study were obtained indirectly by the degree of coexistence of the species in the various plots sampled.

Habitat-generalists, intermediates, and specialists.—Habitat-generalists are species that utilize a broad spectrum of the environment, as indicated by the contingency table indices; they are found in all four major forest areas and have high habitat niche breadth scores (16.0-32.0), as calculated from Levins' index. Habitat-specialists are species apparently restricted in their distributions to one or two of the major forest areas; they seem to live in a narrow range of the environmental spectrum and have low niche breadth scores (1.0-4.0). All other species are referred to as habitat-intermediates. In most instances, the habitat-specialists are the least common species, whereas the habitat-generalists are the most abundant.

Species diversity.—The concept of species diversity consists of two components, species richness and equitability. The former is the number of species, and the latter is the evenness with which the individuals are distributed among the species. A community having a large number of species in which the abundance decreases gradually from the most to the least abundant species is considered to have a high species diversity. According to Whittaker (1970), niche differentiation results in greater species richness through time, whereas a narrowing of habitat distributions tends to increase species equitability. Some investigators propose that species richness depends primarily on the structural diversity of the habitat, whereas equitability is more dependent on the stability of physical conditions. Apparently the more complex the vegetation is vertically, the greater is bird species diversity (MacArthur and MacArthur, 1961; MacArthur, MacArthur, and Preer, 1962; MacArthur, 1964, 1965; and MacArthur, Recher, and Cody, 1966). Pianka (1967) proposed that spatial heterogeneity is the most important single factor determining the number of species of lizards in any given area. One of the most commonly accepted formulas to measure species diversity is the Shannon function (Shannon, 1948). Pielou (1966) discussed its use and disuse. The formula is used to describe an infinitely large population and results in the average diversity per species.

Coefficient of community.—The coefficient of community (CC) is a mathematical measure of relative similarity of samples from two communities (Whittaker, 1970).

ANALYSIS OF ECOLOGICAL DISTRIBUTION

As discussed in the preceding section, each major area is a complex of intrinsic physical environmental parameters, different from those in other areas. Each species is adapted to a particular range of each environmental gradient; the totality of environmental gradients forms the structural niche, or habitat, of the species. One must assume that habitat adaptation is based on the genetic make-up of the individuals of the species in terms of morphology, physiology, behavior, and life cycle. Based on the preceding assumptions, the following hypothesis can be stated: The 62 species of frogs, salamanders, and lizards in the Belém area are distributed in such a manner that environmental resources are partitioned; the consequence of habitat differentiation is highly efficient utilization of the environment.

Several techniques were used to study the ecological distribution and to test the hypothesis; others were used to compare and contrast the species composition within each major area. To avoid confusion, each analysis is presented separately. Included in each section is an explanation of purpose and a presentation and discussion of results; where applicable, advantages and limitations of the analyses are indicated.

The distribution of frogs, salamanders, and lizards as taxonomic groups within five of the major habitats is presented in table 1. The varzea has the highest species richness, with 38 (61.3%) of the 62 species occurring there. Next in terms of species richness is terra firme forest, with 36 species (58.1%). The area with the lowest value is capoeira, with only 20 species (32.2%). The mature forest

TABLE 1.—Distribution of Amphibians and Lizards by Major Taxonomic Groups in Five of the Major Areas. The top numbers are the number of species of a taxonomic group in a given area; percentages are the proportion of the taxonomic group in the area. Numbers in parentheses indicate the sum of the coded relative abundance indices (Table 2) for the taxonomic group in the area.

Group	Terra Firme	Varzea	Igapó	Capoeira	Open & Edge
Frogs and toads	20	22	13	8	24
37 species	54.0%	59.4%	35.1%	21.6%	64.9%
	(36)	(56)	(23)	(12)	(80)
Salamanders	1	1	1	1	0
1 species	100%	100%	100%	100%	----
	(4)	(4)	(2)	(3)	-----
Lizards	15	15	8	11	10
24 species	62.5%	62.5%	33.3%	45.8%	41.7%
	(27)	(29)	(16)	(19)	(23)
Total No. Species	36	38	22	20	34
% Total Species (62)	58.1%	61.3%	35.5%	32.2%	54.8%
Sum Abundance Indices	67	89	41	34	103
Average Species Abundance Index	1.86	2.34	1.86	1.70	3.03

areas likely are highest in species richness due to the greater vegetational diversity, yielding environmental heterogeneity, as contrasted to second growth areas (capoeira) having less structural complexity. Open and edge areas are relatively rich with 34 species (54.8%); 24 species of frogs (62.3% of the total anuran fauna) breed in the numerous ponds in these areas. Abundance indices for each species in each area were coded as follows: 0=apparently absent (none observed); 1=not commonly seen (1-4 observations); 2=moderately common (5-15); 3=common (16-25); and 4=abundant (26 or more observations). The average abundance index (obtained by dividing the sum of the abundance indices for all the species in a given area by the total number of species in that area) is much higher in open and edge areas (3.03) than the next highest which is the varzea forest (2.34); this is partially due to the large congregations of breeding frogs in open and edge areas. In addition, population densities of lizards are higher in open areas than in the forest, although this may be due to censusing methods; lizards are more easily seen in open and edge areas than in the dense forest. The ecological distribution and relative abundance of each species of frog, salamander, and lizard are shown in table 2. It is evident that certain species have a much broader range of ecological distribution than do others. Figures 5-9 indicate the distribution of three species relative to the distribution of water. The salamander, *Bolitoglossa*

TABLE 2.—Ecological Distribution of Frogs, Salamanders, and Lizards. Numbers indicate relative abundance of a species within an area, coded 0-4 as follows: 0=Apparently absent (none observed), 1=Not commonly seen (1-4 observations), 2=Moderately common (5-15), 3=Common (16-25), and 4=Abundant (26 or more observations).

Species	Terra Firme	Varzea	Igapó	Capoeira	Open & Edge
Pipa pipa	0	1	0	0	0
Eleutherodactylus lacrimosus	1	0	1	0	0
Leptodactylus marmoratus	4	4	0	3	0
Leptodactylus mystaceus	1	0	0	0	0
Leptodactylus ocellatus	0	0	0	0	4
Leptodactylus pentadactylus	1	0	0	0	0
Leptodactylus rhodomystax	1	2	0	0	0
Leptodactylus wagneri	1	4	4	0	2
Physalaemus ephippifer	4	4	1	1	4
Physalaemus petersi	3	4	0	0	2
Bufo marinus	0	0	0	0	4
Bufo typhonius	4	4	0	2	0
Dendrobates trivittatus	2	0	0	1	0
Dendrobates ventrimaculatus	0	2	3	0	0
Hyla baumgardneri	0	0	1	0	4
Hyla boesemani	0	0	0	0	4
Hyla calcarata	1	3	0	0	0
Hyla egleri	2	3	2	1	4
Hyla geographica	0	4	0	0	2
Hyla goughi	1	2	1	0	4
Hyla granosa	1	2	3	0	0
Hyla leucophyllata	0	2	1	0	4
Hyla melanargyrea	1	0	0	0	4
Hyla minuta	0	0	0	0	4
Hyla multifasciata	0	2	1	0	4
Hyla nana	1	0	0	0	4
Hyla raniceps	0	1	0	0	4
Hyla rondoniae	0	1	0	0	0
Hyla rubra	1	3	3	1	4
Hyla sp. (large *rubra*)	1	1	0	0	4
Hyla sp. (*rubra*-like)	4	4	1	2	1
Osteocephalus taurinus	0	0	0	0	1
Phrynohyas venulosa	1	0	1	1	3
Phyllomedusa bicolor	0	2	0	0	2
Phyllomedusa hypochondrialis	0	0	0	0	4
Phyllomedusa vaillanti	0	1	0	0	0
Sphaenorhynchus eurhostus	0	0	0	0	3
Bolitoglossa altamazonica	4	4	2	3	0
Gonatodes humeralis	4	4	3	3	0
Hemidactylus mabouia	0	0	0	0	4
Thecadactylus rapicaudus	1	0	0	0	0
Lepidoblepharus festae	0	1	1	0	0
Anolis fuscoauratus	3	3	1	1	0
Anolis ortoni	1	0	0	0	0
Anolis punctatus	1	1	0	1	0
Iguana iguana	0	1	0	0	1
Plica umbra	3	1	1	2	0
Polychrus marmoratus	1	1	1	1	0

TABLE 2.—(*Concluded*)

Species	Terra Firme	Varzea	Igapó	Capoeira	Open & Edge
Tropidurus torquatus	1	0	0	1	4
Uranoscodon superciliosa	1	2	1	1	1
Mabuya mabouya	3	4	4	3	2
Alopoglossus carinicaudatus	0	1	0	0	0
Ameiva ameiva	1	0	0	3	4
Arthrosaura kochii	1	0	0	0	0
Cnemidophorus lemniscatus	0	0	0	0	3
Crocodilurus lacertina	0	1	0	0	0
Dracaena guianensis	0	0	0	0	1
Kentropyx calcaratus	4	4	4	2	0
Leposoma percarinatum	0	2	0	0	1
Prionodactylus argulus	1	2	0	0	0
Tupinambus nigropunctatus	1	1	0	1	2

altamazonica, is abundant in capoeira, terra firme, and varzea areas, but few individuals are found in the terra firme-varzea transition area. *Leptodactylus marmoratus* occurs predominantly in well-drained areas, but *Gonatodes humeralis* tolerates wet and dry areas.

RESOURCE PARTITIONING

Extensive field observations were carried out in an effort to discern whether species do indeed partition environmental resources. Resources examined were those aspects of the habitat which are important to the daily and seasonal activities of the species as follows: frogs—standing bodies of water, calling sites, and vegetation and ground area used for daily activities; salamanders—vegetation used for nocturnal activities; lizards—vegetation and ground area used for basking sites and other diurnal activities.

For purposes of analysis, the environment can be divided into vertical and horizontal components such as arboreal (high and low), terrestrial, aquatic margin, and aquatic. The distribution of species in these subdivisions of each of the five major areas is shown in table 3. Most species studied are either low arboreal or terrestrial.

TABLE 3.—Distribution of Species of Frogs and Lizards Within Subdivisions of Five of the Major Areas. Numbers preceding hyphens are frogs, and numbers following hyphens are lizards.

Subdivision	Terra Firme	Varzea	Igapó	Capoeira	Open & Edge
Arboreal (high)	0-3	1-3	0-1	0-2	1-1
Arboreal (low)	9-6	11-6	9-5	4-4	16-2
Terrestrial	9-6	7-5	3-2	4-5	4-7
Aquatic Margin	1-0	2-0	1-0	0-0	3-0
Aquatic	0-0	1-1	0-0	0-0	0-0

Spatial overlap among some species does exist. Salamanders and *Hyla* sp. (*rubra*-like) overlap greatly in their utilization of low vegetation in terra firme and varzea areas at night, presumably for obtaining food; also present, sharing the same vertical component, are numerous sleeping lizards *(Gonatodes humeralis).* Although these three species are the most abundant vertebrates using this aspect of the environment at night, the population densities appear to be so low that it is unlikely that significant interspecific competition exists.

There is evidence of breeding site partitioning in frogs, probably indicative of differing requirements of various species. Some tree frogs, such as *Hyla baumgardneri, H. egleri,* and *H. goughi* breed in diverse types of ponds and swamps, large or small, deep or shallow; apparently the frogs require only standing water and emergent vegetation. On the other hand, *Hyla minuta, H. raniceps,* and *Phyllomedusa hypochondrialis* are found in only some of the same areas as *H. baumgardneri, egleri,* and *goughi. Hyla raniceps* breeds only in larger bodies of water, at least 8 m by 15 m, usually at least 0.6 m in depth. *Phyllomedusa hypochondrialis* is restricted to ponds bordered by dense vegetation. The distribution of *H. minuta* is more difficult to interpret; the frogs occur in all types of areas, but without any regular pattern. For instance, numerous males call from one pond and not from a nearby pond having similar size, water depth, and emergent vegetation. The population density of this species appears to be lower than those of *H. baumgardneri, H. egleri,* and *H. goughi.* Perhaps male *H. minuta* attract other males to an area for the purpose of forming breeding congregations. This formation would be of greater importance to a less abundant species than to a more common one and would explain the fact that usually these frogs call in groups of at least 15 individuals in contrast to *H. baumgardneri, H. egleri,* and *H. goughi* which often call in groups of 10 or less.

Many species of frogs which breed sympatrically demonstrate calling site segregation (Tables 4 and 5). Most species characteristically call from a certain physiognomic type of vegetation, at a relatively uniform height from the water. The type of vegetation utilized is correlated with the body build and size of the animal. Large, heavy frogs generally call from the ground, sturdy vegetation near the ground, or from branches of trees; small frogs usually call from grass stems or leaves and small branches from emergent and edge vegetation. Some species have a broader range of calling sites than do others. For example, *Hyla goughi* commonly calls from both emergent and edge vegetation, 0.05-1.5 m above the water,

TABLE 4.—Species of Frogs Breeding and/or Calling at Least Partially Sympatrically and Synchronically.

Species	Calling Site	Jan.	Feb.	Mar.	Apr.	May	June	July
Bufo marinus	ground	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX
Physalaemus ephippifer	ground	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	------	------
Leptodactylus ocellatus	ground	------	------	XXXXXX	XXXXXX	------	XXXXXX	XXXXXX
Hyla rubra	ground & low vegetation	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX
Hyla sp. (large *rubra*)	ground & low vegetation	------	------	------	XXXXXX	------	XXXXXX	XXXXXX
Hyla multifasciata	ground & low vegetation	------	XXXXXX	XXXXXX	XXXXXX	XXXXXX	------	------
Hyla baumgardneri	low vegetation	------	------	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX
Hyla boesemani	low vegetation	------	------	XXXXXX	XXXXXX	XXXXXX	XXXXXX	------
Hyla egleri	low vegetation	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX
Hyla goughi	low vegetation	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX
Hyla minuta	low vegetation	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX	XXXXXX
Hyla nana	low vegetation	------	------	------	XXXXXX	XXXXXX	------	XXXXXX
Hyla leucophyllata	low vegetation	XXXXXX	------	XXXXXX	XXXXXX	------	------	XXXXXX

whereas *Phyllomedusa hypochondrialis* always calls from edge vegetation usually 0.6-1.5 m above the ground or water. Complete segregation of calling sites does not exist for all species in all areas. Segregation is partially dependent on species composition at the site, relative abundance of the calling individuals, and on the size of the breeding site relative to the population densities. Generally, in large, mixed congregations segregation tends to break down, and the frogs call from whatever sites are available. Interspecific competition for calling sites is probably significant during times of much reproductive activity. Segregation is more pronounced in large areas with distinct physiognomic vegetational diversity than in smaller areas with less calling site diversity. A commonly accepted explanation for the evolution of partitioning of calling sites is the resultant tendency to reduce the chances of interspecific mating. However, because segregation breaks down in large, mixed congregations at the time it is most needed, I propose that calling site partitioning exists due to the structural and behavioral attributes of each species rather than as a necessary reproductive isolating mechanism; advantages likely include improved mating efficiency and reduced energy expenditure.

There is a definite replacement of several species of tree frogs at breeding sites because of calling site overlap. *Hyla boesemani, H. multifasciata, H. raniceps,* and *H. rubra* all call from thick clumps of emergent vegetation, usually within 20 cm of the water. Individuals of all four species call from the same swampy areas, but not all at the same time; the only two of these species ever found calling sympatrically and synchronically are *H. boesemani* and *H. rubra,* the two smaller species. Every congregation of *Hyla* sp. (large *rubra*) observed was found calling in association with *H. rubra.* Male *Hyla* sp. (large *rubra*) call from the ground or low, thick vegetation. They seem to be dominant over *H. rubra* as indicated by calling site displacement of *H. rubra* when the two species call sympatrically. *Hyla rubra* usually calls from low vegetation, but when *Hyla* sp. (large *rubra*) is also calling from the area, the former calls from higher vegetation.

Perhaps some syntopic species (species with similar habitats) coexist with minimum interspecific competition as a result of temporal partitioning of the environment, in terms of diel and seasonal activities. For example, the nocturnal gecko, *Thecadactylus rapicaudus,* is likely the temporal replacement for diurnal lizards feeding on similar species of insects and utilizing the same habitat. The two species of dendrobatid frogs use the same forest floor by day that several species of leptodactylids utilize at night. Frogs demon-

TABLE 5.—Partitioning of Calling Sites of Species of Frogs.

Species	VARZEA Vegetation			IGAPÓ Vegetation			OPEN & EDGE Vegetation		
	High	Low	Ground	High	Low	Ground	High	Low	Ground
Leptodactylus marmoratus	—	—	X	—	—	—	—	—	—
Leptodactylus ocellatus	—	—	—	—	—	—	—	—	X
Leptodactylus wagneri	—	—	X	—	—	X	—	—	—
Physalaemus ephippifer	—	—	X	—	—	—	—	—	X
Physalaemus petersi	—	—	X	—	—	—	—	—	X
Bufo marinus	—	—	—	—	—	—	—	—	X
Hyla baumgardneri	—	—	—	—	X	—	—	X	—
Hyla boesemani	—	—	—	—	—	—	—	X	—
Hyla calcarata	—	X	—	—	—	—	—	—	—
Hyla egleri	—	X	—	—	X	—	—	X	—
Hyla geographica	—	X	X	—	—	—	—	X	—
Hyla goughi	—	X	—	—	—	—	—	X	—
Hyla granosa	—	X	—	—	X	—	—	—	—
Hyla leucophyllata	—	—	—	—	—	—	—	X	—
Hyla melanargyrea	—	—	—	—	—	—	—	X	—
Hyla minuta	—	—	—	—	—	—	—	X	—
Hyla multifasciata	—	X	—	—	—	—	—	X	—
Hyla nana	—	—	—	—	—	—	—	X	—
Hyla rubra	—	X	—	—	X	—	—	X	—
Hyla sp. (large *rubra*)	—	—	—	—	—	—	—	X	X
Phyllomedusa bicolor	X	—	—	—	—	—	X	—	—
Phyllomedusa hypochondrialis	—	X	—	—	—	—	—	X	—
Sphaenorhynchus eurhostus	—	—	—	—	—	—	—	X	—

TABLE 6.—Known Breeding Cycles of Frogs. The code is: 1=observation only; 2=no adult females examined; A=presence of calling males; B=evidence of breeding (amplexing pairs and/or gravid females and/or egg clutches) and calling; C=presence of known tadpoles and/or juveniles of species; D=presence of presumed tadpoles and/or juveniles of species.

Species	*N*	Jan.	Feb.	Mar.	Apr.	May	June	July
Leptodactylus marmoratus	125-150	BC	BC	BC	BC	2C	2C	2C
Leptodactylus ocellatus	125+	2	2	B	B	2	2A	2A
Leptodactylus wagneri	100+	2A	B	AC	BC	2A	A	2A
Physalaemus ephippifer	125+	A	A	BC	BC	AC	2C	2
Physalaemus petersi	25	2	BC	BC	2AC	2C	C	----
Bufo marinus	40-50	2A	2AC	2AC	2A	2A	2A	2A
Bufo typhonius	60-70	2C	BC	2C	2C	2C	BC	2C
Dendrobates trivittatus	5	----	B	2	2	2	----	----
Dendrobates ventrimaculatus	5	----	----	B	2	1	1	----
Hyla baumgardneri	100+	----	----	A	B	B	A	B
Hyla boesemani	40-50	----	2	A	B	B	A	2
Hyla calcarata	12	----	2	B	2A	----	----	2
Hyla egleri	150+	A	A	BC	BC	BC	BC	BC
Hyla geographica	30	----	B	2A	2	----	2AC	2AC
Hyla goughi	150+	A	A	B	BC	B	A	A
Hyla granosa	20	----	2	2A	2AD	2A	2	----
Hyla leucophyllata	40-45	B	2	B	AC	2	2	A
Hyla melanargyrea	17	----	----	----	2AD	----	----	2
Hyla minuta	90-100	A	A	A	BD	B	A	B
Hyla multifasciata	40-50	2	B	B	AC	A	2	2C
Hyla nana	50-60	----	----	----	B	A	----	A
Hyla raniceps	35-40	----	B	----	2	----	B	BD
Hyla rubra	80-90	B	2A	2A	BC	2A	2A	2AC
Hyla sp. (large *rubra*)	25-30	----	----	----	2AC	----	B	BC
Hyla sp. (*rubra*-like)	37	2	B	2C	2C	----	2	2
Phrynohyas venulosa	20	2	----	2	2C	----	----	2
Phyllomedusa bicolor	15-20	----	----	2A	2A	----	2A	2A
Phyllomedusa hypochondrialis	60-70	AC	AC	A	BC	2C	----	----
Phyllomedusa vaillanti	2	----	----	2	----	----	C	----
Sphaenorhynchus eurhostus	5	----	2	----	2A	----	----	----

strate seasonal partitioning of the environment in terms of breeding activities (Table 6). *Hyla multifasciata* and *H. raniceps* both call from low vegetation in swampy, open areas; they are rather large tree frogs with similar mating calls. The former is a wet season breeder, whereas the latter is a dry season breeder. Most of the frogs are nocturnal (83.8%) and most of the lizards are diurnal (91.7%); the salamander is nocturnal. In the terra firme and varzea forests, 50 percent of the frogs, salamanders, and lizards considered as a group are diurnal; the distribution in the igapó forest is similar, with 45.5 percent diurnal and 54.5 percent nocturnal. Most of the species in open and edge areas are nocturnal (73.5%); breeding tree frogs account for most of this distribution. On the other hand, most of the species in the capoeira area are diurnal (70%); over half of these species are lizards, many of which are heliotherms (Table 7).

CONTINGENCY TABLE ANALYSIS

The contingency table analysis technique, developed by Williams (1952) as an extension of Fisher and Yates' ideas for dealing with frequency counts in two-way tables, is employed here for two reasons: 1) to measure the degree of association between species and plots; and 2) to partition the species-plot association into independent components representative of environmental gradients. The analysis was carried out on 20 species of frogs, salamanders, and lizards from 44 sampling plots, each 20×30 m, from the capoeira-terra firme transition, terra firme-varzea transition, varzea, and igapó areas. All plots received approximately equal amounts of sampling time from mid-January to the end of July. The 20 species were the only species of frogs, salamanders, and lizards found within the boundaries of the particular plots analyzed. The total sample includes 1218 individuals (Table 8). Most individuals were not removed from the habitat, so the relative abundance indices are possibly inclusive of re-counted individuals; each observation was treated as a unit indicative of species-habitat association.

TABLE 7.—Comparison of Activity Cycles of Amphibians and Lizards in Five of the Major Areas. Absolute number of species and percentage of species within each area are given.

Period of Activity	Terra Firme	Varzea	Igapó	Capoeira	Open & Edge
Diurnal	18 50%	19 50%	10 45.5%	14 70%	9 26.5%
Nocturnal	18 50%	19 50%	12 54.5%	6 30%	25 73.5%

TABLE 8.—Summary of the Species × Plot Data Matrix used for Contingency Table Analysis.

Species	*N*	Capoeira-Terra Firme Transition (4 plots)	Terra Firme-Varzea Transition (19 plots)	Varzea (9 plots)	Igapó (12 plots)
Bufo typhonius	123	21	102	------	------
Dendrobates ventrimaculatus	10	------	------	2	8
Hyla baumgardneri	12	------	------	------	12
Hyla egleri	11	------	2	------	9
Hyla geographica	23	------	2	21	------
Hyla granosa	14	------	------	1	13
Hyla rubra	36	5	------	22	9
Hyla sp. (*rubra*-like)	60	34	------	26	------
Leptodactylus marmoratus	190	19	171	------	------
Leptodactylus wagneri	112	------	24	33	55
Physalaemus ephippifer	21	------	21	------	------
Physalaemus petersi	18	------	17	1	------
Bolitoglossa altamazonica	36	21	------	15	------
Anolis fuscoauratus	22	8	3	11	------
Gonatodes humeralis	313	38	158	88	29
Kentropyx calcaratus	142	8	16	36	82
Leposoma percarinatum	4	------	2	2	------
Mabuya mabouya	54	5	4	10	35
Plica umbra	14	9	4	------	1
Uranoscodon superciliosa	3	------	------	3	------
Total No. Individuals	1218	168	526	271	253
Total No. Species	20	10	13	14	10

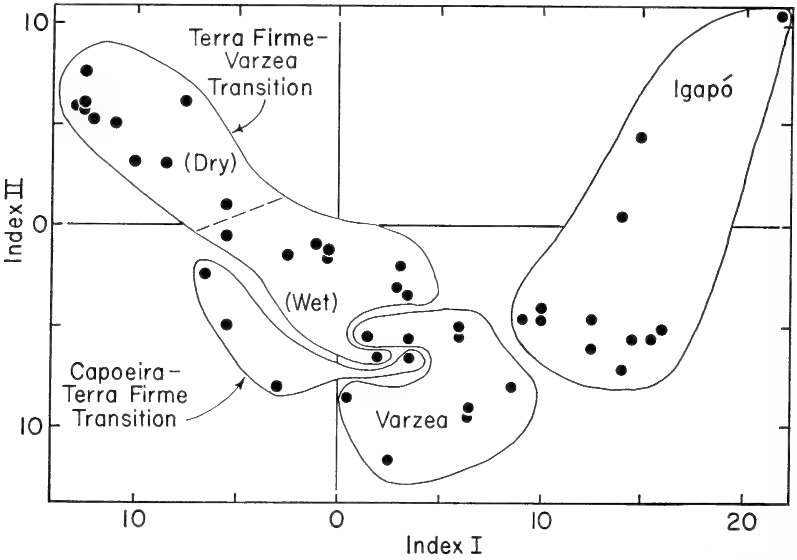


FIG. 12. Scores on index I plotted against scores on index II for each of 44 plots. Each dot represents the position of a particular plot relative to the x and y axes. Index I is a moisture gradient from dry (negative) to wet (positive). Index II is a vegetation density gradient from dense ground cover (negative) to grassy ground cover (positive).

The data were assembled into a species × plot table; the species frequency counts represent the number of individuals of each species which occurred in a particular plot. Williams (1952) showed that when actual environmental measurements were unavailable, scores could be calculated from the data of the contingency table by simply using those sets of scores for which there is maximum correlation. The interpretation is feasible because the scores are adjusted to have a mean of zero and a variance of one.

The computer print-out for the analysis consists of a series of indices, each representing an environmental gradient or a composite of such gradients. Each index maximizes the measure of association between the two sets of variables—species and plots. Index scores relative abundances are presented in table 9. The results are presented by Cartesian (x, y) scattergrams of two sets of scores (Figs. 12-17). In this way, two gradients (two indices) can be studied simultaneously and their interaction examined. Species or plots having similar index scores appear close together on the diagram. Thus, ecologically similar plots and species with similar distributions can be identified.

No actual environmental measurements were taken; resource

TABLE 9.—Tabulation of Relative Abundance, Contingency Table Indices, and Niche Breadth Scores. Numbers are the results from analytical techniques applied to a species × plot data matrix, dimensions 20 × 44, summarized in Table 8.

			Relative Abundance					Contingency Table Indices				
Species	Series Number	*N*	Capoeira-Terra Firme Transition	Terra Firme-Varzea Transition	Varzea	Igapó	Accumulative Relative Abundance (× 1000)	I	II	III	IV	Niche Breadth
Bufo typhonius	1	123	0.01724	0.08375	....	....	101	–12.37	5.20	–0.71	3.94	9.31
Dendrobates ventrimaculatus	2	10	....	....	0.00164	0.00657	8	17.64	–0.79	–2.00	19.24	5.00
Hyla baumgardneri	3	12	....	....	....	0.00985	10	28.11	61.66	21.96	–17.35	1.00
Hyla egleri	4	11	....	0.00164	....	0.00739	9	20.71	52.27	17.26	–12.99	1.46
Hyla geographica	5	23	....	0.00164	0.01725	....	19	6.65	–11.58	–4.05	–25.88	4.30
Hyla granosa	6	14	....	....	0.00082	0.01067	11	21.15	23.56	2.95	0.23	3.27
Hyla rubra	7	36	0.00411	....	0.01806	0.00739	30	9.77	–9.55	12.71	22.48	5.31
Hyla sp. (*rubra*-like)	8	60	0.02792	....	0.02134	....	49	–0.77	–11.79	25.47	–15.48	4.46
Leptodactylus marmoratus	9	190	0.01560	0.14040	....	....	156	–12.97	6.32	–2.56	4.11	10.76
Leptodactylus wagneri	10	112	....	0.01971	0.02709	0.04515	92	10.92	–5.09	–14.36	–7.04	11.86
Physalaemus ephippifer	11	21	....	0.01724	....	....	17	–2.35	–2.59	–21.69	–38.69	6.78
Physalaemus petersi	12	18	....	0.01396	0.00082	....	15	–8.62	4.06	–10.81	–6.31	6.48
Bolitoglossa altamazonica	13	36	0.01724	....	0.01232	....	30	0.11	–11.59	25.01	–6.96	5.59
Anolis fuscoauratus	14	22	0.00656	0.00246	0.00903	....	18	–0.41	–7.63	13.41	7.31	8.34
Gonatodes humeralis	15	313	0.03120	0.12972	0.07224	0.02381	257	–2.43	–1.25	–0.66	–1.45	32.01
Kentropyx calcaratus	16	142	0.00657	0.01313	0.02955	0.06732	117	10.99	–3.77	–4.39	9.44	21.68
Leposoma percarinatum	17	4	....	0.00164	0.00164	....	3	1.09	–3.87	–6.73	–9.25	4.00
Mabuya mabouya	18	54	0.00410	0.00328	0.00822	0.02874	44	12.84	0.31	–0.65	9.66	16.38
Plica umbra	19	14	0.00738	0.00328	....	0.00082	11	–3.13	–4.62	9.63	0.96	5.44
Uranoscodon superciliosa	20	3	....	....	0.00246	....	2	6.91	–11.57	8.64	7.91	3.00

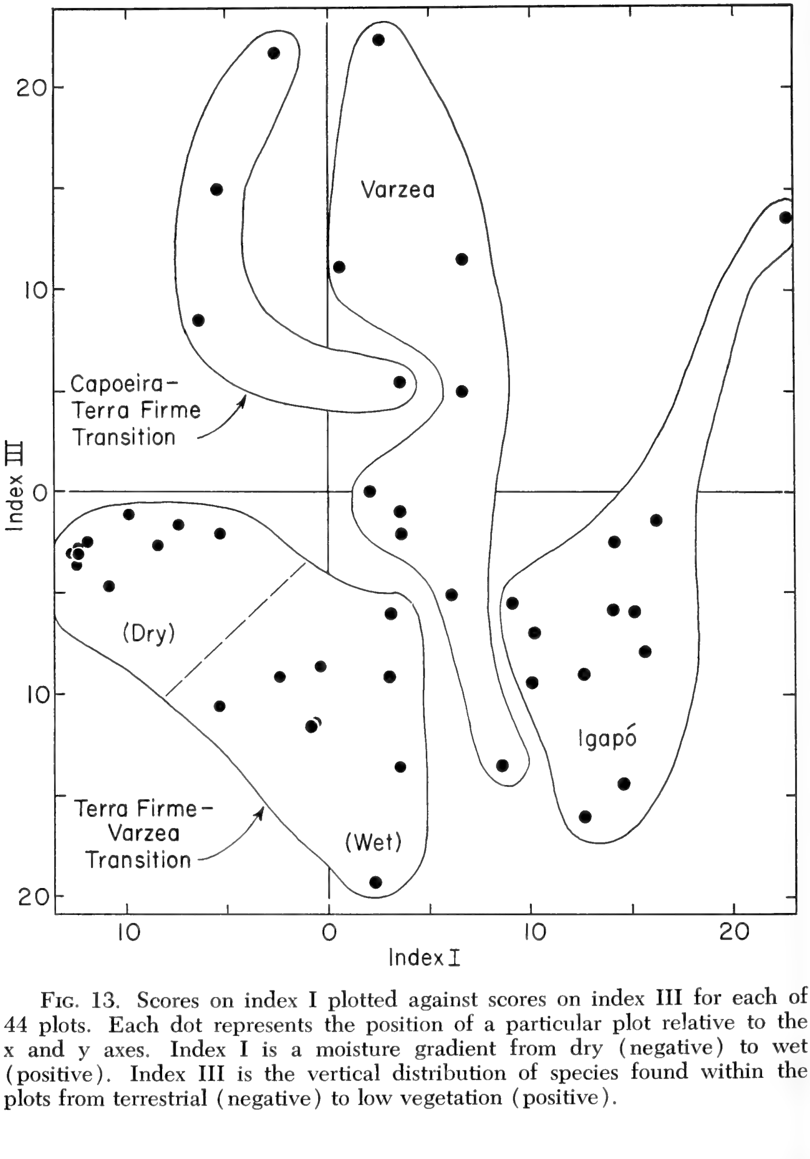


FIG. 13. Scores on index I plotted against scores on index III for each of 44 plots. Each dot represents the position of a particular plot relative to the x and y axes. Index I is a moisture gradient from dry (negative) to wet (positive). Index III is the vertical distribution of species found within the plots from terrestrial (negative) to low vegetation (positive).

requirements for each species were analyzed indirectly by assuming that a given sampling plot provides necessary resources for the species found therein. For this reason interpretation of the indices is inferential.

Environmental gradients.—The first four index scores from the contingency table analysis were analyzed in an attempt to: 1) determine the major limiting environmental parameters affecting the

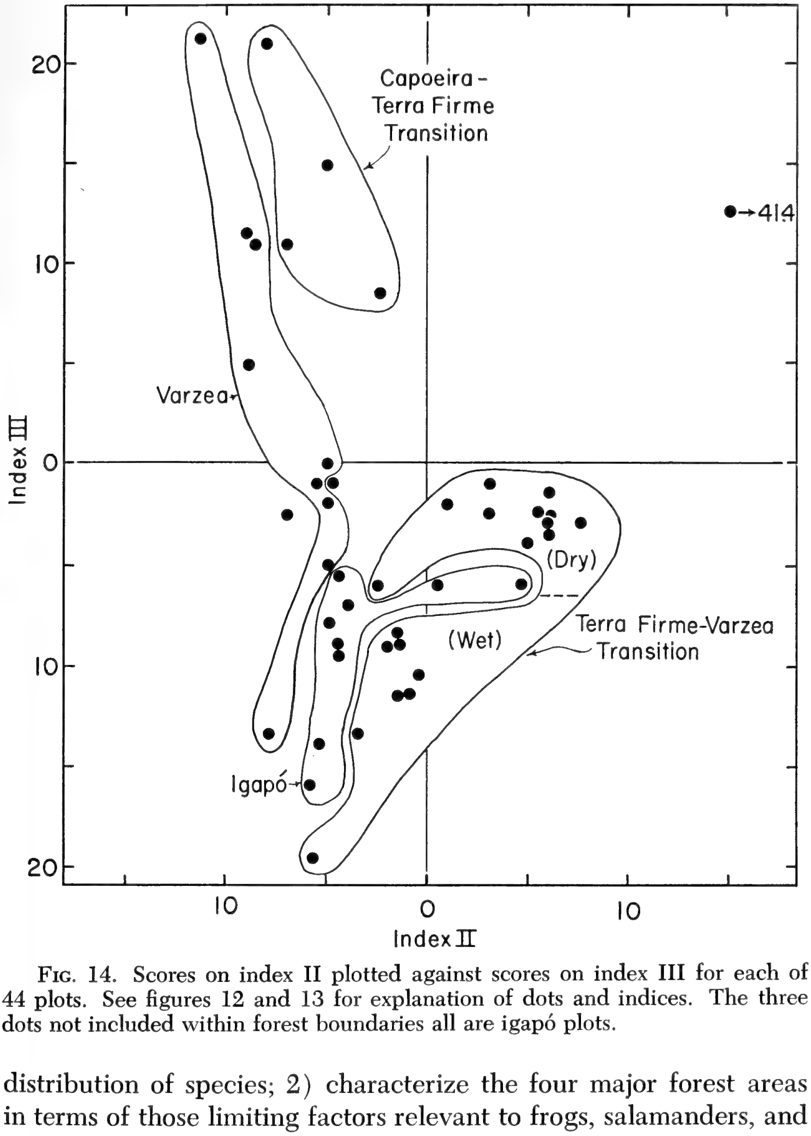


FIG. 14. Scores on index II plotted against scores on index III for each of 44 plots. See figures 12 and 13 for explanation of dots and indices. The three dots not included within forest boundaries all are igapó plots.

distribution of species; 2) characterize the four major forest areas in terms of those limiting factors relevant to frogs, salamanders, and lizards; and 3) identify the habitat of each of the 20 species in terms of the environmental parameters represented by the indices.

The first index indicates a moisture gradient from dry (low values) to wet (high values). Moisture probably is the most critical factor affecting the ecological distribution of amphibians and reptiles in the study area.

Probably the next most critical limiting factor is the physiognomy of the vegetation. The second index is indicative of vegetation

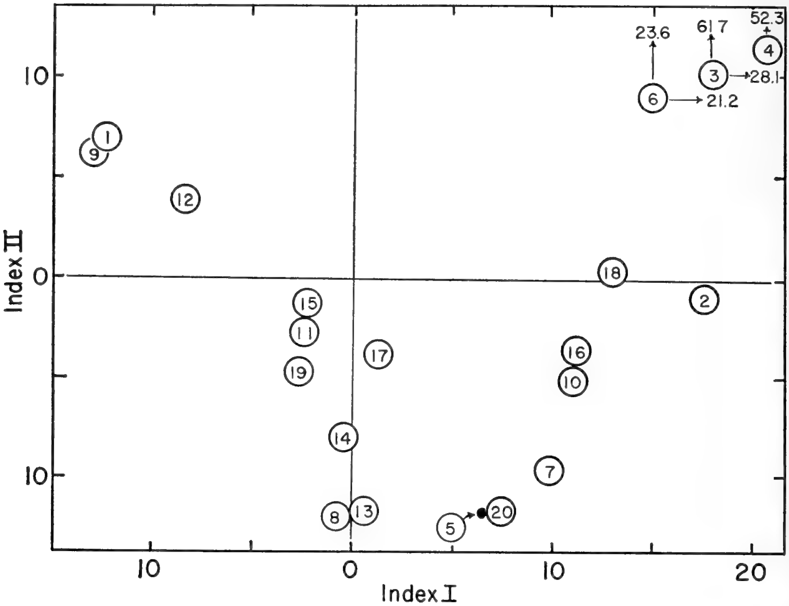


FIG. 15. Scores on index I plotted against scores on index II for each of 20 species. See figure 12 for explanation of the indices. Each circle represents the position of a particular species relative to the x and y axes. The species numbers are associated with species names in table 9, p. 29.

ground cover. The spectrum is from dense ground cover (low values) to grassy areas (high values). The second index may also indicate light intensity, resulting from the structure and density of the vegetation. In general, areas with dense ground cover are darker habitats than are grassy open areas.

The third index probably is a combination of factors affecting vertical distribution. Terrestrial species have low values, and species which inhabit low vegetation have high values. Lizards found on tree trunks and along the boardwalks have intermediate scores.

The fourth index seems to be a composite of many factors. Some of the following may be involved, but no one of them is responsible for the separation of the plot or species scores: 1) temporal activity (diel and seasonal); 2) organism size; 3) phylogenetic position of organisms; 4) heliophilous versus sciophilous organisms; 5) niche breadth of organisms; 6) abundance of animals within plots; and 7) solitary organisms versus congregations. The fourth index segregates the following species pairs, which are similar on the basis of the first three indices: *Hyla rubra* and *Hyla* sp. (*rubra*-like), *Hyla geographica* and *Uranoscodon superciliosa,* and *Hyla rubra* and *Bolitoglossa altamazonica.*

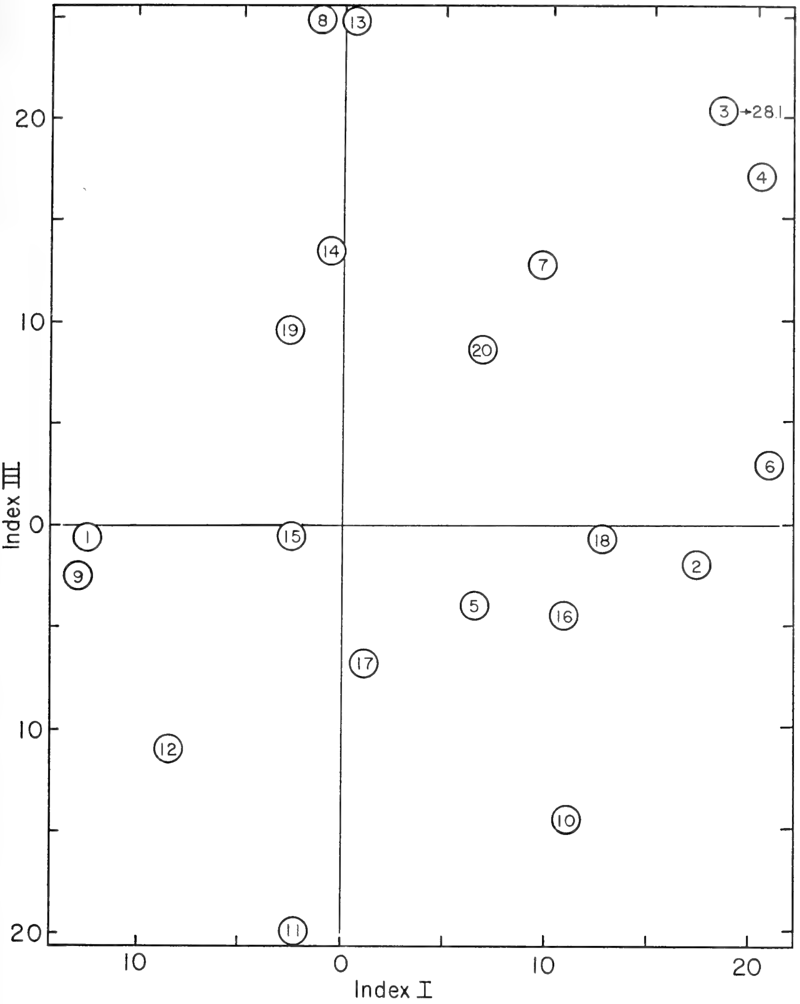


FIG. 16. Scores on index I plotted against scores on index III for each of 20 species. See figures 13 and 15 for explanation of indices and circles/species numbers respectively.

When the scores of the first three indices for the 44 plots (Table 10) are plotted against each other, it is possible to characterize the four major areas in terms of the environmental gradients analyzed (Figs. 12-14). Likewise, when the species scores are plotted, it is possible to get some understanding of the habitat of each species in terms of the environmental gradients inferred from the indices (Figs. 15-17).

Plot index scores.—Four capoeira-terra firme transition plots

Table 10.—Contingency table indices for each of 44 plots analyzed. Plot numbers are located on figures 10 and 11. Indices are plotted on figures 12-14.

Plot No.	Index I	Index II	Index III
1	3.66	–6.77	10.62
4	–3.13	–7.83	20.81
11	–6.50	–2.36	8.60
12	–5.57	–4.80	14.94
15	–5.74	0.88	–1.96
16	–0.67	–1.32	–8.52
17	–8.55	2.79	–2.38
18	–7.60	6.06	–1.55
19	–10.78	4.77	–4.29
20	–12.62	5.93	–2.88
22	–12.39	6.03	–3.31
23	–10.17	3.26	–1.02
24	–12.35	7.34	–3.19
25	–1.16	–0.88	–11.55
26	3.26	–3.47	–13.31
27	–2.30	–1.51	–9.13
28	1.87	–6.29	–25.82
29	–5.26	–0.48	–10.31
30	3.02	–1.95	–8.83
31	–0.67	–1.45	–11.32
33	2.82	–2.87	–6.13
42	–12.05	5.54	–2.63
43	–12.58	6.11	–2.95
44	6.64	–9.18	5.09
45	0.55	–8.65	10.87
46	2.34	–11.48	22.55
49	5.89	–5.08	–4.86
50	1.74	–5.26	–0.18
51	8.56	–8.12	–13.45
52	6.33	–8.77	11.53
53	3.38	–4.85	1.81
54	3.44	–5.34	–0.96
65	22.25	41.36	13.27
66	14.31	–5.39	–14.28
67	15.00	4.45	–5.85
68	13.83	0.45	–5.74
69	13.92	–6.85	–2.69
70	15.77	–4.80	–1.69
71	12.38	–4.32	–8.75
72	15.28	–5.04	–7.98
73	9.76	–4.10	–7.00
74	8.98	–4.33	–5.59
75	9.82	–4.66	–9.33
76	12.64	–5.78	–15.93

were studied. In general, these plots are characterized by low to mid-range values on the first index, fairly low on the second, and high on the third (Figs. 12-14). The area is towards the drier end of the moisture spectrum and near the denser end of the vegetation

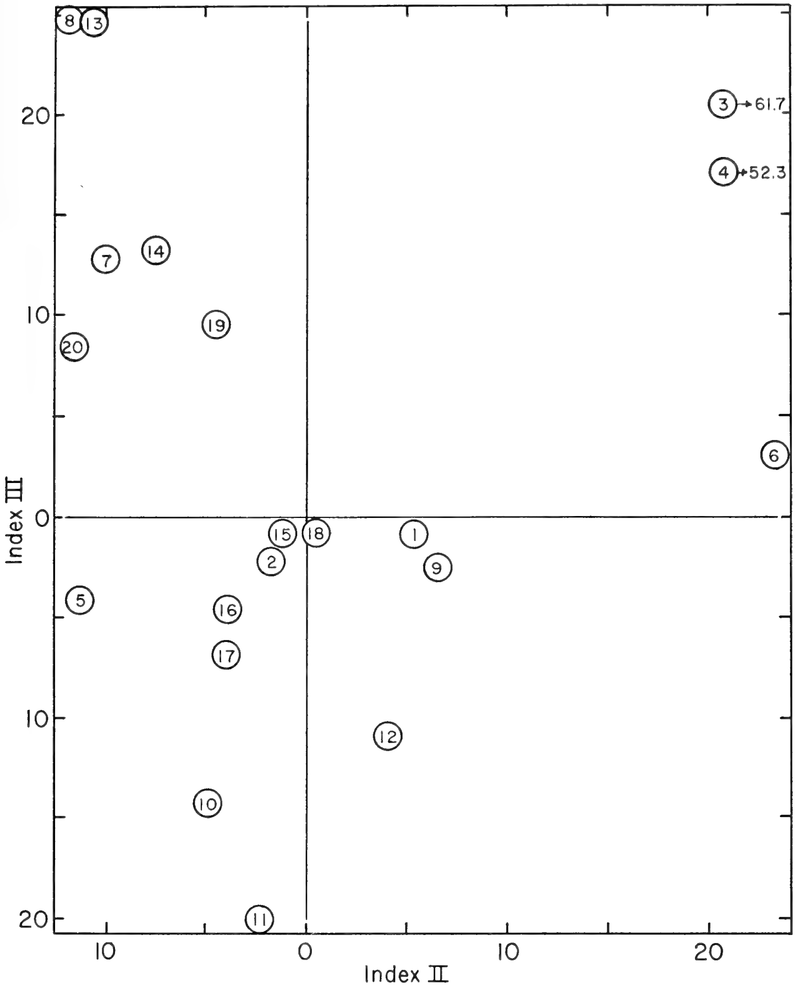


FIG. 17. Scores on index II plotted against scores on index III for each of 20 species. See figures 12 and 13 for an explanation of indices and figure 15 for an explanation of circles.

density spectrum. The value on the third index suggests that the herpetofauna of this area is predominantly found on low vegetation rather than on the ground.

Nineteen plots are terra firme-varzea transition areas, and can be divided into two groups, dry transition and wet transition (Fig. 10). The two transition areas are clearly segregated when the index values are plotted against each other (Figs. 12-14). The entire transition zone is characterized by low to mid-range values on the first index, high on the second, and low to middle on the third. The area represents an intermediate zone with regard to the physical environmental parameters, except on the second index, indicating that the ground cover is relatively grassy. One plot is extremely low on the third and fourth indices and segregates from the other transition plots. The low value on the third index is explained by the many terrestrial leptodactylids found calling from temporary puddles.

Nine varzea plots were analyzed (Fig. 11). There is a very small range of variation on the first and second indices, but a wide range on the third and fourth. In general, most plots have a fairly high value on the first index, low on the second, and from low to high on the third. The varzea is a wet environment with relatively dense ground cover; the organisms are neither predominantly terrestrial nor inhabitants of low vegetation.

Twelve igapó plots were studied. These plots have the highest values on the first index, indicating that the igapó is the wettest area. Most values on the second index range from low to middle and most on the third are low. The igapó forest has a relatively dense to intermediate vegetation ground cover. Most of the lizards are terrestrial or are found predominantly on the boardwalks. When the indices are plotted against each other, one plot is segregated from the other igapó plots by high values on the second and third indices (Figs. 12-14). The second index score is explained by the presence of large clumps of tall emergent grass in the plot. Two species of tree frogs not found elsewhere in the igapó forest utilize the grass for calling sites; this creates a higher third index score than those values for igapó plots in which there are many terrestrial lizards.

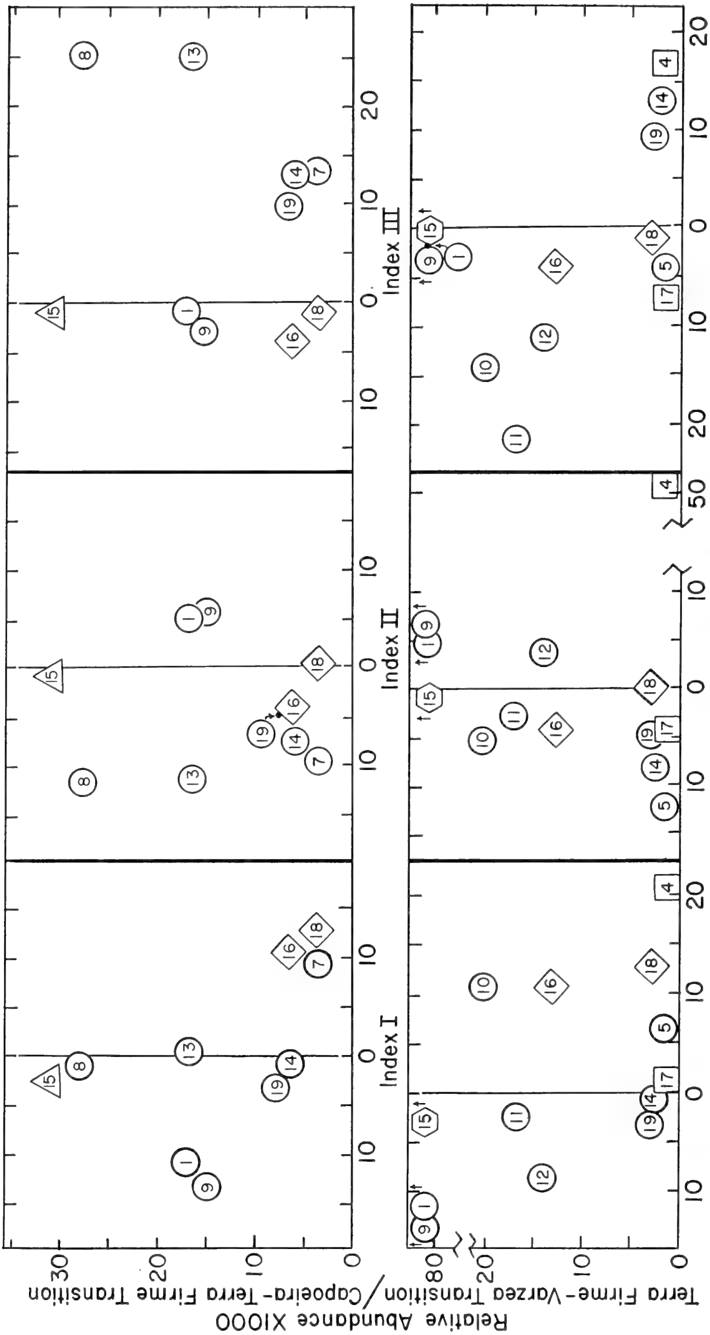
Species index scores.—The Cartesian plots of index values (Figs. 18-21) and the bar diagrams (Figs. 22-24) illustrate that each species has requirements and tolerances with regard to the environmental gradients. Several trends represented by correlations between species abundances and availability of a particular resource are evident (Figs. 22-24). For example, index I represents a moisture gradient; those species with the highest positive values are those found in association with wet areas. Each of the seven species with the highest scores *(Leptodactylus wagneri, Kentropyx calcaratus, Mabuya mabouya, Dendrobates ventrimaculatus, Hyla egleri, H. granosa,* and *H. baumgardneri)* is most abundant in the igapó forest, less abundant in the varzea forest, still less common in the terra firme-varzea transition area, and rare in the capoeira-terra firme transition area, if found in the last two areas at all. The two species with extremely low negative scores on the first index *(Lepto-*

dactylus marmoratus and *Bufo typhonius)* are more abundant in the terra firme-varzea transition area than in capoeira-terra firme transition plots, contrary to what one might expect. The distribution is better understood when the second index scores are considered; both species have positive scores, but neither one is extreme. Apparently these terrestrial species inhabit relatively dry areas but avoid the open areas characteristic of capoeira forest in preference to the denser undergrowth of high ground, dry terra firme-varzea transition areas.

In most instances, those species with scores closest to zero are the most abundant. This is probably because those species requiring neither extreme (considered generalized) are able to utilize more of the environment. If more of the environment is potentially available for exploitation by a species, it can be assumed that the potential carrying capacity of the environment for that species is greater than that for a specialized species restricted to a particular habitat. *Gonatodes humeralis* is the most abundant of the twenty species and has scores near zero on each of the four indices. The three next most abundant species, *Leptodactylus marmoratus, Kentropyx calcaratus,* and *Bufo typhonius,* have scores relatively close to zero on all indices except the first. Species with extremely high positive or low negative scores on index IV are relatively uncommon.

Most species of lizards do not have extreme values on any of the environmental gradients. *Gonatodes humeralis, Kentropyx calcaratus,* and *Mabuya mabouya* are the only species found in all four major areas; none has extreme index values. The combined cumulative relative abundances (the three species from the four areas) represents 509 individuals, or 41.8 percent of the total sampled herpetofauna. *Gonatodes humeralis* is less abundant in the igapó forest than in the other three areas, whereas *K. calcaratus* and *M. mabouya* are most abundant in the igapó forest. The other four species of lizards are relatively uncommon in all of the areas. *Anolis fuscoauratus, Leposoma percarinatum,* and *Plica umbra* have no extreme index scores; the first two species are near zero on the moisture gradient, and *P. umbra* is near zero on the fourth index. *Uranoscodon superciliosa* is relatively generalized with respect to all the environmental gradients except vegetation density; the score on the second index is low, indicative of its occurrence in areas of dense vegetation.

In general, the amphibians demonstrate more extreme environmental requirements than do the lizards. None of the thirteen



FIGS. 18-19. Species scores on each of the three indices plotted against relative abundance × 1000 in capoeira-terra firme
(continued on next page)

species is found in all four areas. The salamander, *Bolitoglossa altamazonica,* has a score near zero on the moisture gradient, but exhibits extreme scores on the second and third indices, indicative of the occurrence of individuals on low vegetation in relatively dense areas. *Physalaemus petersi* is generalized with regard to all of the environmental gradients. *Bufo typhonius* and *Leptodactylus marmoratus* are specialized only with regard to the moisture gradient; they inhabit relatively dry areas. *Hyla granosa* is found in relatively open, very wet areas. This species is more abundant in the igapó forest than in the varzea forest; the fourth index score is almost zero. *Leptodactylus wagneri* is terrestrial, as indicated by the extremely low third index score; the species is more common in the varzea and igapo forests than in the terra firme-varzea transition area, apparently due to the absence of permanent standing water in the transition area. The fourth index yields extreme values for several of the species of frogs. *Physalaemus ephippifer, Hyla geographica, H. baumgardneri, Hyla* sp. (*rubra*-like), and *H. egleri* all have low scores; *Dendrobates ventrimaculatus* and *Hyla rubra* have high values. *Physalaemus ephippifer* is terrestrial, found only in the terra firme-varzea transition area. *Dendrobates ventrimaculatus* occurs in very wet areas of the varzea and igapo forests; the species is relatively uncommon in both areas. *Hyla geographica* and *H. rubra* are found in places of rather dense vegetation. The three most specialized species seem to be *Hyla baumgardneri, H. egleri,* and *Hyla* sp. (*rubra*-like). The first two species are found in very wet, open grassy areas, whereas *Hyla* sp. (*rubra*-like) is found in plots having intermediate values on the moisture gradient, with dense vegetation. All three species are found on low vegetation; all have extremely low values on the fourth index.

Of the twelve species of frogs, the only abundant ones are *Bufo typhonius, Leptodactylus marmoratus,* and *L. wagneri,* all of which are terrestrial, and mainly forest inhabitants. Three species of tree frogs, *Hyla baumgardneri, H. egleri,* and *H. rubra,* are found principally in open, non-forested areas, where they congregate at ponds and swamps to breed, thus explaining their relative uncommonness in the forest plots.

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transition (figure 18, upper) and terra firme-varzea transition (figure 19, lower). See figures 12 and 13 for an explanation of indices. Species numbers are associated with species names in table 9, p. 29. Numbers enclosed in squares indicate species that are habitat specialists; circles are habitat intermediates; diamonds are relatively uncommon generalists; triangles are moderately common generalists, and hexagons are abundant generalists.

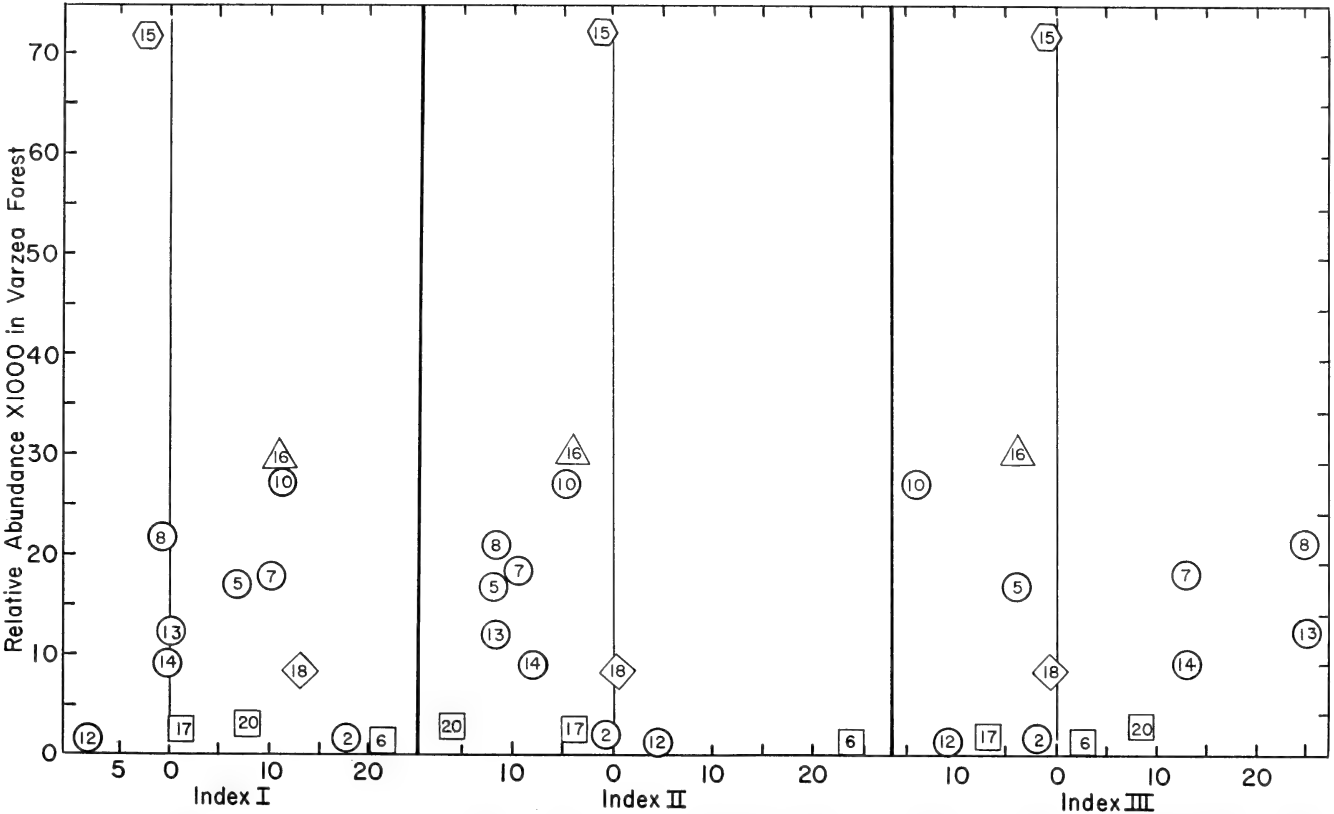

FIG. 20. Species scores on each of the three indices plotted against relative abundance × 1000 in the varzea forest. Refer to figures 18 and 19 for explanation.

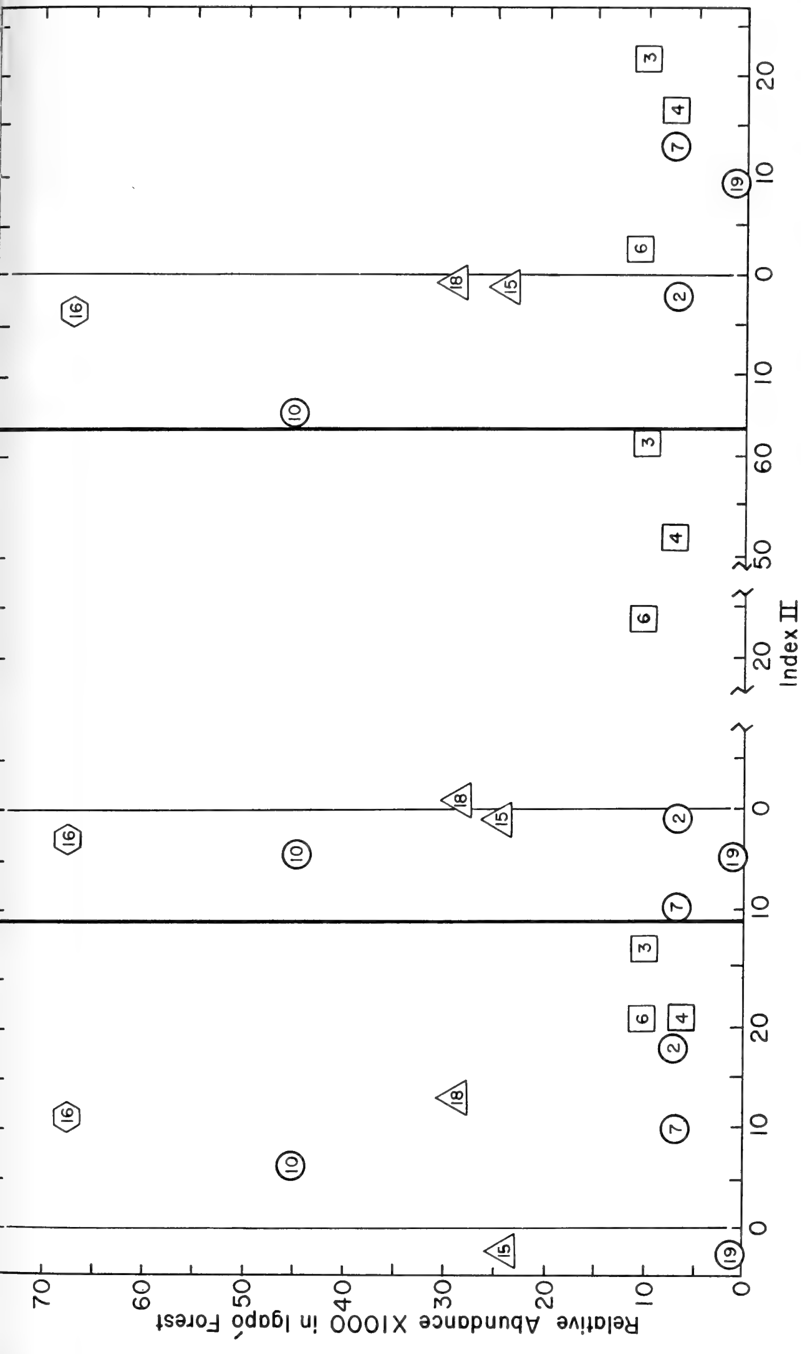

FIG. 21. Species scores on each of the three indices plotted against relative abundance × 1000 in the igapó forest. Refer to figures 18 and 19 for explanation.

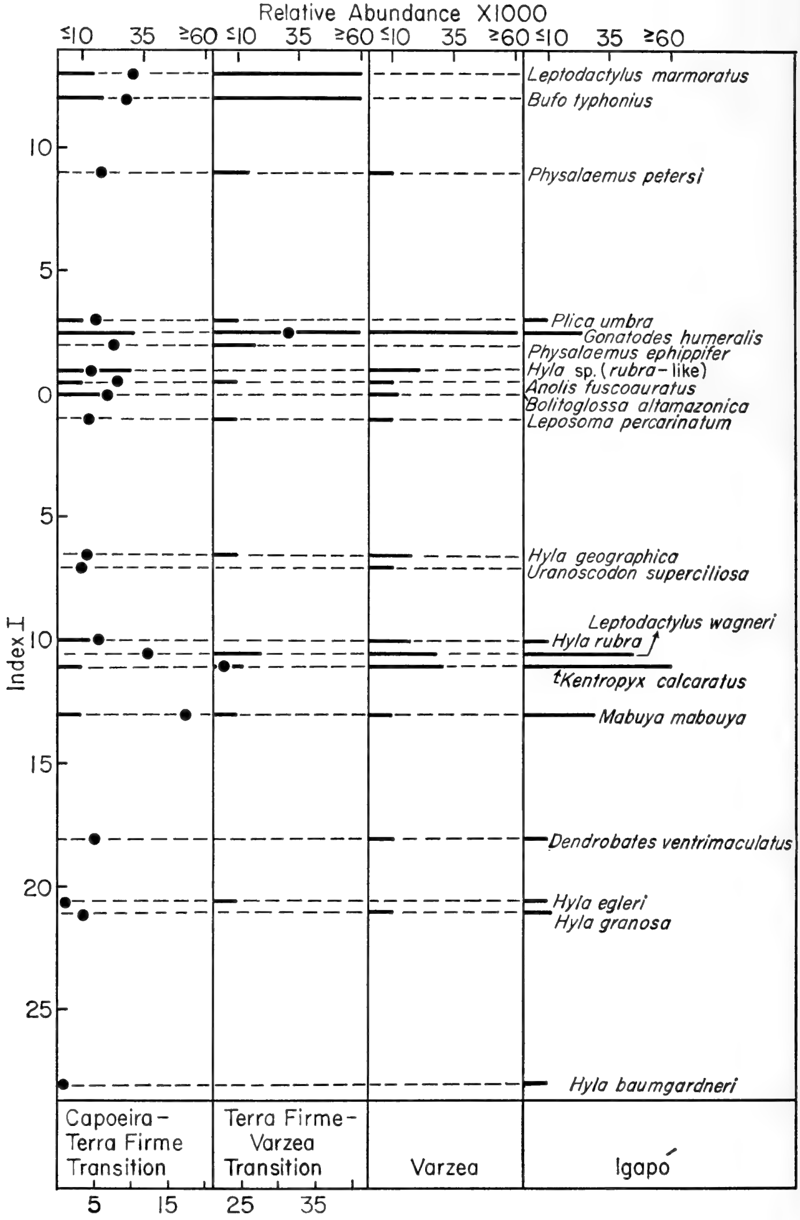

FIG. 22. Relationship of species scores on index I, relative abundance, and niche breadth scores for 20 species in each of the four major areas. Dots represent niche breadth scores. Horizontal bars indicate index scores and relative abundance.

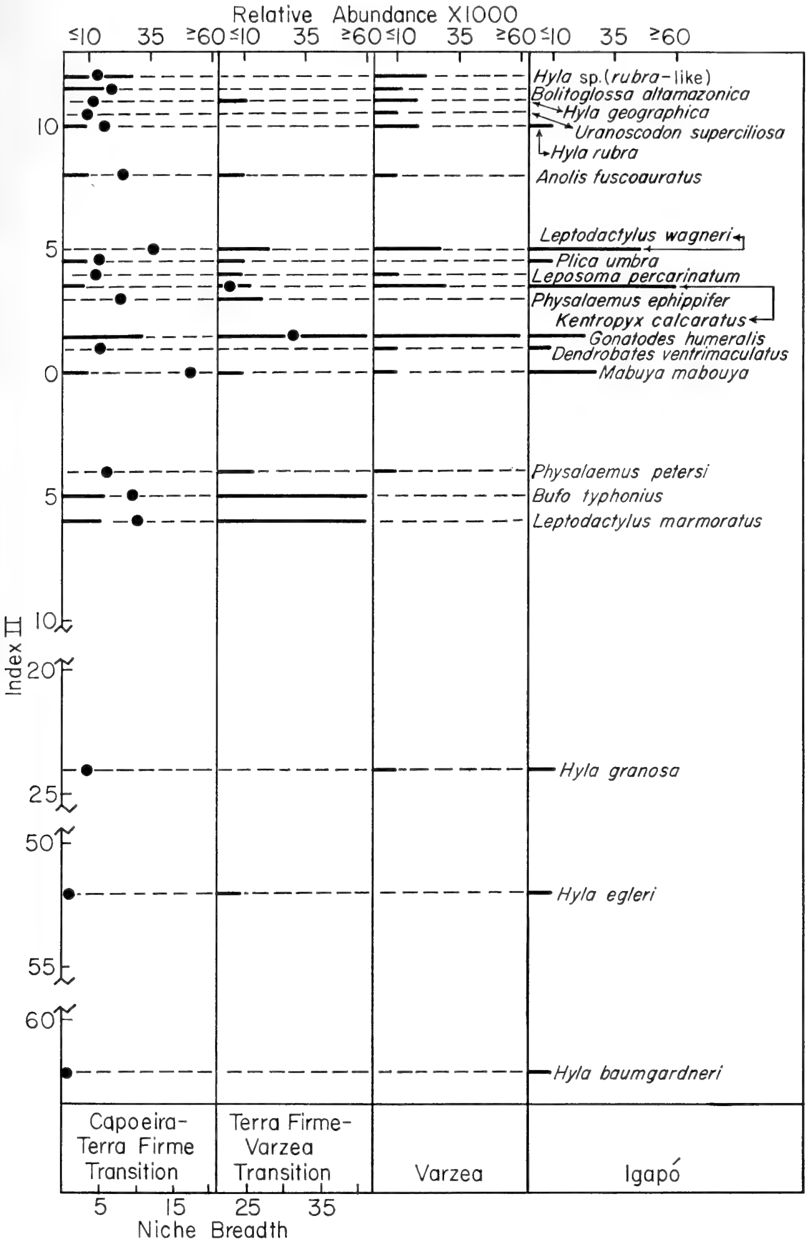

FIG. 23. Relationship of species scores on index II, relative abundance, and niche breadth scores for 20 species in each of the four major areas. See figure 22 for explanation.

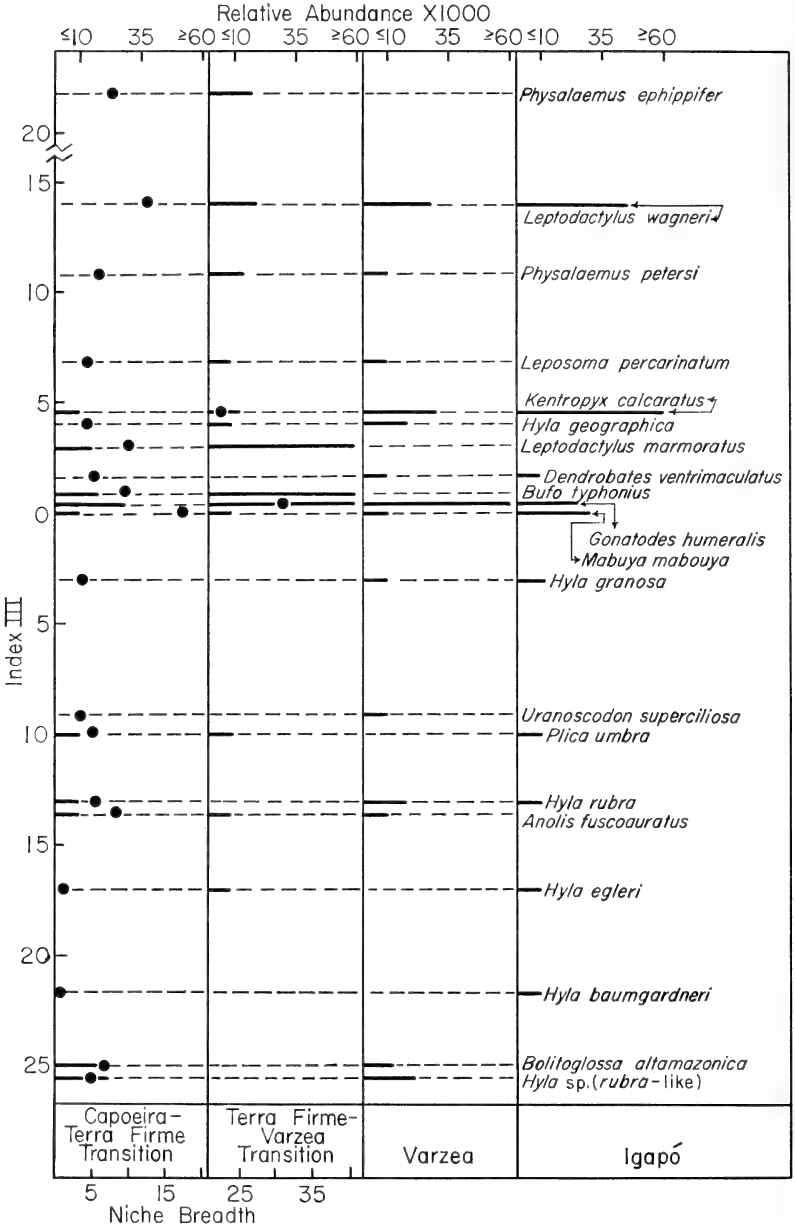

FIG. 24. Relationship of species scores on index III, relative abundance, and niche breadth scores for 20 species in each of the four major areas. See figure 22 for explanation.

Niche Breadth Analysis

Niche breadth is used in this paper to refer to habitat niche breadth and is presumed to be correlated with the range of environmental tolerances. Niche breadth scores were calculated from the standard formula proposed by Levins (1967), where p_{ij} is the proportion of occurrences of species j in plot i, niche breadth of species j (B_j) equals:

$$1/B_j = \sum_i p_{ij}^2$$

No actual environmental measurements were taken; resource requirements for each species were measured indirectly by assuming that a given sampling plot provides the necessary resources for the amphibians and lizards found therein. Although the niche dimension is referred to as being habitat, there may be certain latent biotic interactions influencing the distribution of species which are included in the niche breadth measurement. The limitation of using occurrence in sampling plots as an indirect method of measuring requirements of species is acknowledged. However, the analysis is the only one feasible due to the lack of direct physical environmental measurements. The data are from the matrix (plot × species) used in the contingency table analysis. Niche breadth values are included in table 9. The niche breadth analysis used here was not meant to describe the entire niche of each species, but rather to delimit the spectrum of the habitat dimension of the niche of each species.

Three species of lizards (*Gonatodes humeralis, Kentropyx calcaratus,* and *Mabuya mabouya*) have much higher niche breadth scores (16-32) than the next highest species, *Leptodactylus wagneri* (approximately 12). These three species of lizards are found in all four of the major areas, account for 41.8 percent of the entire sample of 1218 individuals, and do not have extreme scores on any of the contingency table indices representing environmental gradients. These lizards are considered to have wide niche breadths with regard to habitat requirements and tolerances and are referred to as habitat-generalists (Fig. 25). The relative abundances in each major area are plotted in figure 26.

Five species can be considered habitat-specialists; all of them have niche breadth scores in the range of 1-4, indicating that they have very narrow tolerances and specialized requirements with regard to the environmental parameters measured indirectly by the analysis (Fig. 25). Each species is found in only one or two of the four major areas and is relatively uncommon. The cumulative

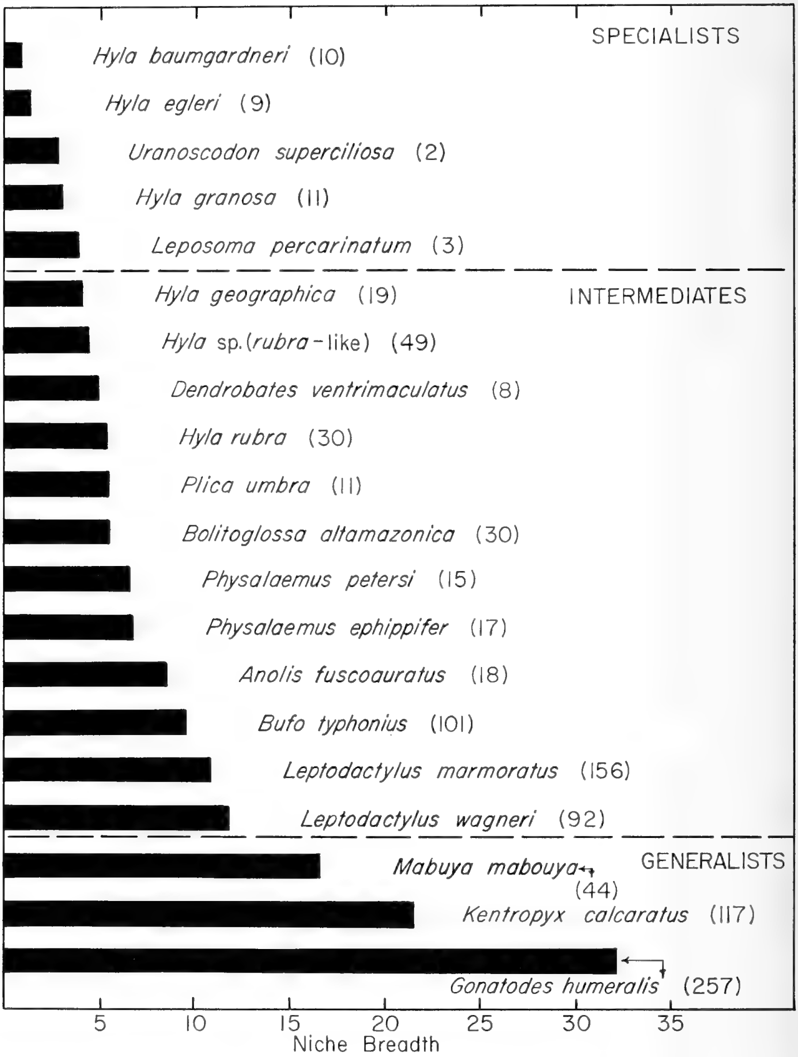

FIG. 25. Niche breadth scores. The bars represent niche breadth scores. Numbers in parentheses indicate the accumulative relative abundance × 1000 in all of the four major areas. The dashed lines separate the species into habitat specialists, intermediates, and generalists.

relative abundance of the five species in all of the areas is only 44 out of the total of 1218 individuals, or 3.6 percent. Two of the habitat-specialists are lizards (*Leposoma percarinatum* and *Uranoscodon superciliosa*), and three are frogs (*Hyla baumgardneri, H. egleri,* and *H. granosa*). *Leposoma percarinatum,* a secretive terrestrial lizard found within the leaf litter by day, is probably more

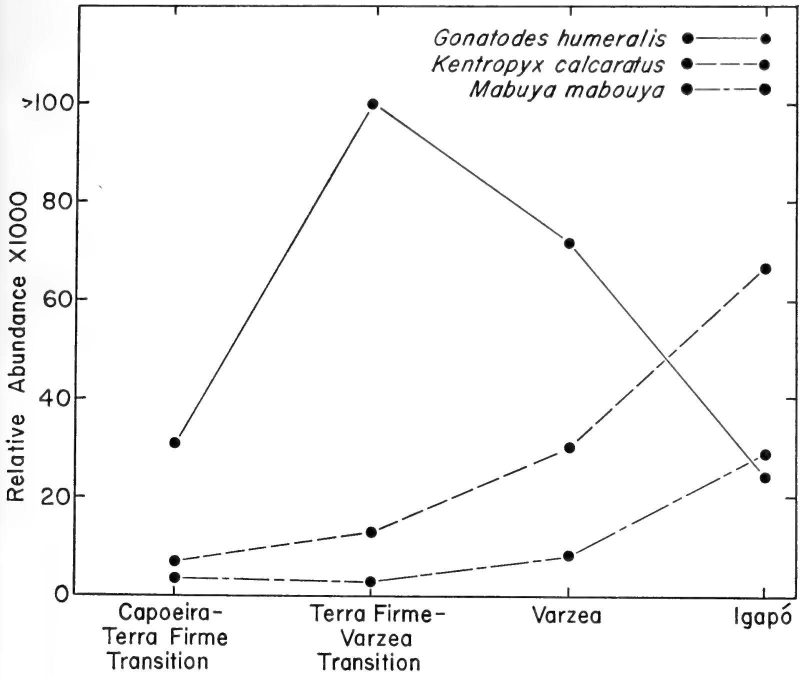

FIG. 26. Relative abundance × 1000 of the three habitat generalists in each of the four major areas.

widely distributed and more abundant than the data indicate. *Uranoscodon superciliosa* is found mainly near pools of standing water in the varzea forest. *Hyla granosa* is predominantly an igapó specialist, not found outside of the forest. The other two species of tree frogs, *H. baumgardneri* and *H. egleri*, are not primarily forest inhabitants, but are found abundantly in open areas; therefore, these two species are not specialized for the particular forest areas, but rather are dependent on standing water. For this reason the species have low niche breadth scores relative to the forest analysis. If a similar study were carried out in open areas, these species would probably have wide habitat niche breadth scores, for they are abundant and seem to have a wide range of environmental tolerances in open areas.

The remaining twelve species are considered to be habitat-intermediates (Fig. 25). In general, these species demonstrate intermediate niche breadth scores, corresponding to relatively few extreme values on the environmental indices from the contingency table analysis. They are generally more abundant and more widely distributed than the habitat-specialists, but less so than the habitat-generalists. This category includes the one species of salamander, two lizards, and nine frogs. Several of the habitat-intermediates have niche breadth scores similar to those of the habitat-specialists. The artificial line separating the two groups is obviously based on more than niche breadth values; representation and relative abundance in the major areas were also considered.

There seems to be a definite relationship between cumulative relative abundance and niche breadth scores (Fig. 27). In general, those species with wide habitat tolerances (high niche breadth values) are more abundant than those with narrow habitat tolerances. The abundant generalist has the highest niche breadth value, the moderately common generalists have lower niche breadth values, and the five habitat-specialists have the lowest niche breadth values and are extremely uncommon.

Another way of looking at the association is to plot index scores against niche breadth values (Fig. 28). All of the habitat-specialists have positive values on the first index, indicative of wet environments. Three of the habitat-specialists are restricted to open, grassy areas. One of the specialists is terrestrial, and the other four are found predominantly on low vegetation. Three of the specialists have more extreme negative values on the fourth index than does the generalist having a negative value. The relationship of niche breadth values to both index scores and relative abundances within each major area is presented (Figs. 22-24).

When index scores are plotted against relative abundance values for each area, it is possible to characterize the areas with regard to species composition in terms of habitat-generalists, intermediates, and specialists (Figs. 18-21). The capoeira-terra firme transition area provides suitable habitat for the three habitat-generalists (one is moderately common and the other two are relatively uncommon), but the five habitat-specialists are absent. The terra firme-varzea transition area is composed of two habitat-specialists, the three generalists, and numerous habitat-intermediates. One of the generalists is very abundant in this area, and the other two species are relatively uncommon; the two specialists are rare. Both of the specialists are found in one additional major area. The varzea area is represented by the three generalists (one abundant, one moderately common, and one relatively uncommon) and three habitat-specialists (all rare); one of the specialists is restricted to the varzea forest. Two of the generalists are moderately common in the igapo forest, and the third is abundant; three habitat-specialists inhabit the area, only one of which *(Hyla baumgardneri)* is restricted to the

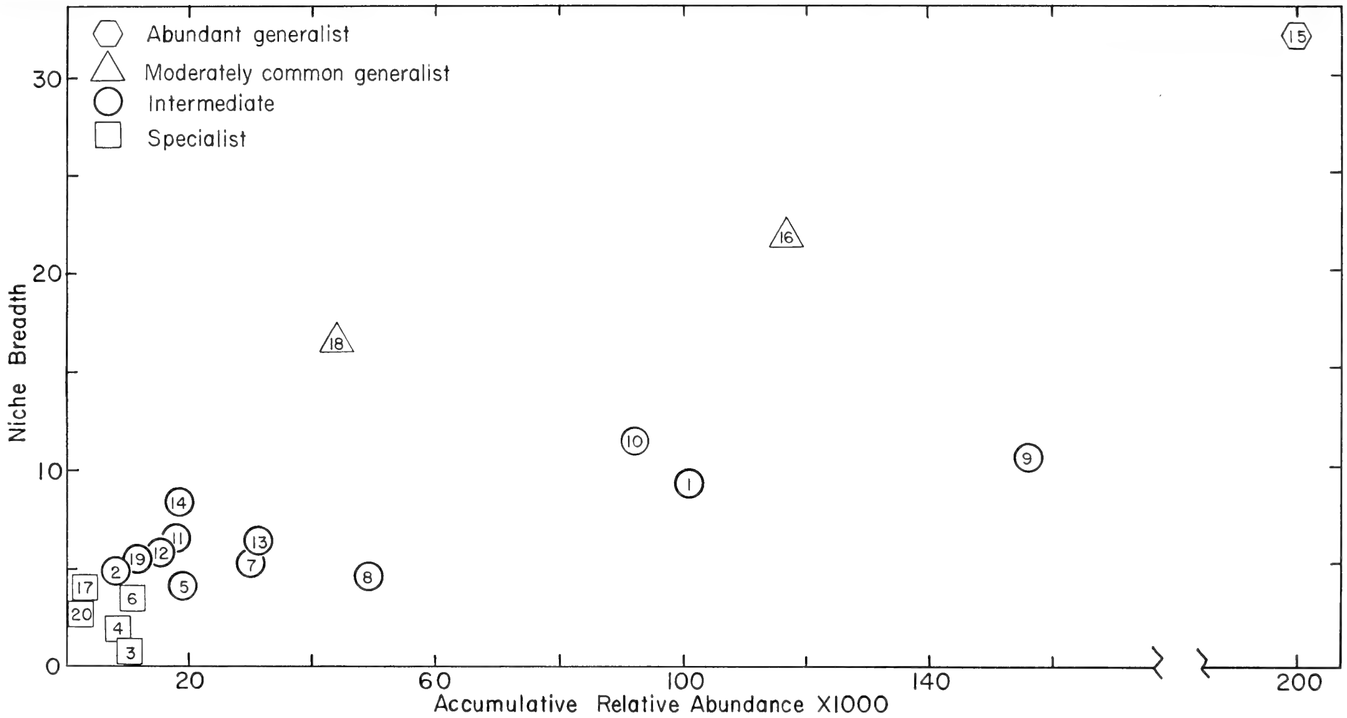

FIG. 27. Accumulative relative abundance × 1000 plotted against niche breadth for each of the 20 species. Species numbers are associated with species names in table 9, p. 29.

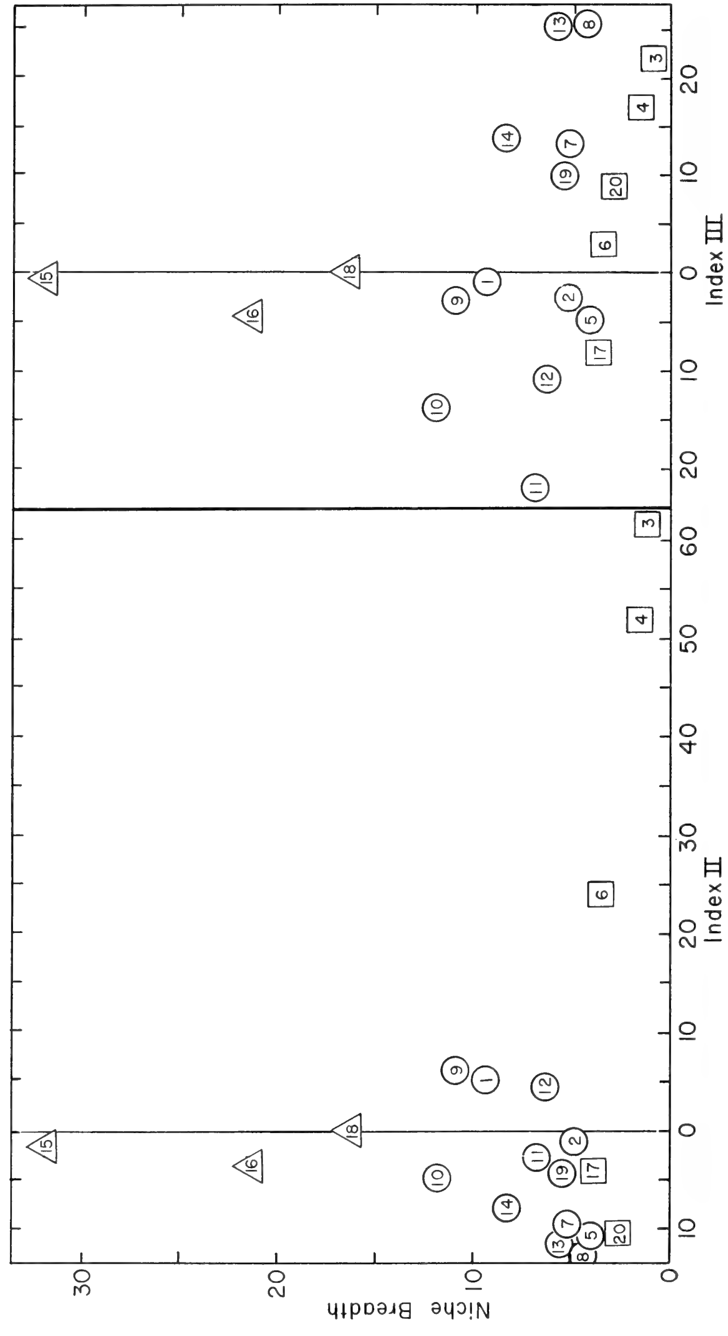

FIG. 28. Species scores on indices II and III plotted against niche breadth for each of the 20 species. Species numbers are associated with species names in table 9, p. 29. Refer to figures 18 and 19 for explanation.

igapó. All three specialists have the highest positive scores of any of the igapó species on the first and second indices, indicating standing water and areas of grassy, emergent vegetation; two species have the highest positive scores on the thtird index. The habitat-specialists in the igapó forest exhibit more extreme index scores and are more abundant than other specialists in other areas.

NICHE OVERLAP ANALYSIS

In a consideration of niche overlap, it is appropriate to ask: Proportionately, how often do species *i* and *j* occur together? Niche overlap can be crudely estimated by plot overlap if we assume that species requirements are intrinsic properties of the plots. The measure does not indicate what the overlapping requirements of the species are, but merely that overlap exists. Niche overlap scores were obtained from a formula suggested by Horn (1966); p_{ij} is the proportion of occurrences of species *j* in plot *i*. Overlap of species *j* and *k* ($\propto jk$) is then estimated by the following:

$$\propto jk = 2 \sum_i p_{ij}\, p_{ik} / (\sum_i p_{ij}^2 + \sum_i p_{ik}^2)$$

The index is from 0.0 (no overlap) to 1.0 (complete overlap). A high niche overlap value for two species indicates they are found together in the same plots. For example, *Hyla baumgardneri* and *H. egleri* have an overlap value of 0.971, the highest of any two species associations; these frogs breed in the same plots in the igapó forest. Other high correlations are *Bufo typhonius* and *Leptodactylus marmoratus* (0.928) and *Hyla* sp. (*rubra*-like) and *Bolitoglossa altamazonica* (0.913). Both species pairs usually occur sympatrically and therefore probably overlap greatly with regard to certain environmental requirements.

The following species pairs frequently occur together and have fairly high correlations, likely indicating similarities in environmental requirements: 1) *Kentropyx calcaratus* and *Mabuya mabouya* (0.718); 2) *Hyla rubra* and *Anolis fuscoauratus* (0.631); 3) *Hyla egleri* and *H. granosa* (0.589); 4) *Leptodactylus marmoratus* and *Physalaemus petersi* (0.586); 5) *Leptodactylus marmoratus* and *Gonatodes humeralis* (0.575); 6) *Hyla baumgardneri* and *H. granosa* (0.547); 7) *Leptodactylus wagneri* and *Mabuya mabouya* (0.539); 8) *Hyla rubra* and *Uranoscodon superciliosa* (0.533); 9) *Bufo typhonius* and *Gonatodes humeralis* (0.529); 10) *Anolis fuscoauratus* and *Plica umbra* (0.513); 11) *Hyla geographica* and *Uranoscodon superciliosa* (0.512); and 12) *Bufo typhonius* and

Physalaemus petersi (0.507). *Physalaemus ephippifer* has the least association with any other species, the highest being with *Physalaemus petersi* (0.210). A complete, ordered tabulation of niche overlap values for every species pair combination is given in table 11.

TABLE 11.—Niche Overlap Scores. In each column the species number (see Table 9) is followed by the niche overlap score, as determined by the Horn formula. Scores are ordered within a column; higher numbers indicate a greater degree of overlap.

Species 1	Species 2	Species 3	Species 4	Species 5	Species 6	Species 7
2 0.000	1 0.000	1 0.000	5 0.000	1 0.000	1 0.000	9 0.000
3 0.000	9 0.000	5 0.000	8 0.000	3 0.000	9 0.000	11 0.000
5 0.000	11 0.000	8 0.000	11 0.000	4 0.000	11 0.000	12 0.009
6 0.000	12 0.000	9 0.000	13 0.000	9 0.000	12 0.000	1 0.023
20 0.000	19 0.000	11 0.000	20 0.000	19 0.000	19 0.000	3 0.047
10 0.022	14 0.057	12 0.000	14 0.010	12 0.025	14 0.015	4 0.052
7 0.023	15 0.091	13 0.000	19 0.015	6 0.104	13 0.033	6 0.080
4 0.035	13 0.117	14 0.000	1 0.035	11 0.109	8 0.054	17 0.095
16 0.063	3 0.167	17 0.000	15 0.047	7 0.144	17 0.064	10 0.126
18 0.102	4 0.185	19 0.000	17 0.049	18 0.159	20 0.074	8 0.135
17 0.182	8 0.188	20 0.000	9 0.052	14 0.202	15 0.076	5 0.144
8 0.191	7 0.215	15 0.025	7 0.052	13 0.211	7 0.080	19 0.160
11 0.198	17 0.222	7 0.047	10 0.057	16 0.218	5 0.104	15 0.188
13 0.203	20 0.250	10 0.049	12 0.072	15 0.228	10 0.206	2 0.215
14 0.208	10 0.251	16 0.081	16 0.096	2 0.362	16 0.248	16 0.280
19 0.231	6 0.282	2 0.167	2 0.185	8 0.374	2 0.282	13 0.332
12 0.507	5 0.362	18 0.175	18 0.207	17 0.405	18 0.461	18 0.396
15 0.529	16 0.378	6 0.547	6 0.589	10 0.436	3 0.547	20 0.533
9 0.928	18 0.426	4 0.971	3 0.971	20 0.512	4 0.589	14 0.631

TABLE 11.—*Continued*

Species 8	Species 9	Species 10	Species 11	Species 12	Species 13	Species 14
3 0.000	2 0.000	19 0.019	2 0.000	2 0.000	3 0.000	3 0.000
4 0.000	3 0.000	1 0.022	3 0.000	3 0.000	4 0.000	11 0.000
11 0.000	5 0.000	9 0.029	4 0.000	6 0.000	11 0.000	4 0.010
12 0.000	6 0.000	14 0 044	6 0.000	8 0.000	12 0.019	6 0.015
6 0.054	7 0 000	3 0.049	7 0.000	20 0.000	6 0.033	10 0.044
9 0.116	20 0.000	4 0 057	8 0.000	7 0.009	10 0.109	2 0.057
10 0.127	10 0.029	11 0.103	13 0.000	13 0.019	2 0.117	17 0.123
7 0.135	16 0.041	13 0.109	14 0.000	5 0.025	9 0.118	12 0.166
16 0.160	4 0.052	7 0.126	20 0.000	18 0.029	17 0.194	9 0.196
2 0.188	18 0.070	8 0.127	18 0.025	16 0.043	16 0.196	5 0.202
1 0.191	8 0.116	12 0.137	10 0.103	19 0.070	1 0.203	1 0.208
17 0.211	13 0.118	20 0.157	5 0.109	4 0.072	5 0.211	18 0.261
20 0.239	11 0.156	6 0.206	16 0.114	10 0.137	20 0.217	16 0.270
18 0.240	19 0.177	2 0.251	17 0.120	14 0.166	18 0.291	8 0.387
15 0.266	14 0.196	17 0.267	9 0.156	11 0.210	15 0.292	15 0.434
19 0.373	17 0.238	15 0.306	19 0.184	15 0.319	7 0.332	13 0.448
5 0.374	15 0 575	5 0.436	15 0.179	17 0.412	19 0.427	20 0.468
14 0.387	12 0.586	16 0.482	1 0.198	1 0.507	14 0.448	19 0.513
13 0.913	1 0.928	18 0 539	12 0.210	9 0.586	8 0.913	7 0.631

SPECIES DIVERSITY AND EQUITABILITY

The Shannon index was used in the present analysis as a means of comparing the four major forest areas. The index is calculated as follows:

$$H' \approx -\sum_i p_i \log p_i \approx \mathrm{C/N}\,(\mathrm{N} \log_{10} \mathrm{N} - \sum_i n_i \log_{10} n_i),$$

TABLE 11.—*Concluded*

Species 15	Species 16	Species 17	Species 18	Species 19	Species 20
3 0.025	9 0.041	3 0.000	11 0.025	2 0.000	1 0.000
4 0.047	12 0.043	19 0.000	12 0.029	3 0.000	3 0.000
6 0.076	1 0.063	4 0.049	9 0.070	5 0.000	4 0.000
2 0.091	3 0.081	6 0.064	1 0.102	6 0.000	9 0.000
11 0.179	4 0.096	7 0.095	17 0.149	17 0.000	11 0.000
20 0.181	11 0.114	11 0.120	5 0.159	20 0.000	12 0.000
7 0.188	19 0.158	14 0.123	19 0.162	4 0.015	19 0.000
17 0.204	8 0.160	18 0.149	3 0.175	10 0.019	6 0.074
5 0.228	17 0.190	1 0.182	20 0.188	12 0.070	10 0.157
8 0.266	13 0.196	16 0.190	4 0.207	16 0.158	15 0.181
19 0.270	20 0.210	13 0.194	8 0.240	7 0.160	18 0.188
13 0.292	5 0.218	15 0.204	14 0.261	18 0.162	16 0.210
10 0.306	6 0.248	8 0.211	13 0.291	11 0.164	13 0.217
12 0.319	14 0.270	2 0.222	15 0.340	9 0.177	8 0.239
18 0.340	7 0.280	9 0.238	7 0.396	1 0.231	2 0.250
14 0.434	2 0.378	10 0.267	2 0.426	15 0.270	17 0.286
16 0.450	15 0.450	20 0.286	6 0.461	8 0.373	14 0.468
1 0.529	10 0.482	5 0.405	10 0.539	13 0.427	5 0.512
9 0.575	18 0.718	12 0.412	16 0.718	14 0.513	7 0.533

where H' = average diversity per species, p_i = probability of encountering the i^{th} species, C = the constant 3.321928 when using Base 2, N = total number of individuals, and n_i = number of individuals in the i^{th} *species.* The values are interpreted as follows. If in Area I there are 20 individuals of species A and 20 individuals of species B, then $H' \approx 2.00$; there are two equally common species. If in Area II there are 40 individuals of species A and 10 individuals of species B, then $H' \approx 1.65$; there are 1.65 equally common species. Area I is considered to have a higher species diversity than Area II. The data used were those in the original data matrix which also served as the basis for the contingency table analysis and niche breadth and overlap analyses.

The calculated species diversity values for the four major forest areas are as follows: capoeira-terra firme transition = 3.00; terra firme-varzea transition = 2.45; varzea = 3.02; and igapó = 2.72. Thus, in terms of the sampling plots analyzed, the varzea is the most diverse area with regard to species richness and evenness; the terra firme-varzea transition area is the least diverse. A determination of statistical and biological significance of these values would require additional data, ideally with an equal number of plots sampled per major area.

MacArthur (1957) proposed a "broken-stick model" dealing with species equitability based on one million individuals of 200 species. The model is based on the equation

$$\pi_r = 1/s \sum_{i=1}^{r} 1/s-i+1),$$

where π_r is the theoretical proportion of individuals in the r^{th} most abundant species ($r = 1, 2, \ldots, s$), each theoretical proportion itself being obtained by summing over r terms ($i = 1, 2, \ldots, r$). By using this formula, it is possible to obtain an apportionment of the individuals among the species in a sample in about as equitable a manner as ever occurs in nature. An advantage of MacArthur's model is that there is no set of parameters into which data must conform; for each possible number of species (s), the equation generates a complete set of s proportions π_r ($r = 1, 2, \ldots, s$). The model yields a curve whereby species abundances are graduated from the rarest to the most common. A maximum equitability curve, whereby for every sample size each species is equally abundant, can also be calculated. Species diversity values (H') obtained from the Shannon index can then be compared to the broken-stick and maximum equitability curves. Any community falling between the two curves is considered to be extremely diverse.

The species diversity values for the four areas were plotted in relation to the curve expected from the broken-stick model and the maximum equitability curve (Fig. 29). All areas fall to the left of the broken-stick distribution with the exception of the capoeira-terra firme transition area; the position of this area suggests that it is highly diverse in terms of species equitability. The validity of this model was questioned by Hairston (1969). He claimed that the broken-stick model lacks ecological meaning, because conformity to the model is largely a function of sample size. He demonstrated that large samples tend to make rare species even more rare and common species even more abundant; the reverse distortion is apparent in small samples. Because of the small sample sizes in the present analysis, the distribution of abundances may be distorted

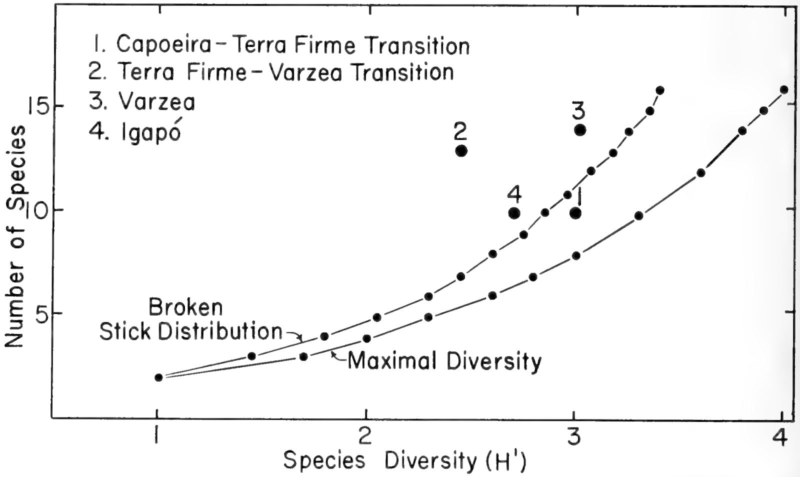

FIG. 29. Relationship of species diversity and numbers of species for each of the four major areas to MacArthur's broken stick distribution and maximal diversity.

such that rare species appear to be more common relative to abundant species than actually is the case.

Lloyd and Ghelardi (1964) proposed an equitability equation for the measure of fit of observed relative abundances of species to those predicted by MacArthur's broken-stick model, as follows:

$$E = s'/s,$$

where s is the actual number of species and s′ is the theoretical number of species that should be present according to the broken-stick model at the actual diversity *(H′)*, as calculated from the Shannon index. Maximum conformation to the model is 1.00. The following equitability indices were calculated from Lloyd and Ghelardi's table: capoeira-terra firme transition = 1.10; terra firme-varzea transition = 0.58; varzea = 0.79; and igapó = 0.90. Because of inequitability in the distribution of individuals among the species, the sample from the capoeira-terra firme transition forest has a species diversity appropriate to a community with 10 percent more species than actually occur in the particular sample. On the other hand, the samples from the terra firme-varzea transition, varzea, and igapó areas have species diversities appropriate to communities with only 58, 79, and 90 percent as many species as actually occur in the respective areas. Therefore, only the capoeira-terra firme transition area is more diverse than would be expected by the

TABLE 12.—Comparisons of Major Areas by Coefficients of Community. Numbers in Roman are the number of shared species of amphibians and lizards between two major areas; numbers in bold face are the actual number of species in a given area; numbers in italics are the coefficient of community values.

Major Areas	Terra Firme	Varzea	Igapó	Capoeira	Open & Edge
Terra Firme	**36**	24	16	20	16
Varzea	*0.480*	**38**	19	16	18
Igapó	*0.381*	*0.463*	**22**	13	12
Capoeira	*0.556*	*0.381*	*0.448*	**20**	10
Open & Edge	*0.296*	*0.333*	*0.273*	*0.227*	**34**

broken-stick model (Fig. 29). Again, because of small sample sizes, the statistical and biological significance of this analysis is uncertain.

COEFFICIENT OF COMMUNITY

The coefficient of community (CC), used to measure the relative similarity of samples from two communities (major areas), is calculated,

$$CC = S_{ab}/(S_a+S_b-S_{ab}),$$

where S_{ab} is the number of species shared by samples A and B, S_a is the total number of species present in sample A, and S_b is the total number of species present in sample B.

Coefficients were calculated for every two area combinations for five major areas: open and edge areas, capoeira, terra firme, varzea, and igapó. The distribution data used are found in table 2, consisting of 62 species of frogs, salamanders, and lizards. The coefficients are presented in table 12, in addition to the actual number of species every two areas have in common. The varzea and terra firme forests have the most species in common (24), but the coefficient of community is the second highest (0.480). The capoeira and terra firme forests have 20 species in common and have the highest coefficient of community (0.556). The capoeira forest and open and edge areas have the fewest species in common (10) and have the lowest coefficient of community (0.227). Likewise, there is low similarity between the igapó forest and open and edge areas (12 shared species, with a coefficient of 0.273).

SUMMARY AND CONCLUSIONS

The ecological distribution of each of 62 species of frogs, salamanders, and lizards was determined by means of continuous sampling throughout the environment from mid-January to the end of July, 1969, two weeks in April 1970, and June-July, 1970. Each species exhibits a characteristic distribution, according to its genetic, morphological, and physiological make-up, its life cycle, its way of relating to the physical environment, and its interactions with other species.

The contingency table analysis was used to obtain a measure of the association between species of amphibians and reptiles and their habitats (plots) and to partition this association into independent components (indices) which determine the distribution of species within four of the major forest areas. The components are interpreted as follows: the first is a moisture gradient; the second, a vegetation density gradient; the third, a vertical distribution gradient, and the fourth seems to be a composite of environmental parameters. Each species can be characterized in terms of the indices. Species with scores near zero are the most generalized with regard to the environmental parameters studied and are generally the most abundant species; those species with extremely high positive or low negative scores are restricted to a particular range of the environmental spectrum and are relatively uncommon. The species of frogs exhibit more environmental extremes than do the lizards, indicating that the particular species of frogs studied have more narrow environmental tolerances than do the lizards included in the analysis. The environment likely produces greater restrictions on frogs than on lizards in the carrying out of life processes due to basic physiological differences between the animals, resulting in more restricted distributions for frogs than for lizards.

Niche breadth scores, as calculated from Levins' formula, are presumed to be correlated with the range of environmental tolerances. Three species of lizards have much higher habitat niche breadth scores than the other 17 species of amphibians and lizards; these three species are the only ones found in all of the major forest areas. There is a definite relationship between cumulative relative abundance and niche breadth values. In general, those species with wide environmental tolerances (high niche breadth scores) are more abundant than those with narrow tolerances (low niche breadth scores).

When niche breadth scores, abundance indices, and scores on the environmental gradients are analyzed together, three species are referred to as habitat-generalists, five species as habitat-specialists, and the remaining twelve as habitat-intermediates. The generalists occur in all major areas, have high niche breadth scores, are abundant, and exhibit no extreme scores on the environmental gradients; the specialists are found in only one or two major areas, have low niche breadth scores, are relatively uncommon, and exhibit extreme requirements on one or more environmental gradient.

Partitioning of resources is evident, in terms of both space and time. One of the most striking examples is the calling site segregation among breeding male frogs in a given area. Habitat niche overlap can be estimated by plot overlap. Many species pairs have relatively high overlap values, thereby indicating that they frequently occur in association with each other. Assuming the plot is indicative of the requirements and tolerances of the species found therein, we can conclude that some niche overlap does exist.

Four of the major forest areas were compared and contrasted by various analytical techniques. Each area was characterized by the contingency table indices. The capoeira-terra firme transition area is relatively dry and has rather dense vegetation; the herpetofauna predominantly inhabits low vegetation and tree trunks. The terra firme-varzea transition area can be divided into high ground transition and low, wet transition. The entire transition zone is an intermediate area with respect to the environmental gradients, except that in many areas the ground cover is less dense than that of the capoeira-terra firme transition area. The varzea plots are relatively wet and have fairly dense ground cover. The igapó forest is the wettest area and has intermediate to relatively dense ground cover; most of the lizards are either terrestrial or are found on the boardwalks, and the frogs are found both on low vegetation and on the ground.

Another way of comparing the areas is in terms of species richness and equitability. Species richness values for five major areas are: varzea—38 species; terra firme—36 species; open and edge areas—34 species; igapó—22 species; and capoeira—20 species. Coefficients of community were calculated on these data to determine relative similarity between every two areas. The highest similarity is between capoeira and terra firme forests (0.556), and the lowest is between capoeira and open-edge areas (0.227). Species diversity (Shannon index) scores were calculated from the contingency table data matrix; the results are: varzea—3.02; capoeira-terra firme transition—3.00; igapó—2.72; and terra firme-varzea transition—2.45. Equitability values were then calculated from the species diversity estimates *(H')* and compared to MacArthur's broken-stick model. The capoeira-terra firme transition area has an equitability of 1.10, indicating that the area is more diverse than would be expected by MacArthur's model. As discussed in the relevant section, the statistical and biological significance of this analysis is uncertain due to small sample size.

The ecological requirements and tolerances characteristic of species in a community vary widely. Every species exploits the available resources in the most effective way possible for that particular species. Some species accomplish this by specializing in part of the environment, whereas others are generalized and utilize a greater spectrum of environmental parameters. It is concluded that the niche segregation existent among the frogs, salamanders, and lizards living in various habitats within the rainforest at Belém permits many species to coexist with highly efficient utilization of environmental resources.

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LITERATURE CITED

Belém Virus Laboratory, Belém, Pará, Brazil
1967. Annual report. Unpublished.

Cain, S. A., G. M. de O. Castro, J. M. Pires, and N. T. da Silva
1956. Application of some phytosociological techniques to Brazilian rain forest. Amer. J. Botany, 43:911-941.

Duellman, W. E.
1967. Courtship isolating mechanisms in Costa Rican hylid frogs. Herpetologica, 23:169-183.

Hairston, N. G., J. D. Allen, R. K. Colwell, D. J. Futuyma, J. Howell, M. D. Lubin, J. Mathias, and J. H. Vandermeer
1968. The relationship between species diversity and stability: an experimental approach with Protozoa and bacteria. Ecology, 49(6):1091-1101.

Hatheway, W. H.
1967. Physiognomic characterizations of three vegetational types at the Guamá Ecological Research Area, Belém, Brazil. Unpublished report to the Smithsonian Institution, June 15, 1967:1-35.

Horn, H. S.
1966. The measurement of "overlap" in comparative ecological studies. Amer. Nat., 100:419-424.

Hutchinson, G. E.
1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology, 22:415-427.

Inger, R. F. and B. Greenberg
1966. Ecological and competitive relations among three species of frogs (genus *Rana*). Ecology, 47(5):746-759.

Kendeigh, S. C.
1961. Animal ecology. Prentice-Hall, Inc., Englewood Cliffs, N.J., 468 pp.

Lloyd, M. and R. J. Ghelardi
1964. A table for calculating the "equitability" component of species diversity. J. Animal Ecol., 33:217-225.

Lloyd M., R. F. Inger, and F. W. King
1968. On the diversity of reptile and amphibian species in a Bornean rain forest. Amer. Nat., 102(928):497-515.

MacArthur, R. H.
1957. On the relative abundance of bird species. Proc. Natl. Acad. Sci. U.S., 43:293-295.
1964. Environmental factors affecting bird species diversity. Amer. Nat., 98:387-398.
1965. Patterns of species diversity. Biol. Rev., 40:510-533.

MacArthur, R. H. and J. W. MacArthur
1961. On bird species diversity. Ecology, 42:594-598.

MacArthur, R. H., J. W. MacArthur, and J. Preer
1962. On bird species diversity: II. Prediction of bird census from habitat measurements. Amer. Nat., 96:167-174.

MacArthur, R. H., H. Recher, and M. Cody
1966. On the relation between habitat selection and species diversity. Amer. Nat., 100:319-332.

Pianka, E. R.
1967. Lizard species diversity. Ecology, 48(3):333-351.

Pielou, E. C.
1966. Shannon's formula as a measure of specific diversity: its use and misuse. Amer. Nat., 100:463-465.

Rand, A. S.
1964. Ecological distribution in anoline lizards of Puerto Rico. Ecology, 45:745-752.

Rand, A. S. and S. S. Humphrey
1968. Interspecific competition in the tropical rain forest: ecological distribution among lizards at Belém, Pará. Proc. U.S. Natl. Mus., 125(3658):1-17.

Schoener, T. W.
1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. Ecology, 49:704-726.
1970. Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology, 51(3):408-418.

Schoener, T. W. and G. C. Gorman
1968. Some niche differences in three Lesser Antillean lizards of the genus *Anolis*. Ecology, 49(5):819-830.

Shannon, C. E.
1948. The mathematical theory of communication. In C. E. Shannon and W. Weaver, The mathematical theory of communication. Univ. Illinois Press, Urbana, 117 pp.

Whittaker, R. H.
1970. Communities and ecosystems. The Macmillan Company, Collier-Macmillan Limited, London, 162 pp.

Williams, E. J.
1952. Use of scores for the analysis of association in contingency tables. Biometrika, 39:274-289.

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A TAXONOMIC REVIEW OF SOUTH AMERICAN HYLID FROGS, GENUS *PHRYNOHYAS*

By

William E. Duellman[1]

Few large South American hylid frogs are so poorly known taxonomically as the widespread *Phrynohyas venulosa* (Laurenti, 1768) and its cogeners. Duellman (1956) included three South American species in the genus; four other species were recognized in Central America and México. Duellman (1966) and McDiarmid (1968) reduced all of the Middle American nominal species to synonyms of *Phrynohyas venulosa.* Duellman (1968) resurrected *Hyla coriacea* Peters from the synonymy of *Phrynohyas venulosa* and showed that *coriacea* was a valid species of *Phrynohyas* in the Guianas and Amazon Basin. Bokermann (1966) listed *Hyla mesophaea* Hensel and *Hyla imitatrix* Miranda-Ribeiro in the genus *Phrynohyas.*

The purposes of the present paper are to: 1) redefine the hylid genus *Phrynohyas,* 2) describe the geographic variation in the widespread *Phrynohyas venulosa,* 3) ascertain the assignments of several nominal species, and 4) present a synopsis of the species in the genus.

Specimens examined are designated by the following abbreviations of depositories:

AMNH	American Museum of Natural History
ANSP	Academy of Natural Sciences, Philadelphia
BMNH	British Museum (Natural History)
CAS	California Academy of Sciences
CAS-SU	Stanford University collection, now in the California Academy of Sciences
FMNH	Field Museum of Natural History

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[1] Curator, Division of Herpetology, Museum of Natural History, University of Kansas.

IRSNB	Institut Royal des Sciences Naturelles Belgique
KU	University of Kansas Museum of Natural History
LACM	Los Angeles County Museum of Natural History
MCZ	Museum of Comparative Zoology, Harvard
MLS	Museo de La Salle, Bogotá
MJP	Museo Javier Prado, Lima
MNHN	Museum National d'Histoire Naturelle, Paris
MNRJ	Museu Nacional, Rio de Janeiro
MZUSP	Museu de Zoología, Universidade de São Paulo
NHMG	Naturhistoriska Museet, Göteborg
NHMW	Naturhistorisches Museum, Wien
NHRM	Naturhistoriska Riksmuseet, Stockholm
RMNH	Riksmuseet van Natuurlijke Histoire, Leiden
SMF	Senckenbergische Museum, Frankfurt
UIMNH	University of Illinois Museum of Natural History
UMMZ	University of Michigan Museum of Zoology
USNM	United States National Museum
UZM	Universitets Zoologiske Museum, Copenhagen
WCAB	Werner C. A. Bokermann, São Paulo, Brasil
ZIUS	Zoologiske Institut, Universitet Stockholm
ZMB	Zoologisches Museum, Berlin
ZSM	Zoologisches Staatssammlung, Munich

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PHRYNOHYAS FITZINGER, 1843

Phrynohyas Fitzinger, 1843:30 [type species, *Hyla zonata* Spix, 1824 (= *Rana venulosa* Laurenti, 1768) by monotypy and declaration of International Commission on Zoological Nomenclature (Opinion No. 520, 1958)].

Acrodytes Fitzinger, 1843:30 [type species, *Hyla venulosa* Daudin, 1803 (= *Rana venulosa* Laurenti, 1768) by monotypy; generic name suppressed by International Commission on Zoological Nomenclature (Opinion No. 520, 1958) for purposes of Law of Priority, but not for those of Law of Homonymy].

Scytopis Cope, 1862:354 [type species, *Scytopis hebes* Cope, 1862, by monotypy].

Diagnostic Definition.—1) Skull slightly broader than long; 2) dermal roofing bones of skull well ossified, lacking exostosis and co-ossification; 3) nasals broad, overlapping anterior edge of sphenethmoid, not articulating with maxillaries: 4) frontoparietals having complete medial articulation, entirely covering frontoparietal fontanelle; posterolateral margin of frontoparietal lying just medial to epiotic eminence; 5) sphenethmoid well ossified with large portion exposed dorsally; 6) maxillary arch complete; pars facialis of maxillary moderately well developed but not articulating with nasal; 7) squamosal weakly articulating with prootic; zygomatic ramus extending about one-half of distance to maxillary; 8) pterygoid robust with complete articulations; 9) dentigerous processes of prevomers curved; 10) parasphenoid large, edentate, acuminate anteriorly; alae oriented posterolaterally; 11) palatines moderately large, widely separated medially, bearing dentigerous ridge; 12) neural arches of vertebrae low, non-imbricate; 13) transverse processes of vertebrae subequal in width; width of processes on third presacral vertebra less than width of sacral diapophyses; 14) sacral diapophyses expanded; 15) ilial shaft long, cylindrical, with low dorsal protuberance; 16) pubis cartilaginous; 17) clavicles expanded distally, strongly arched; 18) coracoids expanded distally and proximally, widely separated medially; 19) epicoracoids broadly overlapping; 20) suprascapula large, well ossified; cleithrum ossification incorporated into suprascapula; 21) vocal sacs paired, lateral, behind angles of jaws; 22) submentalis muscle moderate in size, araphic; 23) intermandibularis muscle undifferentiated, lacking aponeurosis; 24) interhyoideus muscle forming large supramandibular lobes; no myointegumental contact between lobes and sacs; 25) postmandibular septum short, attached to posterior end of intermandibular portion of interhyoideus; 26) length of vocal slits about one-fifth of length of mandible; 27) skin on dorsum thick, glandular, and smooth, granular, or tuberculate; that on venter heavily granular; 28) parotoid glands extensively developed in occipital and scapular regions; 29) diameter of tympanum 50-75 percent of diameter of eye; upper edge covered by supratympanic fold; 30) discs large, round; 31) fingers one-fourth to two-thirds webbed; toes about three-fourths webbed; 32) smooth, horny nuptial excrescences in breeding males; 33) pupil horizontal; 34) palpebrum clear; 35) snout-vent length of adults 50-114 mm; 36) known tadpoles having four upper and six lower rows of teeth.

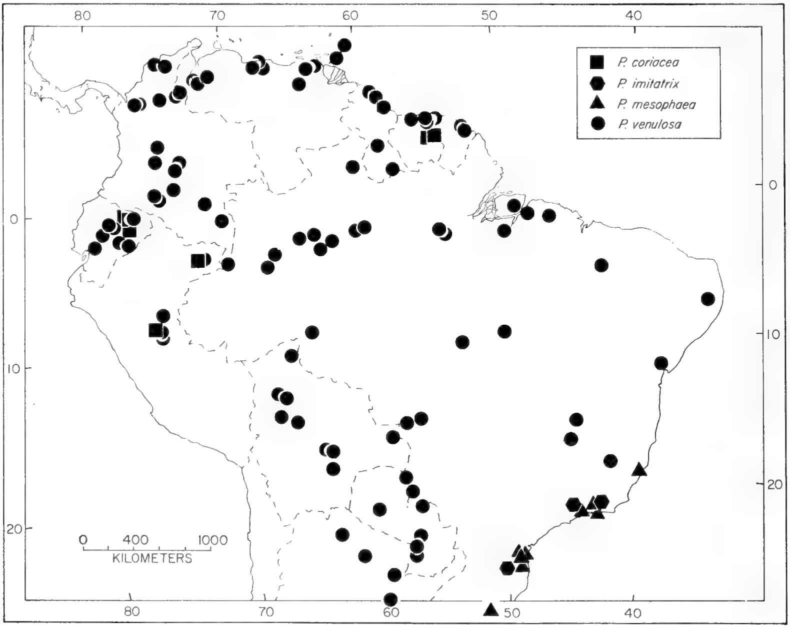

FIG. 1. Map showing locality records for the species of *Phrynohyas.*

Content.—As defined here, the genus contains four species: *P. coriacea* (Peters), *P. imitatrix* (Miranda-Ribeiro), *P. mesophaea* (Hensel), and *P. venulosa* (Laurenti, 1768).

Distribution.—The lowland tropics from Sinaloa and Tamaulipas, México, southward to Chaco, Entre Ríos, and Salta, Argentina, and Rio Grande do Sul, Brasil. The genus occurs on Trinidad and Tobago, but only two specimens are known from the Pacific lowlands of South America (Fig. 1). Most records of occurrence are at elevations of less than 500 m, but the frogs ascend the Amazonian slopes of the Andes to about 800 m and are known to occur at elevations of 1200 m in the Serra do Mar and Serra da Mantiqueira in southeastern Brasil.

Comments.—As pointed out by Trueb and Duellman (1971:38), only four hylid genera have paired lateral vocal sacs; these are *Argenteohyla, Osteocephalus, Phrynohyas,* and *Trachycephalus.* Tyler (1971:349) provided evidence that the paired lateral vocal sacs were derived from single subgular sacs and stated: "Conceivably the very highly specialized vocal sacs of *Phrynohyas* and *Trachycephalus* could have been derived from the simpler structures now found in some species of *Osteocephalus.*" Trueb and Duellman (1971:40) concluded that *Phrynohyas* and *Trachycephalus* probably were representatives of one phyletic line. *Trachycephalus* differs from *Phrynohyas* principally by having a heavily casqued, co-ossified skull and by lacking extensive parotoid glands.

GEOGRAPHIC VARIATION IN *PHRYNOHYAS VENULOSA*

In 1956 I noted the presence of variation in size and coloration in *P. venulosa* in the Amazon Basin; furthermore, I recognized, taxonomically two peripheral populations—*P. hebes* in the Gran Chaco and *P. ingens* in the Maracaibo Basin. Examination of many additional South American specimens reveals that the mosaic of variation is more complex than that described previously.

Size.—In South America very large individuals of *P. venulosa* occur in the Maracaibo Basin (females to 112.5 mm in snout-vent length) and in Amazonian Ecuador (females to 110.2 mm in snout-vent length). Equally large individuals are known from Panamá and Costa Rica (Duellman, 1970:165). Specimens from other areas in South America are noticeably smaller (Table 1). Measurements and proportions of the limbs and head all are positively correlated with snout-vent length. Duellman (1956) suggested that there were interpopulational differences in the size of the tympanum, but data from larger series of specimens negate that suggestion (Table 1). Also, there seems to be no correlation between size and habitat, as suggested by McDiarmid (1968).

Skin.—Considerable variation is apparent in the thickness and texture of the dorsal skin. Most specimens have scattered pustules dorsally; these are especially noticeable in young individuals. In a few specimens, such as KU 126067 from 2 km east of Leticia, Colombia, and especially MNRJ 4054 from Rio Branco, Brasil, the skin on the dorsum is highly pustulate. The parotoid glands result in thickened skin in occipital and scapular regions in most specimens from throughout the range. Many specimens from the upper Amazon Basin in Ecuador, Perú, and Bolivia have thick, leathery skin. McDiarmid (1968) suggested that extensive development of the parotoid glands is a seasonal phenomenon in frogs living in regions having wet and dry seasons, the glands being better developed in the dry season. Dates of collection are not available for many South American specimens of *P. venulosa;* the specimens having such data do not provide strong evidence in support of McDiarmid's proposal. For example, well-developed glands are evident in specimens from the upper Amazon Basin where there is no prolonged dry season;

Table 1.—Variation in Certain Measurements in *Phrynohyas venulosa*. Measurements are in millimeters; means are given in parentheses below observed ranges.

Locality	*N*		Snout-vent Length		Tympanum Length	
	♂	♀	♂	♀	♂	♀
Trinidad	25	6	67.0-82.0 (74.9)	65.0-72.5 (67.8)	4.0-6.0 (4.8)	4.0-4.5 (4.7)
Venezuela: Maracaibo Basin	4	4	75.0-88.0 (84.0)	94.5-112.5 (101.4)	4.5-6.0 (5.3)	6.1-7.0 (6.6)
Brasil: Belém	7	3	58.5-75.3 (66.3)	63.1-68.9 (66.6)	3.9-4.7 (4.4)	4.1-4.7 (4.4)
Colombia: Leticia	5	-	63.9-70.5 (69.2)	-	4.7-5.0 (4.8)	-
Ecuador: Napo-Pastaza	7	3	84.8-92.5 (87.7)	102.8-110.2 (107.6)	5.6-7.4 (6.8)	8.1-9.1 (8.6)
Bolivia: El Beni	7	5	67.5-73.5 (70.9)	71.0-74.5 (73.1)	5.0-5.5 (5.1)	5.0-5.5 (5.1)
Bolivia: Santa Cruz	5	8	65.0-76.0 (69.0)	59.5-88.5 (73.0)	4.5-5.0 (4.7)	4.0-6.0 (4.8)
Paraguay	7	6	64.2-86.0 (78.7)	68.0-89.1 (81.0)	3.8-5.5 (4.9)	5.0-6.2 (5.6)

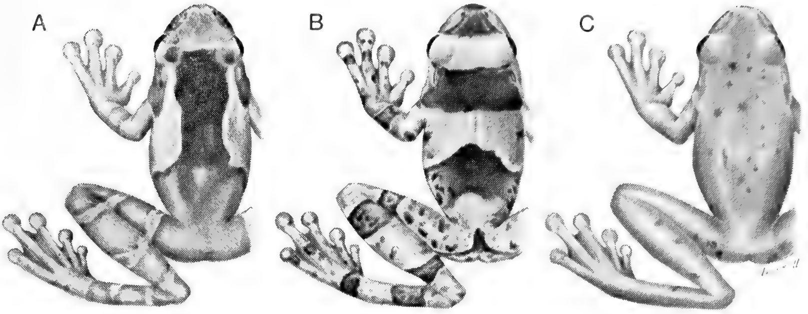

FIG. 2. Dorsal color patterns in *Phrynohyas venulosa*. *A*. Normal, code 4, KU 92258. *B*. Divided, code 3, KU 126067. *C*. *Spotted*, code 2, NHMW 19013 (holotype of *Hyla wettsteini*).

specimens from Napo and Pastaza provinces in Ecuador have more extensive glands than do individuals from the xeric Maracaibo Basin.

Coloration.—All individuals of *P. venulosa* are brown or tan dorsally with or without darker markings. The venter is uniform grayish white or pale tan. The iris is golden with radiating black lines. There is considerable variation in dorsal color pattern, but most of the variants can be grouped into one of four categories; code numbers indicate a decreasing amount of dark pigment dorsally (Fig. 2):

NORMAL: A large middorsal dark blotch extending from the occiput to the rump; blotch divided anteriorly by a longitudinal band of ground color in some specimens (coded 4).

DIVIDED: As above, but blotch divided by a broad transverse band of ground color (coded 3).

SPOTTED: Dorsal pattern consisting of irregular small dark spots (coded 2).

PLAIN: Dorsum uniform brown (coded 1).

The various color patterns are found throughout most of the range of the species in South America (Table 2). The only region in which all specimens have the normal pattern is Paraguay; the next highest percentage of specimens having the normal pattern is Trinidad (93%). All four color pattern types were found in only four of 14 pooled samples; normal and plain patterns occurred in 12 samples, and divided and spotted patterns occurred in eight samples. In the only large sample (151 specimens from Maracay, Venezuela) the following percentages occur: normal 14.6, divided 44.3, spotted 7.9, and plain 33.2. Each of the various patterns has been found in males, females, and juveniles. All four patterns, save the spotted one, are found in Central America.

TABLE 2.—Variation in Dorsal Color Pattern in *Phrynohyas venulosa*. See text for explanation of patterns and scoring.

Locality	*N*	Normal	Divided	Spotted	Plain	Score
Trinidad	32	30	1	1	0	3.91
Venezuela: Maracaibo Basin	8	0	0	7	1	1.89
Venezuela: Maracay	151	22	67	12	50	2.38
Surinam	21	15	0	2	4	3.28
Brasil: Belém	26	23	1	0	2	3.73
Brasil: Mato Grosso	15	2	0	12	1	2.20
Brasil: Manáus	8	3	3	0	2	2.87
Colombia: Leticia	5	1	1	0	3	2.00
Ecuador: Napo-Pastaza	13	0	1	0	12	1.25
Perú: Pebas	10	4	0	4	2	2.60
Perú: Pucallpa	12	6	0	0	6	2.50
Bolivia: El Beni	16	1	1	2	12	1.44
Bolivia: Santa Cruz	15	4	1	3	7	2.13
Paraguay	14	14	0	0	0	4.00

Remarks.—It is evident that the various characters considered to be of taxonomic value in this group vary independently of one another in *P. venulosa*. Refined quantitative analysis must await the acquisition of large series of specimens from throughout the range of the species. Currently, karyological, larval, and biosonic data are

TABLE 3.—Alphabetical Synonymy of the Species of *Phrynohyas*.

Trivial Name, Original Generic Name, Author, and Date	Current Name
adenoderma (Hyla) Lutz, 1968	*P. venulosa*
bufona (Hyla) Spix, 1824	*P. venulosa*
corasterias (Phrynohyas) Shannon and Humphrey, 1957	*P. venulosa*
coriacea (Hyla) Peters, 1867	*P. coriacea*
hebes (Scytopis) Cope, 1862	*P. venulosa*
imitatrix (Hyla) Miranda-Ribeiro, 1926	*P. imitatrix*
inflata (Acrodytes) Taylor, 1944	*P. venulosa*
ingens (Phrynohyas) Duellman, 1956	*P. venulosa*
latifasciata (Phrynohyas) Duellman, 1956	*P. venulosa*
lichenosa (Hyla) Günther, 1859	*P. venulosa*
macrotis (Hyla) Andersson, 1945	*P. venulosa*
mesophaea (Hyla) Hensel, 1867	*P. mesophaea*
modesta (Acrodytes) Taylor and Smith, 1945	*P. venulosa*
nigropunctata (Hyla) Boulenger, 1882	*P. venulosa*
paenulata (Hyla) Brocchi, 1879	*P. venulosa*
palpebrogranulata (Hyla) Andersson, 1906	*P. venulosa*
quadrangulum (Hyla) Boulenger, 1882	*P. coriacea*
resinifictrix (Hyla) Goeldi, 1907	*P. venulosa*
spilomma (Hyla) Cope, 1877	*P. venulosa*
venulosa (Rana) Laurenti, 1768	*P. venulosa*
vermiculata (Hyla) Duméril and Bibron, 1841	*P. venulosa*
wettsteini (Hyla) Ahl, 1933	*P. venulosa*
zernyi (Hyla) Ahl, 1933	*P. venulosa*
zonata (Hyla) Spix, 1824	*P. venulosa*

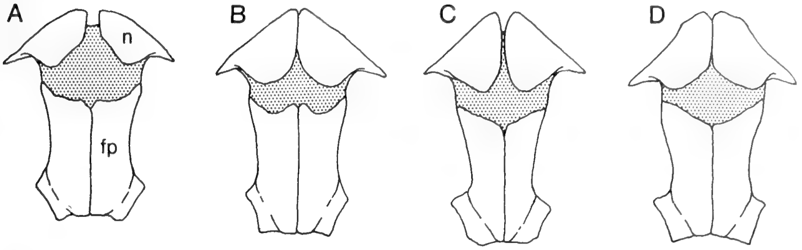

FIG. 3. Anterior cranial roofing bones showing positions of nasals and proportion of dorsal exposure of the sphenethmoid. *A. P. coriacea,* KU 105249. *B. P. imitatrix,* KU 92249. *C. P. mesophaea,* KU 92257. *D. P. venulosa,* KU 138830. Abbreviations: fp = frontoparietal, n = nasal; sphenethmoid is stippled.

lacking. Until such data are available for a more sophisticated analysis, we must be content to base conclusions on the present inadequate series of preserved specimens, which have formed the basis for my broad definition of *Phrynohyas venulosa.*

TAXONOMY OF *PHRYNOHYAS*

Data taken from series of preserved specimens, some living frogs, skeletal preparations, and radiographs provide a basis for the recognition of four species in the genus *Phrynohyas* (Table 3). Diagnostic external morphological characters and features of coloration are used in the following key. Osteological characters that are important at the species level are discussed below.

Nasals.—The size and position (relative to one another) of the nasals are distinctive (Fig. 3). In *P. imitatrix* and *venulosa* the nasals are juxtaposed; in *mesophaea* they are narrowly separated, and in *coriacea* they are widely separated.

Sphenethmoid.—The sphenethmoid is well ossified in all species. The proportion of the element exposed dorsally shows interspecific differences (Fig. 3); the area of exposure is dependent on the relative sizes and positions of adjacent dermal roofing bones—the nasals anteriorly and the frontoparietals posteriorly. The sphenethmoid is least exposed in *P. imitatrix* and moderately exposed in *mesophaea* and *venulosa.* A relatively large area of the sphenethmoid is exposed in *coriacea,* in which the nasals are widely separated.

Prevomers.—The dentigerous processes are curved and separated medially in all species. The curvature is slight and the separation moderate in *P. imitatrix* and *venulosa,* slight and widely separated in *coriacea,* and strongly curved and narrowly separated in *mesophaea.*

Sacral Diapophyses.—The diapophyses are dilated in all species; this dilation is symmetrical in *P. mesophaea* and *venulosa* and asymmetrical (greater dilation posteriorly) in *imitatrix* and *coriacea.*

KEY TO THE SPECIES OF *Phrynohyas*

1. Dorsal quadrangular mark outlined with white and terminating in sacral region; thighs lacking dark transverse bars; black post-tympanic spot present; red "flash-colors" in life .... *P. coriacea*

   Dorsal quadrangular mark, if present, usually not outlined with white; thighs usually having dark transverse bars (if blotches present on dorsum); black post-tympanic spot absent; no red "flash-colors" in life 2

2. Dorsum and flanks dark brown with broad cream dorsolateral stripe from eyelid to groin; limbs unicolor or faintly barred dorsally .... *P. mesophaea*

   Dorsal pattern variable, but lacking dorsolateral cream strips; limbs usually distinctly barred, if blotch present on dorsum 3

3. Dorsal markings consisting of large brown blotch anteriorly and usually round spots or blotches posteriorly, darkest peripherally; limbs with distinct dark brown, light bordered bars; dorsal skin distinctly tuberculate .... *P. imitatrix*

   Dorsal markings absent or consisting of large dark blotch (transversely divided in some) or small dark spots; limbs unicolor or barred, lacking light borders; dorsal skin variable ...... *P. venulosa*

Phrynohyas coriacea (Peters)

Hyla coriacea Peters, 1867:711 [syntypes, ZMB 5807 (3 specimens) from Surinam; H. Kappler collector].
Hyla quadrangulum Boulenger, 1882:367 [holotype, BMNH 1947.2.13.75 from "western Ecuador"; Mr. Fraser collector]. New synonymy.
Phrynohyas coriacea—Duellman, 1968:205.

Distribution.—Surinam and the upper Amazon Basin in Ecuador and Perú at known elevations of less than 500 m (Fig. 1). The record for Machala on the Pacific coast of Ecuador probably is erroneous. 29 specimens from 11 localities.

Remarks.—The three syntypes (ZMB 5807) were reported on by Duellman (1968). The holotype of *Hyla quadrangulum* (BMNH 1947.2.13.75) is an adult female having a snout-vent length of 57.5 mm and morphological characters which render it indistinguishable from *P. coriacea*. The color pattern consists of a dark brown quadrangular dorsal blotch faintly outlined with cream on a tan dorsum; the limbs are distinctly barred, and a dark post-tympanic spot is evident.

The type locality of "western Ecuador" cannot be taken seriously; several species contained in the Fraser collections supposedly from western Ecuador have been found subsequently only in the Amazon Basin and eastern slopes of the Andes.

Phrynohyas imitatrix (Miranda-Ribeiro)

Hyla imitatrix Miranda-Ribeiro, 1926:77 [syntypes, MNRJ 154 (2 specimens) from Teresópolis, Rio de Janeiro, Brasil; Alipio de Miranda-Ribeiro collector].

Phrynohyas mesophaea—Bokermann, 1966:55.

Distribution.—Mountains of southeastern Brasil—Serra do Mar, Serra da Bocaina, and Serra da Mantiqueira—in the states of Rio de Janeiro, São Paulo, and Santa Catarina (Fig. 1); the known localities are at elevations between 800 and 1200 m. Eight specimens from three localities.

Phrynohyas mesophaea (Hensel)

Hyla mesophaea Hensel, 1867:154 [holotype, ZMB 6810 from Porto Alegre, Rio Grande do Sul, Brasil; Reinhold Hensel collector].

Phrynohyas mesophaea—Bokerman, 1966:55.

Distribution.—Coastal lowlands of southeastern Brasil from Bahia to Rio Grande do Sul (Fig. 1). 259 specimens from 13 localities.

Phrynohyas venulosa (Laurenti)

Rana venulosa Laurenti, 1768:31 [based on a plate in Seba (1734, vol. 1, pl. 72, fig. 4)].

Hyla venulosa—Daudin, 1803:71.

Hyla zonata Spix, 1824-41 [type formerly in ZSM, now lost, from Lago Tefé, Amazonas, Brasil; collector unknown].

Hyla bufonia Spix, 1824:42 [type formerly in ZSM, now lost, from Eca (= Tefé), Amazonas, Brasil; collector unknown].

Hyla vermiculata Duméril and Bibron, 1841:563 [holotype, MNHN 4797 from "Amerique Sept."; presented by Mr. Harlan].

Phrynohyas zonata—Fitzinger, 1843:30.

Acrodytes venulosa—Fitzinger, 1843:30.

Hyla lichenosa Günther, 1859 [lectotype, BMNH 1936.12.3.119 from Amazonas, Brasil; collector unknown].

Scytopis hebes Cope, 1862:354 [holotype, USNM 5837 from "Paraguay" (restricted to Asunción by Duellman, 1956:16); T. J. Page collector]. New synonymy.

Scytopis venulosus—Cope, 1866:85.

Hyla spilomma Cope, 1877:86 [holotype, unknown, apparently lost, from Cosamaloapam, Veracruz, México; Francis Sumichrast collector].

Hyla paenulata Brocchi, 1879:21 [holotype, formerly in MNHN, now lost, from western (= southern ?) Guatemala; collector unknown].

Hyla nigropunctata Boulenger, 1882:366 [syntypes, BMNH 59.9.20.2 and 81.10.31.20 from Jalapa, Veracruz, México; Alphonse Hoege collector].

Hyla palpebrogranulata Andersson, 1906:14 [holotype, ZIUS A133 from Tatarenda, Santa Cruz, Bolivia; Erland Nordenskiold collector]. New synonymy.

Hyla resinifictrix Goeldi, 1907:135 [holotype, BMNH 1947.2.23.24 from San Antonio do Prata, Pará, Brasil; Emil Goeldi collector].

Hyla zernyi Ahl, 1933:27 [holotype, NHMW 16503 from Taperinha, near Santarém, Pará, Brasil; H. Zerny collector]. New synonymy.

Hyla zeryni Ahl, 1933:27 [holotype, NHMW 16503 from Taperinha, near Santarém, Pará, Brasil; H. Zerny collector]. New Synonymy.

Acrodytes inflata Taylor, 1944:63 [holotype, FMNH 100046 from La Venta, Guerrero, México; Edward H. Taylor collector].

Acrodytes spilomma—Taylor, 1944:64.

Acrodytes modesta Taylor and Smith, 1945:594 [holotype, USNM 115013 from Cruz de Piedra, near Acacoyaqua, Chiapas, México; Hobart M. Smith collector].

Hyla macrotis Andersson, 1945:70 [holotype, NHRM 1958 from the Río Pastaza watershed, Ecuador; William Clarke-MacIntyre collector]. New synonymy.

Phrynohyas hebes—Duellman, 1956:16.

Phrynohyas inflata—Duellman, 1956:19.

Phrynohyas ingens Duellman, 1956:22 [holotype, UMMZ 55570 from La Fría, Pueblo Nuevo, Zulia, Venezuela; H. B. Baker collector]. New synonymy.

Phrynohyas latifasciata Duellman, 1956:24 [holotype, BMNH 83.2.7.1 from Presidio, Sinaloa, México; Alfonso Forrer collector].

Phrynohyas modesta—Duellman, 1956:25.

Phrynohyas spilomma—Duellman, 1956:28.

Phrynohyas corasterias Shannon and Humphrey, 1957:15 [holotype, UIMNH 67060 from 4.8 miles east of San Blas, Nayarit, México; Francis L. Humphrey and Frederick A. Shannon collectors].

Phrynohyas venulosa—Hemming, 1958:172.

Hyla tibiatrix tibiatrix—Rivero, 1961:127.

Hyla tibiatrix ingens—Rivero, 1961:131.

Hyla venulosa venulosa—Rivero, 1964:493.

Hyla adenoderma Lutz, 1968:3 [holotype, MNRJ 4054 from Rio Branco, a tributary of the Rio Madeira, Rondonia, Brasil; F. Casper collector]. New synonymy.

Distribution.—In South America—the Caribbean lowlands, including Trinidad and Tobago, the Amazon Basin, the Chaco, and northeastern Brasil (Fig. 1). Only one specimen is known from the Pacific lowlands; Duellman (1956:42) reported that specimen as being from Hacienda San Miguel, Milagro, Guayas Province, Ecuador, but James A. Peters, the collector, informed me that it actually came from 7 kilometers southeast of Buenavista, El Oro Province, Ecuador. All specimens are from elevations of less than 800 m. 475 specimens from 107 localities.

Remarks.—This widespread, variable species has received 19 names in 200 years. The earliest name, *Rana venulosa* Laurenti, 1768, was based on a plate in Seba's "Thesaurus" (1734). Type specimens of *Hyla zonata* Spix, *H. bufonia* Spix, *H. spilomma* Cope, and *H. paenulata* Brocchi are no longer extant. I have examined the types of the other 14 nominal species. Duellman (1961) provided evidence that *P. corasterias* Shannon and Humphrey, 1957, was not specifically distinct from *P. inflata* (Taylor, 1944). Duellman (1966) showed that *P. modesta* (Taylor and Smith, 1945) was a color morph of *P. spilomma* (Cope, 1877). McDiarmid (1968) analyzed variation in Middle American *Phrynohyas* and concluded that *P. spilomma* (Cope, 1877), *P. inflata* (Taylor, 1944), and *P. latifasciata* Duellman, 1956, were synonymous with *P. venulosa* (Laurenti, 1768). My recent studies (Duellman, 1970) support McDiarmid's conclusions; all Middle American populations seem to be correctly allocated to *Phrynohyas venulosa.*

Of the names in the foregoing synonymy, Duellman (1956) listed *Hyla vermiculata* Duméril and Bibron, *H. lichenosa* Günther, and *H. resinifictrix* Goeldi in the synonymy of *Phrynohyas zonata* (Spix) [= *P. venulosa* (Laurenti)]. Duellman (1956) included *Hyla nigropunctata* Boulenger in the synonymy of *Phrynohyas spilomma* (Cope), now considered to be a synonym of *P. venulosa* (Laurenti).

Duellman (1956) distinguished *Phrynohyas hebes* from *venulosa* by the wider dark limb bands in the former. Examination of additional material from throughout the range of *venulosa* and especially from Argentina, Bolivia, Paraguay, and southern Brasil reveals that the supposed differences between *venulosa* and *hebes* are not constant. Thus, I now consider *Scytopis hebes* Cope, 1862, to be a junior synonym of *Phrynohyas venulosa* (Laurenti, 1768).

Duellman (1956) distinguished *Phrynohyas ingens* from *venulosa* chiefly on the basis of the larger size of the former and by its dorsal coloration consisting of small brown spots on a tan ground color, as opposed to a large dark blotch on the dorsum in *venulosa.* It is now apparent that the coloration considered to be diagnostic of *ingens* appears in populations throughout most of the range of *venulosa* (Table 2). Furthermore, the size of *ingens* is equaled or exceeded by some individuals from Ecuador and Costa Rica. Consequently, I now consider *Phrynohyas ingens* Duellman, 1956, to be a junior synonym of *Phrynohyas venulosa* (Laurenti, 1768).

The holotype of *Hyla vermiculata* Duméril and Bibron (MNHN 4797) is an adult male having a snout-vent length of 65.2 mm. The specimen is soft and has been abraded. The dorsum is medium brown with distinct reddish brown marks; dark marbling is evident on the flanks and posterior surfaces of the thighs. The remnants of the color pattern are reminiscent of one of the color morphs of *Phrynohyas venulosa* common in northeastern South America.

Hyla lichenosa Günther was based on several juveniles; Smith and Taylor (1948:75) designated BMNH 1936.12.3.119 as the lectotype. This specimen has the usual tuberculate skin of young *Phrynohyas,* and it has a color pattern resembling that of young *P. venulosa* from Belém, Pará, Brasil.

The holotype of *Hyla resinifictrix* Goeldi (BMNH 1947.2.23.24) is a male having a snout-vent length of 75.3 mm. The color pattern is well preserved. The ground color is golden tan; anteriorly, on the dorsum, there is a reddish brown blotch, which is narrowly separated from a large, posterior blotch. The limbs bear distinct cross bars; the skin on the dorsum is distinctly pustulate. In features of structure and coloration the holotype is like most individuals of *P. venulosa* from the lower Amazon Basin.

The holotype of *Hyla palpebrogranulata* Andersson (ZIUS A133) is a juvenile having a snout-vent length of 32.3 mm. The skin on the dorsum is tubercular. The dorsum is yellowish tan with a large brown blotch beginning on the head and extending nearly to the vent. Broad brown cross bars are present on the limbs. A pair of pigment clusters above the anal opening suggest that the specimen is a recently metamorphosed young. The iris has the markings characteristic of *P. venulosa;* broad black streaks radiate from the pupil. This juvenile specimen certainly is a *Phrynohyas venulosa.* Cochran and Goin (1970) recognized a monotypic *"Hyla palpebrogranulata* group." I have examined all of the Colombian specimens that they referred to *H. palpebrogranulata* and find that all are young *Osteocephalus taurinus.*

The holotype of *Hyla wettsteini* Ahl (NHMW 19013) is a female having a snout-vent length of 61.3 mm and a moderately tuberculate dorsum. The dorsal surfaces of the head, body, and limbs are pale brown with scattered small brown spots (Fig. 2c). The pattern is identical to that of many individuals of *P. venulosa* from the middle and upper Amazon Basin and from Venezuela and Guyana.

The holotype of *Hyla zernyi* Ahl (NHMW 16503) is a juvenile having a snout-vent length of 20.4 mm and only slightly tubercular skin on the dorsum. The dorsum is pale tan with a narrow, elongate brown blotch beginning on the eyelids and extending to the sacrum. The flanks are brown, and the limbs are marked with irregular dark brown cross bars. The upper lips are boldly marked by three vertical bars, the first two of which fuse with a broad, diffuse canthal stripe, whereas the third enters the orbit. A broad, postorbital brown stripe encompasses the tympanum and is confluent with the dark flanks. The edge of the lower jaw is dark brown interrupted by creamy white spots. In structure, this specimen is like juvenile *P. venulosa;* the color pattern is bold but falls within the range of variation of *P. venulosa*

The holotype of *Hyla macrotis* Andersson (NHRM 1958) is an adult female having a snout-vent length of 110.2 mm. The skin on the dorsum is thick and glandular; the parotoid glands are extensive, diffuse, and form a moderately heavy supratympanic fold. The dorsum is uniform reddish brown; the loreal region is slightly paler brown, and the tympanum and groin are pale cream. The dentigerous processes of the prevomers are nearly transverse elevations between the choanae and bear 10-10 teeth. Specimens resembling the type have been examined from several localities in Amazonian Ecuador; some of these have small dark spots on the dorsum and thus resemble the smaller spotted color morph known from Amazonian Brasil, Perú, and Bolivia. One of the large *macrotis*-like frogs was prepared as a skeleton; no osteological differences between that specimen and several of *P. venulosa* were apparent. Consequently, *Hyla macrotis* Andersson, 1945, is considered to be a junior synonym of *Phrynohyas venulosa* (Laurenti, 1768).

The holotype of *Hyla adenoderma* Lutz, 1968 (MNRJ 4054) is a female having a snout-vent length of 66.0 mm. The skin on the dorsal surfaces of the head and body is greatly thickened and glandular, more so than in any other specimen of *Phrynohyas* that I have seen. The dorsal color pattern consists of a network of bold dark brown reticulations on a tan ground color (Lutz, 1968, fig. 1); dark brown cross bars are evident on the limbs. The following data supplement Lutz's description: The discs on the hands are large and equal in diameter to the tympanum, the upper edge of which is covered by a heavy supratympanic fold. There are 7-9 prevomerine teeth on narrowly separated transverse elevations between the choanae. Although the iris is faded, there is a faint indication of radiating black streaks. This specimen seems to represent an extreme in glandular development of the skin and of a bold reticulated pattern. Otherwise, it is unquestionably a *P. venulosa*. Individuals having a fainter reticulated pattern are known from various localities in the Amazon Basin and Guianas. One specimen from Leticia, Colombia (KU 126067), has dorsal skin nearly as thick and glandular as that of the type of *Hyla adenoderma*, but the Colombian specimen has a large divided blotch on the dorsum. I consider *Hyla adenoderma* Lutz, 1968, to be a junior synonym of *Phrynohyas venulosa* (Laurenti, 1768).

SUMMARY

Phrynohyas is one of four genera in the Hylidae having paired lateral vocal sacs behind the angles of the jaws; the other genera are *Argenteohyla*, *Osteocephalus*, and *Trachycephalus*. The four species of *Phrynohyas* exhibit differences in size, external structural

features, coloration, and cranial osteology. *Phrynohyas venulosa* is widespread in the tropical lowlands from northern México to northern Argentina; the other three species have much more restricted distributions—*P. coriacea* in Surinam and the upper Amazon Basin, *P. mesophaea* on the coastal lowlands of southeastern Brasil, and *P. imitatrix* in the uplands of the coastal ranges of southeastern Brasil. Only *P. coriacea* and *venulosa* are known to occur sympatrically.

The variability in size, coloration, and texture of the skin on the dorsum in *P. venulosa* has resulted in 19 specific names being proposed for this species. Seven nominal species are herein relegated to the synonymy of *Phrynohyas venulosa* (Laurenti, 1768); these are: *Scytopis hebes* Cope, 1862; *Hyla palpebrogranulata* Andersson, 1906; *Hyla wettsteini* Ahl, 1933; *Hyla zernyi* Ahl, 1933; *Hyla macrotis* Andersson, 1945; *Phrynohyas ingens* Duellman, 1956; and *Hyla adenoderma* Lutz, 1968. *Hyla quadrangulum* Boulenger, 1882, is placed in the synonymy of *Phrynohyas coriacea* (Peters, 1867).

RESUMEN

Phrynohyas es uno de cuatro géneros en la familia Hylidae que poseén sacos vocales laterales apareados, localizados detrás de los ángulos de las articulaciones mandibulares; los otros géneros son: *Argenteohyla, Osteocephalus,* y *Trachycephalus.* Las cuatro especies de *Phrynohyas* exiben diferencias en tamaño, rasgos estructurales externos, coloración, y osteología cranial. *Phrynohyas venulosa* está ampliamente distribuida en las tierras bajas tropicales, desde el norte de México al norte de Argentina; las otras tres especies tienen distribuciones más restringidas—*P. coriacea* en Surinam y la parte alta de la cuenca amazónica, *P. mesophaea* en las tierras bajas de la costa del sureste del Brasil, y *P. imitatrix* en las tierras altas que costean el sureste brasileño. Se sabe, que sólo *P. coriacea* y *venulosa* ocurren simpatricamente.

Diez y nueve nombres específicados han sido propuestos para *P. venulosa,* debido a la variabilidad del tamaño, coloración, y textura de la piel dorsal de esta especie. Siete especies nominales son relegadas aquí a la sinonimia de *Phrynohyas venulosa* (Laurenti, 1768); estas son: *Scytopis hebes* Cope, 1862; *Hyla palpebrogranulata* Andersson, 1906; *Hyla wettsteini* Ahl, 1933; *Hyla zernyi* Ahl, 1933; *Hyla macrotis* Andersson, 1945; *Phrynohyas ingens* Duellman, 1956; y *Hyla adenoderma* Lutz, 1968. *Hyla quadrangulum* Boulenger, 1882, es puesta en la sinonimia de *Phrynohyas coriacea* (Peters, 1867).

SPECIMENS EXAMINED

The localities for each of the specimens examined are given below. The arrangement of the data is as follows: alphabetically by country, state (department or province), and locality; alphabetically by the first letter in the abbreviations for the museum, and numerically after each museum abbreviation. Specimens lacking precise locality data are listed first in the most restricted political unit possible; localities which have not been found on maps or which are too vague to be located precisely are given in quotation marks. Where more than one specimen is included under one museum number, the number of specimens is given in parentheses after the museum number. Unless noted otherwise, all specimens are preserved in alcohol.

Phrynohyas coriacea

ECUADOR: "western Ecuador," BMNH 1947.2.13.75. *El Oro:* Machala, WCAB 40100. *Napo:* Lago Agrio, KU 126656; Limón Cocha, KU 107025, UIMNH 87799, 90315-6; Santa Cecilia, KU 105249, UMMZ 129323. *Pastaza:* "Río Pastaza watershed," NHRM 1950 (7).

PERÚ: *Loreto:* Pebas, CAS-SU 12622; Puerto Oriente, 5 km. above Contamana, Río Ucayali, UMMZ 123915.

SURINAM: No specific locality, BMNH 70.3.10.69, ZMB 5807 (3); "Spoorban," RMNH 9606. *Marowijne:* Albino, Río Maroni, ZMB 7606 (3); Maroni, ZMB 7605 (2); Nassaugebergte, RMNH 7296.

Phrynohyas imitatrix

BRASIL: *Rio de Janeiro:* Teresópolis, MNHN 31/45-46, NHMW 18433.5, SMF 58269. *Santa Catarina:* Rio Vermelho, KU 92249 (skeleton), 92250-1. *São Paulo:* São José do Barreiro, Serra da Bocaina, SMF 62562.

Phrynohyas mesophaea

BRASIL: No specific locality, UZM 14223, ZMB 3122. *Bahia:* Santa Cruz, ZMB 30444. *Guanabara:* Rio de Janeiro, KU 92252-6, 92257 (skeleton), SMF 30024-9. *Rio de Janeiro:* Angra dos Reis, ZSM 60/1947; "Guapy," SMF 39251-3; 36 km from Rio Petrópolis road, BMNH 1940.4.14.13; Teresópolis, SMF 2515, ZMB 26322. *Rio Grande do Sul:* Porto Alegre, ZMB 6256, 6810. *Santa Catarina:* No specific locality, UZM 14224; Blumenau, NHMW 6279-80; Hansa (= Corupá), BMNH 1928.11.5.89-106, SMF 2500-14, 30998, 31001-27; Jaraguá, NHMW 6293 (4); Joinville, MNHN 6310 (5), NHMW 6282-3, 6287 (4), 6288 (21), 6289 (2), 6290 (6), 6291 (5), 6294 (5), 6295 (7), 6296 (6), 6297 (5), 6298 (6), 6299 (9), 6300 (6), 6301 (6), 6302 (7), 6303 (4), 6304 (3), 6305 (3), 6306 (7), 6307 (9), 6309 (3), SMF 2516-34, 5120, 5131; "Rio Humboldt," BMNH 1910.7.26.3-6, 1923.6.1.84-91; "Rio Novo," NHMW 6286 (5), 6295 (5).

Phrynohyas venulosa

AMERICA: No specific locality, MNHN 4797.

ARGENTINA: No specific locality, USNM 73523. *Chaco:* Ciervo Petizo, KU 128948-50; Colonia Eliza, NHRM 1503. *Entre Ríos:* Puerto Marquez, 2 km N La Paz, SMF 43634. *Salta:* Río Pescado, KU 128946-7.

BOLIVIA: No specific locality, NHMW 6177 (3). *Cochabamba:* Río Chaparé, ZSM 9/1948. *El Beni:* Esperanza, BMNH 1920.11.29.15-16; Rerrenabaque, UMMZ 57528, 57531 (2). *La Paz:* Ixiamas, MCZ 10087, UMMZ 57529 (4), 57530 (3); Santa Ana de Movimas, BMNH 98.6.9.38. *Santa Cruz:* Buenavista, BMNH 1927.8.185-6, CM 2582, 3828, 3892-3, 3971, 3974, 3986, 4467-8, UMMZ 60526, 63960 (2), 66559-60; Río de la Cal, ZMB 32107; Santa Cruz, BMNH 1904.10.29.177, 1907.10.31.72, 1927.8.1.87, CM 2514; Tatarenda, ZIUS A133.

BRASIL: "lower Amazonia," USNM 28926-7. *Amazonas:* No specific locality, BMNH 1936.12.3.119; Aiapuá, ZMB 30303; Fonte Boa, NHMW 6104; Manacapurú, Rio Solimões, ZMB 37080, ZSM 23/1924; Manáus, AMNH 51755, IRSNB 2681 (14), KU 92258-61, UMMZ 66647; Rio Caicara, NHMW 6111 (2), 6119 (2), 13262 (2); Rio Juruá, BMNH 1904.11.4.12; Rio Purús, ZMB 30307; Tefé, NHMW 6100. *Bahia:* No specific locality, BMNH 64.1.19.34, NHMW 6281. São Gonçalo, 30 km SW Feira de Santana, KU 29438, MCZ 1531. *Mato Grosso:* Barro do Tapirapé, CAS-SU 12304-10, 12312, KU 40219; Chapada dos Guimarães, BMNH 1903.3.26.54-6; Posto Jacarú, Rio Xingú, KU 92262-3; Villa Murtinho, UMMZ 56770. *Minas Gerais:* La Filomena, NHMW 6102 (2), 6112 (2), 6114 (3), 6115; Manga, Rio São Francisco, UMMZ 108894; Piraporinha, USNM 98536-7; São Luís dos Caceres, CAS-SU 12298-9. *Pará:* Belém (= Pará), BMNH 45.8.25.143, 96.1.7.2, CAS-SU 12390-3, NHMW 6098, ZMB 33189, ZSM 119/1911 (2); Cachoeira de Arari, Ilha de Marajó, ZMB 29999, ZSM 120/1911; Cametá, Rio Tocantins, NHMW 6099, 6107, 6113; "Ilha de Marajó," BMNH 1923.11.9.26; IPEAN, 3 km E Belém, KU 127963-4, 128557-61, 130121-6; Livramento, CAS-SU 12383-7; "San Antonio do Prata," BMNH 1947.2.23.24; Santarém, BMNH 56.3.25.14 (2); Taperinha, near Santarém, NHMW 16503, 19013. *Pernambuco:* No specific locality, BMNH 58.11.28.48; Bonita, MCZ 4998. *Piaui:* Bosqus, BMNH 1926.5.26.4. *Rondonia:* Rio Branco, MNRJ 4054. *Roraima:* Serra Grande, below Boa Vista, Rio Branco, NHMW 15893.

COLOMBIA: *Amazonas:* Leticia, KU 124897-900, 124955-6 (tadpoles); 2 km E Leticia, KU 126067. *Caquetá:* Morelia, ANSP 25313. *Cundinamarca:* Honda, MLS 1-2. *Magdalena:* Barranquilla, MLS 3; Fundación, UMMZ 48263. *Norte de Santander:* Río Zulia, N of Cucutá, MLS 4.

ECUADOR: No specific locality, USNM 14054. *El Oro:* 7 km SE Buenavista, USNM 192507. *Napo:* Avila, USNM 165979-80; Lago Agrio, KU 126657; Rio Cotapino, KU 138736, USNM 165977-8. *Pastaza:* Montalvo, CAS-SU 10318:9, USNM 165981 (skeleton), 165982-3; Río Bobonaza, USNM 165984; upper Río Oglán, USNM 165986; "Río Pastaza watershed," NHRM 1958; Río Villano, USNM 165988.

FRENCH GUIANA: *Cayenne:* Cayenne, BMNH 53.2.89-90, NHMW 6101, 6103; Mt. Cabasson, LACM 44638.

GUYANA: *East Demerara:* Georgetown, MCZ 2618, UMMZ 80495. *Essequibo:* Better Hope, BMNH 80.11.22.5-6. *Mazaruni-Potaro:* Kaieteur Falls, AMNH 23128. *North West:* Santa Rosa Island, Moruka River, UMMZ 55834. *Rupununi:* north of Acaray Mts., west of New River, KU 69778-82.

PARAGUAY: No specific locality, AMNH 19916-7, 19919, USNM 5837; "Alto Paraguay," ZMB 26181. *Boquerón:* Loma Plata, KU 73432. *Central:* Asunción, BMNH 94.3.14.168; Patiño, FMNH 10799. *Concepción:* Apa-Bergland, ZSM 137/1933. *La Cordillera:* San Berbardino, NHMW 6106 (2), ZMB 26054, 26115. *Olimpo:* Puerto 14 de Mayo, Bahia Negra, BMNH 98.6.3.19.

PERÚ: *Loreto:* "Caseirio Libertad, Río Amazonas," MJP 514; Orellana, USNM 127168-9, 127180; Pebas, CAS-SU 3159, 6376, 12622; Pucallpa, MJP 84, 86 (3), 90, 92, 93 (2), 95, 97 (2), 99; Río Ucayali, FMNH 3562, UMMZ 48210; Roaboya, AMNH 43316, 43534; "Transval, near Pebas," CAS-SU 3162.

SURINAM: No specific locality, BMNH 70.3.10.68-9, NHMW 6097, 6109 (2), USNM 14618. *Brokopondo:* Brokopondo, RMNH 16692 (2). *Coronie:* Coronieweg, RMNH 16693. *Marowijne:* Camp 3, RMNH 16694. *Suriname:*

Berg en Dal, ZMB 7267; Coropina Creek, RMNH 16695; Kwattaweg, RMNH 16696; "Lelydorp," RMNH 16697 (2); Paramaraibo, AMNH 4009, ANSP 2169-70, BMNH 1946.4.2.24-25, MCZ 7662, RMNH 16698 (9), USNM 13820-1, ZMB 25966 (2), 26076.

TRINIDAD AND TOBAGO: *Tobago:* Milford Bay, MCZ 4087; "Whim," BMNH 1926.1.19.1. *Trinidad:* No specific locality, FMNH 41683, MCZ 3517, 5971; "Churchill-Roosevelt Hwy," AMNH 55712-15 (16), 55717-19; "Cumpia," SMF 2646-47; Fyzabad, BMNH 1929.11.25.6; "Imperial College of Agriculture," BMNH 1932.9.16.41; "Mt. Harris," FMNH 49701; "Mt. Thabor," CM 5257; "Oarino River," BMNH 1929.11.25.4; "Piarco," KU 84714; "St. Augustine," AMNH 55716.

VENEZUELA: "Los Canales," USNM 128792. Anzoátequi: Carapa, USNM 80612. *Aragua:* Maracay, ZSM 304/1929 (20), 305/1929 (46), 61/1930 (22), 120/1930 (4), 292/1933 (6), 43/1934 (10), 105/1935 (11), 196/1965 (5). *Distrito Federal:* Caracas, SMF 2645; La Guaira, USNM 22545, 27797. *Monagas:* Caicara, AMNH 16904-6, 16911-2, USNM 36377; Caripito, USNM 117098-9. *Trujillo:* Savana de Mendoza, UMMZ 57397. *Zulia:* La Fría, Pueblo Nuevo, UMMZ 55567-70; Oropé, FMNH 2604.

LITERATURE CITED

AHL, E.
1933. Über einige neue Frósche aus Brasilien. Zool. Anz., 104:25-32.

ANDERSSON, L. G.
1906. On batrachians from Bolivia, Argentina, and Peru collected by Erland Nordenskiold and Nils Holmgren 1901-1902 and 1904-1905. Arkiv Zool., 3 (12):1-19.
1945. Batrachians from east Ecuador collected 1937, 1938 by Wm. Clarke-MacIntyre and Rolf Blomberg. *Ibid,* 37A (2):1-88.

BOKERMANN, W. C. A.
1966. Lista anotada das localidades tipo de anfíbios Brasileiros. São Paulo, 183 pp.

BOULENGER, G. A.
1882. Catalogue of the Batrachia Salientia s. Ecaudata in the collection of the British Museum, ed. 2, London, xvi+503 pp.

BROCCHI, P.
1879. Sur divers batrachiens anoures de l''Amerique Centrale. Bull. Soc. Philom. Paris, ser. 7, 3:19-24.

COCHRAN, D. M., and C. J. GOIN
1970. Frogs of Colombia. Bull. U. S. Natl. Mus., 288:xii+655 pp.

COPE, E. D.
1862. Catalogue of the reptiles obtained during the explorations of the Parana, Paraguay, Vermejo, and Uruguay rivers, by Capt. Thos. J. Page, U.S.N., and of those procured by Lieut. N. Michler, U.S. Top. Eng., Commander of the expedition conducting the survey of the Atrato River. Proc. Acad. Nat. Sci. Philadelphia, 14:346-359.
1866. On the structures and distribution of the genera of arciferous Anura. Journ. Acad. Nat. Sci. Philadelphia, ser. 2, 6:67-112.
1877. Tenth contribution to the herpetology of tropical America. Proc. Amer. Philos. Soc., 17:85-98.

DAUDIN, F. M.
1803. Histoire naturelle et particuliere des reptiles. Paris, 8: 439 pp.

DUELLMAN, W. E.
1956. The frogs of the hylid genus *Phrynohyas* Fitzinger, 1843. Misc. Publ. Mus. Zool. Univ. Michigan, 96:1-47.

DUELLMAN, W. E.
1961. The amphibians and reptiles of Michoacán, México. Univ. Kansas Publ. Mus. Nat. Hist., 15:1-148.
1966. Taxonomic notes on some Mexican and Central American hylid frogs. *Ibid,* 17:263-379.
1968. The taxonomic status of some American hylid frogs. Herpetologica, 24:194-207.
1970. The hylid frogs of Middle America. Monog. Mus. Nat. Hist., Univ. Kansas, 1: xi+753 pp.

DUMÉRIL, A. M. C., and G. BIBRON
1841. Erpétologie générale ou histoire naturelle compléte des reptiles. Paris, 8:792 pp.

FITZINGER, L.
1843. Systema reptilium. Vienna, ix+106 pp.

GOELDI, E.
1907. Description of *Hyla resinifictrix* Goeldi, a new Amazonian tree frog peculiar for its breeding habits. Proc. Zool. Soc. London (1907):135-140.

GÜNTHER, A. L. C.
1859. Catalogue of the Batrachia Salientia in the collection of the British Museum. London, xvi+160 pp.

HEMMING, F. (editor)
1958. Opinion 520. Suppression under the plenary powers of the specific name *tibiatrix* Laurenti, 1768, as published in the combination *Hyla tibiatrix,* and of the generic name *Acrodytes* Fitzinger, 1843, and interpretation of *Rana venulosa* Laurenti, 1768 (Class Amphibia). Opin. Declar. Intl. Comm. Zool. Nomencl., 19:169-200.

HENSEL, R. F.
1867. Beitrage zur Kenntniss der Wirbelthiere Südbrasiliens. Wiegmann's Arch. Naturg., 33:120-162.

LAURENTI, J. N.
1768. Specimen medicum, exhibens synopsin Reptilium emendatum cum experimentis circa venena et antidota reptilium Austriacorum. Vienna, 214 pp.

LUTZ, B.
1968. New Brazilian forms of *Hyla.* Pearce-Sellards Ser., 10:1-18.

McDIARMID, R. W.
1968. Populational variation in the frog genus *Phrynohyas* in Middle America. Contr. Sci. Los Angeles Co. Mus., 134:1-25.

MIRANDA-RIBEIRO, A. DE
1926. Notas para servirem ao estudio dos Gymnobatrachios (Anura) brasileiros. Arch. Mus. Nac. Rio de Janeiro, 27: 227 pp.

PETERS, W.
1867. Über Flederthiere und Amphibien. Monats. Akad. Wissen. Berlin (1867):703-712.

RIVERO, J. A.
1961. Salientia of Venezuela. Bull. Mus. Comp. Zool., 126:1-207.
1964. The distribution of Venezuelan frogs VI. The llanos and the delta region. Caribbean Jour. Sci., 4:491-495.

SEBA, A.
1734. Locupletissimi rerum naturalium thesauri accurata descriptio, et inconibus artificissimis expressio, per universam physices historiam. Amsterdam, 1: xxxiv+178 pp, 111 pls.

SHANNON, F. A., and F. L. HUMPHREY
1957. A new species of *Phrynohyas* from Nayarit. Herpetologica, 13:15-18.

SMITH, H. M., and E. H. TAYLOR
1948. An annotated checklist and key to the Amphibia of Mexico. Bull. U. S. Natl. Mus., 194:iv+118 pp.

SPIX, J. B. VON
1824. Animalia nova, sive species novae testudinum et ranarum, quas in itinere per Brasiliam, annis 1817-1820. Monaco, 53 pp.

TAYLOR, E. H.
1944. The hylid genus *Acrodytes* with comments on the Mexican forms. Univ. Kansas Sci. Bull., 30:63-68.

TAYLOR, E. H., and H. M. SMITH
1945. Summary of the collection of amphibians made in México under the Walter Rathbone Bacon Traveling Scholarship. Proc. U. S. Natl. Mus., 95:521-613.

TRUEB, L., and W. E. DUELLMAN
1971. A synopsis of Neotropical hylid frogs, genus *Osteocephalus*. Occas. Papers Mus. Nat. Hist. Univ. Kansas, 1:1-47.

TYLER, M. J.
1971. The phylogenetic significance of vocal sac structure in hylid frogs. Univ. Kansas Publ. Mus. Nat. Hist., 19:319-360.

DUELLMAN, W. E.
1961. The amphibians and reptiles of Michoacán, México. Univ. Kansas Publ. Mus. Nat. Hist., 15:1-148.
1966. Taxonomic notes on some Mexican and Central American hylid frogs. *Ibid,* 17:263-379.
1968. The taxonomic status of some American hylid frogs. Herpetologica, 24:194-207.
1970. The hylid frogs of Middle America. Monog. Mus. Nat. Hist., Univ. Kansas, 1: xi+753 pp.
DUMÉRIL, A. M. C., and G. BIBRON
1841. Erpétologie générale ou histoire naturelle compléte des reptiles. Paris, 8:792 pp.
FITZINGER, L.
1843. Systema reptilium. Vienna, ix+106 pp.
GOELDI, E.
1907. Description of *Hyla resinifictrix* Goeldi, a new Amazonian tree frog peculiar for its breeding habits. Proc. Zool. Soc. London (1907):135-140.
GÜNTHER, A. L. C.
1859. Catalogue of the Batrachia Salientia in the collection of the British Museum. London, xvi+160 pp.
HEMMING, F. (editor)
1958. Opinion 520. Suppression under the plenary powers of the specific name *tibiatrix* Laurenti, 1768, as published in the combination *Hyla tibiatrix,* and of the generic name *Acrodytes* Fitzinger, 1843, and interpretation of *Rana venulosa* Laurenti, 1768 (Class Amphibia). Opin. Declar. Intl. Comm. Zool. Nomencl., 19:169-200.
HENSEL, R. F.
1867. Beitrage zur Kenntniss der Wirbelthiere Südbrasiliens. Wiegmann's Arch. Naturg., 33:120-162.
LAURENTI, J. N.
1768. Specimen medicum, exhibens synopsin Reptilium emendatum cum experimentis circa venena et antidota reptilium Austriacorum. Vienna, 214 pp.
LUTZ, B.
1968. New Brazilian forms of *Hyla.* Pearce-Sellards Ser., 10:1-18.
McDIARMID, R. W.
1968. Populational variation in the frog genus *Phrynohyas* in Middle America. Contr. Sci. Los Angeles Co. Mus., 134:1-25.
MIRANDA-RIBEIRO, A. DE
1926. Notas para servirem ao estudio dos Gymnobatrachios (Anura) brasileiros. Arch. Mus. Nac. Rio de Janeiro, 27: 227 pp.
PETERS, W.
1867. Über Flederthiere und Amphibien. Monats. Akad. Wissen. Berlin (1867):703-712.
RIVERO, J. A.
1961. Salientia of Venezuela. Bull. Mus. Comp. Zool., 126:1-207.
1964. The distribution of Venezuelan frogs VI. The llanos and the delta region. Caribbean Jour. Sci., 4:491-495.
SEBA, A.
1734. Locupletissimi rerum naturalium thesauri accurata descriptio, et inconibus artificissimis expressio, per universam physices historiam. Amsterdam, 1: xxxiv+178 pp, 111 pls.
SHANNON, F. A., and F. L. HUMPHREY
1957. A new species of *Phrynohyas* from Nayarit. Herpetologica, 13:15-18.

SMITH, H. M., and E. H. TAYLOR
1948. An annotated checklist and key to the Amphibia of Mexico. Bull. U. S. Natl. Mus., 194:iv+118 pp.
SPIX, J. B. VON
1824. Animalia nova, sive species novae testudinum et ranarum, quas in itinere per Brasiliam, annis 1817-1820. Monaco, 53 pp.
TAYLOR, E. H.
1944. The hylid genus *Acrodytes* with comments on the Mexican forms. Univ. Kansas Sci. Bull., 30:63-68.
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1945. Summary of the collection of amphibians made in México under the Walter Rathbone Bacon Traveling Scholarship. Proc. U. S. Natl. Mus., 95:521-613.
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A NEW SPECIES OF SPINY POCKET MOUSE (GENUS *LIOMYS*) FROM JALISCO, MEXICO

By

HUGH H. GENOWAYS[1]

In the course of a systematic revision of the spiny pocket mice of the genus *Liomys*, a series of large, brightly colored mice from several localities in southeastern Jalisco was studied. Individuals in this series appeared to be morphologically distinct from mice typical of *Liomys pictus plantinarensis* Merriam, 1902, taken in the same traplines at several localities, and from specimens of *Liomys irroratus jaliscensis* (J. A. Allen, 1906), a taxon that also occurs in southeastern Jalisco. My studies now have progressed to the point where the large and distinctively colored mice from Jalisco can be defined as a new species which is distinct from, but closely related to, *Liomys pictus*. The new species is named and described below.

Liomys spectabilis new species

Holotype.—Adult male, skin and skull, no. 96051 Museum of Natural History, The University of Kansas (KU); from 2.2 mi NE Contla, 3850 ft, Jalisco; obtained on 20 September 1963 by Percy L. Clifton; original no. 5244.

Geographic distribution.—Known only from southeastern Jalisco (presently known limits from a point 8.5 mi S Mazamitla, 5300 ft in the north to a place 8 mi SW Tecalitlán in the south—see Fig. 1).

Description.—Size large, both externally and cranially (see measurements and Table 1); skull proportionally similar to that of *L. pictus*, but much larger (Fig. 2); six plantar tubercles; dorsal coloration reddish brown, lateral stripe bright ochraceous; under-

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[1] Research Assistant, Division of Mammals, Museum of Natural History, University of Kansas.

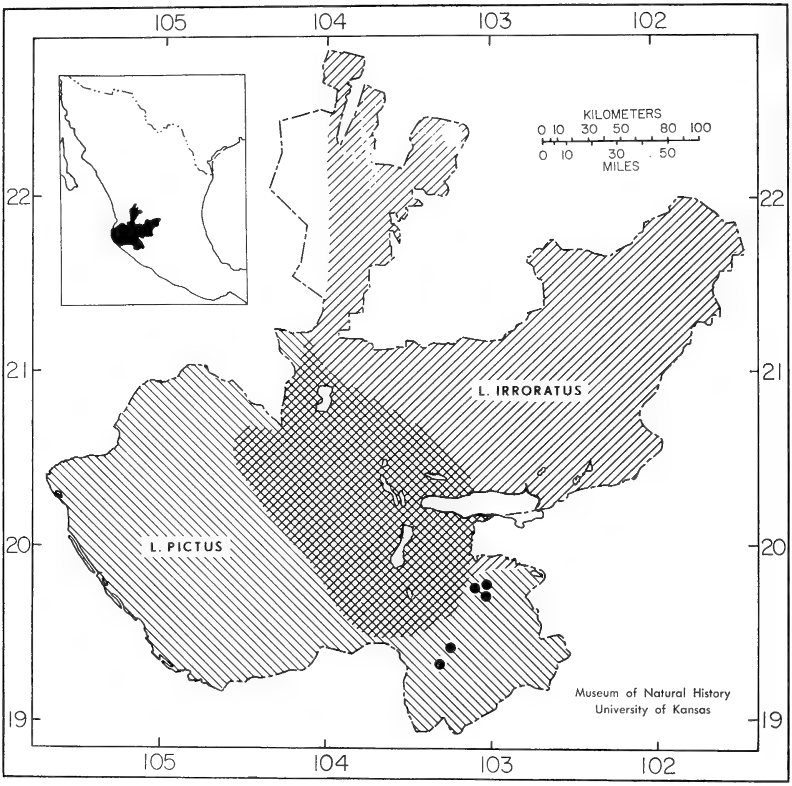

FIG. 1.—Geographic distribution of three species of *Liomys* in Jalisco, México. Closed circles indicate localities from which *Liomys spectabilis* has been taken. The inset map in the upper, left-hand corner indicates the position of the state of Jalisco in western México.

parts white; bacular morphology similar to that described for *L. pictus* (Burt, 1960:44 and pl. 11).

Measurements.—External measurements (in millimeters) of the male holotype, followed by the mean (and extremes) of four adult females for the first two measurements and eight for the second two measurements are: total length, 280, 249.5 (242-261); length of tail, 142, 129.0 (122-134); length of hind foot, 31, 30.4 (29.5-32); length of ear, 17, 16.9 (16.5-17.5). Weights of the holotype and another adult male were respectively, 69.3 and 67.1 grams; seven nonpregnant adult females averaged 51.2 (48.6-56.1) grams in weight. Cranial measurements of the specimens of *Liomys spectabilis* are given in Table 1 along with comparative measurements of *Liomys pictus plantinarensis* and *Liomys pictus pictus.*

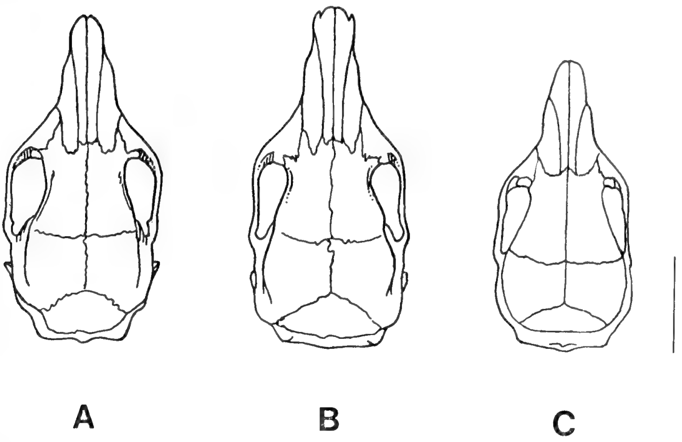

FIG. 2.—Dorsal view of the crania of three taxa of *Liomys:* A. *Liomys pictus pictus* (KU 112276, ♂, San Sebastián, Jalisco); B. *Liomys spectabilis* (KU 96051, ♂, 2.2 mi NE Contla, Jalisco); C. *Liomys pictus plantinarensis* (KU 96048, ♂, 2.2 mi NE Contla, Jalisco). Scale at right is 10 mm.

Comparisons.—From *Liomys pictus plantinarensis* with which it occurs sympatrically, *Liomys spectabilis* can be distinguished easily by its much larger size (Table 1). There is no overlap in measurements of adults of the two taxa for total length, length of hind foot, greatest length of skull, interorbital constriction, mastoid breadth, length of nasals, and length of rostrum, and *spectabilis* averages significantly larger in all other measurements analyzed (Fig. 2). Middorsal coloration of *L. spectabilis* is significantly darker than that of *L. p. plantinarensis* as revealed by use of a Photovolt Photoelectric Reflection Meter, Model 610. Mean reflectance values for *L. spectabilis,* followed in parentheses by those for typical *L. p. plantinarensis,* were: red, 11.0 (14.6); green, 6.3 (7.9); blue, 5.8 (7.1).

From *Liomys pictus pictus* of the coastal and montane areas of western Jalisco, *L. spectabilis* is again distinguished by its larger size, although the difference is not as striking as in the case of *plantinarensis* (Table 1, Fig. 2). Only in greatest length of skull and length of rostrum is there no overlap in the measurements of the two taxa, although *spectabilis* averages larger in all measurements except for interparietal length of females. A useful character in separating these two taxa externally is length of the hind foot, which is rarely less than 30 in *spectabilis* and rarely more than 30 in *pictus.* The only subspecies of *L. pictus* that approaches *L. spectabilis* in size is *annectens* from the mountains of Guerrero and Oaxaca. From this race, *spectabilis* can be distinguished by its slightly larger over-

TABLE 1.—Cranial measurements of three taxa of *Liomys* from Jalisco. The specimens of *L. spectabilis* and *L. p. plantinarensis* are from southeastern Jalisco and those of *L. p. pictus* are from northwestern Jalisco.

	Greatest length of skull	Zygomatic breadth	Interorbital constriction	Mastoid breadth	Length of nasals	Length of rostrum	Length of maxillary toothrow	Depth of cranium	Inter-parietal width	Inter-parietal length
					Liomys spectabilis					
Males										
N	3	2	3	3	3	2	2	2	3	3
Mean	35.0	--------	8.2	14.6	14.5	--------	--------	--------	9.0	4.8
Minimum	34.7	15.2	8.1	13.9	14.0	15.8	5.0	8.5	8.7	4.6
Maximum	35.2	16.3	8.2	15.1	15.5	16.0	5.4	8.6	9.2	4.9
2 SE	±0.30	--------	±0.07	±0.72	±0.97	--------	--------	--------	±0.29	±0.18
Females										
N	8	6	8	8	8	8	8	7	8	8
Mean	34.1	15.6	8.0	14.5	13.6	15.5	5.2	8.4	8.5	4.4
Minimum	33.0	14.8	7.5	14.0	12.6	14.8	5.0	8.2	7.8	4.0
Maximum	35.3	16.0	8.4	15.4	14.2	16.2	5.6	8.6	9.0	4.8
2 SE	±0.59	±0.37	±0.21	±0.33	±0.40	±0.35	±0.12	±0.12	±0.28	±0.19
					Liomys pictus plantinarensis					
Males										
N	20	19	21	20	22	22	22	19	20	21
Mean	30.4	14.0	7.3	13.5	11.7	13.0	4.8	8.1	8.3	3.8
Minimum	28.9	13.4	6.7	12.8	10.5	12.2	4.6	7.5	7.8	3.4
Maximum	32.0	14.8	7.9	13.8	12.8	13.9	5.3	8.6	8.8	4.5
2 SE	±0.42	±0.16	±0.12	±0.12	±0.25	±0.20	±0.08	±0.11	±0.12	±0.13

Females										
N	26	23	27	27	27	24	27	23	26	27
Mean	29.6	13.9	7.1	13.4	11.2	12.6	4.8	7.9	8.3	3.7
Minimum	28.0	13.3	6.7	13.0	10.4	11.1	4.5	7.3	7.5	3.3
Maximum	31.4	14.9	7.4	13.9	12.2	13.6	5.3	8.4	8.9	4.2
2 SE	±0.27	±0.17	±0.07	±0.09	±0.19	±0.24	±0.07	±0.11	±0.13	±0.09
					Liomys pictus pictus					
Males										
N	20	16	22	20	23	17	22	17	20	20
Mean	32.1	15.0	7.7	13.9	13.1	14.2	5.0	8.2	8.9	4.6
Minimum	30.3	13.9	7.1	12.7	11.7	13.7	4.6	7.8	8.1	4.1
Maximum	33.2	15.9	8.2	14.5	13.7	15.0	5.6	8.5	9.7	5.2
2 SE	±0.33	±0.26	±0.13	±0.19	±0.20	±0.18	±0.10	±0.08	±0.19	±0.12
Females										
N	16	16	19	16	19	13	15	10	15	16
Mean	31.7	14.7	7.7	13.9	12.7	13.9	4.9	8.0	9.0	4.6
Minimum	30.4	13.9	7.2	13.1	11.9	13.2	4.4	7.7	7.8	4.2
Maximum	32.8	15.4	8.5	14.7	13.6	14.8	5.3	8.4	9.9	5.2
2 SE	±0.40	±0.18	±0.14	±0.22	±0.21	±0.28	±0.12	±0.13	±0.30	±0.15

all size, proportionately shallower cranium, and paler dorsal coloration.

Liomys spectabilis can be distinguished from *Liomys irroratus jaliscensis* from southeastern Jalisco by its generally longer but proportionately narrower cranium (greatest length of *irroratus* males, 33.4, females, 31.8; mastoid breadth, 14.9 and 14.4). Other characteristics distinguishing *spectabilis* from *irroratus* are those characters that also serve to distinguish *pictus* from *irroratus*—for example, differences in bacular morphology (Burt, 1960:44), six (*spectabilis* and *pictus*) rather than five plantar tubercles on the hind feet, and reddish brown dorsal coloration and a bright ochraceous lateral stripe (as compared to grayish brown coloration and a pale pinkish lateral stripe in *irroratus*).

Remarks.—*Liomys spectabilis* appears to be a member of the *Liomys pictus*-group as defined by Goldman (1911). *L. spectabilis* occupies a restricted distribution near the eastern limits of the geographic range of *L. pictus* in Jalisco. It seems plausible that the precursor of these two species occurred throughout this area of México, and that the parental stock was split into two parts in response to changing environmental conditions. One segment probably was restricted to coastal regions of western México and gave rise to *L. pictus*, whereas the other was isolated in interior Jalisco and gave rise to *L. spectabilis.* Subsequent to speciation, *L. pictus* has reinvaded inland areas of Jalisco and now occurs sympatrically with *spectabilis* at several localities.

The area northeast of Contla, Jalisco, in the vicinity of the type locality is under heavy agricultural use. All trapping in this area was conducted in the immediate vicinity of a highway which follows a shallow valley northeastward from Contla. The road right-of-way is about 40 to 50 feet wide at most points and has been allowed to grow to weeds, low brush, and trees; cornfields were present beyond the right-of-way in relatively level areas. Around the edges of these cornfields were rock or wire fences that were heavily overgrown with weeds and brush. On adjacent hillsides, where the slope became too steep to plant corn the grass was heavily grazed in most places and was interspersed with clumps of dense, low brush. It was along fencerows and in pastureland of the type described that P. L. Clifton obtained the original series of the new species between 17 and 27 September 1963. During that period Clifton obtained specimens of *Liomys spectabilis* and *Liomys pictus plantinarensis* in the same traplines at three localities as follows: 3.3 mi NE Contla (four *spectabilis* and two *plantinarensis*), 3 mi NE Contla (one *spectabilis* and one *plantinarensis*), 2.2 mi NE Contla (seven *spectabilis* and 11 *plantinarensis*). Along with Larry C. Watkins and Elmer C. Birney, I revisited this same area on 7 August 1969 and obtained a specimen of *L. spectabilis* at a place 6 km NE Contla, at the edge of a dense clump of brush in a pasture. In early March 1964, P. L. Clifton trapped three additional specimens of *spectabilis* 8½ mi S Mazamitla. Traps in which these specimens were taken were set along a brush fence between a cornfield and a grove of oak. Nothing is known of the circumstances under which the specimens from near Tecalitlán and Pihuano were taken.

Only one of the six adult females of *spectabilis* evinced gross reproductive activity; a female taken on 26 September 1963 at a place 2.2 mi NE Contla carried five embryos that measured 4 mm in crown-rump length. Four adult males taken between 17 and 20 September 1963 had testes that averaged 21.5 (21-22) in length.

Specimens examined (21).—All localities are in Jalisco (those in italics are not plotted on Fig. 1 because undue crowding of symbols would have resulted): 8½ mi S Mazamitla, 5300 ft, 3 (KU 97182-84); 8 km N Contla, 4300 ft, 3 (KU 96035-37); *6 km NE Contla, 1310 m,* 1 (KU 120606); *3.3 mi NE Contla, 3900 ft,* 4 (KU 96042-45); *3 mi NE Contla, 3850 ft,* 1 (KU 96039); 2.2 mi NE Contla, 3850 ft, 7 (KU 96049-54, 96064); 12 mi NE Pihuano, 3150 ft, 1 (Michigan State University, 11496); 8 mi SW Tecalitlán, 1 (California Academy of Science, 13961).

LITERATURE CITED

Burt, W. H.
1960. Bacula of North American mammals. Misc. Publ. Mus. Zool., Univ. Michigan, 113:1-76.

Goldman, E. A.
1911. Revision of the spiny pocket mice (genera Heteromys and Liomys). N. Amer. Fauna, 34:1-70.

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MAMMALS FROM THE MEXICAN STATE OF SINALOA. II. CHIROPTERA

By

J. Knox Jones, Jr.,[1] Jerry R. Choate,[2]
and Alberto Cadena[3]

The Mexican state of Sinaloa is strategically located in the transition zone between the temperate and tropical regions of North America. The zoogeographic significance of this part of western México is particularly evidenced by distributional patterns of bats (Koopman, 1961), but no attempt has been made previously to document the occurrence and distribution of Sinaloan Chiroptera on a state-wide basis. In the period 1950 to 1968, field parties and representatives from the Museum of Natural History at The University of Kansas collected mammals in Sinaloa, and this report is based on specimens thus obtained, some material in other museums, and a perusal of the pertinent literature.

To date, 44 species of bats have been taken in Sinaloa. Two additional species, *Eumops underwoodi* and *Tadarida aurispinosa*, are known in western México from both north and south of the state, and likely will be found there. Furthermore, certain other Neotropical species, such as *Myotis nigricans* and *Micronycteris sylvestris*, have been recorded from as far north as central Nayarit, and may occur in suitable habitats in southern Sinaloa.

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[1] Dean, Graduate School, Texas Tech University, Lubbock, and Associate in Mammalogy, Museum of Natural History, University of Kansas.

[2] Assistant Professor, Division of Biological Sciences, Fort Hays Kansas State College, Hays, Kansas.

[3] Curatorial Assistant, Division of Mammals, Museum of Natural History, University of Kansas.

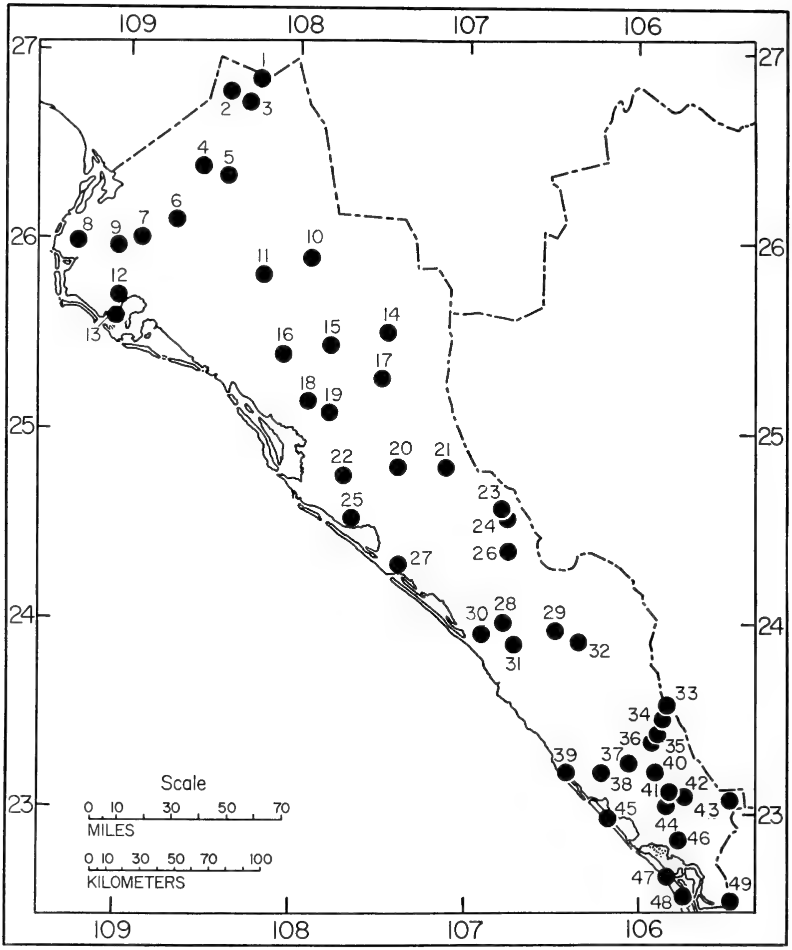

FIG. 1.—Map of Sinaloa showing location of place-names used in this report. From north to south, these are: 1, El Cajón; 2, Vaca; 3, Choix; 4, El Fuerte; 5, Chinobampo; 6, San Blas; 7, El Carrizo; 8, Zaragosa; 9, San Miguel; 10, Bacubirito; 11, Sinaloa; 12, Los Mochis; 13, Topolobampo; 14, Alisos; 15, San Benito; 16, Guamúchil; 17, Badiraguato; 18, Terrero; 19, Pericos; 20, Culiacán; 21, Presa Sanalona; 22, Navolato; 23, Aguacaliente; 24, Casa Blanca; 25, El Molino; 26, Cosalá; 27, El Dorado; 28, Elota; 29, San Ignacio; 30, La Cruz; 31, Camino Real and Piaxtla (one symbol); 32, San Juan; 33, Palmito (Palmarito); 34, Santa Lucía; 35, Pánuco; 36, Copala; 37, Concordia; 38, Villa Unión (including Presidio); 39, Mazatlán; 40, Chele; 41, Cacalotán; 42, Matatán; 43, Plomosas; 44, Rosario; 45, Isla Palmito de la Virgen; 46, Escuinapa; 47, Palmito, Isla Palmito del Verde; 48, Teacapán, Isla Palmito del Verde; 49, Concepción.

This is the second in a series of publications intended eventually to encompass the entire mammalian fauna of Sinaloa. A useful summary of the environment of the state was provided by Hardy and McDiarmid (1969) in their report on the herpetofauna. Additional commentary as relates to mammals has been published by Armstrong and Jones (1971), Birney and Jones (1971), Dunnigan (1967), and Koopman (1961). An analysis of zoogeographic relationships of the mammalian fauna of Sinaloa will appear later.

Measurements and weights, given where appropriate in the following accounts, are in millimeters and grams, respectively. The arrangement of localities in lists of specimens examined and additional records is from north to south. Location of place-names mentioned in text is shown on Fig. 1. Gordon B. Corbet and J. E. Hill of the British Museum (Natural History), A. M. Husson of the Rijksmuseum van Natuurlijke Historie in Leiden, and Robert J. Baker of Texas Tech University allowed us to study Sinaloan bats in their charge. The majority of the specimens examined (those without institutional designation) are in the collection of The University of Kansas Museum of Natural History. We are grateful to the many persons from the Museum who participated in field studies in Sinaloa, particularly J. R. Alcorn, P. L. Clifton, and M. R. Lee, under permits granted by the Dirección General de la Fauna Silvestre de México. Field work was supported principally by the Kansas University Endowment Association and a contract (DA-49-193-MD-2215) with the U.S. Army Medical Research and Development Command. We are indebted also to Hugh H. Genoways and R. Laurie Hendricksen for their considerable aid in readying this report for publication.

ACCOUNTS OF SPECIES

Family EMBALLONURIDAE

Balantiopteryx plicata plicata Peters, 1867

Specimens examined (162).—10 km S, 38 km E Sinaloa, 800 ft, 2; 20 km N, 5 km E Badiraguato, 1800 ft, 14; 1.5 mi N Badiraguato, 750 ft, 3; 17 mi SSE Guamúchil, 1; 4 mi N Terrero, 2; 1 mi S Pericos, 3; 2 mi E Aguacaliente, 800 ft, 10; 32 mi SSE Culiacán, 1; San Ignacio, 700 ft, 7; 0.5 mi E Piaxtla, 1; Santa Lucía, 3600 ft, 8; 2.5 km E Santa Lucía, 3200 ft, 31; Pánuco, 2050 ft, 13; 2.5 mi NE Concordia, 3; 5 mi NW Mazatlán, 29; Mazatlán, 2 (Leiden Mus.); 1 mi SE Mazatlán, 10 ft, 16; Isla Palmito de la Virgen, 15 ft, 2; 0.5 mi W Rosario, 100 ft, 3; 5 mi SSE Rosario, 2; Tatemales, near Rosario, 6 (BM); 10 mi SE Escuinapa, 1; N end Isla Palmito del Verde, 10 ft, 2.

Additional records (Villa-R., 1967:152, unless otherwise noted).—[Cueva de] la Chinacatera, Monte Largo, 23 km W Pericos; Mazatlán (Sanborn, 1937: 352); "cerro El Faro, Mazatlán"; "Cueva de Don Cristino," [*ca.*] 20 km E Mazatlán; "34 mi (54.4 km) [direction not given] Mazatlán"; Rosario (Koopman, 1961:536); Escuinapa (J. A. Allen, 1906:235).

TABLE 1.—Selected measurements of two subspecies of *Balantiopteryx plicata* from Sinaloa.
Superscript numbers indicate fewer specimens averaged than listed in left-hand margin.

Number averaged and sex	Length of forearm	Greatest length of skull	Zygomatic breadth	Postorbital constriction	Breadth of braincase	Mastoid breadth	Length of maxillary toothrow
Balantiopteryx plicata plicata, 5 mi NW Mazatlán							
Average (10♂)	41.0	14.1^{3}	9.1^{9}	3.4	7.2	8.4	5.4
Minimum	40.0	13.8	9.0	3.3	7.0	8.1	5.3
Maximum	42.1	14.4	9.3	3.5	7.3	8.6	5.5
Average (12♀)	42.2	14.5^{4}	9.2	3.3	7.0	8.3	5.4
Minimum	41.0	14.2	8.8	3.1	6.7	8.0	5.3
Maximum	43.5	14.8	9.4	3.5	7.2	8.6	5.6
Balantiopteryx plicata pallida, 10 mi NNW Los Mochis							
Average (7♂)	39.6	13.4	8.5	3.3	6.8	7.8	5.1
Minimum	38.0	13.0	8.3	3.0	6.5	7.5	5.0
Maximum	40.4	13.8	8.7	3.5	7.0	8.0	5.4
Average (10♀)	41.0	13.7	8.6	3.1	6.8	7.8	5.2
Minimum	39.4	13.4	8.5	2.9	6.5	7.6	5.0
Maximum	42.5	13.8	8.9	3.4	7.0	8.0	5.3

Specimens herein assigned to the subspecies *B. p. plicata* average significantly larger (Table 1) and have darker (usually brownish rather than gray) and more luxuriant pelage than do specimens assigned to *B. p. pallida.* Bats labeled with reference to Santa Lucía and Culiacán resemble those from the vicinity of Mazatlán but have paler pelage. Specimens from 4 mi N Terrero, 1 mi S Pericos, and 17 mi SSE Guamúchil are intergrades (slightly nearer *plicata* in size) between the two subspecies. Those listed with reference to Sinaloa and Badiraguato also are intergrades; their pelage is paler than that of most other *plicata,* but they are provisionally referred to that subspecies because they most closely approach typical specimens in cranial features.

The series from 5 mi NW Mazatlán was collected in an old mine in the side of a cliff facing the sea. Some of the specimens from near Santa Lucía also were taken in a mine. Most other specimens in our collection were shot or netted. Ten males and 12 females from the vicinity of Mazatlán had an average weight of 5.2 (5.0-6.0) and 5.6 (4.5-6.5) gms, respectively.

Six females taken in June carried embryos (crown-rump length 12 to 16 mm), as did three obtained in July (crown-rump length 21 to 23 mm).

Balantiopteryx plicata pallida Burt, 1948

Specimens examined (48).—0.5 mi SE Vaca, 650 ft, 2; 2 mi N San Blas, 50 ft, 4; 3 mi NE San Miguel, 300 ft, 5; 10 mi NNW Los Mochis, 32; 1.5 mi NW Topolobampo, 10 ft, 5.

The pelage of the specimens from 1.5 mi NW Topolobampo is as darkly pigmented as that of individuals of the subspecies *plicata* from southern Sinaloa, but cranial dimensions clearly show their affinities to be with the subspecies *pallida.*

Some specimens from 10 mi NNW Los Mochis were collected in shallow caves, whereas those from 1.5 mi NW Topolobampo were removed from cracks in the ceiling of a rocky hollow near the coast. Other bats in our collection were shot as they foraged. Eight females collected in early June were pregnant, containing embryos having crown-rump lengths of 11-15 mm.

Family NOCTILIONIDAE

Noctilio leporinus mexicanus Goldman, 1915

Specimens examined (13).—San Benito, 400 ft, 1; 1.5 mi N Badiraguato, 750 ft, 1; Isla Palmito de la Virgen, 15 ft, 11.

Additional record.—Chele, 400 ft (Koopman, 1961:536).

Specimens of the big fish-eating bat from Isla Palmito de la Virgen were caught in a mist net over a small, freshwater pond where terns had been observed feeding during the day. The one specimen from San Benito, which constitutes the northernmost record of the species, was netted over the middle of a wide (30 feet) but shallow part of the Río Mocorito, and the one from north of Badiraguato also was netted over a stream.

Three of seven females taken in mid-June were lactating, and three males had testes ranging in length from 5 to 10 mm.

Family CHILONYCTERIDAE

Pteronotus parnellii mexicanus (Miller, 1902)

Specimens examined (111).—12 mi NE San Benito, 1000 ft, 1; 20 km N, 5 km E Bardiraguato, 1800 ft, 1; 7 mi ENE Presa Sanalona, 600 ft, 1; 4 mi S Casa Blanca, 1200 ft, 1; 3 mi SE Camino Real, 500 ft, 35; 1 mi E Santa Lucía, 3650 ft, 2; 1.5 km S Santa Lucía, 3200 ft, 14; Pánuco, 2050 ft, 44; 1.5 km W Copala, 1400 ft, 4; 2.5 mi NE Concordia, 1; 12 km N Villa Unión, 400 ft, 3; 5 mi WSW Plomosas, 800 ft, 3; 0.5 mi S Concepción, 250 ft, 1.

Additional records.—Monte Largo, *ca.* 14 mi W Pericos (Constantine, 1959: 442—also reported as Cueva de la Chinacatera, 60 km NW Culiacán by Villa-R., 1967:176); Río Piaxtla (on Mexican Highway 15 at Camino Real) (Baker, 1967:426); Hda. Chele, 300 ft, 15 mi N Rosario (Hooper, 1955:8).

Parnell's mustached bat occurs throughout the length of Sinaloa at low to moderate elevations. Most of our specimens were obtained in or near caves or mines; an estimated 800 were discovered in an old gold mine 3 mi SE Camino Real, where they were associated with *Glossophaga soricina leachii, Macrotus waterhousii bulleri,* and *Desmodus rotundus murinus.*

One female taken in May carried an embryo that was 17 mm in crown-rump length, one captured in June was pregnant (embryo 30 mm), and another obtained at the same time had recently given birth and was lactating. Three females taken in July evidenced lactation.

Pteronotus psilotis (Dobson, 1878)

Specimens examined (19).—0.5 mi SE Vaca, 650 ft, 2; 1 mi S, 6 mi E El Carrizo, 3; La Cruz, 30 ft, 1; 1.5 mi N Badiraguato, 750 ft, 6; 1 mi W Matatán, 2; Isla Palmito de la Virgen, 15 ft, 1; 0.5 mi S Concepción, 250 ft, 4.

Additional record.—Cueva de la Chinacatera, 23 km W Pericos (Baker and Christianson, 1966:311).

Our specimens were netted or shot as they flew over water courses, mostly in otherwise relatively xeric habitats. A female caught in June on Isla Palmito de la Virgen contained an embryo that had a crown-rump length of 17 mm.

Pteronotus davyi fulvus (Thomas, 1892)

Specimens examined (47).—1 mi E Sinaloa, 180 ft, 1; 1 mi S, 6 mi E El Carrizo, 5; San Juan, 8 mi SE San Ignacio, 1; 1 mi E Santa Lucía, 3650 ft, 1; Pánuco, 2050 ft, 36; 3 mi SE Plomosas, 4000 ft, 1; 5 mi WSW Plomosas, 800 ft, 2.

Additional records.—[Cueva de] la Chinacatera, Monte Largo, 23 km W Pericos (Villa-R., 1967:181); Escuinapa (J. A. Allen, 1906:236).

Specimens of Davy's naked-backed bat were collected at Pánuco by natives, who found them in small mines. The remainder of our series was netted or shot near ponds or rivers. One female obtained 1 mi E Santa Lucía on 22 June 1955 carried an embryo 21 mm in crown-rump length.

Mormoops megalophylla megalophylla Peters, 1864

Specimens examined (39).—1 mi E Santa Lucía, 3650 ft, 1; 1.5 km S Santa Lucía, 3200 ft, 6; Pánuco, 29; 3 mi SE Plomosas, 4000 ft, 2; 0.5 mi W Rosario, 100 ft, 1.

Additional record.—Rosario (Davis and Carter, 1962a:66).

Most of our specimens of *Mormoops* were collected in mines where they usually clustered as far as possible from the entrance. At both Pánuco and Santa Lucía, this bat was taken in mines containing standing water. Other specimens listed herein were netted. The species no doubt is widely distributed in suitable habitats in Sinaloa, even though all of our records are from the southern part of the state.

Davis and Carter (1962a:66) assigned Sinaloan representatives of *M. megalophylla* to the subspecies *M. m. rufescens*. However, pending publication of a revision of the genus by J. D. Smith, we follow Villa-R. (1967:187-189) in recognizing only one subspecies in México.

Family PHYLLOSTOMATIDAE

Macrotus waterhousii bulleri H. Allen, 1890

Specimens examined (50).—3 mi SE Camino Real, 500 ft, 1; 6 mi W Santa Lucía, 3650 ft, 1; Santa Lucía, 3600 ft, 4; 1 km NE Pánuco, 2700 ft, 13; Pánuco, 2050 ft, 31.

Additional record.—Copala (Anderson and Nelson, 1965:31).

The subspecies *bulleri* reaches the northern limit of its distribution in Sinaloa. Intergradation between *bulleri* and the more northerly subspecies *californicus* no doubt will be demonstrated in north-central Sinaloa when material is available from that area. Most of our specimens of this species were collected in caves or abandoned mines, but a few were netted over streams, ponds, or roads, or brought in by natives. Lactating females and young of the year were taken in July.

Macrotus waterhousii californicus Baird, 1859

Specimens examined (36).—13 km NNE Vaca, 1300 ft, 1; 1 mi S, 6 mi E El Carrizo, 1; 12 mi N, 3 mi W Los Mochis, 34.

This subspecies is known in Sinaloa only from the northern part of the state, south to the drainage basin of the Río del Fuerte. *Macrotus w. californicus* differs from *M. w. bulleri* of the southern part of Sinaloa principally in having larger ears and bullae, a narrower interorbital region, and paler coloration (Anderson and Nelson, 1965).

Glossophaga commissarisi Gardner, 1962

Specimens examined (9).—20 km N, 5 km E Badiraguato, 1800 ft, 4; Santa Lucía, 3600 ft, 5.

Our Sinaloan specimens of this long-tongued bat, all females, represent the northernmost known locality for the species; the previous northernmost records are from southern Durango (Baker and Greer, 1962:67) and central Nayarit (Villa-R., 1964:388). The series from Santa Lucía was obtained by natives in a cave; bats from northeast of Badiraguato were netted over a large stream. Each of four females taken on 27 January was gravid with a single embryo (6.5-10 mm in crown-rump length), whereas only one of five taken at Santa Lucía on 14 July was pregnant (embryo 8 mm in length).

Glossophaga commissarisi markedly resembles its congener *G. soricina* in size and other external features, and the two frequently

TABLE 2.—Selected measurements of two species of *Glossophaga* from Sinaloa.

Number averaged, or catalogue number, and sex	Length of forearm	Greatest length of skull	Zygomatic breadth	Breadth of braincase	Mastoid breadth	Length of maxillary toothrow
	Glossophaga commissarisi					
KU 94744, ♀	34.9	20.5	9.6	8.7	9.2	7.0
KU 96461, ♀	35.7	21.2	9.7	8.8	9.5	7.3
KU 96463, ♀	35.4	21.0	9.4	8.7	9.3	7.4
	Glossophaga soricina leachii					
Average, 10 (1♀, 9♂)	35.1	21.4	9.5	8.7	9.2	7.4
Minimum	34.0	20.7	9.0	8.5	8.9	7.0
Maximum	36.2	22.0	10.0	8.9	9.4	7.7

are difficult to distinguish in the field. A number of subtle cranial characters serve to distinguish the two, however; the most trenchant are: first upper incisors less procumbent in *commissarisi* and the two pairs nearly the same size (inner pair noticeably larger than outer teeth in *soricina*); premaxillary more or less evenly rounded anteriorly in *commissarisi,* not attenuate; lower incisors usually small and peglike in *commissarisi,* with evident space between middle pair and frequently between all teeth (usually robust and filling the gap between the canines in *soricina*); presphenoid ridge flattened subterminally in *commissarisi.* Comparative measurements of Sinaloan specimens of the two species are given in table 2.

Glossophaga soricina leachii (Gray, 1844)

Specimens examined (299).—18 km NNE Choix, 1; 16 mi NNE Choix, 1700 ft, 16; 0.5 mi E El Cajón, 1800 ft, 4; 0.5 mi SE Vaca, 650 ft, 2; 6 km E El Fuerte, 400 ft, 2; 6 km SW San Blas, 30 ft, 2; 1.5 mi N Badiraguato, 750 ft, 3; Cosalá, 1300 ft, 1; 6 km E Cosalá, 1500 ft, 3; El Dorado, 13; 1 mi S El Dorado, 1; La Cruz, 30 ft, 8; San Ignacio, 700 ft, 5; San Juan, 2; Piaxtla, 100 ft, 1; 3 mi SE Camino Real, 500 ft, 93; 6 mi W Santa Lucía, 3650 ft, 1; Santa Lucía, 3600 ft, 31; 2.5 km E Santa Lucía, 3200 ft, 3; 1 km NE Pánuco, 2700 ft, 2; Pánuco, 2050 ft, 23; 1.5 km W Copala, 1400 ft, 9; Copala, 1; 12 km N Villa Unión, 400 ft, 4; 8 km N Villa Unión, 450 ft, 6; 5 mi NW Mazatlán, 1; 1 mi SE Mazatlán, 10 ft, 1; Matatán, 550 ft, 5; Plomosas, 2500 ft, 19; 5 mi WSW Plomosas, 800 ft, 7; 4 mi N Rosario, 9; 0.5 mi W Rosario, 15; N end Isla Palmito del Verde, 5.

Additional records.—El Molino (Koopman, 1961:536); Río Piaxtla (on Mexican Highway 15 at Camino Real) (Baker, 1967:427); 8 mi (by road) N Mazatlán (Ingles, 1959:382); 3-4 mi N Mazatlán (Villa-R., 1967:231); Rosario (Koopman, 1961:536); 8 mi SE Rosario (Koopman, 1961:536); Escuinapa (J. A. Allen, 1906:236).

Pallas' long-tongued bat is one of the commonest and most widespread Neotropical species in Sinaloa, occurring the length of the state at low and moderate elevations. From at least the vicinity of El Molino and El Dorado southward, *G. soricina* occupies suitable habitat from sea level to about 3600 feet along streams on the Pacific slope of the Sierra Madre Occidental. Farther north, the species seemingly avoids arid coastal areas, but is known from a number of localities along the Río del Fuerte and its tributaries above San Blas.

Many of our specimens were trapped or shot in mines and caves; others were taken in mist nets in a variety of situations, mostly over water. Gravid females have been taken in the months of March, May, and August through January.

Anoura geoffroyi lasiopyga (Peters, 1868)

Specimens examined (16).—12 mi NE San Benito, 1000 ft, 1; 1 km NE Santa Lucía, 3700 ft, 1; Santa Lucía, 3600 ft, 12; 1.5 km S Santa Lucía, 3200 ft, 1; Matatán, 550 ft, 1.

This species first was reported from Sinaloa by Jones (1964:510). The bat from 12 mi NE San Benito represents the northernmost record in western México. Most of our specimens were captured in mist nets set in mango or banana groves; one was netted over a small stream, and another (from Matatán) was taken in a mine tunnel.

None of six females taken in July was reproductively active. Testes of a male captured on 25 June were 1.5 mm in length, whereas those of two taken in mid-July each measured 6 mm.

Choeronycteris mexicana Tschudi, 1844

Specimens examined (14).—18 km NNE Choix, 1; 16 km NNE Choix, 1700 ft, 2; 1 mi S El Cajón, 1800 ft, 1; 12 mi N, 4 mi W Los Mochis, 2; 10 km S, 38 km E Sinaloa, 800 ft, 3; 20 km N, 5 km E Badiraguato, 1800 ft, 2; La Cruz, 30 ft, 1; Pánuco, 2050 ft, 2.

Additional record.—6 mi E Santa Lucía (Schaldach and McLaughlin, 1960:8).

This long-tongued species is widely distributed at low to moderate elevations throughout western Sinaloa but evidently is nowhere especially common. All bats at hand are from elevations of 1800 feet or less, and *C. mexicana* may not occur regularly at higher elevations in the eastern part of the state. The specimen reported by Schaldach and McLaughlin (1960:8), however, probably is from an area above 3000 feet in elevation, suggesting that some individuals occur in major river valleys to the border of Durango and beyond.

Many of our specimens were obtained in caves, but others were netted over streams, arroyos, or roads. The only pregnant female was taken 1 mi S El Cajón on 11 February 1965 (embryo 14 mm in crown-rump length).

Choeroniscus godmani (Thomas, 1903)

The one specimen, a pregnant female from San Ignacio, 700 feet, reported by Jones (1964:510), remains the only Sinaloan record of this relatively rare glossophagine. It was captured by P. L. Clifton on the night of 18-19 July 1962 in a mist net over a small, fig-lined creek.

Leptonycteris nivalis (Saussure, 1860)

This long-nosed bat is known from Sinaloa only by two females collected "in the pine-oak zone" 10.3 mi (by road) W Palmito [Palmarito], 6000 feet, on 18 February 1964 (Baker and Cockrum, 1966:330). Means by which *L. nivalis* can be distinguished from the commoner and more widely distributed (in western México) *L. sanborni* have been enumerated by Davis and Carter (1962b: 194-197), Phillips *et al.* (1969:1368-1369), and Jones and Genoways (1970:14-15).

Leptonycteris sanborni Hoffmeister, 1957

Specimens examined (42).—6 km SW San Blas, 30 ft, 3; 1 mi N, 0.5 mi E San Miguel, 1; 1.5 mi N Badiraguato, 750 ft, 1; El Dorado, 8; 2 mi E Aguacaliente, 800 ft, 1; La Cruz, 30 ft, 3; San Ignacio, 700 ft, 1; Pánuco, 2050 ft, 19; 8 km N Villa Unión, 450 ft, 1; Matatán, 550 ft, 4.

Additional records.—Elota (Baker and Cockrum, 1966:329); Escuinapa (Hoffmeister, 1957:457).

Leptonycteris sanborni occurs at low to moderate elevations throughout Sinaloa. Pánuco, at 2050 feet, is the highest altitude in the state from which specimens thus far have been reported. Baker and Cockrum (1966:330), who recorded the only known representatives of *Leptonycteris nivalis* from Sinaloa, believed *sanborni* and *nivalis* to be "ecologically isolated," with the latter occurring at higher elevations than the former. Many of our specimens of *sanborni* were taken in mist nets set over streams or in banana or mango groves. Some were captured in abandoned mines, and one from 8 km N Villa Unión was taken in a road culvert.

The only pregnant females in our material are one taken near Aguacaliente on 21 February (crown-rump length of embryo 17 mm), one from La Cruz in early July (embryo 17 mm), and a third from El Dorado on 13 November (embryo 20 mm). Adult males had testes 2 mm in length in October (two) and November (one), and 4 mm in June (three).

Sturnira lilium parvidens Goldman, 1917

Specimens examined (60).—1 mi S El Cajón, 1800 ft, 1; 13 km NNE Vaca, 1300 ft, 2; 6 km SW San Blas, 30 ft, 5; 12 mi NE San Benito, 1000 ft, 4; 20 km N, 5 km E Badiraguato, 1800 ft, 15; 7 mi ENE Presa Sanalona, 600 ft, 4; 2 km E Aguacaliente, 800 ft, 1; 32 mi SSE Culiacán, 1; 1 mi S El Dorado, 1; La Cruz, 30 ft, 4; San Ignacio, 700 ft, 3; 1 mi E Santa

Lucía, 3650 ft, 10; Pánuco, 2050 ft, 4; 12 km N Villa Unión, 400 ft, 1; Plomosas, 2500 ft, 1; 5 mi WSW Plomosas, 800 ft, 3.

Additional record.—Elota (Cockrum and Bradshaw, 1963:6).

Most Sinaloan specimens of this species were captured in mist nets set over creeks or arroyos. *Sturnira lilium* occupies low tropical habitats in the state where fruits are available throughout the year. At elevations above 2000 feet, this species occurs primarily in the vicinity of water courses and the tropical deciduous forest associated with them; 3650 feet is the highest elevation from which *S. lilium* is known in the state.

Pregnant females were taken in May (embryo 28 mm in crown-rump length), June (embryo 8 mm), and August (two, embryos 25 and 27 mm). Two bats netted in June were noted as lactating by the collector, and one taken in November had enlarged mammae, indicating past or present lactation.

Sturnira ludovici occidentalis Jones and Phillips, 1964

Specimens examined (6).—5 km SW Palmito [Palmarito], 6100 ft, 2; Santa Lucía, 3600 ft, 3; Plomosas, 2500 ft, 1 (the holotype).

Sinaloan specimens of this species were caught in nets set near orchards around which the dominant vegetation consisted of oak or pine. Although *S. ludovici* has been taken sympatrically with *S. lilium* at one locality (the type locality of *occidentalis*—see Jones and Phillips, 1964:478, 480) in Sinaloa, the two species generally seem to be separated ecologically; *S. ludovici* dwells near sources of fruit at elevations where oak and even pine predominate, whereas *S. lilium* prefers tropical lowlands.

Selected measurements of the holotype, a female, followed by those of two males from Santa Lucía and one from 5 km SW Palmito, respectively, are: length of forearm, 42.5, 42.3, 43.5, 44.4 mm; greatest length of skull, 22.0, 22.7, 23.1, 23.5 mm; zygomatic breadth, 12.5, 13.1, 13.4, 13.5 mm; mastoid breadth, 11.4, 11.5, 11.9, 11.8 mm; postorbital constriction, 5.3, 5.8, 5.8, 6.0 mm; length of maxillary toothrow, 6.1, 6.3, 6.5, 6.5 mm. The three males weighed 19.6, 22.4, and 22.0 gms, respectively. The specimen listed last, taken on 17 July, had testes 4.5 mm long.

Artibeus aztecus aztecus Andersen, 1906

Specimens examined (45).—5 km SW Palmito [Palmarito], 6100 ft, 2; Santa Lucía, 3600 ft, 34; 2.5 km E Santa Lucía, 3200 ft, 9.

Additional records.—Rancho Batel, 5 mi NE Santa Lucía, 5200 ft (Koopman, 1961:536); near Santa Lucía (Davis, 1969:22).

The Aztec fruit-eating bat, first reported from Sinaloa by Koopman (1961:536), is known from several localities at relatively high

TABLE 3.—Comparative measurements of selected adult specimens of six species of *Artibeus* from Sinaloa.
Weights do not include those of pregnant females. Superscript numbers indicate fewer specimens averaged than listed in the left-hand margin.

Number averaged and sex	Length of forearm	Greatest length of skull	Zygomatic breadth	Mastoid breadth	Postorbital constriction	Length of maxillary toothrow	Weight in grams
			Artibeus aztecus aztecus				
Average (10♂, 5♀)	44.1	21.9	12.8	11.4	5.6	7.0	21.4
Minimum	43.2	21.4	12.4	10.8	5.3	6.7	17.8
Maximum	45.8	22.4	13.2	12.1	6.2	7.3	26.0
			Artibeus hirsutus				
Average (5♂, 5♀)	54.3	26.7^{8}	16.3	13.9^{8}	6.7	9.7	33.3
Minimum	53.2	26.2	16.0	13.5	6.5	9.5	28.4
Maximum	55.5	27.0	16.8	14.5	7.2	9.9	39.0
			Artibeus jamaicensis triomylus				
Average (5♂, 5♀)	55.6	27.1	17.0	14.2^{9}	6.8	9.6	38.1
Minimum	54.4	26.2	16.5	13.8	6.7	9.4	27.0
Maximum	57.7	27.9	17.4	14.5	6.9	9.9	45.3
			Artibeus lituratus palmarum				
Average (5♂, 5♀)	65.2	28.9	18.3	15.9	6.5	10.2	56.6
Minimum	63.0	28.3	17.8	15.5	6.2	10.0	43.5
Maximum	68.0	29.5	18.9	16.5	6.8	10.4	69.0
			Artibeus phaeotis nanus				
Average (5♂, 5♀)	36.9	18.6	11.6	10.0	4.6	5.9	10.1^{6}
Minimum	35.5	17.7	11.2	9.4	4.2	5.7	8.1
Maximum	38.5	19.0	11.8	10.2	4.8	6.1	11.5
			Artibeus toltecus hesperus				
Average (5♂, 5♀)	39.6	20.2	12.1	10.7	5.0	6.6	14.8
Minimum	38.6	19.7	11.9	10.6	4.7	6.4	12.4
Maximum	41.0	20.5	12.4	11.0	5.2	7.0	16.7

elevations (3200 to 6100 feet) in the southern part of the state. In the vicinity of Santa Lucía, *A. aztecus* has been taken with four other species of the genus (*hirsutus, jamaicensis, lituratus,* and *toltecus*). Jones (1964:512) published measurements of a series of *aztecus* from that locality (Table 3).

Seventeen of 23 females, collected near Santa Lucía in the period 14 to 28 July 1963, were pregnant; embryos ranged from 19 to 29 mm in crown-rump length. Additionally, a pregnant female (embryo 26 mm) was taken southwest of Palmito on 17 July of the same year. Our specimens were netted in orchards or captured in mines by native collectors.

Artibeus hirsutus Andersen, 1906

Specimens examined (22).—3 mi NE El Fuerte, 200 ft, 1; El Fuerte, 3; 2 mi N San Blas, 50 ft, 1; 6 km SW San Blas, 30 ft, 10; 1 mi N Zaragoza, 30 ft, 1; 6 km E Cosalá, 1500 ft, 1; Santa Lucía, 3600 ft, 4; Pánuco, 2050 ft, 1.

Additional record.—Sinaloa de Leyva (Villa-R., 1967:305).

This medium-sized member of the genus occurs the length of Sinaloa in lowland areas; the highest recorded elevation of occurrence in the state is 3600 feet. Most of our specimens were captured in mist nets over ponds or streams, or in mango groves. One from 1 mi N Zaragoza was taken from a small cave in a rocky hillside where another individual and many *Balantiopteryx plicata* were observed. A specimen from 3 mi NE El Fuerte was shot as it sought food in a strangler fig. *Artibeus hirsutus* is the only one of the six species of the genus occurring in Sinaloa that does not reach its northern distributional limits in the state.

Four of seven females collected on 6 August were pregnant (embryos 22-30 mm in crown-rump length); a fifth aborted a term fetus (forearm 17.8 mm), whereas one taken on 7 June was lactating. Two other females (taken in July and December) were not reproductively active. Two males taken in December and one in July each had testes 5 mm in length.

Artibeus jamaicensis triomylus Handley, 1966

Specimens examined (71).—10 km S, 38 km E Sinaloa, 800 ft, 5; 12 mi NE San Benito, 1000 ft, 11; San Benito, 400 ft, 5; 20 km N, 5 km E Badiraguato, 1800 ft, 14; 1.5 km N Badiraguato, 750 ft, 1; 7 mi ENE Presa Sanalona, 600 ft, 3; 2 mi E Aguacaliente, 800 ft, 1; 32 mi SSE Culiacán, 1; 1 mi S El Dorado, 1; 6 km E Cosalá, 1500 ft, 6; La Cruz, 30 ft, 1; San Ignacio, 700 ft, 5; 0.5 mi E Piaxtla, 2; 1 km NE Santa Lucía, 3700 ft, 3; Santa Lucía, 3600 ft, 1; 1 mi E Santa Lucía, 3650 ft, 1; 8 km N Villa Unión, 450 ft, 5; Plomosas, 2500 ft, 1; 5 mi WSW Plomosas, 800 ft, 3; S end, Isla Palmito del Verde, 1.

Additional records.—Sinaloa de Leyva (Villa-R., 1967:296); Río Piaxtla (on Mexican Highway 15 at Camino Real) (Baker, 1967:427).

The Jamaican fruit-eating bat is one of the commonest chiropterans in areas of Sinaloa where fruits are available throughout the year. Most of our specimens were netted over streams lined with fruit trees or in orchards. At a village known locally as Cahuinahuato (between Tule and Mocorito at a place 10 km S, 38 km E Sinaloa), individuals of this species were seen emerging from a hollow limb of a fig tree. They foraged higher in the tree, some returning in approximately 10 minutes with cut green figs to the hollow.

Pregnant females were collected in January, February, and April through July, and those in lactation were caught in September and November. Five males had the following testicular lengths in the months listed: April (7 mm), July (5, 8, 8 mm), October (6 mm).

Handley (1966:299) indicated that 96.5 per cent of the specimens of *A. j. triomylus* he examined from western México had the M3 present in both maxillae. We found this tooth lacking (on both sides) in only one of 30 skulls examined from Sinaloa.

Artibeus lituratus palmarum J. A. Allen and Chapman, 1897

Specimens examined (101).—12 mi NE San Benito, 1000 ft, 1; 20 km N, 5 km E Badiraguato, 1800 ft, 10; 12 mi NE Presa Sanalona, 600 ft, 3; 7 mi ENE Presa Sanalona, 600 ft, 2; El Dorado, 12; 1 mi S El Dorado, 10; Cosalá, 1300 ft, 3; 6 km E Cosalá, 1500 ft, 4; San Juan, 8 mi SE San Ignacio, 1; 1 km NE Santa Lucía, 3700 ft, 3; Santa Lucía, 3600 ft, 7; 2.5 km E Santa Lucía, 3200 ft, 5; 5 km SW Santa Lucía, 2150 ft, 2; Pánuco, 2050 ft, 21; 1 km S Pánuco, 2600 ft, 9; 1.5 km W Copala, 1400 ft, 1; 3 mi SE Plomosas, 4000 ft, 3; 5 mi WSW Plomosas, 800 ft, 2; 6 mi NW Teacapán, 1; S end, Isla Palmito del Verde, 1.

Additional record.—Río Piaxtla (on Mexican Highway 15 at Camino Real) (Baker, 1967:427).

Artibeus lituratus apparently reaches the northern limit of its range in northern Sinaloa. Like most other frugivorous bats, this species is restricted in distribution to areas in which palatable fruits are available throughout the year. Most of our specimens were netted in orchards or over streams lined with fruit-bearing trees.

Females carrying embryos were collected in February, April, June, and July, and females in lactation were caught in July and October. Thus, reproductive activity in Sinaloan representatives of this species seemingly parallels closely that of the related *A. jamaicensis.* Testes of six males taken in November had an average length of 6.1 (4-7.5) mm; those of two collected in June measured 5 and 7 mm, whereas single males from January, July, and October had testes 4, 6, and 7 mm long, respectively.

Artibeus phaeotis nanus Andersen, 1906

Specimens examined (17).—San Ignacio, 700 ft, 1; La Cruz, 30 ft, 7; Pánuco, 2050 ft, 1; 8 km N Villa Unión, 450 ft, 5; 5 mi WSW Plomosas, 800 ft, 3.

Additional records.—Río Piaxtla (on Mexican Highway 15 at Camino Real) (Baker, 1967:428); Puerta de las Canoas, 11 mi N, 2.5 mi E Mazatlán (Davis, 1970:400); 5 mi SE Copala, 750 ft (Baker and Greer, 1962:70); Presidio (Andersen, 1908:310); Cacalotán (Koopman, 1961:536).

This small fruit-eating bat inhabits the lowlands of southern Sinaloa, the northernmost records being from just south of the 24th parallel at La Cruz, San Ignacio, and Camino Real. All of our specimens were trapped in mist nets over streams or among fruit trees.

Of five females in our series, four taken at La Cruz on 6 July 1962 were pregnant (embryos 21-28 mm in crown-rump length), whereas one obtained on 15 October 1963 evinced no gross reproductive activity. A July-taken male had testes that measured 3 mm, and those of two collected in October measured 5.5 and 6 mm.

Artibeus toltecus hesperus Davis, 1969

Specimens examined (45).—12 mi NE San Benito, 1000 ft, 4; 20 km N, 5 km E Badiraguato, 1800 ft, 18; 7 mi ENE Presa Sanalona, 600 ft, 2; San Ignacio, 700 ft, 1; San Juan, 8 mi SE San Ignacio, 2; Santa Lucía, 3600 ft, 1; Pánuco, 2050 ft, 3; 8 km N Villa Unión, 450 ft, 6; 3 mi SE Plomosas, 4000 ft, 6; 5 mi WSW Plomosas, 800 ft, 2.

Additional records.—Escuinapa (J. A. Allen, 1906:237—see Koopman, 1961:536); 2 mi NW Palmito (Davis, 1969:26—we do not know to which of the several Palmitos in Sinaloa this name refers).

Artibeus toltecus is a common inhabitant of lowlands in the southern half of Sinaloa and occurs northward along the base of the Sierra Madre Occidental at least as far as the vicinity of San Benito, the northernmost locality of record for the species. Altitudinally, *A. toltecus* is most widely distributed below 1000 feet, but has been taken in protected situations along water courses as high as 3600 feet at Santa Lucía and to 4000 feet southeast of Plomosas. All of our specimens were captured in mist nets, most often over water courses near wild fig trees, or in fruit groves.

We have taken pregnant females in January, May, and October, and lactating females in May. Two males collected on 23 October 1963 each had testes measuring 4 mm in length. Jones (1964:512) and Davis (1969:25) published measurements of Sinaloan specimens (Table 3).

Chiroderma salvini scopaeum Handley, 1966

Specimens examined (14).—20 km N, 5 km E Badiraguato, 1800 ft, 1; 1.5 mi N Badiraguato, 750 ft, 1; Santa Lucía, 3600 ft, 8; 1 mi E Santa Lucía, 3650 ft, 1; 8 km N Villa Unión, 450 ft, 1; 5 mi WSW Plomosas, 800 ft, 2.

All of the white-lined bats collected thus far in Sinaloa have been netted under deciduous canopies, frequently over water, and often in the vicinity of trees bearing ripe fruit. For instance, a net placed under a fig tree replete with ripe fruits on 26 January 1964, at a place 20 km N and 5 km E Badiraguato, yielded 51 bats of three genera (*Artibeus, Chiroderma,* and *Sturnira*) by 9:30 PM.

A female obtained on 22 January contained one embryo that measured 4 mm in crown-rump length. Males taken in January, July, and October each had testes measuring 5 mm in length. Flying young were netted in early May and late July.

Centurio senex senex Gray, 1842

Specimens examined (4).—12 mi NE San Benito, 1000 ft, 2; 5 mi WSW Plomosas, 800 ft, 2.

An adult male and female netted over a fig-lined stream at a place 12 mi NE San Benito on 22 November 1964 provide the northernmost locality for the wrinkle-faced bat in western México. Two males (one immature, with one deciduous upper incisor still in place) were netted 5 mi WSW Plomosas on 4 May 1964 in an arroyo flanked by oak-covered hills.

Selected measurements of a male and female from 12 mi NE San Benito, followed by those of an adult male from 5 mi WSW Plomosas, are, respectively: total length, 59, 59, 61; length of hind foot, 13, 13.5, 15; length of ear, 16, 15, 15; length of forearm, 42.6, 41.2, 42.5; weight, 24.1, 16.4, 23.5; greatest length of skull, 18.9, 19.0, 18.7; condylobasal length, 14.5, 14.8, 14.4; zygomatic breadth, 14.6, 14.5, 14.5; length of maxillary toothrow, 4.6, 5.1, 5.0; breadth across upper molars, 10.2, 10.5, 10.6.

Desmodus rotundus murinus Wagner, 1840

Specimens examined (54).—16 km NNE Choix, 1700 ft, 7; 20 km N, 5 km E Badiraguato, 1800 ft, 1; 6 km E Cosalá, 1500 ft, 1; 8 km SE Elota, 250 ft, 3; 3 mi SE Camino Real, 500 ft, 8; 1 km NE Santa Lucía, 3700 ft, 1; Santa Lucía, 3600 ft, 1; 1.5 km W Copala, 1400 ft, 4; 7.3 km SW Copala, 1400 ft, 5; 5 mi NW Mazatlán, 2; 8 km N Villa Unión, 450 ft, 8; Matatán, 550 ft, 1; Plomosas, 2500 ft, 8; 5 mi WSW Plomosas, 800 ft, 1; Teacapán, Isla Palmito del Verde, 3.

Additional records.—12 km NE Chinobampo (Villa-R., 1953:429); [Cueva de] la Chinacatera, Monte Largo, 23 km E Pericos (Villa-R., 1959:377); Elota (Villa-R., 1953:429).

Sinaloan specimens of the vampire bat were removed from crevices in caves and mines or were netted over water. In March of 1961, for example, eight individuals were taken from an estimated 35 or so roosting at the end of an abandoned tunnel of a gold mine near Camino Real; other bats inhabiting the tunnel included an estimated 600 *Glossophaga soricina,* 150 *Pteronotus parnellii,* and one *Macrotus waterhousii.*

Pregnant females were obtained only during the dry season. An individual carrying an embryo that measured 12 mm in crown-rump length was obtained in December, a female caught in January contained an embryo 15 mm long, one taken in March bore an embryo that measured 16 mm, and a female obtained in May carried a near-term fetus that measured 29 mm.

Family NATALIDAE

Natalus stramineus mexicanus Miller, 1902

Specimens examined (132).—1 mi SE El Cajón, 1800 ft, 4; Santa Lucía, 3600 ft, 9; Pánuco, 2050 ft, 55; 1.5 km W Copala, 1400 ft, 1; Copala, 8;

5 mi NW Mazatlán, 26; Matatán, 550 ft, 6; Plomosas, 2500 ft, 17; 0.5 mi W Rosario, 100 ft, 6.

Additional records.—Rosario (Koopman, 1961:536); Escuinapa (J. A. Allen, 1906:236).

Most of the specimens of *Natalus stramineus* in our collections were taken in abandoned mines. At a place 5 mi NW Mazatlán, for example, specimens were obtained from a horizontal tunnel in a rocky cliff facing the sea; funnel-eared bats were concentrated in the darkest part of the tunnel along with scattered clusters of *Desmodus rotundus,* whereas *Balantiopteryx plicata* was abundant near the entrance and several *Glossophaga soricina* were taken elsewhere in the mine. Bats from Pánuco were collected in an old gold-silver mine in which the atmosphere was notably hot and humid. Other species taken in the same mine, in approximate decreasing order of abundance, included *Pteronotus parnellii, Mormoops megalophylla, Glossophaga soricina,* and *Macrotus waterhousii.*

Koopman (1961:536-537) considered funnel-eared bats from southern Sinaloa to be intergrades between the subspecies *N. s. mexicanus* to the north and *N. s. saturatus* to the south (see also Goodwin, 1959:6-7). On the basis of characters listed by Goodwin (*loc. cit.*), we tentatively refer all our Sinaloan specimens to the subspecies *mexicanus,* realizing, however, the need for a thorough study of infraspecific variation in this species. Several authors have reported different color phases in *N. stramineus,* but our Sinaloan series suggests that such differences are due, in part at least, to "foxing" of the pelage and subsequent (annual) molt. Fresh adult pelage is pale tawny in color, replacing worn yellowish to orangish hairs dorsally, beginning over the shoulders and spreading both anteriorly and posteriorly.

A female taken on 26 June 1962 contained an embryo that measured 15 mm in crown-rump length. One obtained on 15 July 1963 was lactating.

Family VESPERTILIONIDAE

Myotis californicus mexicanus (Saussure, 1860)

Specimens examined (3).—5 mi E Plomosas, 5500 ft, 2; 3 mi SE Plomosas, 4000 ft, 1.

Sinaloan specimens of this species were netted or shot in pine-oak forest. A female, taken on 30 April 1965, contained an embryo measuring 10 mm in crown-rump length. Measurements and weights of this and other species of *Myotis* that occur in the state were recorded by Jones *et al.* (1971).

Myotis fortidens fortidens Miller and Allen, 1928

Specimens examined (7).—Cosalá, 1300 ft, 1; 6 km E Cosalá, 1500 ft, 3; Isla Palmito de la Virgen, 15 ft, 3.

Additional record.—Escuinapa (Hall and Dalquest, 1950:583).

At Cosalá specimens were taken in mist nets over streams, whereas those from the barrier island of Palmito de la Virgen were caught, along with *Noctilio leporinus* and *Rhogeessa parvula,* in nets over a freshwater pond. Four of five females taken in June were pregnant, containing embryos measuring 4, 7, 10, and 12 mm in crown-rump length.

Myotis fortidens sonoriensis Findley and Jones, 1967

Our collections contain a single specimen of this large, relatively dark race of *fortidens*—from the Río del Fuerte, 1 mi N and 0.5 mi E San Miguel. Measurements of this specimen and of those of the preceding subspecies were recorded by Jones *et al.* (1971).

Myotis velifer velifer (J. A. Allen, 1890)

Specimens examined (84).—0.5 mi SE Vaca, 650 ft, 1; El Fuerte, 150 m, 2; Río del Fuerte, 1 mi N, 0.5 mi E San Miguel, 1; 10 mi NNW Los Mochis, 1; La Cruz, 30 ft, 1; 1 km NE Santa Lucía, 3700 ft, 16; Santa Lucía, 3600 ft, 4; 1 mi E Santa Lucía, 3650 ft, 52; 1 km NE Pánuco, 2700 ft, 1; 7 mi ENE Plomosas, 6000 ft, 2; 3 mi SE Plomosas, 4000 ft, 3.

Additional record.—Monte Largo, *ca.* 14 mi W Pericos (Constantine, 1959:442).

The cave myotis is the most abundant and widely distributed vespertilionid in Sinaloa, where it occurs from coastal areas to at least 6000 feet in elevation and probably higher. Most of our specimens were captured in mist nets or shot in flight as they foraged. External and cranial measurements of a series from the vicinity of Santa Lucía were given by Jones *et al.* (1971).

Nineteen of 27 June-taken females from Sinaloa were pregnant and five were lactating; we took lactating females as late as 23 July, when flying young of the year also were caught. Thirteen embryos from females taken in the vicinity of Santa Lucía in late June varied from 14 to 30 mm (average 20.2) in crown-rump length.

Myotis yumanensis lutosus Miller and Allen, 1928

Specimens examined (6).—0.5 mi SE Vaca, 650 ft, 3; 6 km NE El Fuerte, 150 m, 1; 2 mi E Aguacaliente, 800 ft, 1; Cosalá, 1300 ft, 1.

Sinaloan specimens of the Yuma myotis were netted or shot over streams bordered with deciduous trees. In the vicinity of Vaca, the deciduous vegetation was replaced abruptly by thorn forest away from the tributaries of the Río del Fuerte. A female from Cosalá netted on 15 June 1962 carried an embryo that measured 14 mm in crown-rump length.

Jones *et al.* (1971) commented on the taxonomic status of bats of this species in western México and listed measurements of Sinaloan specimens.

Pipistrellus hesperus hesperus (H. Allen, 1864)

Specimens examined (5).—6 km NE El Fuerte, 150 m, 1; 10 mi NNW Los Mochis, 3; 1 mi E Santa Lucía, 3650 ft, 1.

Additional record.—73 mi S Navajoa, Sonora (and 2 mi W Mexican Highway 15) (Findley and Traut, 1970:760).

Reasons for use of the subspecific name *P. h. hesperus* instead of *P. h. australis* for pipistrelles from western México were given by Findley and Traut (1970). Specimens labeled from El Fuerte and Los Mochis were shot as they flew among trees along the Río del Fuerte; most of the land beyond the deciduous border of the river was fenced and cultivated. The bat from 1 mi E Santa Lucía was netted over a small stream.

Neither of two females taken in June from near Los Mochis was reproductively active, but a female (in alcohol) obtained northwest of El Fuerte on 13 June had enlarged mammae and presumably was lactating.

Eptesicus fuscus miradorensis (H. Allen, 1866)

Specimens examined (2).—7 mi ENE Plomosas, 6000 ft, 1; 3 mi SE Plomosas, 4000 ft, 1.

Additional records.—30 mi SW El Salto [Durango], 2160 m (Villa-R., 1967:402); 2 km W Palmito [Palmarito], 6000 ft (Irwin and Baker, 1967: 195); 1 km W Palmito [Palmarito] (Baker and Patton, 1967:285).

Subspecific identity of big brown bats from Sinaloa and the remainder of western México is uncertain, and assignment here of Sinaloan specimens to *E. f. miradorensis* is tentative pending study of geographic variation throughout the range of the species. Specimens from Sinaloa are not notably different with respect to size or color than specimens at hand from Jalisco, Zacatecas, Guerrero, and Sonora, but are slightly paler than specimens from eastern México—Nuevo León, Puebla, and Veracruz (near the type locality of *miradorensis*). On the other hand, specimens from western México that we have examined are conspicuously darker than typical Great Plains and Great Basin representatives of *E. f. pallidus,* a subspecific name that frequently has been applied to populations of *E. fuscus* in northwestern México.

One of our two specimens, both males, was shot as it foraged in pine-oak woods; the other was netted over a small, mountain stream in the pine-oak zone. All records of this bat from Sinaloa are from the mountainous eastern part of the state.

Lasiurus borealis teliotis (H. Allen, 1891)

Specimens examined (5).—10 mi NNW Los Mochis, 1; 5 mi WSW Plomosas, 800 ft, 2; 3 mi SE Plomosas, 4000 ft, 1; Tatemales (near Rosario), 1 (BM).

Additional record.—2 km W Palmito [Palmarito], 6000 ft (Irwin and Baker, 1967:195).

The red bat apparently is relatively uncommon in Sinaloa. The earliest date on which a specimen has been taken in the state is 1 February; other specimens of which we have record, all non-reproductive females (weights of three, 8.0, 7.7, and 6.9 gms), were obtained on 26 April, 4 and 5 May, and 1 and 8 June. It is not known whether red bats are migratory in western México.

Lasiurus cinereus cinereus (Palisot de Beauvois, 1796)

A male netted 2 km W Palmito [Palmarito] at an elevation of 6000 feet, on 1 February 1966 (Irwin and Baker, 1967:195; Baker and Patton, 1967:285), is the only hoary bat thus far reported from the state. The season of capture suggests that this species may be a winter resident in mountainous eastern Sinaloa. Possibly, too, some migrants pass through that part of the state in autumn and again in late winter or early spring.

Lasiurus ega xanthinus (Thomas, 1897)

Specimens examined (3).—0.5 mi SE Vaca, 650 ft, 1; 1 mi S Pericos, 1; Mazatlán, 1.

Additional record.—Escuinapa (Handley, 1960:475).

This yellow bat apparently is an uncommon resident of Sinaloa. A male from 0.5 mi SE Vaca was netted over a pool in the Río del Fuerte. No precise data are available on the circumstances of capture of our other two specimens, one an adult female and the other an immature male (13 July).

Lasiurus intermedius intermedius H. Allen, 1862

A female, shot on 30 June 1962 from a coco palm 3 mi N Mazatlán (Loomis and Jones, 1964:32), is the only northern yellow bat known from Sinaloa and the northernmost record for the species in western México. This bat carried two embryos, each 25 mm in crown-rump length.

Rhogeessa parvula parvula H. Allen, 1866

Specimens examined (33).—16 km NNE Choix, 1700 ft, 3; 1 mi S El Cajón, 1800 ft, 1; 6 km NE El Fuerte, 150 m, 6; 1 mi E Sinaloa, 180 ft, 1; 1 mi S, 6 mi E El Carrizo, 1; 7 mi ESE Presa Sanalona, 600 ft, 1; La Cruz, 30 ft, 3; 0.5 mi E Piaxtla, 6; 12 km N Villa Unión, 400 ft, 1; 5 mi

WSW Plomosas, 800 ft, 5; Isla Palmito de la Virgen, 15 ft, 1; 2 mi E Palmito, 10 ft, Isla Palmito del Verde, 4.

Additional record.—El Molino (Koopman, 1961:537).

Most of the specimens of this small bat in our collection were netted over ponds or streams. The species occurs the entire length of the state at low and moderate (up to 1800 feet) elevations, and reaches the northernmost limits of its range in western México in adjacent southern Sonora.

Four females taken in May each contained two embryos (6, 10, 10, and 10 mm in crown-rump length). Two of seven females caught in June were gravid (twins, 10 and 13 mm in crown-rump length), whereas the remainder had enlarged mammae indicating past or present lactation; a female taken in July also had enlarged mammae. A male obtained on 30 October had testes 6 mm in length.

Goodwin (1958) reviewed the taxonomy of the genus and listed selected measurements for specimens of *R. p. parvula* from Sonora and Nayarit. Two Sinaloan males and a nonpregnant female weighed 3.3, 3.2, and 3.1 gms, respectively, whereas one of the pregnant females taken in May weighed 4.7 gms.

Family MOLOSSIDAE

Tadarida brasiliensis mexicana (Saussure, 1860)

Specimens examined (59).—0.5 mi SE Vaca, 650 ft, 3; El Fuerte, 150 m, 47; 1 mi S, 6 mi E El Carrizo, 1; 13 mi ESE Badiraguato, 800 ft, 5; Pericos, 1; Mazatlán, 10 ft, 2.

Additional records.—Bacubirito (Villa-R., 1967:442); 3 km N, 8 km W Topolobampo, 10 m (Davis and Loomis, 1971:453); Monte Largo, *ca.* 14 mi W Pericos (Constantine, 1959:442); Navolato (Villa-R. and Cockrum, 1962:54); Culiacán (Shamel, 1931:24); 2 km W Palmito [Palmarito], 6000 ft (Irwin and Baker, 1967:195); Esquinapa (J. A. Allen, 1906:236).

Aside from a series taken in June from El Fuerte and a female from Pericos that was obtained on 14 June 1954, free-tailed bats of this species were taken in Sinaloa only in the cold months (November through February). Specimens were obtained at El Fuerte in December and on 14-15 June. At the latter time, two males and 26 females (25 of which were pregnant, with crown-rump lengths of embryos ranging from 16 to 32 mm) were removed from the attic of an old building. The large size of embryos suggests that this concentration may have represented an incipient maternity colony. No other such colonies have been reported from Sinaloa, however, and Cockrum (1969:310) reported that most pregnant females arrive at maternity roosts in Arizona a few days prior to parturition.

A large number of crania of *T. b. mexicana* was found in owl pellets taken from a cave 1.5 mi NW Topolobampo. Remains of several *T. femorosacca* and one *Macrotis waterhousii* also were found in these pellets, along with those of numerous rodents.

Tadarida femorosacca (Merriam, 1889)

Specimens examined (15).—1.5 mi NW Topolobampo, 10 ft, 6; Rosario, 500 ft, 9.

Additional records.—3 km N, 8 km W Topolobampo, 10 m (Davis and Loomis, 1971:453); 4.3 km NW Topolobampo (Loomis and Webb, 1969:41).

Six specimens from northwest of Topolobampo, all adult males, were shot on 18 December 1961 by P. L. Clifton and J. H. Bodley in a cave some 50 yards inland from the coastline of the Pacific Ocean. The cave was approximately 50 feet wide, 25 feet deep, and 15 feet high; it was open and light, with the bats clustered in narrow crevices in the ceiling. One other species (*Balantiopteryx plicata*) was taken in the cave, and droppings of fruit-eating bats were found on the floor and around the entrance. Clifton also found remains of *T. femorosacca* (see previous account) in owl pellets collected there. The specimens listed by Loomis and Webb (1969:41) may have been obtained in this same cave. The bats from Rosario (six adult males and three adult females) were taken in a church by natives on 22 June 1962. One of three females was pregnant (crown-rump length of single embryo, 18 mm).

Three species of the *Tadarida laticaudata* group—*T. aurispinosa, T. femorosacca,* and *T. macrotis*—are known from western México. The two species listed last are on record from Sinaloa, and *aurispinosa* undoubtedly occurs there because specimens are on record both from southern Sonora and from Nayarit. Of the three, *macrotis* is the largest, *aurispinosa* is intermediate in size, and *femorosacca* is the smallest. In addition to the characters mentioned by Gardner (1963:43), *femorosacca* differs from *aurispinosa* in being smaller externally and cranially, in having smaller teeth, and in having a noticeably less inflated braincase (both dorsally and laterally) and rostral area. Also, all specimens of *femorosacca* examined by us are grayish brown dorsally, whereas those of *aurispinosa* are a rich, dark brown; both species have white-based hairs. Cranial measurements of Sinaloan specimens of *femorosacca* and *macrotis* are given in table 4. Cranial measurements for *aurispinosa* were presented by Gardner (1963:42).

Average and extreme external dimensions of six males from 1.5 mi NW Topolobampo, those for five males from Rosario, and measurements of a single female from Rosario are, respectively, as follows: total length, 105.5 (103-109), 103.8 (100-110), 108 mm;

TABLE 4.—Selected cranial measurements of *Tadarida femorosacca* and *Tadarida macrotis* from Sinaloa.

Number averaged or catalogue number, and sex	Greatest length of skull	Zygomatic breadth	Postorbital constriction	Breadth of braincase	Mastoid breadth	Length of maxillary toothrow
			Tadarida macrotis, vicinity Plomosas			
KU 97087, ♂	23.9	12.7	4.2	9.8	11.7	9.2
KU 97090, ♂	23.8	12.6	4.1	10.0	11.5	9.1
KU 97091, ♂	24.3	12.7	4.0	10.4	11.7	9.0
			Tadarida femorosacca 1.5 mi NW Topolobampo			
Average (4♂)	19.5	10.6	3.6	9.0	10.3	7.4
Minimum	19.3	10.5	3.4	8.8	10.2	7.3
Maximum	19.8	10.8	3.7	9.3	10.5	7.5
			Rosario			
Average (5♂)	19.6	10.6	3.6	9.1	10.3	7.4
Minimum	19.3	10.4	3.5	8.9	10.1	7.3
Maximum	19.8	10.9	3.7	9.3	10.4	7.5
KU 90762, ♀	19.2	10.3	3.4	8.8	10.3	7.3

length of tail, 37.8 (34-42), 40.4 (37-44), 41 mm; length of hind foot, 11.2 (11-12), 10.8 (10-11), 11 mm; length of ear, 23.0 (22-24), 23.8 (23-24), 23 mm; length of forearm, 46.8 (45.6-47.8), 47.1 (46.3-47.7), 48.7 mm; weight, 15.2 (13.0-18.0), 12.0 (11.5-13.5), 14.5 gms.

Tadarida macrotis (Gray, 1839)

Specimens examined (5).—3 mi SE Plomosas, 4000 ft, 1; 5 mi WSW Plomosas, 800 ft, 4.

Specimens listed herein, all taken in early May of 1964, provide the first records for the big free-tailed bat in Sinaloa. At the first locality listed, a male was netted over a mountain stream in pine-oak forest. Specimens from the second locality, two males and two nonpregnant females, were netted in an arroyo. It seems likely that this species will be found elsewhere in the state at moderate elevations in areas along the western edge of the Sierra Madre Occidental.

External measurements of three adult males are: total length, 150, 124, 137 mm; length of tail, 59, 45, 52 mm; length of hind foot, 13, 12.5, 13 mm; length of ear, 33, 31, 33 mm; length of forearm, 61.8, 60.8, 62.2 mm; weight, 22.7, 20.2, 22.5 gms. Cranial measurements are given in the same order in table 4. The forearms of two females preserved in spirits measured 60.6 and 63.2 mm.

Eumops perotis californicus (Merriam, 1890)

A male, taken by Robert J. Baker and associates of Texas Tech University in a mist net at kilometer marker 1665 on Mexican Highway 15, a few miles south of the Sonoran border, provides the only record of the greater mastiff bat from Sinaloa. The series of nets in which this bat was captured were stretched across a pond that provided the water supply for local residents; *Pteronotus parnellii, Rhogeessa parvula,* and *Tadarida brasiliensis* were collected at the same place.

Molossus ater nigricans Miller, 1902

Specimens examined (30).—1 mi S Pericos, 2; 32 mi SSE Culiacán, 9; La Cruz, 30 ft, 2; 1 mi SE Camino Real, 400 ft, 7; 0.5 mi E Piaxtla, 1; Rosario, 1 (BM); Tatemales (near Rosario), 5 (BM); Palmito, Isla Palmito de la Virgen, 20 ft, 3.

This bat is widely distributed in lowlands of western Sinaloa, north at least to the vicinity of Pericos. As indicated by Jones *et al.* (1962:155), specimens listed from Camino Real and Piaxtla were obtained along the Río Piaxtla at approximately the same place.

A female from 32 mi SSE Culiacán, taken on 18 June, contained an embryo 18 mm in crown-rump length, whereas two obtained at La Cruz on 4 July carried embryos measuring 7 and 13 mm. Females collected on 1 March near Camino Real evidenced no reproductive activity; two males from this same place and date had testes 7 and 8 mm in length.

Molossus molossus aztecus Saussure, 1860

An individual reported by Gardner (1966:5) from Alisos is the only specimen of this small mastiff bat thus far reported from Sinaloa.

Molossus sinaloae sinaloae J. A. Allen, 1906

The holotype and paratype of *M. s. sinaloae,* from Escuinapa, remain the only specimens of this bat known from the state.

DISTRIBUTIONAL SUMMARY

Among the 44 chiropteran species presently recorded from Sinaloa, there is one representative each of the families Emballonuridae and Noctilionidae, four chilionycterids, 19 phyllostomatids, a single natalid, 11 species of Vespertilionidae and seven of Molossidae. The majority of species are closely associated with the Neotropics—tropical or subtropical in their affinities—and distributed at low or middle altitudes in Sinaloa.

The emballonurid, noctilionid, and four chilonycterids all are Neotropical taxa, but only one (*Noctilio leporinus*) reaches its northernmost distribution in Sinaloa; all of the others occur northward in western México at least as far as adjacent southern Sonora.

The 19 species of Phyllostomatidae, all with Neotropical affinities, are about evenly divided between those that reach northern distributional limits in Sinaloa (11 species) and those that occur also to the north of the state. Species that are found no farther north than Sinaloa include the glossophagines *Glossophaga commissarisi, Anoura geoffroyi, Choeroniscus godmani,* and *Leptonycteris nivalis* (occurs northward to Texas east of the Sierra Madre Occidental), and the stenodermine taxa *Sturnira ludovici, Artibeus aztecus, A. lituratus, A. phaeotis, A. toltecus, Chiroderma salvini* (recorded also from southwestern Chihuahua), and *Centurio senex.* The one species of Natalidae, *Natalus stramineus,* is widespread in the Neotropics, reaching distributional limits in western México in Baja California and Sonora.

The 11 kinds of vespertilionids present an interesting array of zoogeographic affinities. Four (*Myotis californicus, M. velifer, M. yumanensis,* and *Pipistrellus hesperus*) are temperate species, four more (*Myotis fortidens, Lasiurus ega, L. intermedius,* and *Rhogeessa parvula*) are Neotropical taxa, whereas the remaining three (*Eptesicus fuscus, Lasiurus borealis,* and *L. cinereus*) are best categorized as "widespread" species, all occurring in temperate and tropical regions and in both North and South America. The four species of *Lasiurus* are especially interesting in that the widespread *borealis* and *cinereus* may occur in Sinaloa only as migrants, wintering to the south and probably occurring far to the north in summer, whereas *ega* and *intermedius* probably migrate only locally and are year-round residents in western México. *Lasiurus intermedius* is the only vespertilionid thought to reach distributional limits in Sinaloa.

New World molossid bats all are basically Neotropical elements, but several, most notably *Tadarida brasiliensis* and *T. macrotis,* occur far northward into temperate regions as warm-season migrants. In contrast, the three species of *Molossus* known from the state (*ater*, *molossus*, and *sinaloae*) are relatively sedentary and reach their northernmost known distribution in Sinaloa.

In summary, the known chiropteran fauna of Sinaloa is composed of a preponderance of species (37) with Neotropical affinities. The remaining seven taxa recorded from the state, all vespertilionids, include four that are temperate in association and three that are widely distributed and not readily assignable to any major faunal unit. However, of the latter, *Eptesicus fuscus* has a wide distribution in temperate North America, barely reaches South America, and, where it occurs in Central America, generally is found at relatively high altitudes, whereas *Lasiurus cinereus*, a species with a disjunct South American distributional segment, inhabits temperate environs in North America in the warm season and migrates southward to highlands in México and northern Middle America in winter.

Relatively little geographic variation has been detected in bats in Sinaloa. Only three species—*Balantiopteryx plicata*, *Macrotis waterhousii*, and *Myotis fortidens*—are represented in the state by two subspecies; in each case the races are separated on a north-south basis.

RESUMEN

Previamente se ha publicado poco con respecto a la fauna mastozoológica de Sinaloa, México. En esta publicación se resumen los datos sistemáticos y ecológicos de los Chiroptera conocidos de este estado. Cuarenta y cuatro especies están representadas por cinco familias: Emballonuridae (1 especie), Noctilionidae (1), Chilonycteridae (4), Phyllostomatidae (19), Natalidae (1), Vespertilionidae (11), y Molossidae (7).

De esas 44 especies, 37 tienen afinidades Neotropicales, y 16 de estas alcanzan en Sinaloa, su extrema distribución nórdica en el occidente de México. Las siete especies restantes, todas vespertilionidos, se dividen en dos grupos: cuatro con afinidades temperadas, y tres (*Eptesicus fuscus*, *Lasiurus borealis*, *L. cinereus*), con una distribución muy amplia en las Américas.

Entre los murciélagos que se encuentran en Sinaloa, se observó muy poca variación geográfica. Solo tres especies tienen mas de una subespecie con una distribución de norte a sur.

LITERATURE CITED

ALLEN, J. A.
1906. Mammals from the states of Sinaloa and Jalisco, Mexico, collected by J. H. Batty during 1904 and 1905. Bull. Amer. Mus. Nat. Hist., 22:191-262.
ANDERSEN, K.
1908. A monograph of the chiropteran genera Uroderma, Enchisthenes, and Artibeus. Proc. Zool. Soc. London, 204-319.
ANDERSON, S., and C. E. NELSON
1965. A systematic revision of *Macrotus* (Chiroptera). Amer. Mus. Novit., 2212:1-39.
ARMSTRONG, D. M., and J. K. JONES, JR.
1971. Mammals from the Mexican state of Sinaloa. I. Marsupialia, Insectivora, Edentata, and Lagomorpha. Jour. Mamm., 52:747-757.
BAKER, R. H., and J. K. GREER
1962. Mammals of the Mexican state of Durango. Publ. Mus., Michigan State Univ., Biol. Ser., 2:25-154.
BAKER, R. J.
1967. Karyotypes of bats of the family Phyllostomidae and their taxonomic implications. Southwestern Nat., 12:407-428.
BAKER, R. J., and L. CHRISTIANSON
1966. Notes on bats from Sonora, Mexico. *Ibid.*, 11:310-311.
BAKER, R. J., and E. L. COCKRUM
1966. Geographic and ecological range of the long-nosed bats, *Leptonycteris.* Jour. Mamm., 47:329-331.
BAKER, R. J., and J. L. PATTON
1967. Karyotypes and karyotypic variation of North American vespertilionid bats. *Ibid.*, 48:270-286.
BIRNEY, E. C., and J. K. JONES, JR.
1971. Woodrats (genus Neotoma) of Sinaloa, Mexico. Trans. Kansas Acad. Sci., in press.
COCKRUM, E. L.
1969. Migration in the guano bat, Tadarida brasiliensis. Misc. Publ. Mus. Nat. Hist., Univ. Kansas, 51:303-336.
COCKRUM, E. L., and G. V. R. BRADSHAW
1963. Notes on mammals from Sonora, Mexico. Amer. Mus. Novit., 2138: 1-9.
CONSTANTINE, D. G.
1959. *Pteronotus davyi* in northwestern Mexico. Jour. Mamm., 40:442.
DALQUEST, W. W., and E. R. HALL
1949. A new subspecies of funnel-eared bat (*Natalus mexicanus*) from eastern Mexico. Proc. Biol. Soc. Washington, 62:153-154.
DAVIS, R. M., and R. B. LOOMIS
1971. The intranasal chigger *Microtrombicula merrihewi* (Acarina: Trombiculidae) in the North American free-tailed bat, *Tadarida brasiliensis.* Southwestern Nat., 15:437-458.
DAVIS, W. B.
1969. A review of the small fruit bats (genus *Artibeus*) of Middle America. *Ibid.*, 14:15-29.
1970. A review of the small fruit bats (genus *Artibeus*) of Middle America. Part II. *Ibid.*, 14:389-402.
DAVIS, W. B., and D. C. CARTER
1962a. Notes on Central American bats with description of a new subspecies of Mormoops. *Ibid.*, 7:64-74.
1962b. Review of the genus *Leptonycteris* (Mammalia: Chiroptera). Proc. Biol. Soc. Washington, 75:193-198.

DUNNIGAN, P. B.

1967. Pocket gophers of the genus Thomomys of the Mexican state of Sinaloa. Radford Rev., 21:139-168.

FINDLEY, J. S., and G. L. TRAUT

1970. Geographic variation in *Pipistrellus hesperus*. Jour. Mamm., 51: 741-765.

GARDNER, A. L.

1963. Nota acerca de la distribución de los murciélagos en México. Rev. Soc. Mexicana Hist. Nat., 24:41-44.

1966. A new subspecies of the Aztec mastiff bat, *Molossus aztecus* Saussure, from southern Mexico. Contrib. Sci., Los Angeles Co. Mus., 111:1-5.

GOODWIN, G. G.

1958. Bats of the genus *Rhogeessa*. Amer. Mus. Novit., 1923:1-17.

1959. Bats of the subgenus *Natalus*. *Ibid.*, 1977:1-22.

HANDLEY, C. O., JR.

1960. Descriptions of new bats from Panama. Proc. U.S. Natl. Mus., 112:459-479.

1966. Descriptions of new bats (*Chiroderma* and *Artibeus*) from Mexico. An. Inst. Biol., 36:297-301.

HARDY, L. M., and R. W. MCDIARMID

1969. The amphibians and reptiles of Sinaloa, México. Univ. Kansas Publ., Mus. Nat. Hist., 18:39-252.

HOFFMEISTER, D. F.

1957. Review of the long-nosed bats of the genus *Leptonycteris*. Jour. Mamm., 38:454-461.

HOOPER, E. T.

1955. Notes on mammals of western Mexico. Occas. Papers Mus. Zool., Univ. Michigan, 565:1-26.

INGLES, L. G.

1959. Notas acerca de los mamíferos Mexicanos. An. Inst. Biol., 29: 379-408.

IRWIN, D. W., and R. J. BAKER

1967. Additional records of bats from Arizona and Sinaloa. Southwestern Nat., 12:195.

JONES, J. K., JR.

1964. Bats from western and southern Mexico. Trans. Kansas Acad. Sci., 67:509-516.

JONES, J. K., JR., T. ALVAREZ, and M. R. LEE

1962. Noteworthy mammals from Sinaloa, Mexico. Univ. Kansas Publ., Mus. Nat. Hist., 14:145-159.

JONES, J. K., JR., and H. H. GENOWAYS

1970. Chiropteran systematics. Pp. 3-21, *in* About bats (B. H. Slaughter and D. W. Walton, eds.), Southern Methodist Univ. Press, vii + 339 pp.

JONES, J. K., JR., H. H. GENOWAYS, and L. C. WATKINS

1971. Bats of the genus Myotis from western Mexico, with a key to species. Trans. Kansas Acad. Sci., 73:409-418.

JONES, J. K., JR., and G. L. PHILLIPS

1964. A new subspecies of the fruit-eating bat, Sturnira ludovici, from western Mexico. Univ. Kansas Publ., Mus. Nat. Hist., 14:475-481.

KOOPMAN, K. F.

1961. A collection of bats from Sinaloa, with remarks on the limits of the Neotropical region in northwestern Mexico. Jour. Mamm., 42:536-538.

LOOMIS, R. B., and J. K. JONES, JR.
1964. The northern yellow bat in Sinaloa, Mexico. Bull. Southern California Acad. Sci., 63:32.
LOOMIS, R. B., and J. P. WEBB, JR.
1969. A new species of *Speleocola* (Acarina: Trombiculidae), off a bat, *Pizonyx vivesi,* from Baja California, Mexico. *Ibid.,* 68:36-42.
PHILLIPS, C. J., J. K. JONES, JR., and F. J. RADOVSKY
1969. Macronyssid mites in oral mucosa of long-nosed bats: occurrence and associated pathology. Science, 165:1368-1369.
SANBORN, C. C.
1937. American bats of the subfamily Emballonurinae. Zool. Ser., Field Mus. Nat. Hist., 20:321-354.
SCHALDACH, W. J., and C. A. MCLAUGHLIN
1960. A new genus and species of glossophagine bat from Colima, Mexico. Contrib. Sci., Los Angeles Co. Mus., 37:1-8.
SHAMEL, H. H.
1931. Notes on the American bats of the genus Tadarida. Proc. U.S. Natl. Mus., 78:1-27.
VILLA-R., B.
1953. Distribución en México de los murciélagos vampiros familia Desmodontidae. Bol. Oficina Sanitaria Panamericana, 35:426-432.
1959. *Pteronotus davyi fulvus.* El murciélago de espaldas desnudas en el norte de Sonora, México. An. Inst. Biol., 29:375-378.
1964. Reflexiones acerca de la posición taxonómica de los murciélagos siricoteros de México, género *Glossophaga. Ibid.,* 34:381-391.
1967. Los murciélagos de México. Univ. Nac. Autónoma México, xvi + 491 pp.
VILLA-R., B., and E. L. COCKRUM
1962. Migration in the guano bat *Tadarida brasiliensis mexicana* (Saussure). Jour. Mamm., 43:43-64.

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NEW TREE FROGS OF THE GENUS *HYLA* FROM THE CLOUD FORESTS OF WESTERN GUERRERO, MÉXICO

By

KRAIG ADLER[1] and DAVID M. DENNIS[2]

Because of the difficulty of travel in the mountainous regions of western Guerrero, this major area of uplift has remained one of the poorest known in México. Therefore, it is not surprising that a number of new species of amphibians and reptiles has been discovered in this region; only a few of these species have been described to date. These montane species occur in cloud forests in the Sierra Madre del Sur, which is flanked by the arid Río Balsas basin to the north and west and by the Pacific Ocean to the south. This mountain range extends eastward into Oaxaca; however, several high but dry valleys interrupt the crest and create discontinuities in the cloud forest. The two new frogs described below are representatives of two species groups. Although representatives of both of these groups occur in the Sierra Madre del Sur in Oaxaca, the apparently closest known relatives of the two new species occur to the northeast, in the high mountains between México and Veracruz.

Hyla trux new species

(Figure 1; Plate 1)

Holotype.—Adult male, KU 137551, from 11.4 km (by road) southwest of Puerto del Gallo, Guerrero, México [about 35 km

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[1] Department of Biology, University of Notre Dame, Notre Dame, Indiana 46556.

[2] College of Biological Sciences, The Ohio State University, Columbus, Ohio 43210.

airline northeast of Atoyác de Álvarez], elevation 1985 meters; collected 20 December 1969, by K. Adler, D. M. Dennis and D. H. Snyder.

Paratypes.—FMNH 171784, LACM 64882, USNM 192304, all 10.2 km (by road) SSW of Asoleadero, 2120 m, collected 17 December 1969; AMNH 84584, BMNH 1971.441, both 5.6 km (by road) NE of Yerbabuena, 2000 m, collected 17 December 1969; KU 137550, 10.4 km (by road) SW of Puerto del Gallo, 1940 m, collected 20 December 1969; UMMZ 130154, same data as holotype; and UMMZ 130155, 11.5 km (by road) NNE of El Paraíso, 1760 m, collected 20 December 1969; all from Guerrero, México; same collectors as for holotype.

Diagnosis.—A large member of the *Hyla taeniopus* species group (males to 81.0 mm snout-vent length) possessing, as an adult, a brown dorsum spotted with irregularly-shaped, chocolate-brown blotches, and banded limbs in life; a clear, brown-edged palpebral membrane; vocal slits in males; tarsal folds; prevomerine teeth; and no axillary membranes. The fingers are one-half webbed, the toes three-fourths webbed. *Hyla trux* differs from other known members of the *taeniopus* group in having extensive nuptial excrescences (largely confined to the thumb but also found on all other fingers) and a hypertrophied web between toes one and two (in sexually mature males).

Description of Holotype.—The holotype is an adult male with a snout-vent length of 81.0 mm. The head is broad and moderately flat (25.7 mm long, 24.1 mm wide) with slightly protuberant nostrils, which are horizontally oval; the internarial distance is 5.3 mm. The canthus is distinct and straight in profile; the loreal region is slightly concave. From above the snout is long and moderately pointed, with no rostral keel, and is round in lateral profile. The eye length is 7.6 mm; the upper eyelid is 5.8 mm wide, and the interorbital distance is 6.5 mm. The tympanum is small, distinct, round, and 3.5 mm long; there is a strong supratympanic fold extending from posterior border of eye to above the insertion of the arm and barely covering the upper edge of the tympanum. The length of the hand is 22.9 mm (Fig. 1a). The fingers are moderately long, $1 < 4 < 2 < 3$, and about one-half webbed. The fourth finger and outer side of the third are webbed to the base of the penultimate phalanx; the inner side of third finger is webbed to the middle of the antepenultimate phalanx; the outer side of the second finger is webbed to the middle of the penultimate phalanx, and the first finger and inner side of the second are webbed to the distal end of the antepenultimate phalanx. The

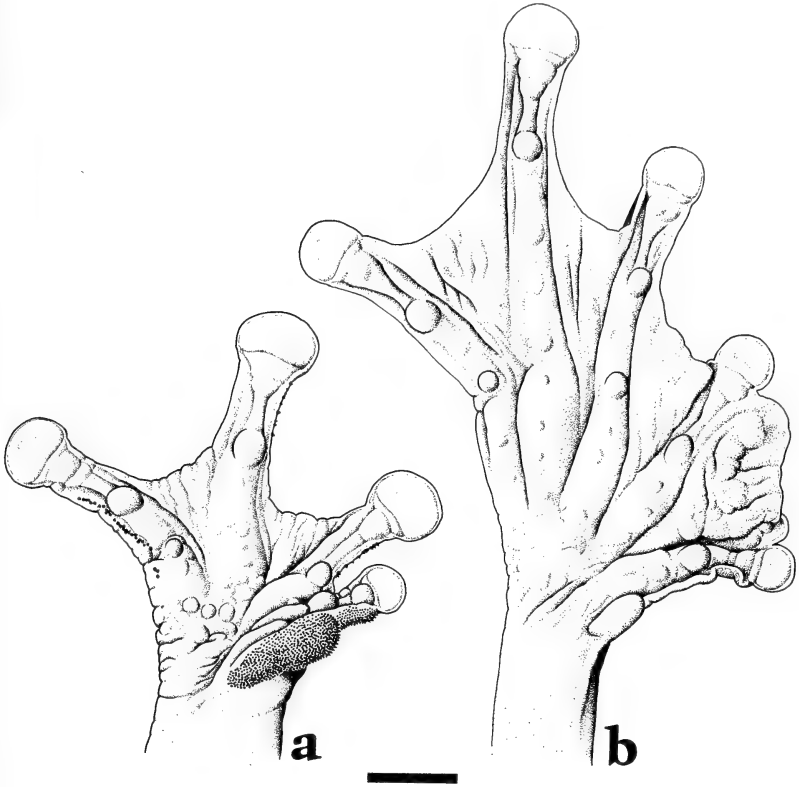

FIG. 1. Hand (a) and foot (b) of *Hyla trux* (KU 137551, mature male; holotype). Scale is 5 mm in length.

discs are moderately large; that of the third finger is 3.5 mm wide. The prepollex is moderately enlarged with an elongate, non-projecting prepollical spine which, from radiographs, appears to be only moderately ossified. The prepollex and inner side of the first finger are extensively covered with nuptial spines; isolated groups of spines also occur on the inner edges of the penultimate phalanx of the second and third fingers and on the outer edge of the entire fourth finger. The subarticular tubercles are round; none is bifid. Distinct supernumerary tubercles are present on the palm and proximal segments of the fingers; there is also a longitudinal row of pustules on a raised ridge along the ventrolateral edge of the forearm. There is a fold on the wrist. The length of the foot is 36.0 mm (Fig. 1b). The toes are moderately long, $1 < 2 < 5 < 3 < 4$, and about three-fourths webbed. The first, second, and fifth toes are webbed to the base of the disc; the fourth toe is webbed to the base of the penultimate phalanx, and the third toe is webbed to the distal end of the penultimate phalanx. The webbing between the first and second toes is greatly hypertrophied, the edge of the web being deflected dorsally and folded into a flap. The inner metatarsal tubercle is distinct and elliptical; there is a small but distinct outer metatarsal tubercle. The tarsal fold is indistinct. The subarticular tubercles are round; none is bifid. Indistinct supernumerary tubercles are present on the soles and proximal segments of the toes. The discs are moderately large; that of the fourth toe is 3.5 mm wide. The length of the tibia is 39.8 mm; the tibiotarsal articulation extends to the tympanum, and the heels overlap 9.0 mm when the legs are flexed and held at right angles to the body. The cloacal sheath is moderately long, directed posteroventrally, and opens at the mid-level of the thighs; there is a transverse dermal fold above the sheath and large, distinct pustules below its aperture. The skin of the dorsum and undersurfaces of arms, head and lower legs is smooth; the skin of the venter of the body and thighs is granular. There is no axillary membrane. The dentigerous processes of the prevomers are each the same size as a choana, oval, and oriented transversely between the choanae, nearer one another than to choanae; there are 3-4 prevomerine teeth. The choanae are oval, each 1.5 mm long. The vocal slits are paired and extend from the midlateral base of the tongue to the angle of the jaws; the vocal sac is apparently barely distensible. The tongue is elongate, cordiform, and one-sixth free and slightly notched posteriorly. The left testis is 17.0 mm long; the right is 15.1 mm. As determined from radiographs, the quadratojugals are well-developed but lack a bony articulation with the maxilla on one side.

Color in life: The dorsum of head, body, limbs, hands and feet are pale brown with small to large, irregularly shaped, dark chocolate-brown blotches on the head, body and upper arms, and bands of the same color on other parts of the limbs (Plate I). Clusters of iridophores are superimposed unevenly over the body, head, and limbs. The ground color of the flanks is paler, tending towards yellowish brown. A wash of chocolate-brown extends from the lip to the nostril and below the canthus, to the eye, and from the eye to the tympanum. The iris is yellowish golden with black reticula-

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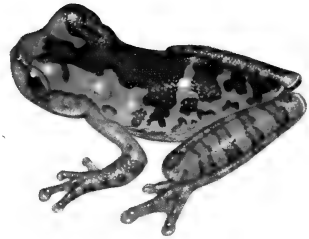
PLATE 1. *Hyla trux:* A. Guerrero, 28.0 mm snout-vent length (BMNH 1971.441, juvenile female; paratype). B. Guerrero, 51.2 mm (KU 137550, immature female; paratype). C. Guerrero, 81.0 mm (KU 137551, mature male; holotype). →

PLATE 1



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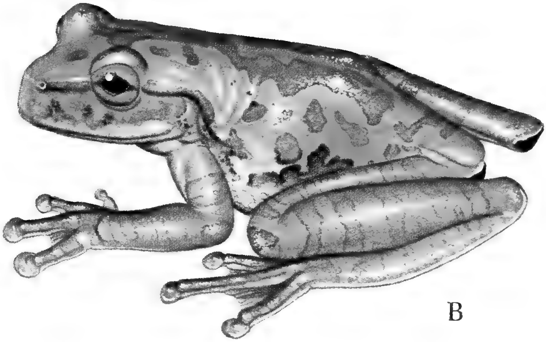

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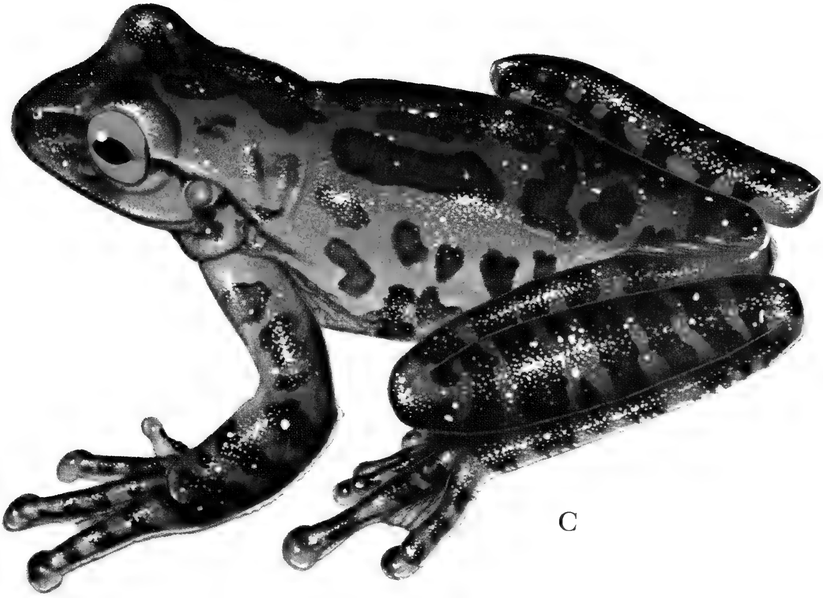

C

tions; the tympanum is pale brown. The lateral edges of the lower limbs and outermost digits are creamy white. The axillae and groin are pale blue; the webbing of the hands and feet is pale blue, laced with thin black lines. The venter is dull creamy brown, with the greatest concentration of melanophores on the throat, abdomen and thighs. The nuptial spines are dark brown.

Color in alcohol: As in life, except that all browns are darker, making detection of the dorsal blotches more difficult. The iris is dark bluish brown, the webbing slate gray, and the nuptial spines dark yellowish brown. The creamy-white color of the borders of the limbs and digits is not evident, and the belly and throat are suffused with grayish brown.

Variation.—The snouts of both large males (79.1 and 81.0 mm snout-vent length) are pointed, but those of smaller males (up to 67 mm) and the largest female (51.2 mm, immature) are noticeably more rounded from above. This apparently represents an ontogenetic change found also in the closely-related *H. taeniopus* (see Duellman, 1965). The peculiar, hypertrophied web between toes one and two is found only in the two large, sexually mature males (Fig. 1b). The quadratojugal is slightly reduced in most individuals and does not have bony contact with the maxilla; in one, only a short spine is present. On one or both sides in three individuals the quadratojugal is in bony contact with the maxilla. The testes of the two mature males range in length from 15.1 to 17.1 mm (mean, 16.4). Morphological variation in some mensural characters is given in table 1.

The considerable color variation apparently is only partly ontogenetic (Plate I). Only the two adult males have blue webbing. In a juvenile female (28.0 mm snout-vent) and several subadult males (59.2-67.0 mm), the dorsal ground color is a rich orange-brown; this ground color is superimposed with the chocolate brown blotches (golden-edged in the males) and iridophores found in the full-grown males. The flanks are yellowish (greenish in one male), and the hands and feet, including webbing, are pale to vivid orange; in several of the half-grown males, there is a chocolate brown band below the tarsal fold which extends to the heel. The rear of the thigh has a greenish tinge, and the border along the lateral edges of the lower limbs and outer edges of the digits is golden white. In the juvenile female, the brown blotches on the dorsum are bordered by black, and the bands on the limbs are orange with brown borders; the rear of the thighs is orange. In two immature females (34.1 and 51.2 mm) the dorsal ground color is a pale yellowish tan with dark-bordered tan or greenish tan

TABLE 1. Morphological variation in the type series of two Mexican *Hyla*.
(All measurements in mm; means in parentheses below ranges.)

Species	*Hyla mykter*			*Hyla trux*		
Sex and age	adult ♀	immature ♂	adult ♂	immature ♀♀	immature ♂♂	adult ♂♂
Number	1	1	1	4	3	2
Snout-vent	50.9 ----	30.8 ----	40.1 ----	28.0-51.2 (38.3)	59.2-67.0 (64.4)	79.1-81.0 (80.1)
Tibia/ snout-vent	0.436 ----	0.481 ----	0.509 ----	0.464-0.486 (0.473)	0.496-0.510 (0.505)	0.432-0.491 (0.462)
Foot/ snout-vent	0.452 ----	0.438 ----	0.504 ----	0.421-0.469 (0.447)	0.454-0.465 (0.460)	0.429-0.444 (0.437)
Hand/ snout-vent	0.301 ----	0.325 ----	0.339 ----	0.287-0.309 (0.299)	0.307-0.318 (0.311)	0.268-0.283 (0.276)
Head width/ snout-vent	0.314 ----	0.334 ----	0.327 ----	0.342-0.364 (0.351)	0.312-0.338 (0.324)	0.295-0.298 (0.297)
Head length/ snout-vent	0.275 ----	0.296 ----	0.282 ----	0.314-0.357 (0.332)	0.297-0.320 (0.310)	0.313-0.317 (0.315)
Prevomerine teeth (total)	8 ----	7 ----	9 ----	5-11 (7.8)	10-15 (11.7)	7-17 (12)

blotches; in the larger female, the flanks are pale blue; the throats of these two individuals are pale yellow in one and golden white in the other. Little metachrosis was noticed, except for darkening which was especially apparent in the adult males.

Habitat and Habits.—These frogs were found along cascading mountain streams flowing through cool, moist, oak-pine or (at the lower elevations) bamboo-tree fern cloud forests near Cerro Teotepec, Guerrero, at elevations between 1760 and 2120 meters. At one ridge-top locality the general habitat was dry, but frogs were found along a lush, plant-shrouded stream in a ravine; all were collected within 2 m of the stream. One frog was wedged among rocks and a root system behind a small waterfall in such a way that water continuously flowed around the animal. Another individual was 1 m from the stream, well camouflaged among some relatively dry rocks in an outcropping, whereas another was caught on a cliff face beneath a loose patch of moss through which water constantly percolated. All of these individuals were collected in mid-morning. At night, an immature female was found abroad on a moss-covered rock by a stream. Both large males were found, during the early evening, sitting in root systems 2-3 m directly above open pools in the stream. Another immature female collected at night was completely exposed on a heavy vine over the stream. The climate at these localities was moderate. It often rained by night and day, but the temperatures never reached the near-freezing levels experienced at night at higher elevations in this area. These frogs were quiescent when discovered but became very active after capture. Although males possess vocal slits, none was heard calling. Other frogs taken at the same time along these streams were *Eleutherodactylus saltator, E. rugulosus, Hyla mykter, H. pentheter* and *Ptychohyla* sp.

Remarks.—The combination of a large adult size, a brown dorsum with darker brown blotches, a clear palpebral membrane, a tarsal fold, and absence of an axillary membrane places *Hyla trux* in the *Hyla taeniopus* species group as characterized by Duellman (1970). However, *trux* differs from all three previously described species of that group. The quadratojugals in *taeniopus, chaneque* and *altipotens* are well ossified and articulate with the maxillae. Radiographs show that the quadratojugal in *trux* is more slender, often reduced, and only rarely articulates with the maxilla. The nuptial excrescences of *trux*, as described for the holotype, are more extensive than those found in the other members of the group (these are apparently lacking altogether in *altipotens*). Finally, the hypertrophied webbing between toes one and two of mature males is not found in any other member of the species group; the function of this enlarged web and its condition in adult female *trux* are not known.

Hyla trux differs from other members of its species group in several details. It differs from *taeniopus* in having an elongate (rather than sickle-shaped) prepollical spine, a shorter anal sheath, and more extensively webbed hands. *Hyla trux* is distinguished from *chaneque* by the absence of a tuberculate dorsum and the presence of a pointed snout (at least in adult males), an elongate (rather than sickle-shaped) prepollical spine, more extensively webbed hands, shorter legs, and a shorter head. *Hyla trux* differs most noticeably from *altipotens* by possession of vocal slits and nuptial excrescences in mature males, shorter legs, and a longer head. It also lacks the bronze-bordered canthus, the creamy yellow reticulations on the flanks and thigh, and the middorsal stripe found in some *altipotens.* An ossified prepollical spine cannot be detected with certainty in the two available skeletons of *altipotens* (mature male and female), although radiographs suggest it is ossified at the proximal end.

Of these three species, *Hyla trux* shares the greatest number of characteristics with *taeniopus.* These two species are more similar to each other in body, limb and head proportions, and in general coloration than either is to any of the other two species. Furthermore, the development of a pointed snout at maturity in males of *taeniopus* occurs also in males of *trux.* Adult males of both species have vocal slits; the nuptial excrescences of *taeniopus,* although not as well developed as those of *trux,* are considerably more extensive than are those of males of *chaneque.* All four species are found in cloud forests at intermediate elevations in southern México: *Hyla taeniopus* (Hidalgo, Puebla and Veracruz, 1200-2100 m), *trux* (Guerrero, 1760-2120 m), *chaneque* (Oaxaca and Chiapas, 800-2200 m) and *altipotens* (Oaxaca, 1100-1900 m).

Etymology.—The Latin name *trux,* meaning fierce or ferocious, refers to the liberally spined fingers.

Distribution.—Known only from localities in the vicinity of Cerro Teotepec in the Sierra Madre del Sur of Guerrero, at elevations between 1760 and 2120 m.

Hyla mykter new species

(Figure 2; Plate 2)

Holotype.—Adult male, KU 137553, from 11.4 km (by road) southwest of Puerto del Gallo, Guerrero, México [about 35 km airline northeast of Atoyác de Álvarez], elevation 1985 meters; collected 20 December 1969, by K. Adler, D. M. Dennis and D. H. Snyder.

Paratypes.—KU 137552, Asoleadero, elevation 2520 m, collected 17 December 1969; USNM 192421, 8.2 km (by road) SW of Puerto del Gallo, elevation 2050 m, collected 20 December 1969; all from Guerrero, México; same collectors as for holotype.

Diagnosis.—A medium-sized member of the *Hyla bistincta* species group (males to 40.1 mm snout-vent length, females to 50.9 mm) possessing long fingers with vestigial webbing (except outermost which are one-fifth webbed) and a prominent, non-projecting prepollical spine; a rounded, truncate snout with slight rostral keel; toes four-fifths webbed; a weakly defined thoracic fold; nuptial excrescences on the prepollex of adult males; moderately long legs; no quadratojugal; no axillary membrane or vocal slits; and a yellowish, olive-green or light gray-brown dorsum with mottled flanks and thighs in life.

Description of Holotype.—The holotype is an adult male with a snout-vent length of 40.1 mm. The head is broad and moderately flat (11.3 mm long, 13.1 mm wide) with slightly protuberant nostrils which are horizontally oval; the internarial distance is 3.0 mm. The canthus is rounded but distinct and slightly concave in profile; the loreal region is slightly concave. As seen from above the snout is long and slightly pointed, with a moderately distinct rostral keel, and is round in lateral profile. The eye length is 3.7 mm; the upper eyelid is 3.5 mm wide, and the interorbital distance is 3.5 mm. The tympanum is small, distinct, round, and 2.1 mm long; there is a strong supratympanic fold extending from posterior border of eye to above the insertion of the arm and barely covering the upper edge of the tympanum. The length of the hand is 13.6 mm (Fig. 2a). The fingers are long, $1 < 4 < 2 < 3$, with greatly reduced webbing. The webbing between first and second fingers is vestigial; that between second and third fingers extends to the distal end of the antepenultimate phalanx, and the webbing between the third and fourth fingers extends to the middle of the antepenultimate phalanx. The discs are moderately large; that of the third finger is 1.9 mm wide. The prepollex is moderately enlarged with a large, spine-shaped, non-projecting prepollical spine. The prepollex and inner edge of the first finger are extensively covered with nuptial spines; isolated groups of spines also occur on the outer edge of the first finger below the disc, along the entire inner edge of the second finger, on the inner edges of the two outermost subarticular tubercles of the third finger, and in tiny patches along outer edges of the two outermost subarticular tubercles of the fourth finger.

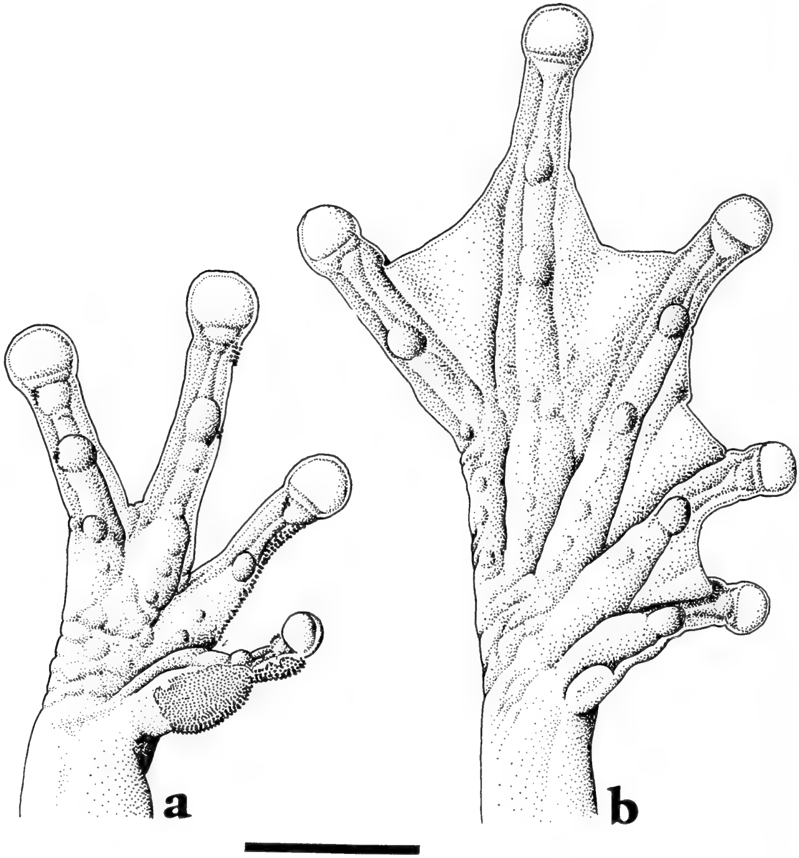

Fig. 2. Hand (a) and foot (b) of *Hyla mykter* (KU 137553, mature male; holotype). Scale is 5 mm in length.

The subarticular tubercles are round or oval; none is bifid. Distinct supernumerary tubercles are present on the proximal segments of the fingers but are indistinct on the palms; a few small pustules are present along the ventrolateral edge of the forearm but are not raised into a ridge. There is a fold on the wrist. The length of the foot is 20.2 mm (Fig. 2b). The toes are moderately long, 1 < 2 < 5 < 3 < 4, and about four-fifths webbed. The first, fifth, and

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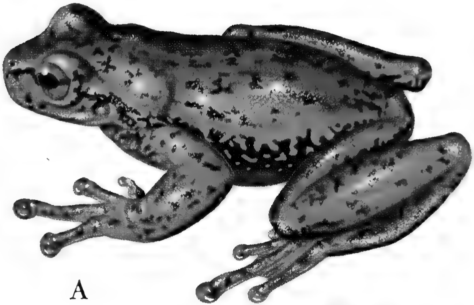
Plate 2. *Hyla mykter:* A. Guerrero, 40.1 mm snout-vent length (KU 137553, mature male; holotype). B. Guerrero, 50.9 mm (KU 137552, mature female; paratype). *Hyla bogertae:* C. Oaxaca, 43.3 mm (LACM 44403, mature female; paratype). D. Oaxaca, 49.0 mm (LACM 44402, mature female, paratype). →

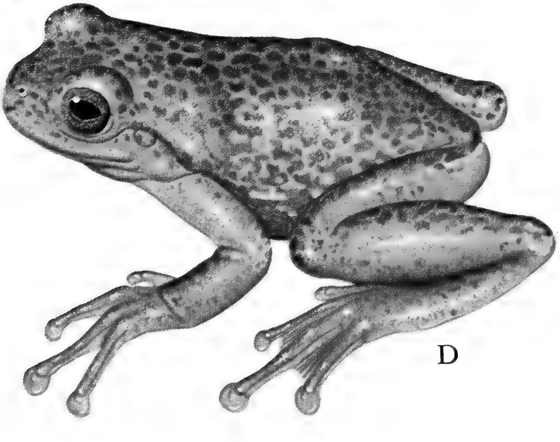
PLATE 2



A

B

C



D

outer sides of the second and third toes are webbed to the base of the disc; the inner side of the second toe is webbed to the base of the penultimate phalanx, and the fourth toe and inner side of the third are webbed to distal end of antepenultimate phalanx. The inner metatarsal tubercle is distinct and elliptical; there is no outer metatarsal tubercle. The tarsal fold is short and faint. The subarticular tubercles are round or oval; none is bifid. Indistinct supernumerary tubercles are present on the soles and proximal segments of the toes. The discs are moderately large, that of the fourth toe is 2.0 mm wide. The tibia length is 20.4 mm; the tibiotarsal articulation extends to the middle of the eye, and the heels overlap 5.7 mm when the legs are flexed and held at right angles to the body. The cloacal sheath is moderately long, grooved medially, directed posteroventrally, and opens just below the midlevel of the thighs; there is a transverse dermal fold above the sheath and large, distinct pustules on the thigh adjacent to its aperture. The skin is only slightly thickened; that of the dorsum and undersurfaces of arms, chest, and lower legs is smooth; that of the throat, abdomen, and undersurfaces of the thighs is granular. There is no enlarged axillary membrane. The dentigerous processes of the prevomers are each the same size as a choana, oval, and oriented transversely between the choanae, nearer one another than to choanae; there are 4-5 prevomerine teeth. The choanae are oval, each 1.0 mm long. Vocal slits are absent. The tongue is cordiform, slightly notched and one-sixth free posteriorly. As determined from radiographs, quadratojugals are absent.

Color in life: The dorsum of the head and body is pale yellowish green, and the limbs are pale yellowish brown, all covered with black reticulations and spots; the flanks and rear of the legs and lower arms are mottled with black and pale yellow (Plate 2). The canthus and supratympanic fold are black-edged and the tympanum is brownish green. The iris is golden orange with black reticulations. The knee and ventrolateral edges of the forearms and legs are black-edged. The venter is mottled dusky brown, tending toward deep purplish gray or chocolate brown around the perimeter, overlaid with some brassy pigment. The nuptial spines are dark brown.

Color in alcohol: The body is dull grayish brown above with gray reticulations; gray mottling is present on the flanks. The gray or brown edging of venter and the yellow and green ground color of the dorsum are not evident. The ventral surfaces are pale yellowish cream with gray mottling. The iris is bluish, and the webbing is pale gray. The nuptial spines are brown.

Variation.—The snout of the adult females (50.9 mm snout-vent length) as well as that of an immature male (30.8 mm) are pointed and possess a rostral keel. The female has only vestigial webbing between all fingers. The female has noticeably shorter legs and feet, proportionate to body length, than have either of the males. The female is also more robust than either male but has a slightly narrower head. The quadratojugal is lacking in all three individuals. Morphological variation in some mensural characters is given in table 1.

Apparently only moderate color variation exists in this species (Plate 2). The adult female was pale gray-brown with a little dark flecking above, with a gray tympanum. There was a green wash along the upper rear edge of the thigh and in the groin, and some brassy overlay on the venter including throat; there were a few yellow spots or blotches along the flank and front edge of arm. The immature male was a deep olive-green dorsally mottled with black flecks and reticulations. Little metachrosis was noticed, except that most individuals were dark greenish or dark yellowish tan if sluggish when first caught, and only later lightened to the colors described above.

Habitat and Habits.—These frogs were taken in a variety of locations, all in cool, moist, oak-pine or (at the lower elevations) bamboo-tree fern cloud forests near Cerro Teotepec, at elevations between 1985 and 2520 meters. All specimens of *Hyla mykter* were taken in December. The female (which has large pigmented eggs) was found early in the morning in a bromeliad 2 m above ground in a pine tree, at the edge of a large clearing at Asoleadero (2520 meters). The vegetation and climate at this locality have been described by Musser (1964) and Adler (1965). The day was warm (21° C maximally) and dry, but temperatures fell to near, or below, freezing at night; there was considerable frost on the logs and boulders in the clearing at daybreak. The two males were taken along lush, cascading mountain streams at considerably lower elevations. The habitat at the type locality is dominated by tree ferns, bamboo, pine and oak, and dissected by deep ravines containing plant-shrouded streams (this is also the type locality for *H. trux*). The holotype was collected at 8:30 PM, fully exposed on vegetation directly over a stream; whereas, the smaller male was found at night in a bromeliad which had fallen along a wide, open stream. The climate at these localities was considerably warmer than at Asoleadero. None of the males was heard to call. Other frogs taken at the same time along these streams include *Hyla trux, H. pentheter* and *Eleutherodactylus saltator.*

Remarks.—The relationships of *Hyla mykter* appear to lie with presumably the most advanced members of the *Hyla bistincta* species group. These species (namely *bogertae, crassa, pachyderma, robertsorum* and *siopela*) possess thick glandular skin, blunt heads, large webbed feet, and nuptial excrescences, and lack axillary membranes and vocal slits. We have not seen specimens of *pachyderma* or *crassa,* and have relied on Duellman (1970) for accounts of their characteristics. *Hyla mykter* differs from the latter two species and *bogertae* in having a weak tarsal fold, the outer fingers slightly webbed, a small spine-shaped quadratojugal, a rostral keel and a less robust body. It is distinguished from *crassa* by having feet four-fifths webbed and a well-defined tympanum. *Hyla mykter* differs from *pachyderma* in possessing smaller nuptial spines, a weak thoracic fold, and a well-defined tympanum in males (indistinct only in male *pachyderma*). The species is distinguished from *bogertae*[3] by its rounded canthus and a gray-mottled belly. *Hyla mykter* differs from *robertsorum* in having a small quadratojugal, a more pointed snout with a better-developed rostral keel, more extensively webbed outer fingers, and, in males, a long cloacal sheath and less robust body shape. In two or three females of the *robertsorum* examined, the snout is slightly pointed, and in one there is a faint trace of a rostral keel; a few individuals of both sexes have a trace of webbing between the outer fingers, but in none of them is it as well developed as it is in *siopela* and *mykter.*

Hyla mykter and *siopela* seem to be closely related because they share more characteristics than either does with other members of the subgroup. Both have a trace of webbing between the outer fingers and have a rostral keel (rarely absent in *siopela*), although the snout is more truncate (in both dorsal and side views) and the canthus more angular in *siopela.* When viewed from above, the nostrils of *siopela* are more anterior than are those of *mykter,* which are located dorsal to the margin of the upper lip. Nuptial excrescences are restricted to the first and second fingers in *siopela* (2 males examined) but at least some spines are found on all fingers in *mykter* (1 mature male); however, this difference may not hold in larger samples. The toes are slightly more fully webbed in *mykter,* although the difference is not as great as a comparison

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[3] The availability of specimens and colored slides of the recently described *Hyla bogertae* has made it possible to illustrate certain features of this form not given in the type description. In an effort to maintain the uniformity of treatment used by Duellman (1970), we have included color illustrations of adults (Plate 2) and drawings of the hands and feet (Fig. 3) because of the usefulness of these features in hylid systematics.

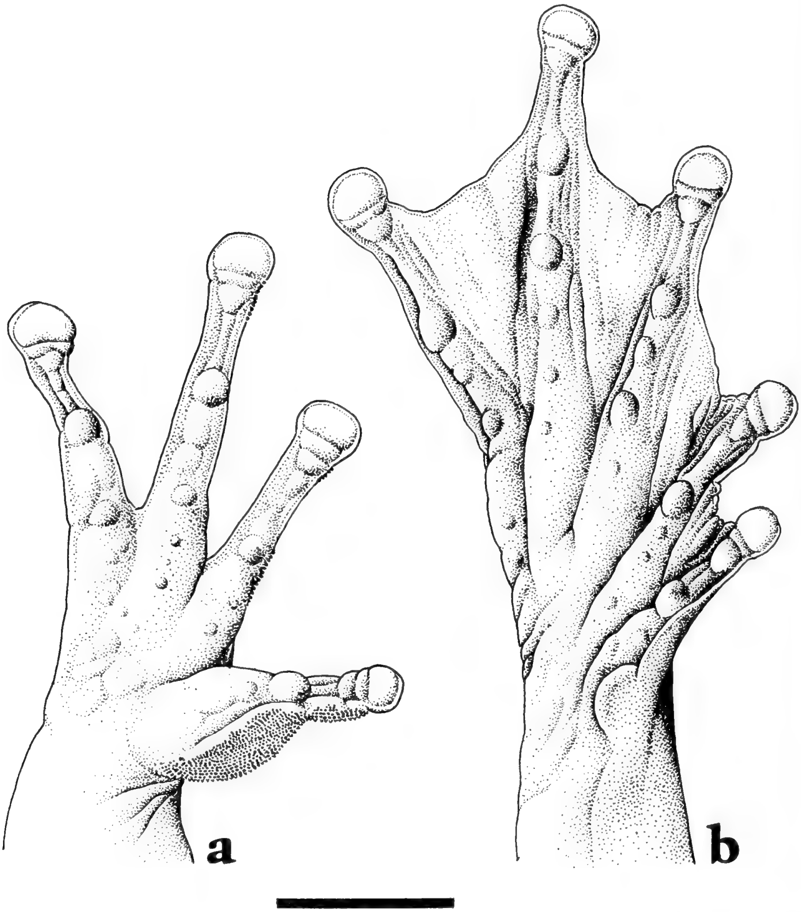

FIG. 3. Hand (a) and foot (b) of *Hyla bogertae* (LACM 44401, mature male; paratype). Scale is 5 mm in length.

of our drawing (Fig. 2) with that of *siopela* (Duellman, 1970, fig. 235-C) suggests; the latter figure shows an individual with less webbing than typifies most of the individuals we have seen of that species. The cloacal sheath of the single adult male *mykter* is longer than that of either of the two male *siopela*. *Hyla mykter* differs further in having a weak, instead of a well-developed, tarsal fold and in having proportionately longer legs. *Hyla siopela* and *mykter* are the only two members of this subgroup which typically have rostral keels and traces of webbing between the two outermost fingers. They also are the most thin-skinned and least robust of the six species. Of the remaining four species, *robertsorum* most closely approaches *siopela* and *mykter* in these characteristics and presumably is closely related to them. The members of this subgroup of the *Hyla bistincta* species group typically are found in moist oak-pine forests at intermediate to high elevations in southern México and can be subdivided further into two series. The species in the first are more robust, have more glandular skin and include *bogertae* (Oaxaca, 2650 m), *crassa* (Oaxaca, 2300 m), and *pachyderma* (Veracruz, 1600 m); whereas in the second series the species are less robust, have thinner skin and include *mykter* (Guerrero, 1985-2520 m), *robertsorum* (Puebla and Hidalgo, 2250-3100 m) and *siopela* (Veracruz, 2500-2650 m).

Several frogs referred to the *Hyla bistincta* group have been recorded from Guerrero. The types and only known specimens of *Hyla chryses* were collected between 2540 and 2600 meters near Asoleadero. (This species is readily distinguished from *mykter* by the well-developed axillary membrane, the more slender and thinner-skinned body, and the absence of nuptial spines in *chryses.*) The three metamorphosing frogs from nearby Omiltemi (UIMNH 38023-25), referred to *bistincta* (by Duellman, 1964, and many subsequent authors including Adler, 1965), have been reexamined. All have tiny tailbuds (specimens collected in August, 1940), a mottled pattern on the dorsum, and long, virtually webless fingers. Newly metamorphosed individuals of *chryses* and *mykter* are not available; thus, these three specimens cannot be referred to any of the species known from Guerrero, although they seem to be allied to the *Hyla bistincta* group. They might even be referrable to an as-yet-unnamed form in this species group based on an examination of eight frogs (IPN CB 149-156) collected in April 1963 at Agua Fria, a logging camp about 10 km E of Cerro Teotepec; these are the same specimens referred to *bistincta* by Duellman (1970, p. 698) as from "22 kilometers southwest of Yextla." All are in a poor state of preservation and exact measurements cannot be made; the snout-vent lengths of the three males are about 38, 39 and 39 mm; those of females range from 34 to 39 mm. They lack the long cloacal sheath, vocal slits, and flank pattern characteristic of *bistincta* and *pentheter,* and also lack the axillary membranes found in *chryses.* Their fingers are long, and the males have nuptial excresences on the prepollex and smaller patches of spines on all other fingers; however, they have no webbing between the fingers, and lack the rostral keel and mottled venter characteristic of *mykter.* They were found by day in and along the edge of a pond at 2600 meters; their identity must await the acquisition of fresh material.

One other frog from Guerrero (UMMZ 125376, an adult female from near Asoleadero) also has been referred to *bistincta* (by Adler, 1965, and subsequent authors). A reexamination of this specimen shows this determination to be incorrect; the specimen lacks the bold markings on the flanks characteristic of *bistincta,* has a dark venter, is considerably smaller in size, and, according to radiographs, lacks a prepollical spine. It differs from *mykter* in the character of the prepollical spine, in having longer legs, and in several features of coloration; it is also dissimilar to the unnamed Agua Fria specimens in being larger, possessing reticulations on the flanks, and lacking a prepollical spine.

Thus, apparently none of the published references of *Hyla bistincta* in Guerrero is, in fact, based on specimens clearly referrable to that species. Together with David H. Snyder, we collected four adult *bistincta* (KU 140420-23) in a moist cove along a dry, rocky canyon 4.5 km (by road) E of El Limón (about 6 km SW of Chilapa), Guerrero, at 1525 m elevation. The only other member of this species group known from Guerrero is *H. pentheter,* previously known only from Oaxaca; we obtained three individuals (KU 140424-26) at an elevation of 2000 m in the vicinity of Cerro Teotepec.

Etymology.—The specific name is from the Greek μυκτήρ, meaning nose, and is given in allusion to this frog's distinctive snout.

Distribution.—Known only from localities in the vicinity of Cerro Teotepec in the Sierra Madre del Sur of Guerrero, at elevations between 1985 and 2520 m.

SUMMARY

Two new frogs of the family Hylidae are described from the cloud forests of the Sierra Madre del Sur of Guerrero. They are members of two different species groups which have representatives primarily in the mountains of eastern and southern México. Both are illustrated (hands and feet; juveniles and adults in color).

Hyla trux, a member of the *H. taeniopus* species group, is a large species (males to 81.0 mm snout-vent length) with a mottled brown dorsum, vocal slits and blue webbing in adult males, absence of an axillary membrane, presence of a tarsal fold, nuptial spines on all fingers of mature males, and a hypertrophied web between toes one and two (in mature males). Specimens were taken at elevations between 1760 and 2120 m at several localities, all within 30 km of Cerro Teotepec. This species seems to be closely related to *H. taeniopus* Günther of the states of Puebla, Veracruz, and Hidalgo.

Hyla mykter, a member of the *H. bistincta* species group, is a medium-sized species (males to 40.1 mm; females to 50.9 mm) with a yellowish olive or pale gray-brown dorsum, absence of vocal slits and axillary membranes, no quadratojugal, nuptial spines on all fingers of mature males, long fingers with vestigial webbing, and a weak rostral keel. Specimens were taken at elevations between 1985 and 2520 m at several localities, all within 35 km of Cerro Teotepec. This species seems to be most closely related to *H. siopela* Duellman of the state of Veracruz.

Hyla bogertae Straughan & Wright, a member of the *H. bistincta* species group recently described from Oaxaca, is illustrated (hand and foot; adults in color).

RESUMEN

Dos nuevas ranas de la familia Hylidae, procedentes de las selvas nubladas de la Sierra Madre del Sur (México, Edo. Guerrero), son descritas en el presente trabajo. Estas especies pertenecen a dos grupos distintos de especies incluídas en el genero *Hyla* y con representantes el las áreas montañosas del sur y extremo este de México. Ambas especies son ilustradas (manos y pies; juveniles y adultos en color).

Hyla trux es un miembro del grupo *taeniopus;* se trata de una especie grande, machos con 81 mm de longitud naso-ventral y dorso irregularmente manchado de marrón; fisuras vocales y membrana interdigital de color azul; membrana axilar ausente; pliegue tarsal presente. Espinas nupciales presentes en todos los dedos de machos sexualmente maduros. Membrana interdigital entre los dedos uno y dos, hipertrofiada. Los ejemplares fueron colectados en varias localidades ubicadas entre 1760 y 2120 m altura, todas ellas a unos 30 kms del Cerro Teotepec. Esta especie parece estar relacionada a *H. taeniopus* Günther de los estados de Puebla, Veracruz e Hidalgo.

Hyla mykter es un integrante del grupo *bistincta.* Es una especie de talla media (longitud maxima de los machos, 40.1 mm; hembras 50.9). Coloración dorsal amarillo-oliváceo o marrón-grisáceo claro. Fisuras vocales y membranas axilares ausentes; quadratojugales ausentes. Espinas nupciales presentes en todos los dedos de los machos maduros; dedos largos con membranas interdigitales vestigiales. Cresta rostral débil. Los ejemplares fueron colectados en varias localidades ubicadas entre los 1985 y 2520 m altura, a unos 35 kms del Cerro Teotepec. Esta especie parece relacionada a *H. siopela* Duellman del Estado de Veracruz.

Hyla bogertae Straughan y Wright, miembro del grupo *bistincta,* recientemente descrita de Oaxaca, es ilustrada (mano y pié; adulto en color).

ACKNOWLEDGMENTS AND METHODS

We thank David H. Snyder (University of Notre Dame) for field assistance and for comments on the manuscript. William E. Duellman (University of Kansas) kindly provided relevant portions of his monograph of Middle American hylid frogs in advance of publication and loaned a large collection of comparative material (designated KU). Other museum abbreviations are: University of Michigan Museum of Zoology (UMMZ), University of Illinois Museum of Natural History (UIMNH), Los Angeles County Museum of Natural History (LACM), Instituto Politechnico Nacional, Ciéncias Biológicas, México (IPN CB), United States National Museum of Natural History (USNM), Field Museum of Natural History (FMNH), American Museum of Natural History (AMNH), and British Museum (Natural History) (BMNH). Certain individuals loaned specimens from several of these institutions, namely Joseph T. Collins, Ticul Alvarez S., John W. Wright, Mrs. Dorothy M. Smith, and Charles F. Walker. James P. Collins and Arnold G. Kluge (both UMMZ) assisted in making x-rays. We thank Alfredo Sartorius Z. and his colleagues of Puerto del Gallo, Guerrero, for their hospitality, and Juan Luís Cifuentes L. (formerly of the Secretaria de Indústria y Comércio, México) who provided our collecting permit. Carlos Machado-Allison (University of Notre Dame) translated the summary into Spanish. Field work involved in this study was supported incidental to research on salamander reproductive biology assisted by a grant from the Society of the Sigma Xi.

Methods of measurement of morphological features and of geographic distances are as indicated in Adler (1965:16).

SPECIMENS EXAMINED

Hyla altipotens Duellman. Oaxaca: 33-37 km N San Gabriel Mixtepec, KU 101002-06, 101008; 104341-42 (skeletons).

Hyla bogertae Straughan & Wright. Oaxaca: 1.6 km S La Cofradia, LACM 44401-03.

Hyla chaneque Duellman. Oaxaca: 4.2-16 km S Vista Hermosa, KU 86961-66, 86968, 86971; 84907-08 (skeletons); 8 km S Yetla, KU 86967.

Hyla charadricola Duellman. Puebla: 14.4 km W Huachinango, KU 53813-15, 58415-22; 55624, 59813 (skeletons).

Hyla chryses Adler. Guerrero: 38 km airline WNW of Chilpancingo, UMMZ 125372-73, 125375; KU 106306.

Hyla mykter, new species. Guerrero: the type series, as listed above.

Hyla robertsorum Taylor. Hidalgo: El Chico Parque Naciońal KU 71265-95; 59824-25, 71757 (skeletons).

Hyla siopela Duellman. Veracruz: W slope Cofre de Perote, KU 100976-80, 100982-85, 105628-29; 117428-29 (skeletons); Cofre de Perote, KU 117430 (skeleton).

Hyla taeniopus Günther. Hidalgo: 3 km W Xochicoatlán, KU 53820-23, 53825-26; 55623, 59826 (skeletons); 2.5-4 km SW Tianguistengo, KU 53827-30. Puebla: 3.7 km NNE Tezuitlán, KU 53832-37, 57827; 55602-03 (skeletons).

Hyla trux, new species. Guerrero: the type series, as listed above.

Hyla, species uncertain. Guerrero: Omiltemi, UIMNH 38023-25; Agua Fria, 10 km E Cerro Teotepec, IPN CB 149-56; between Puerto Chico and Asoleadero, UMMZ 125376.

LITERATURE CITED

Adler, K.
1965. Three new frogs of the genus *Hyla* from the Sierra Madre del Sur of México. Occas. Papers Mus. Zool. Univ. Michigan, 642:1-18, pl. 1.

Duellman, W. E.
1964. A review of the frogs of the Hyla bistincta group. Univ. Kansas Publ. Mus. Nat. Hist., 15:469-491.
1965. Frogs of the *Hyla taeniopus* group. Copeia 1965 (2):159-168.
1970. The hylid frogs of Middle America. Monogr. Mus. Nat. Hist. Univ. Kansas, 1:xii+1-753, pl. 1-72.

Musser, G. G.
1964. Notes on geographic distribution, habitat, and taxonomy of some Mexican mammals. Occas. Papers Mus. Zool. Univ. Michigan, 636: 1-22.

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VARIATION IN THE CENTRAL AMERICAN IGUANID LIZARD, *ANOLIS CUPREUS*, WITH THE DESCRIPTION OF A NEW SUBSPECIES

By

HENRY S. FITCH,[1] ANTHONY A. ECHELLE
AND ALICE F. ECHELLE[2]

In the course of ecological studies of Costa Rican lizards conducted by the senior author from October 1967 to March 1970, *Anolis cupreus* Hallowell was found in larger numbers and at more localities than any other species of lizard. Approximately 3450 individuals of this small Pacific coast anole were processed and recorded in the field in a mark-and-recapture program. Notable differences were observed between individuals, geographic populations, and the sexes. The recent resurrection of *Anolis hoffmanni* Peters (a species long considered a synonym of *A. cupreus*) by Williams and Smith (1966) together with variation observed among our samples, suggested that more than one taxon was represented in our accumulated field records. In order to determine the number of taxa involved, series of specimens were collected throughout the range of *Anolis cupreus* in Costa Rica and near the northern end of the range of the species in Guatemala. Additional preserved specimens from Costa Rica and western Nicaragua were examined in the University of Kansas Museum of Natural History (KU). Localities represented by our collections are shown in figure 1. Populations of *A. cupreus* at or near all Costa Rican localities shown in figure 1 were studied in all seasons, thereby providing information on population structure and other aspects of natural history.

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[1] University of Kansas Natural History Reservation, Lawrence, Kansas 66044.

[2] University of Oklahoma Biological Station, Willis, Oklahoma 73462.

The large series of specimens from those localities permitted study of individual variation and sexual differences. Knowledge of such factors enhances the validity of geographic comparisons.

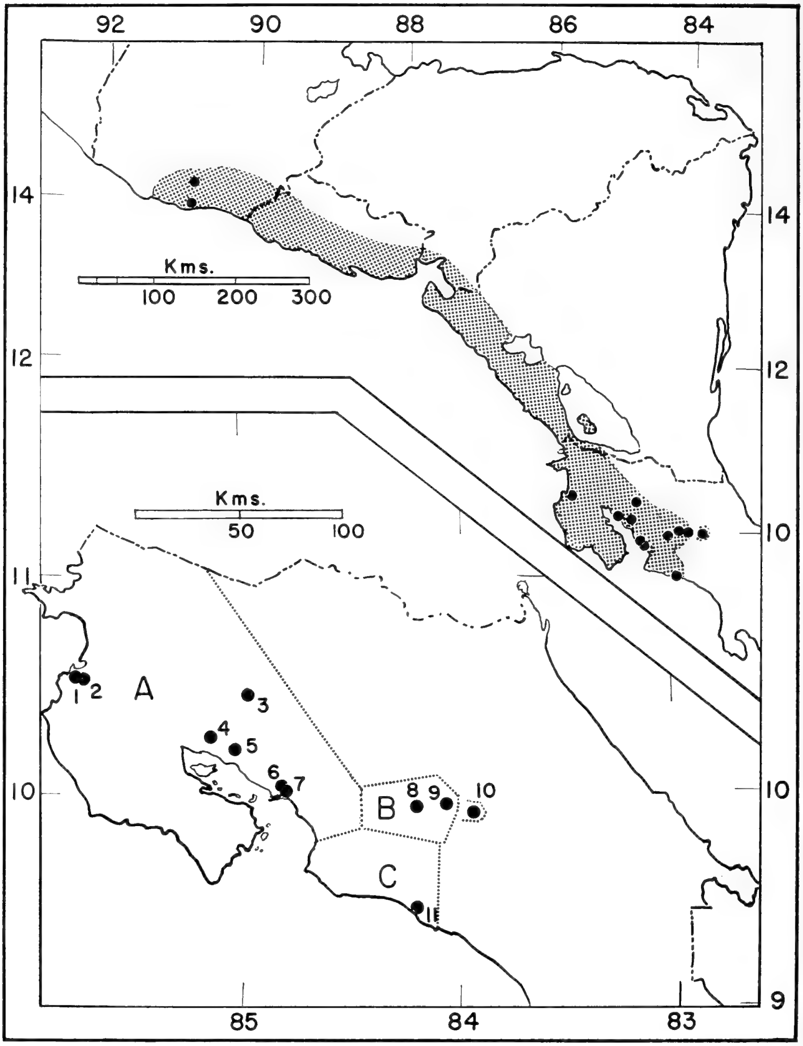

FIG. 1. Map of Central America showing probable range of *Anolis cupreus* (shaded) based on specimens collected by the authors and examined in life (dots), museum specimens, and published records and statements by Taylor (1956), Stuart (1955), and Peters and Donoso-Barros (1970). Inset below is a map of Costa Rica showing probable ranges of three subspecies of *Anolis cupreus:* A. *A. c. cupreus;* B. *A. c. hoffmanni;* C. *A. c. spilomelas.* The localities from which series were examined are: 1. Playa del Coco, 2. Sardinal, 3. Tilarán, 4. Río Higueron, 5. Río Congo, La Irma, 6. Río Naranjo, 7. Boca de Barranca, 8. Turrúcares, 9. San José, 10. Cartago, 11. Quepos.

MATERIALS AND METHODS

Our field data were gathered on six trips to Costa Rica (2 February to 28 March 1965, 13 October 1967 to 16 July 1968, 10 August to 8 September 1968, 18 January to 13 March and 8 August to 8 September 1969, 29 January to 14 March 1970) and one trip to Guatemala, 15 to 24 February 1971, by H. S. Fitch. A. F. Echelle participated in the 1967-68 field trip, and all three authors made the 1970 and 1971 trips together. Population samples, mostly based on live anoles, examined but not killed or removed, were obtained from Costa Rica as follows: on 13 days in eight different months at Boca de Barranca; on two days in one month at Cartago; on 26 days in nine months at La Irma; on 17 days in nine months at Quepos; on three days in three months at Río Naranjo; on 75 days in 19 months at San José; on 15 days in nine months at Sardinal, and on three days in two months at Turrúcares. The samples from Guatemala were obtained on 17, 18 and 19 February, 1971. The small samples that we used from Tilarán and Taboga are in the Museum of Natural History at the University of Kansas.

Many variable characters were examined. Each character was found to have limitations, and each was used on relatively small but representative series of specimens. The conventional characters used in the classification of anoles are those that can be seen in preserved specimens. However, some characters that we found to be equally useful can be seen only in living or freshly killed anoles.

Color and pattern, especially, were found to be useful for showing differences between geographic populations, between age groups, and between the sexes. Because these differences are obscured in preserved specimens, we recorded them only from live or freshly killed anoles. Snout-vent length was measured to the nearest millimeter, and most of the measurements were taken from live lizards or those that were freshly killed. Live weights of most of the anoles processed in 1970 and 1971 were recorded in the field with Oskar Ludi spring scales, to the nearest hundredth of a gram. Length of tail was also recorded for each anole, with regenerated parts noted separately. Relatively large amounts of data were therefore available for size and tail length, and both were found to show significant differences between populations and between the sexes. For comparison of size between populations, only adults were used. Females of 35 mm snout-vent length often contained uterine eggs or enlarged follicles while those that were smaller rarely contained either, hence females of 35 mm in length or larger were considered adults. Males of 40 mm or longer were considered adults; those that were smaller were found to be still growing rapidly.

Other characters that were used were based upon preserved specimens. Number of scale rows around the body varied significantly between geographic populations and between the sexes, but recording them was tedious because of the small granular scales, and was inexact because of irregularities in the rows. Therefore the counts were made on relatively small series of museum specimens.

VARIATION WITHIN AND BETWEEN POPULATIONS

Size.—In *A. cupreus,* as in most iguanids, the male attains a larger size than the female (Figs. 2 and 3). In every series examined, the males were somewhat larger in maximum size (Fig. 3). There is little or no weight difference between males and females of comparable size. Because of continued growth after attaining sexual maturity, the age structure and date of collection influence the comparisons. Most samples are similar in adult size (Fig. 3), but both sexes from Quepos and males from Escuintla are significantly larger. Respectively, these are the southern- and northernmost populations of *A. cupreus* sampled. Sexual difference in size is least in samples from San José and Cartago.

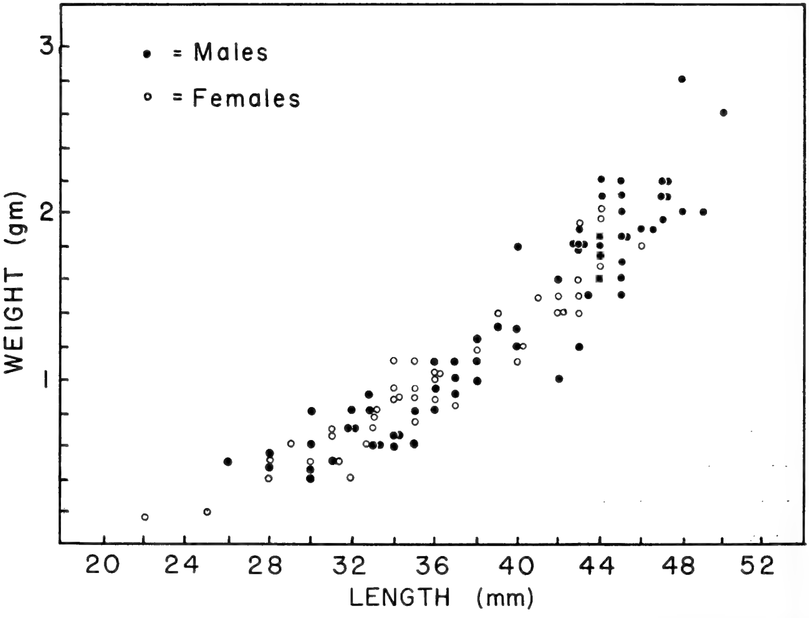

FIG. 2. The relationship between weight and snout-vent length in *Anolis cupreus* collected at San José, San José Province, Costa Rica, February 1970.

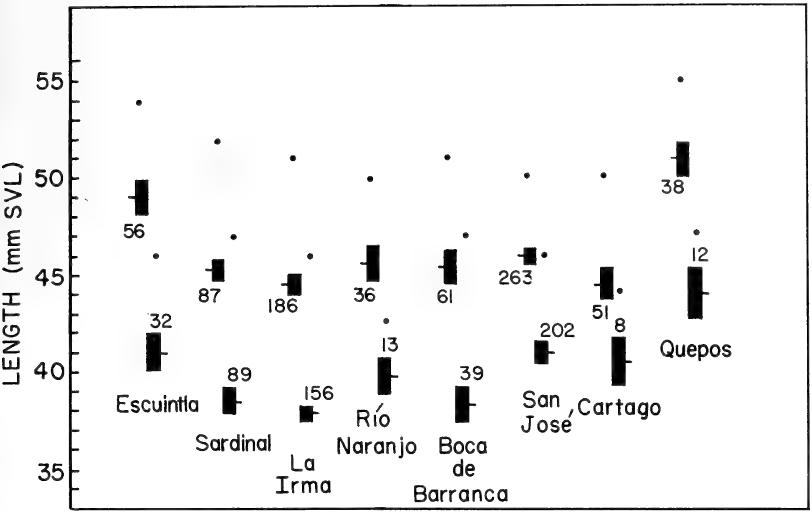

FIG. 3. Snout-vent lengths in adult *Anolis cupreus,* 35 mm or more in females (lower series of figures), 40 mm or more in males (upper series) from eight localities in Guatemala and Costa Rica. Dots indicate maximum lengths; horizontal lines represent means; bars show two standard errors on each side of the means; numbers are sample sizes.

Tail length.—Intact tails are proportionately longer in adults than in young. At Sardinal, Guanacaste Province, Costa Rica, the ratio of tail length to snout-vent length in 203 adults having snout-vent lengths of 40 mm or more is 1.60-2.00 (mean 1.77). Twenty hatchlings (probably in their first month of life) from the same locality have snout-vent lengths of 20 mm or less; the ratio of tail length to snout-vent length is 1.42-1.84 (mean 1.57). Adult males have relatively longer tails than females. Sexual dimorphism in tail length is less, if it exists at all, in hatchlings. In the adult series from Sardinal, the average ratio of tail length to snout-vent length is 1.80 in 112 males and 1.74 in 91 females. The series from the northern (Escuintla) and southern (Quepos) ends of the range have relatively long tails; whereas those from San José on the Meseta Central of Costa Rica are somewhat intermediate, and those from the lowlands of western Costa Rica (Sardinal, La Irma, Boca de Barranca) have relatively short tails (Table 1). The high ratio in females from Escuintla, slightly exceeding the male ratio, probably is an artifact of the small sample size.

Hind Limb.—No geographic variation could be demonstrated in our samples. In 77 per cent of 159 specimens, the fourth toe of the adpressed hind limb lies at a level between the anterior and

TABLE 1.—Comparisons of Various Populations of *Anolis cupreus*.

(Numbers in Parentheses = Sample Sizes)

	Escuintla	Playa del Coco	Sardinal	Taboga	Tilarán	La Irma	Río Naranjo	Boca de Barranca	Turrúcares	San José	Cartago	Quepos
Ratio of Tail Length to Snout-vent Length (Per cent)												
Males	(40)	—	(112)	—	—	(77)	—	(43)	—	(88)	—	(38)
Mean	186.5	—	180.0	—	—	178.8	—	180.2	—	184.4	—	186.9
Range	158-208	—	160-198	—	—	150-193	—	160-198	—	154-214	—	162-205
Females	(28)	—	(91)	—	—	(37)	—	(29)	—	(65)	—	(15)
Mean	186.8	—	173.9	—	—	174.8	—	175.3	—	177.1	—	179.4
Range	171-204	—	157-201	—	—	153-195	—	154-194	—	158-200	—	162-194
Scales around Midbody												
Males	(20)	(9)	—	(6)	(8)	(18)	(19)	—	(12)	(7)	(14)	(28)
Mean	134.0	132.4	—	135.8	119.5	115.1	122.0	—	116.8	114.4	106.8	136.4
Range	112-152	120-140	—	127-147	112-129	101-130	115-141	—	107-128	108-120	100-115	127-150
Females	(10)	(1)	—	(2)	(2)	(10)	(6)	—	(11)	(13)	(8)	(4)
Mean	120.0	120.0	—	125.0	123.5	112.4	118.8	—	110.6	110.6	102.1	127.7
Range	98-140	—	—	125	118-130	99-120	115-123	—	97-123	104-119	94-108	125-133
Digital Lamellae												
Mean	(20)	(11)	—	(8)	(8)	(24)	(25)	—	(23)	(22)	(23)	(32)

Both Sexes	8.70	8.45	—	8.25	7.63	8.46	9.60	—	8.92	8.65	8.83	9.30
Males	9.00	8.50	—	8.28	7.71	8.65	9.68	—	8.92	8.77	9.21	9.60
Females	8.40	8.00	—	8.00	7.00	8.20	9.33	—	8.90	8.44	8.22	8.44
Mode												
Males	9	9	—	9	8	9	10	—	9	9	9	10
Females	8	8	—	8	7	8-9	9	—	9	8	9	8
Contact of Supraoculars with Supraorbital Semicircles (Per cent)												
	(40)	(10)	—	(8)	(10)	(28)	(25)	—	(23)	(20)	(22)	(32)
	38	30	—	25	63	64	64	—	59	75	73	39
Frequency of Occurrence of Pattern Types in Females (Per cent)												
	(33)	—	(52)	—	—	(16)	(12)	—	(21)	(46)	(10)	(6)
Stripe	9.1	—	0.0	—	—	12.5	16.6	—	33.3	35.8	50.0	33.3
Diamonds	18.7	—	0.0	—	—	18.7	8.3	—	33.3	23.9	10.0	33.3
Chevrons	39.4	—	67.0	—	—	18.7	8.3	—	16.7	17.4	0.0	16.7
Nondescript	33.3	—	33.0	—	—	50.0	66.6	—	16.7	23.9	40.0	16.7

posterior corners of the eye; in 21 per cent it lies between the anterior edge of the ear and the eye, and in two per cent it lies slightly anterior to the eye. In six samples the hind limb is proportionately longer in males than in females, but in three samples the opposite is true.

Dewlap area.—The area of the extended dewlap was determined for live adult males (40 mm or more in snout-vent length) according to the method described by Echelle, Echelle and Fitch (1971). There is extensive overlap among the various populations in the ratio between the area of the dewlap and snout-vent length. The most divergent regression line is that for the sample from Escuintla in which the color pattern of the dewlap is also distinctive (Fig. 4).

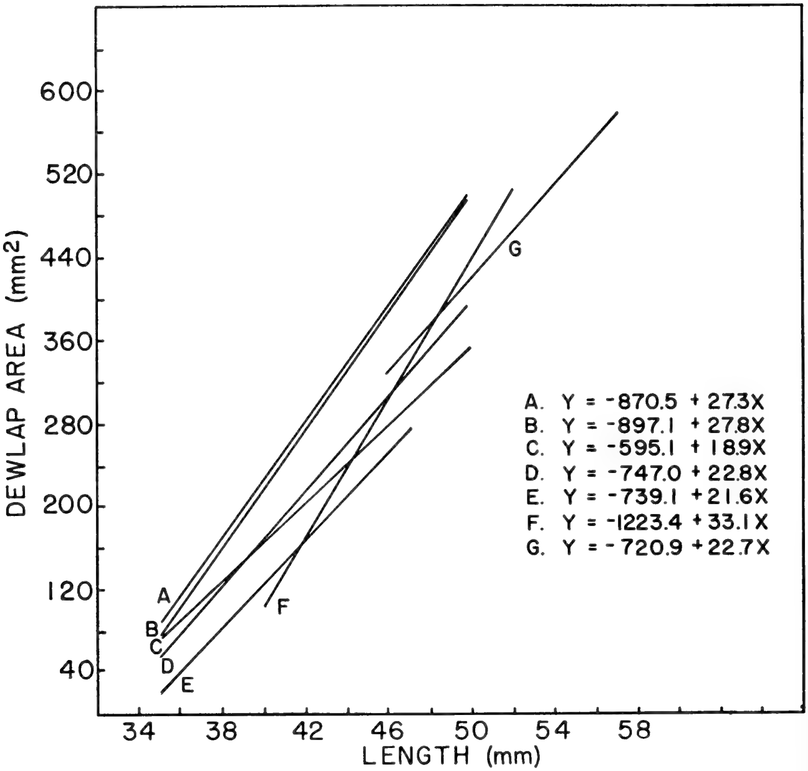

FIG. 4. Dewlap area on one side versus snout-vent length in adult males of *Anolis cupreus* from A. Río Naranjo; B. Turrúcares; C. San José; D. Cartago; E. Sardinal; F. Escuintla; G. Quepos.

Scale rows.—The number of scale rows around the middle of the body was a major character used by Williams and Smith (1966) to separate *A. cupreus* and *A. hoffmanni;* the latter authors stated that six *"hoffmanni"* had 91 to 120 rows and eight *"cupreus"* had 134 to 145. The character is subject to much individual variation. Also there is an average difference between the sexes in number of scales (Table 1), a fact that apparently has not been noted previously. Because the dewlap is exceptionally large in male *A. cupreus*, extending slightly past mid-body, it probably affects the scale count. The scales of the dewlap and those of the belly and dorsum are relatively coarse, and variation in counts results partly from the granular scales of the sides being in irregular rows, making consistent counts difficult.

Anolis cupreus from the northern and southern ends of the range and from most other localities in the Pacific lowlands have relatively high numbers of scales around the body. The series from Turrúcares at an intermediate elevation (639 m) has lower numbers than most of the lowland series, and those from San José (1172 m) and Cartago (1435 m) have progressively lower numbers (Table 1). There is little or no overlap between the series from Cartago and those from the lowlands.

The type of *Anolis hoffmanni* had "approximately 92" scales around midbody (Williams and Smith, 1966), fewer than in any of the 211 specimens we counted. Williams and Smith also stated that counts of 91 [the type?], 108, 111, 114, 120, and 120 were obtained from specimens of *hoffmanni*. The lowest counts that we obtained (minimum 94) were in the series from Cartago; therefore, it seems most likely that the type of *A. hoffmanni* came from the Meseta Central, and perhaps, from the vicinity of Cartago.

Supraorbital semicircles.—In all specimens examined, the supraorbital semicircles are separated from the interparietal plate by small scales. Two scales occur more often (59%) than three (32%), and three more often than four (9%). In the small series from Tilarán and Río Naranjo the trend is reversed with three scales occurring more often than two. In all specimens examined, the supraorbital semicircles are separated by small scales that are variable in size, shape, and number. In each series the modal number is two (78% of total) with one (14%) and three (8%) occurring less frequently. No geographic variation is evident in this character.

Separation of supposed *Anolis hoffmanni* from *A. cupreus* by Williams and Smith (1966) depended largely on whether the large supraoculars were in contact with the supraorbital semicircles *(hoffmanni)* or separated from them in whole or in part by small intercalated scales *(cupreus)*. We examined this character in specimens from various localities; none of the populations is entirely

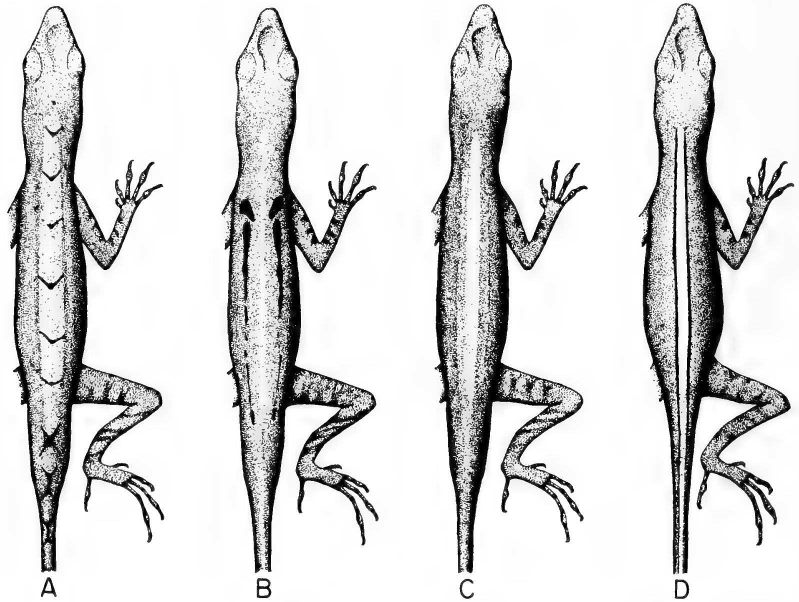

FIG. 5. Dorsal color patterns of *Anolis cupreus:* A. *A. c. cupreus* male with chevron pattern; B. *A. c. spilomelas* male with black shoulder patch and broken dorsolateral stripes; C. *A. c. hoffmanni* male with broad dull whitish middorsal stripe; D. *A. c. spilomelas* female with orange middorsal stripe edged with black. × 1.2.

"*hoffmanni*-like" (Table 1). Anoles from the Meseta Central (San José and Cartago) most commonly have the scales in contact, and samples from the Pacific lowlands most frequently have small intercalated scales. Samples from intermediate altitudes at Tilarán and Turrúcares are intermediate in character. The series from La Irma and Río Naranjo were unlike the other lowland samples in having more individuals which resemble upland populations with the supraoculars and semicircles in contact.

Digital lamellae.—The numbers of widened lamellar pads on the fourth toe vary as follows: 9 in 46.5%, 8 in 27.8%, 10 in 17.6%, 11 in 2.2%, 12 and 6 each in 0.6%. The number of lamellae is slightly higher in males than in females and possibly the character varies geographically (Table 1).

Coloration.—The color pattern of adult males is much less variable than that of females. There are three main pattern types with many intermediates or combinations: 1) White dorsum—a broad, poorly defined, dirty white middorsal area (Fig. 5C) edged with black or with tan tinged with ochre, which merges with the darker flanks. This pattern is most prevalent in populations on the Meseta Central (San José and Cartago) and is uncommon in lowland populations. Ordinarily it is not seen in juveniles, which have a chevron or nondescript pattern like adults of the Pacific lowlands.

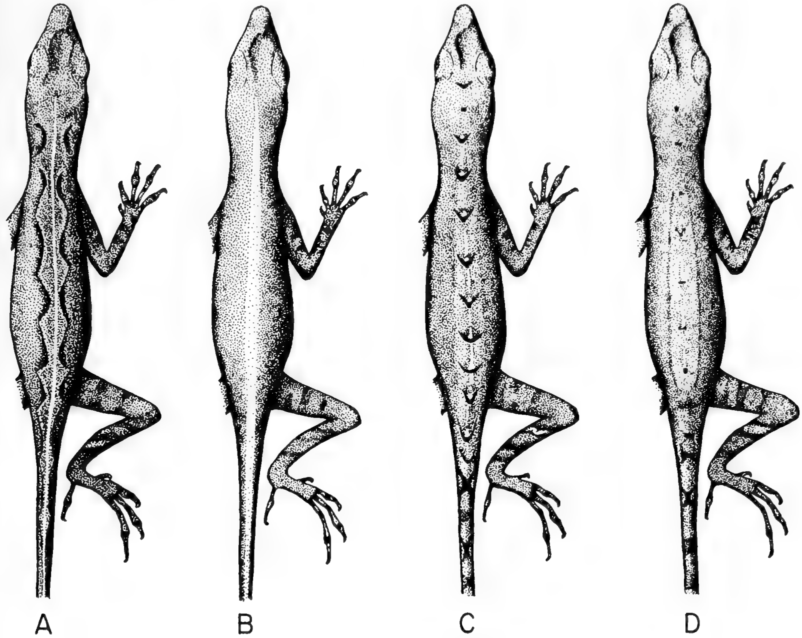

FIG. 6. Dorsal color patterns of female *Anolis cupreus:* A. *A. c. hoffmanni* with striped and diamond pattern; B. *A. c. hoffmanni* with broad, cream-colored dorsal stripe; C. *A. c. cupreus* with dorsal chevrons; D. *A. c. cupreus* with nondescript pattern. × 1.2.

2) Chevron markings—a series of middorsal transverse black marks that are usually chevron-shaped (Fig. 5A). Typically there are four or five chevrons on the body and two or three on the proximal part of the tail. In some individuals the markings are reduced to dots and the middorsal area bearing the dots is slightly paler than the sides. If the middorsal area is not set off as a pale band and if the chevrons are lacking, the pattern is referred to as "nondescript." The nondescript (sometimes nearly uniform drab brown) and chevron patterns are the common patterns in the Pacific lowlands. 3) Black-sided—heavy black pigmentation dorsolaterally, especially anteriorly (Fig. 5B). A black shoulder spot is prominent in some specimens. Variation includes a continuous but irregular streak, or a series of irregular spots and streaks on each side. The dorsal area between the black marks has chevrons or is nondescript. Although the tendency to have heavy pigmentation is most evident in the samples from Quepos, some individuals were found to be pale colored.

Like many other anoles, *Anolis cupreus* is characterized by pattern polymorphism in the females. At one locality as many as three distinctive patterns may be present among females. The frequency of occurrence of the different patterns varies from one area to another, and a pattern that is common at one place may be absent at another. In one type of pattern there is a pale longitudinal middorsal stripe (Fig. 6B). The stripe varies in width from narrow to broad, and in color from creamy white to tan or bright orange; the margins of the stripe are darkened or boldly outlined in black. A second type of pattern consists of a longitudinal series of diamond shaped middorsal marks (Fig. 6A); usually the marks overlap, so that the posterior corner of one merges with the anterior part of the next. The markings are usually dark brown, but may be outlined by pale edges, and may enclose paler areas. The half of a diamond on one side of the midline may be displaced backward or forward from the other half so that the diamond markings are asymmetrical. Many individuals combine the diamond pattern with a pale middorsal stripe; in others the diamonds are not associated with such a stripe. A third type of pattern (Fig. 6C) lacks longitudinal lines and diamond markings but may have a series of middorsal black chevrons typical of some males. There are various degrees of intermediacy among the three types of patterns. Also there is some capacity for color change. Depending on temperature, illumination, and degree of excitation, there is darkening or lightening of general color, and markings that are well defined at one time may become faint at another. However, one type of pattern does not change to another. For the purposes of comparison, females lacking a dorsal stripe, diamond markings, and chevrons are termed "nondescript." The dorsum may be almost uniform brown, or have dark spots, dots, or flecks, usually middorsally. The flanks may bear tan or yellowish dots, or flecks.

At every locality where samples were obtained, the female pattern was highly variable (Table 1). At Cartago and San José on the Meseta Central the commonest type of pattern is the dorsal stripe (Figs. 6A and 6B); it occurs in one-third of the females from Quepos and Turrúcares. Farther north relatively few individuals are striped. Most females from Sardinal and La Irma have chevrons (Fig. 6C) or a nondescript pattern (Fig. 6D).

According to Williams and Smith (1966), an important difference between *A. cupreus* and *A. hoffmanni* is the dorsal color which is dark brown in *cupreus* and pale brown in *hoffmanni*. We suspect that this merely reflects individual variation; every population that we observed in the field was composed of some dark and light individuals with others being intermediate.

The dewlap is rudimentary and barely distensible in female *A. cupreus*. In all those from Guatemala, Guanacaste (Sardinal and La Irma) and Río Naranjo, the throat, or dewlap region, is plain white, whereas in those females from Quepos it is white mottled with gray. Females from the Meseta Central are distinctive in having a trace of the pinkish orange like that which occurs on the male dewlap. Only two of 39 females from San José and one of 12 from Cartago have plain white throats that lack pinkish or orange. Specimens from Turrúcares are intermediate; only four of 21 have any color on the throat, and in each of these four the color is fainter than in most San José and Cartago specimens.

In general, characters of the dewlap are useful only when the living or freshly killed lizards are available. The dewlap cannot be spread in specimens preserved with it collapsed; moreover, on preservation, the colors become dull and nondescript. In male *Anolis cupreus* the dewlap is bicolor; the inner part is darker and sharply set off from the paler outer portion. In anoles from near Escuintla, and El Salto in Guatemala, the dark inner area is approximately half as large as that of Costa Rican specimens.

Almost every individul of *Anolis cupreus* has dusky bands on the arms, thighs, shanks, fingers and toes. Usually the bands are obscure, and they vary according to stage of molt and temperature. In our Guatemalan samples the bands seem to be more sharply defined on the digits than in the other samples.

RELATIONSHIPS

Our study focused on intraspecific variation, but various other species of anoles were observed in the field and/or examined in the laboratory. These observations, plus data from the literature, permitted us to form opinions regarding interspecific relationships. According to Etheridge (1960), *Anolis cupreus* belongs to the *chrysolepis* series of the Beta division of the genus *Anolis*. The *chrysolepis* series can be divided into several natural groups; many of the species are strikingly different from *A. cupreus*.

Anolis cupreus is the dominant anole on the Pacific versant of Central America from southeastern Guatemala to central Costa Rica. None of the numerous sympatric species seems to be closely related to it. *Anolis townsendi*, of Cocos Island (a remote Pacific island located almost midway between Costa Rica and the Galapagos) is remarkably like *cupreus* in size, most scale characters, and the stereotyped pattern of its aggressive display (see Carpenter, 1965). Possibly *A. townsendi* is a derivative of a *cupreus*-like ancestor which reached the island by rafting (Echelle, Echelle, and Fitch, 1971). Another close relative may be *Anolis cuprinus* Smith, as yet known only from the type locality near Zanatepec, Oaxaca, México. It differs in having a unicolor dewlap that is smaller (reaching only to midthorax), and in having broad, V-shaped bands across the body. Stuart (1955:16) suggested that *Anolis dollfusianus* in Guatemala is a near relative of *A. cupreus.* This species seems to replace *cupreus* in the western two-thirds of Guatemala on the Pacific versant. Sympatric populations of the two species have not been recorded, but Stuart (1955:17) stated that *A. dollfusianus* occurs ". . . from about the level of Escuintla westward . . ." and we found *A. cupreus* to be abundant in the Escuintla area. *Anolis dollfusianus* differs from *cupreus* in smaller size (snout-vent length to 45 mm in 54 adults from near Retalhuleu), in having a smaller, yellowish dewlap, and in more rugose head shields. Its habits resemble those of *cupreus,* but the species is more slender and agile, similar in superficial appearance to *A. limifrons* of the Caribbean versant.

TAXONOMY

On the basis of our findings, *Anolis cupreus* is redescribed below; four subspecies, one named herein, are recognized.

Anolis cupreus Hallowell

Anolis cupreus Hallowell, 1860, Proc. Acad. Nat. Sci. Philadelphia, 1860:481.

Description.—Snout-vent length 35-57 mm in adults (males 40-57, mean 46; females 35-50, mean 40); brownish; scales on top of head large, rugose; ventral scales rhomboidal, imbricate, keeled, rounded posteriorly, much larger than dorsals; four median rows of dorsals larger than others; dorsal scales smallest about midlaterally, granular, in oblique and irregular rows; six or seven supralabials; seven or eight infralabials; two elongate supraciliaries; supraoculars keeled, in contact with supraorbital semicircles or separated by small intercalated scales, left and right sides often differing in this respect; six or seven rows of loreals; supraorbital semicircles usually separated from each other by one or two rows of scales; occipital nearly twice size of ear opening, separated from supraorbital semicircles on each side by two or three scales; caudal scales large, hexagonal, heavily keeled; most limb scales larger than those of body; some enlarged scales on dorsum of upper arm, anterior surfaces of forearm and thigh, and ventral surface of tibia; adpressed hind limb extending to region of eye; adpressed forelimb extending to region between eye and nostril; intact tail of adults 1.5-2.1 times snout-vent length (usually 1.8-1.9 in males and 1.7-1.8 in females); 6-12 (usually 8 or 9) lamellar pads on penultimate phalanx of fourth toe; dorsum nearly uniform pale or dark brown, or variously marked with whitish, yellow, tan or orange, middorsal stripe edged with black or not, or with a series of middorsal black marks, usually chevron-shaped; black shoulder spots and black spots or streaks in dorsolateral area occasionally present; belly dull white with dusky suffusion; limbs somewhat paler than body; dusky bands, sometimes faint, on limbs and digits; dewlap of male large, rounded, extending from chin to midbelly or slightly beyond, bicolor, with dark amber-orange inner portion and pinkish rose outer portion.

Range.—Anolis cupreus inhabits Central America on, or near, the Pacific Coast (sea level to 1435 m) from southeastern Guatemala to Quepos in Costa Rica; it extends into the Caribbean versant, at least in the vicinities of Lago de Managua, Lago de Nicaragua, and Cartago in Costa Rica, but is confined to seasonally dry climates.

Anolis cupreus cupreus Hallowell

Anolis cupreus Hallowell, 1860. Proc. Acad. Nat. Sci. Philadelphia, 12:481.

Types.—None designated in original description; Stuart (1968: 62) listed 14 syntypes as follows: U.S. National Museum 12211 (11), Museum of Comparative Zoology 17631-32, and University of Illinois Museum of Natural History 40733, all from Nicaragua.

Diagnosis.—1) Small (average 45 mm snout-vent in adult males, 38 mm in adult females); 2) usually nondescript brown, lacking well defined pattern or with series of chevron-like middorsal marks in both sexes; 3) throat white in female; 4) average number of scales around mid-body more than 130 in males and more than 120 in females; 5) supraorbital semicircles in contact with supraoculars more often than not; 6) average ratio of tail length to snout-vent length approximately 1.80 in males and 1.75 in females.

The nominate subspecies differs from *A. c. hoffmanni* in having more scales around mid-body, white instead of pinkish or orange throat in female, and lower frequency of females having middorsal stripe and diamond pattern. The dark basal area of dewlap is approximately twice as large as in *A. c. macrophallus* and banding of the toes is less distinct. *Anolis c. cupreus* is smaller than *A. c. macrophallus* and *A. c. spilomelas;* it differs from the latter subspecies in the low frequency of males having black dorsolateral markings.

Range.—Anolis cupreus cupreus occurs in the Pacific lowlands from the northern part of Puntarenas Province through Guanacaste Province in Costa Rica, and northwest in Nicaragua to at least Managua, and probably to Honduras; it occurs in the Caribbean versant on the west shore of Lago de Nicaragua (Sapóa), on Isla Ometepe, and on the south shore of Lago de Managua (Sabana Grande). We have not seen live material from Nicaragua but assume that the anoles there are similar to those from adjacent Guanacaste; in preservative they appear to be.

Anolis cupreus hoffmanni Peters
New combination

Anolis hoffmanni Peters, 1862, Monatsb. Akad. Wiss. Berlin, 1862:142.

Holotype.—Zoological Museum of Humboldt University, Berlin, 4690 from "Costa Rica" collected by C. Hoffmann. The type locality is hereby restricted to Cartago, Cartago Province, Costa Rica, because only in that area have anoles been found approximating the low number of scales around mid-body of the type. Although Hoffmann's itinerary has not been documented, the descriptions of his herpetological collection (Peters 1859, 1863) suggest that he must have travelled widely on the Atlantic and Pacific lowlands and in the Meseta Central.

Diagnosis.—1) Small (average 45 mm snout-vent in adult males, 40 mm in adult females); 2) adult males usually with broad, pale gray or brown middorsal band; females often with narrow, sharply defined middorsal stripe and/or a series of diamond shaped marks; 3) females with faint suffusion of pinkish or orange in throat area; 4) fewer than 120 scales around mid-body; 5) supraorbital semicircles usually in contact with supraoculars; 6) ratio of tail length to snout-vent approximately 1.84 in males and 1.77 in females.

This subspecies differs from other subspecies of *Anolis cupreus* in having fewer scales around mid-body, greater frequency of contact between supraoculars and supraorbital semicircles, and pink or orange on throat of female. *Anolis cupreus hoffmanni* is distinguished from *A. c. macrophallus* and *A. c. spilomelas* by its smaller average and maximum size.

Range.—Anolis cupreus hoffmanni occurs on the Meseta Central in Costa Rica, from approximately 600 m to 1435 m; chiefly on the Pacific versant but in the Cartago area on the Caribbean versant there is a population separated from the main population by the continental divide.

Anolis cupreus macrophallus Werner
New combination

Anolis macrophallus Werner, 1917, Jahrb. Hamburg Miss. Anat., 34:31.

Holotype.—Formerly in Zoologisches Museum, Hamburg, but destroyed in World War II (*fide* Stuart, 1955:15), from San José, Department of Escuintla, Guatemala.

Diagnosis.—1) Large (average 49 mm snout-vent in adult males, 41 mm in adult females); 2) nondescript in both sexes, usually brown with no well defined pattern or with series of chevron-like middorsal marks; 3) throat white in female whereas dewlap in male is pinkish or rose with a darker, orange basal area which is relatively small, only about half as large as in the other subspecies; 4) average number of scales around mid-body 134 in males and 120 in females; 5) supraorbital semicircles in contact with supraoculars in approximately one-third of specimens; 6) ratio of tail length to snout-vent approximately 1.87 in both sexes.

This subspecies differs from *Anolis cupreus spilomelas* in its smaller size and lack of black dorsolateral marks. *Anolis c. macrophallus* differs from *A. c. cupreus* and *A. c. hoffmanni* in its larger size and is uniquely distinguished by the relatively small, darkened (orange) area at base of male dewlap.

Range.—*Anolis cupreus macrophallus* occurs in southeastern Guatemala in lowlands and at intermediate elevations (to 1400 m), from San José, Escuintla and Palin across the southern part of El Salvador. Mertens (1952:41) listed and described 21 specimens from nine localities in El Salvador.

Presumably *Anolis cupreus* has a continuous range along the Pacific Coast of Central America, at least from San José, Guatemala to Quepos, Costa Rica, but records are lacking from the 300 km interval between Cuscatlán, El Salvador and Managua, Nicaragua. The gap separating known populations of *A. c. macrophallus* and *A. c. cupreus* includes the Honduran coast at the Gulf of Fonseca and the areas adjacent to it in El Salvador on the west and Nicaragua on the south and east.

Anolis cupreus spilomelas new subspecies

Holotype.—KU 140593 from Quepos, Puntarenas Province, Costa Rica, obtained by H. S. Fitch, on 23-24 February, 1970.

Paratypes.—KU 140594-605, 140607-19, California Academy of Sciences 133124-6, Museum of Comparative Zoology 129776-8, same data as holotype.

Diagnosis.—1) Large (average 51 mm snout-vent in adult males, 44 mm in adult females); 2) heavy black dorsolateral spots, streaks or lines; female pattern variable with pale middorsal stripe or diamond shaped markings or chevrons, or nondescript; 3) throat white, mottled with gray in female; 4) average number of scales around mid-body 136 in males, 128 in females; 5) supraorbital semicircles separated from supraoculars in majority (61 per cent) of specimens;

6) ratio of tail length to snout-vent approximately 1.87 in males and 1.79 in females.

Description of holotype.—Snout-vent length 51 mm, tail 63 mm, head 9 mm long, snout 6 mm wide; adpressed hind limb extending forward to middle of eye; 133 scales around mid-body; 8 supralabials on each side, seventh beneath middle of eye; 7 postrostrals; 9 scales between nasals; 4 scales between frontal ridges at widest point; 2 scales between supraorbital semicircles; 3 scales between semicircles and occipital; occipital slightly larger than ear; 8 loreals on each side; 2 large superciliaries on each side; 8 canthals on left, 7 on right; 4 large suboculars left and right; scales on top of head strongly keeled; canthus rostralis strongly developed; 9 infralabials on each side, the 8th below middle of eye; 4 rows of enlarged mid-dorsal scales on body; 9 lamellae on penultimate phalanx of fourth toe on each side; eye 1.5 times diameter of ear opening; a large black rounded shoulder spot on each side followed by black streaks that extend to mid-body.

Range.—Anolis cupreus spilomelas occurs on the coastal plain and adjacent foothills of northern Puntarenas Province in the Quepos-Parrita area of Costa Rica. Almost certainly the range is continuous with that of *A. c. cupreus* to the northwest, but material is lacking from a 77-km interval between Boca de Barranca, the southernmost station for *A. c. cupreus* and Parrita, the northernmost station for *A. c. spilomelas.*

Etymology.—The subspecific name *spilomelas* is from Greek, *spilos*—spot and *melas*—black, referring to the prominent black marks often present on the shoulder and dorsolateral region.

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RESUMEN

Anolis cupreus se encuentra distribuido en el sureste de Guatemala, extendiendose hacia el sureste especialmente en las tierras bajas del Pacifico, hasta Costa Rica. Además, su distribución se extiende hacia el caribe en áreas relativamente áridas del Lago Nicaragua y en el centro de Costa Rica en los alrededores de Cartago. El tamaño del cuerpo, la proporción de cabeza y cola, el número de escamas alrededor del cuerpo, el diveño del saco gular, el color de la quihoda, el diseño dorsal del cuerpo, y detalles en la escamación de la cabeza varian geograficamente y están subjectos a mucha variación individual, con marcadas diferencias entre los sexos. El polimorfismo en el diseño de las manchas del cuerpo de las hembras es comón. Varios autores han considerado a menudo *Anolis hoffmanni* Peters, como un sinónimo de *A. cupreus,* pero también autores contemporaneos los han catalogado como diferentes especies. Sin embargo, todas las características descritas para *Anolis hoffmanni* se encuentran presentes en las poblaciones de *A. cupreus.* Las cuales están muy bien desarrolladas en la población de la Meseta Central en Costa Rica. Consideramos que *Anolis cupreus hoffmanni* es una subespecie endémica de esta area, caracterizada por el tamaño relativamente pequeño, por el diseño en lineas, y por el color rosado o anaranjado de la quijada de las hembras. Otras subespecies son: *A. c. spilomelas* del área Quepos-Parrita en Costa Rica, distinquiéndose por su tamaño grande, y por las marcas dorsolaterales negras; *A. c. cupreus* que aparece desde Puntarenas extendiendose al noroeste de Costa Rica, hasta el occidente de Nicaragua, distinquiéndose por su tamaño pequeño y con diseños indifinibles o con manchas angulares mediodorsales; y *A. c. macrophallus* de El Salvador y sureste de Guatemala, el cual se distingue por una mancha oscura relativamente pequeña en la base del saco gular del macho.

SPECIMENS EXAMINED

Anolis cupreus cupreus. COSTA RICA, *Guanacaste:* Finca Bosco, KU 40743; Finca Taboga, KU 129253; 5 km W Liberia, 100 m, KU 66866; La Irma, Río Congo, KU 125703-8, 140565-92; Las Cañas, KU 40747-51; 16 km SSE Las Cañas, KU 66865; Ojotal, 2 km SW El Coco, KU 66860-61; "Pacific slope," KU 40744-46; Playa del Coco, KU 129245-52; Río Bebedero 2.5 km S Bebedero, KU 66862-64; 4-5 km ENE Tilarán, KU 40752-63 and 40995; 7 mi NE Tilarán, KU 86555. *Puntarenas:* 6 mi E Esparta, KU 56032; Marbella Hotel, KU 40739-40 and 40742.

NICARAGUA, *Managua:* 2 mi N Sabana Grande, 50 m, KU 85637. *Rivas:* Isla Ometepe, 40 m, 3 km N Moyogalpa, KU 85641; Río Javillo, 3 km N and 4 km W Sapóa, 40 m KU 85368-40.

Anolis cupreus hoffmanni. COSTA RICA, *Alajuela:* 5-10 km E Sarchi, KU 40737-38; Turrúcares, KU 140620-63. *Cartago:* Cartago, KU 140664-738. *San José:* Las Pavas, 4.8 km W San José, KU 125681-89; San José, KU 40741, 125613-80, 125690-92, 125817-22, 140739-69.

Anolis cupreus macrophallus. GUATEMALA, *Escuintla:* El Salto, near

Escuintla, KU 140862-75; 0.5 mi S Escuintla, KU 140770-832; 4.6 mi S Escuintla, KU 140833-46, 140848, 140850-61.

Anolis cupreus spilomelas. COSTA RICA, *Puntarenas:* Quepos, CAS 133124-6, KU 125693-94, 140594-605, 140607-19, MCZ 129776-8; 2.4 km E Quepos, KU 125695; 6.4 km NNW Quepos, KU 125696; 1.6 km N Quepos, KU 125701-02; 2.4 km N Río Cañas, KU 125697-700.

LITERATURE CITED

Carpenter, C. C.

1965. The display of the Cocos Island anole. Herpetologica, 21(4):256-260.

Echelle, A. A., A. F. Echelle and H. S. Fitch

1971. A comparative analysis of aggressive display in nine species of Costa Rican *Anolis.* Herpetologica, 27:271-288.

Etheridge, R. E.

1960. The relationships of the anoles (Reptilia: Sauria: Iguanidae): an interpretation based on skeletal morphology. Ph.D. Thesis. Univ. Michigan, Ann Arbor. 236 p.

Mertens, R.

1952. Die Amphibien und Reptilien von El Salvador. Abh. Senckenburg. Naturforsch. Ges., 487, 83 p.

Peters, J. A. and R. Donoso-Barros

1970. Catalogue of the Neotropical Squamata: Part II. Lizards and Amphisbaenians. Smithson. Inst. Bull., 297, viii + 293 pp.

Peters, W.

1859. Über die von Hrn Dr. Hoffmann in Costa Rica gesammelten und aus die königl. Zoologische Museum gesandten Schlangen. Monatsb könig. preuss Akad. Wiss. Berlin, 1859:275-278.

1863. Eine mittheilung über einige neue Arten der Saurier-Gattung *Anolis.* Monatsb. Akad. Wiss. Berlin, 1862:135-149.

Stuart, L. C.

1955. A brief review of the Guatemalan lizards of the genus *Anolis.* Misc. Publ. Mus. Zool. Univ. Michigan, no. 91, 31 pp.

1963. A checklist of the herpetofauna of Guatemala. Misc. Publ. Mus. Zool. Univ. Michigan, no. 122, 150 pp.

Taylor, E. H.

1956. A review of the lizards of Costa Rica. Univ. Kansas Sci. Bull., 28, pt. 1, no. 1, 322 pp.

Williams, K. L. and H. M. Smith

1966. Noteworthy lizards of the genus *Anolis* from Costa Rica. Carib. Jour. Sci., 6(3-4):163-166.

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A TAXONOMIC REVIEW OF THE SOUTHERN ANDEAN MARSUPIAL FROGS (HYLIDAE: *GASTROTHECA*)

By

WILLIAM E. DUELLMAN[1] AND THOMAS H. FRITTS[2]

Marsupial frogs of the genus *Gastrotheca* are unique in their mode of reproduction and therefore are of considerable interest to biologists. Yet the taxonomy of the genus is chaotic; the nomenclature and distribution of the most common and widespread Andean species are usually erroneously reported in the literature. Consequently, in order to facilitate study of biological problems of these frogs, the basic taxonomy must be treated first.

From September 1969 through July 1970 Fritts carried out field work in the Andes of Ecuador, Perú, and Bolivia. In January 1971 both of us concentrated field work on *Gastrotheca* in central and southern Perú, and Duellman collected in Ecuador in the summer and fall of 1971. As the result of this field work we accumulated large series of *Gastrotheca* and extensive data on the ecology, life history, and distribution of several species. In the present paper we are concerned only with the species occurring in the Andes south of the Huancabamba Depression in northern Perú. We have relied mostly on our own collections and data but have studied Argentinean material provided by Raymond F. Laurent. Also, we have examined all extant type specimens of Andean *Gastrotheca* and much material in other museums.

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[1] Curator, Division of Herpetology, Museum of Natural History, University of Kansas.

[2] Research Fellow, Museum of Natural History, University of Kansas. Present address: Department of Biology, St. Edwards University, Austin, Texas, 78704.

The purposes of the present paper are to 1) define as a natural group the marsupial frogs in the southern Andes; 2) allocate the appropriate trivial names; 3) diagnose the species and define their ranges; 4) describe two new species from the Peruvian Andes. We have examined 913 specimens from Perú, Bolivia, and Argentina. Reference to all specimens is by the abbreviations of the collections as given in the acknowledgments; the Museum of Natural History, University of Kansas is abbreviated KU.

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HISTORICAL RESUMÉ

Duméril and Bibron (1841:593) named *Hyla marsupiata* from Cuzco, Perú. Their description and color illustrations could apply equally to specimens from southern Perú or from Ecuador. The holotype (MNHN 4877) is a female having a snout-vent length of 48.2 mm, 3 mm larger than any other specimen from southern Perú that we have seen, but within the size range of specimens from Quito, Ecuador. The holotype is now soft and rubbed; the color pattern is completely faded. Under the catalogue number MNHN 4878 are four small specimens from Quito, Ecuador. Jean Guibé carefully rechecked the catalogue and stated that there was no reason to suspect that the holotype was not part of the collection made in vicinity of Cuzco by Pentland. Because of the poor condition of the holotype, we could not rely on external characters for assigning it to a known population. However, radiographs revealed that the cranial characters of the holotype are like those of specimens from southern Perú and not like specimens from Ecuador. Thus, we disagree with Laurent's (1969a:129) suggestion that Vellard's (1957:19) allocation of the trivial name *marsupiata* to the population at Cuzco was erroneous.

Hyla marsupiata is the type species of *Gastrotheca* Fitzinger, 1843. Günther (1859:115) proposed the substitute generic name *Nototrema,* which was commonly used until Miranda-Ribeiro (1920:328) resurrected *Gastrotheca.*

Cope (1877:37) named *Chorophilus cuzcanus* on the basis of a specimen obtained by the Orton Expedition. Although no locality is given in the description, the specific name apparently is derived from Cuzco. The holotype cannot be found, but the description applies well to young *Gastrotheca marsupiata* from southern Perú; consequently, we consider *Chorophilus cuzcanus* Cope, 1877, to be a junior synonym of *Gastrotheca marsupiata* (Duméril and Bibron, 1841).

Steindachner (1892:840) named *Nototrema bolivianum* on the basis of six specimens from Puerto de San Mateo, Departamento

Cochabamba, Bolivia. These specimens (NHMW 16490-91) are in excellent condition; NHMW 16490, an adult female having a snout-vent length of 42.8 mm, is hereby designated as the lectotype. Thus, the five specimens catalogued under NHMW 16491 become lectoparatypes. *Hylodes caeruleomaculatus* Werner (1899:482), based on two syntypes (NHMW 16496) from "Bolivia," was placed in the synonymy of *Nototrema bolivianum* by Nieden (1923:320). The largest of the syntypes is a male having a snout-vent length of 28.8 mm. Comparison of the syntypes with the types of *N. bolivianum* and with other specimens from Bolivia and southern Perú reveals that the syntypes of *Hylodes caeruleomaculatus* are juveniles of the species earlier named *Nototrema bolivianum.*

Five syntypes (BMNH 1900.6.20-46-50) were designated by Boulenger (1900:181) in his description of *Nototrema peruanum* from "Carao" (=Caraz), Departamento Ancash, Perú. The type series consists of four adult males having snout-vent lengths of 38.3-41.5 mm and a juvenile (BMNH 1900.6.20.50) having a snout-vent length of 28.9 mm.

Thus, at the beginning of the present century three species of marsupial frogs were recognized in the genus *Nototrema* in the Andes of western South America, viz. *bolivianum, peruanum,* and *marsupiatum;* the latter name was used for populations in Ecuador, as well as that at Cuzco, Perú. Barbour and Noble (1920a:611) applied the name *Gastrotheca boliviana* to specimens from southern Perú and placed *Eleutherodactylus binghami* Stejneger, 1913, in the synonymy of *Gastrotheca boliviana* (Steindachner, 1892). We examined the holotype of *E. binghami* (USNM 49559), a juvenile from Cuzco, Perú, having a snout-vent length of 20.9 mm, and concur with Barbour and Noble that the specimen is a juvenile *Gastrotheca.*

Barbour and Noble (1920b:426) named *Gastrotheca monticola* from Huancabamba, Departamento Piura, Perú, and Parker (1932:25) named *Gastrotheca marsupiata lojana* from Loja, Provincia Loja, Ecuador. Shreve (1941:82) studied series of *Gastrotheca* from central Perú and concluded that they were subspecifically distinct from *G. boliviana;* he named *Gastrotheca boliviana griswoldi* from Maraynioc, Departamento Junín, Perú. The holotype (MCZ 24102) is a female having a snout-vent length of 38.6 mm.

Vellard (1957) reviewed the Peruvian marsupial frogs and recognized the following taxa in Andean Perú: *marsupiata* (two subspecies) *boliviana, peruana* (three subspecies), *lojana,* and *monticola.* We are not concerned here with *lojana* and *monticola,* both of which belong to the northern Andean complex of *Gastro-*

theca. Vellard (1957:22) considered *G. boliviana griswoldi* Shreve to be a synonym of *G. m. marsupiata* (Duméril and Bibron) and named *G. marsupiata bifasciata* from Paccha, Departamento Junín, Perú. Of the three syntypes of that subspecies (MJP 129), two are juveniles; the other is an adult male having a snout-vent length of 33.5 mm. Vellard named two subspecies of *G. peruana—G. peruana dissimilis* from Huamachuco, Departamento La Libertad, Perú, and *G. peruana junensis* from Lago de Punrún, Departamento Junín, Perú. The type series of *dissimilis* (MJP 245) contains 48 specimens, one of which is a *Telmatobius;* the holotype of *junensis* (MJP 195) is a male having a snout-vent length of 36.5 mm. Vellard's application of names to populations in central and southern Perú was influenced by his having only limited topotypic material of *G. marsupiata,* a species about which he obviously was confused.

Laurent (1967, 1969a-b) has made the most recent contributions to the systematics of southern Andean *Gastrotheca.* He named *G. christiani* from the "Monumento de la ruta de Valle Grande, 50 km de Calilegua," Provincia Jujuy, Argentina, and *G. gracilis* from La Banderita, Provincia Catamarca, Argentina. Moreover, Laurent (1969a:129) misinterpreted Vellard's (1957) allocation of *G. marsupiata.* Laurent considered *G. marsupiata bifasciata* to be a species distinct from *G. marsupiata.* He proposed the name *Gastrotheca bifasciata vellardi* for the populations in southern Perú recognized as *G. marsupiata marsupiata* by Vellard.

At the time of this writing, the taxonomy of the southern Andean *Gastrotheca* is as follows (synonyms in brackets): *G. bifasciata bifasciata* Vellard, *G. bifasciata vellardi* Laurent, *G. boliviana* (Steindachner) [*H. caeruleomaculatus* Werner, *E. binghami* Stejneger], *G. christiani* Laurent, *G. gracilis* Laurent, *G. marsupiata* (Duméril and Bibron) [*G. boliviana griswoldi* Shreve], *G. peruana peruana* (Boulenger), *G. peruana dissimilis* Vellard, and *G. peruana junensis* Vellard.

It is obvious from statements made by Barbour and Noble (1920a), Vellard (1957), and Laurent (1969a) that these authors were confused about the allocation of the specific name *marsupiata.* With the exception of Vellard, these authors and others have based their definitions of *marsupiata* on specimens from Ecuador and generally have placed all Peruvian specimens in *boliviana, bifasciata,* or *peruana.* Vellard (1957) assumed that Ecuadorian "*marsupiata*" were different from the nominate race at Cuzco; he proposed the name *Gastrotheca marsupiata ecuatoriensis* for Ecuadorian populations.

PROPOSED TAXONOMY

The examination of type specimens and large series of fresh specimens has provided the basis for a re-evaluation of the taxonomy of southern Andean *Gastrotheca.* Supportive data for taxonomic changes are presented here, whereas diagnoses, accounts of variation, and ranges of the recognized species are given in the accounts of the species.

The most widespread species of marsupial frog in the southern Andes is *G. marsupiata* (Duméril and Bibron). Comparison of the types of *G. marsupiata* and *G. boliviana* revealed no structural differences between the specimens. Comparison of these types with series of specimens from Bolivia and southern Perú demonstrated that many individuals, including the lectotype of *G. boliviana,* lack dorsal dark markings and have small pale spots on the dorsum. Thus, we place *G. boliviana* (Steindachner, 1892) in the synonymy of *G. marsupiata* (Duméril and Bibron, 1841). Four names (*Chorophilus cuzcanus,* Cope, 1877; *Hylodes caeruleomaculatus* Werner, 1899; *Eleutherodactylus binghami* Stejneger, 1913; *Eleutherodactylus footei* Stejneger, 1913) are based on juvenile *Gastrotheca.* We have examined the types of all but *C. cuzcanus* (type lost) and conclude that all four names are synonyms of *G. marsupiata.* Due to Laurent's (1969a) misinterpretation of Vellard's (1957) allocation of *G. marsupiata,* the substitute name *G. bifasciata vellardi* Laurent, 1969, is a synonym of *G. marsupiata.*

Vellard (1957) recognized three subspecies of *G. peruana* (Boulenger, 1900). Although certain minor differences in coloration and pustularity exist among populations of *G. peruana* throughout its range in northern and central Perú, these differences are not consistent. Thus we do not recognize subspecies of *G. peruana* and consider *G. peruana dissimilis* Vellard, 1957, and *G. peruana junensis* Vellard, 1957, to be junior synonyms of *G. peruana* (Boulenger, 1900).

Gastrotheca boliviana griswoldi Shreve, 1941, is not conspecific with *G. boliviana* (=*marsupiata*). Shreve's assignment of the population in central Perú as a subspecies of *G. boliviana* was incorrect; as a consequence, Vellard (1957) named the same population as *G. marsupiata bifasciata.* Our studies of series of specimens from Junín and Pasco and examination of the types revealed that *G. marsupiata bifasciata* Vellard, 1957, is a junior synonym of *G. griswoldi* Shreve, 1941.

Examination of limited material suggests that *G. christiani* Laurent, 1967, and *G. gracilis* Laurent, 1969, are valid species. Our

TABLE 1.—Alphabetical synonymy of species in the *Gastrotheca marsupiata* group.

Trivial Name, Original Combination, Author, Date	Current Name
bifasciata (*Gastrotheca bifasciata*) Vellard, 1957	*G. griswoldi*
binghami (*Eleutherodactylus*) Stejneger, 1913	*G. marsupiata*
bolivianum (*Nototrema*) Steindachner, 1892	*G. marsupiata*
caeruleomaculatus (*Hylodes*) Werner, 1899	*G. marsupiata*
christiani (*Gastrotheca*) Laurent, 1967	*G. christiani*
cuzcanus (*Chorophilus*) Cope, 1877	*G. marsupiata*
dissimilis (*Gastrotheca peruana*) Vellard, 1957	*G. peruana*
excubitor (*Gastrotheca*) new species	*G. excubitor*
footei (*Eleutherodactylus*) Stejneger, 1913	*G. marsupiata*
gracilis (*Gastrotheca*) Laurent, 1969	*G. gracilis*
griswoldi (*Gastrotheca boliviana*) Shreve, 1941	*G. griswoldi*
junensis (*Gastrotheca peruana*) Vellard, 1957	*G. peruana*
marsupiata (*Hyla*) Duméril and Bibron, 1841	*G. marsupiata*
ochoai (*Gastrotheca*) new species	*G. ochoai*
peruanum (*Nototrema*) Boulenger, 1900	*G. peruana*
vellardi (*Gastrotheca bifasciata*) Laurent, 1969	*G. marsupiata*

own collections contain series of two additional unnamed species from Perú. Thus, we recognize seven species of *Gastrotheca* in the Andes south of the Huancabamba Depression; 16 trivial names have been proposed for these seven species (Table 1).

DEFINITION OF SPECIES GROUPS

The marsupial frogs of the southern Andes can be distinguished from those species occurring in the northern Andes and at low elevations. For ease in discussion we refer to the southern species collectively as the *Gastrotheca marsupiata* group and to the northern species as the *Gastrotheca argenteovirens* group. In the latter group we place *G. argenteovirens* (Boettger), *G. lojana* Parker, *G. monticola* Barbour and Noble, *G. plumbea* (Boulenger), and the Ecuadorian populations formerly assigned to *G. marsupiata;* the Colombian species *G. aureomaculata* Cochran and Goin and *G. mertensi* Cochran and Goin also can be associated with the *argenteovirens* group. Other species groups, such as the casque-headed species in Colombia and Venezuela and the long-legged arboreal species in the tropical lowlands, are not considered here.

The most profound difference between the *G. marsupiata* and *G. argenteovirens* groups is the nature of the frontoparietals. In both groups the frontoparietals articulate anteriorly with the dermal sphenethmoid and medially with one another. In members of the *marsupiata* group, the frontoparietals are not expanded laterally and do not extend over the otic region; a frontoparietal fontanelle is evident. The nasals, pars facialis of the maxillary, dermal sphenethmoid, and frontoparietals are smooth in the smaller species and in small individuals of the larger species, whereas in larger individuals exostosis is evident on the frontoparietals and decreasingly so on the nasals, dermal sphenethmoid, and pars facialis of the maxillary. In members of the *argenteovirens* group the frontoparietals are expanded laterally so as to form a supraorbital flange that is broadest posteriorly; the frontoparietal fontanelle is covered with bone. In the fully developed condition in the larger species, the frontoparietals extend over the otic region and articulate with the squamosals. Exostosis is well developed on the nasals, dermal sphenethmoid, frontoparietals, and pars facialis of the maxillary; in large individuals exostosis is present on the premaxillaries and squamosals (Fig. 1).

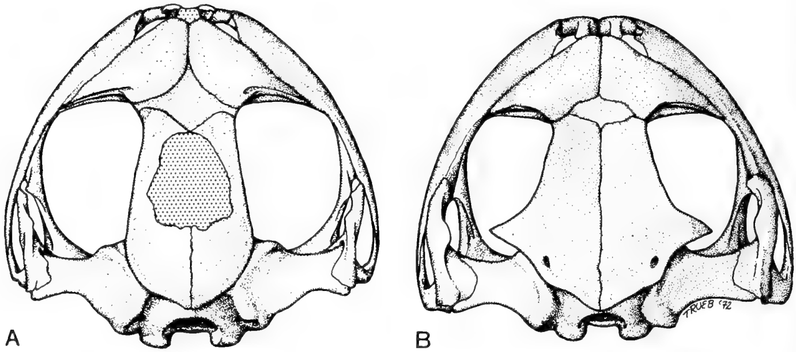

Fig. 1. Dorsal views of skulls of *Gastrotheca*. A. *G. marsupiata*, KU 138372, ♀ 14.1 mm in width. B. *G. riobambae*, KU 99128, ♀ 18.2 mm in width.

These osteological differences are closely correlated with size; larger frogs have better developed frontoparietal flanges and increased exostosis. Frogs in the *marsupiata* group are smaller than those in the *argenteovirens* group. The largest species in the *marsupiata* group is *G. peruana*, females of which attain snout-vent lengths of 53 mm, whereas females of *G. argenteovirens, lojana,* and *monticola* attain snout-vent lengths of 65, 68, and 77 mm, respectively.

All members of the *argenteovirens* group have free-swimming tadpoles. Three species in the *marsupiata* group have free-swimming tadpoles, but in three others development is known to be completed in the maternal pouch.

STATUS OF ECUADORIAN "*GASTROTHECA MARSUPIATA*"

Although Duméril and Bibron (1841:598) based their description of *Gastrotheca marsupiata* on a specimen from Cuzco, Perú, the color patterns of the specimens illustrated in their atlas (Duméril and Bibron, 1854, pl. 98) suggest that the specimens probably came from Ecuador. At the time of the publication of the atlas only one specimen of *Gastrotheca marsupiata* (the type) existed in the Paris museum; however, several Ecuadorian specimens were in the collection at that time and likely served as the basis for the illustrations. Most literature references to *Gastrotheca marsupiata* have dealt with Ecuadorian populations. It is now evident that these populations are not conspecific with the population at Cuzco, Perú, the type locality of *G. marsupiata.* Consequently, another name must be assigned to the Ecuadorian populations. In so doing it is desirable to point out certain problems concerning distribution and variation in the Ecuadorian populations.

We have examined 740 specimens from Ecuador and have seen approximately 250 of these alive. There is considerable variation within and between populations. The most obvious differences are in coloration and involve: 1) presence or absence of dark blotches dorsally, 2) brown versus green dorsal coloration, 3) blue or green in the groin and on the posterior surfaces of the thighs, 4) extent and color of mottling on the flanks, and 5) development of ventral spotting. In addition to differences in coloration, there are differences in size and in glandularity of the dorsal skin.

Polymorphism in dorsal color pattern (uniform versus blotched) occurs within some populations, such as those at such widely separated localities as Biblián, Guaranda, and Papallacta. Frogs from Guaranda and Papallacta are green, whether blotched or plain. Most frogs from Otavalo, Riobamba, and Quito are blotched; most specimens from Otavalo are brown. Both green and brown frogs occur at Riobamba and Quito. At the latter locality the two colors occur in about equal frequency, whereas at Riobamba brown frogs are more frequent in collections made in the dry season and green ones more common in collections made in the rainy season.

Likewise, size is highly variable. Seemingly larger individuals are found on the outer Andean slopes (Guaranda, Baños, Papallacta) than in the interandean valleys (Cuenca, Riobamba, Quito, Otavalo). Specimens from Quito are larger than those from other interandean valleys.

We have not undertaken a detailed analysis of the Ecuadorian populations, which may represent one highly variable species or two or more species. Until such time that the Ecuadorian populations are better known and can be shown to represent more than one species, we propose that they be treated nomenclaturally as one species, *Gastrotheca riobambae* (Fowler).

Fowler (1913:157) named *Hyla riobambae* on the basis of two specimens collected at Riobamba, Provincia Chimborazo, Ecuador, by C. N. Rhoads. The holotype (ANSP 16161) is a male having a snout-vent length of 48.3 mm. The type is in good condition and obviously is a *Gastrotheca.* This is the oldest name applicable to the Ecuadorian populations formerly called *Gastrotheca marsupiata.*

Two other names apply to the same species. Fowler (1913:159) named *Hyla quitoe,* based on three juveniles from Quito, Provincia Pichincha, Ecuador. The holotype (ANSP 18235) has a snout-vent length of 18.8 mm. All three specimens are partially desiccated; no color pattern is evident, although Fowler's illustration (1913, Pl. VII) shows a pattern common in juveniles of *Gastrotheca* from Quito. Acting as first revisors, we have selected *Hyla riobambae* as having priority over *Hyla quitoe,* because: 1) *riobambae* has page priority, 2) the holotype of *riobambae* is an adult in good condition, and 3) the holotype of *quitoe* is a juvenile in poor condition.

Andersson (1945:85) named *Chorophilus olivaceus* from "Rio Napo, 400 m," Ecuador. Examination of the holotype (NHRM 1965) reveals that it is a male *Gastrotheca* having a snout-vent length of 41.7 mm. The specimen is somewhat darkened by formalin, but a faint pattern of dark longitudinal markings is evident on the gray-brown dorsum. The flanks and thighs are plain gray except for faint dark mottling in the groin and on the distal posterior surfaces of the thighs. The type seems to be the same as *Gastrotheca riobambae.* Evidently the type locality is erroneous. The specimen was in a collection received by the Naturhistoriska Riksmuseet in Stockholm from William Clark-MacIntyre, who collected in the Pastaza valley from Baños down to the Amazon lowlands; many of his specimens came from Baños, where *Gastrotheca riobambae* is abundant. The specimen does not bear an attached original tag, so an error in recording the data is possible. The specimen probably came from the vicinity of Baños, the lowest known locality for *G. riobambae* in the Pastaza valley.

A nomenclatural summary of *Gastrotheca riobambae* follows:

Gastrotheca riobambae (Fowler)

New Combination

Hyla riobambae Fowler, 1913:157 [Holotype.—ANSP 16161 from Riobamba, Provincia Chimborazo, Ecuador; S. N. Rhoads collector].

Hyla quitoe Fowler, 1913:159 [Holotype.—ANSP 18238 from Quito, Provincia Pichincha, Ecuador; S. N. Rhoads collector]. New synonymy.

Chorophilus olivaceus Andersson, 1945:85 [Holotype.—NHRM 1965 from "Rio Napo, 400 m." (= ? Banñs, Provincia Tungurahua, Ecuador), William Clarke-MacIntyre collector]. New synonymy.

Gastrotheca m[arsupiata] ecuatoriensis Vellard, 1957:43 [*Nomen nudum*]. New synonymy.

Distribution.—*Gastrotheca riobambae* occurs throughout the Andes, including Amazonian and Pacific slopes and interandean valleys of Ecuador from Tulcán south to the slopes of Cerro Tinajillas, Provincia Azuay. The known altitudinal range is between 1800 and 3960 m. The species probably occurs in the Andes of southern Colombia. To the south of its known range, *Gastrotheca riobambae* apparently is replaced in the Saraguro Valley by *G. monticola* and in the Loja Valley by *G. lojana.*

ACCOUNTS OF SPECIES

In the following accounts the synonymies include all names and combinations thereof applicable to a given taxon. The diagnoses are designed to distinguish the species from other *Gastrotheca* in the southern Andes. Discussions of variation deal principally with coloration, especially in life. An account of geographic and altitudinal distribution is given for each species.

Gastrotheca peruana (Boulenger)

Nototrema peruanum Boulenger, 1900:181 [Syntypes.—BMNH 1900.6.20.46-50 (RR 1947.2.22.42-46) from "Carao" (= Caraz), Departamento Ancash, Perú; P. O. Simons collector].

Gastrotheca peruana peruana—Vellard, 1957:27.

Gastrotheca peruana dissimilis Vellard, 1957:30 [Syntypes.—MJP 245 (47 specimens) from Huamachuco, Departamento La Libertad, Perú; W. Weyrauch collector]. New synonymy.

Gastrotheca peruana junensis Vellard, 1957:33 [Holotype.—MJP 195 from Lago de Punrún, Departamento Junín, Perú; Hernando de Macedo and J. Vellard collectors]. New synonymy.

Diagnosis.—1) Snout-vent length attaining 53.8 mm in males, 52.8 mm in females; 2) snout pointed in dorsal aspect, inclined posterodorsally in profile; 3) canthus acutely rounded; 4) loreal region flat; 5) tympanum round; 6) supratympanic fold heavy, granular; 7) subarticular tubercules on hand large, round; 8) supernumerary tubercles on hand large, round; 9) palmar tubercle large, trifid; 10) webbing absent on hand; 11) webbing present basally on foot, extending to base of antepenultimate phalange of fourth toe; 12) tarsal fold extending full length of tarsus; 13) inner metatarsal tubercles elliptical, not visible from above; 14) outer metatarsal tubercle large, round; 15) subarticular tubercles on foot large, subconical; 16) supernumerary tubercles on foot large, conical, in one row on proximal segments; 17) discs round; 18) dorsal skin strongly granular with longitudinally ovoid tubercles; 19) dorsum predominantly gray or tan with darker gray or brown markings (with pale green centers in some individuals) consisting of pair of supraorbital marks, connected or not to pair of longitudinal blotches or series of dashes; 20) facial pattern consisting of broad, dark canthal stripe, dark postorbital mark extending from supratympanic fold to jaw and not continuous with postaxillary mark, creamy white labial stripe posterior to orbit (absent in some specimens); 21) flanks plain or with few dark flecks; 22) dorsal surfaces of limbs having broad transverse dark bars about equal in width to interspaces; 23) posterior surfaces of thighs brown with or without pale cream spots; 24) venter uniform creamy white; 25) free-swimming tadpoles.

Gastrotheca peruana can be distinguished from the other species by its pointed snout that is inclined posterodorsally in profile. Patterned individuals usually have a large spot on each eyelid (connected with dorsolateral blotch in some individuals) and no interorbital bar; these features of coloration are unique to *G. peruana*. Unpatterned individuals can be distinguished on the basis of the shape of the snout, amount of webbing, and texture of the dorsal skin.

Variation.—Adults are predominantly gray or tan with brown or green markings. An interorbital bar is always absent. The majority of specimens have a dark spot on each eyelid, connected or not with a broad, irregular, longitudinal dark mark; the longitudinal markings are continuous to the sacral region or variously fragmented (Figs. 2 A-D, 3). Most specimens have a dark blotch posterior to the sacrum. Unpatterned individuals are rare.

The following descriptions of coloration in life are excerpted from the authors' field notes.

Cajamarca, Cajamarca, 2800 m (1 specimen): "Dorsum pale gray with dark copper blotches having slight greenish suffusion in concave area of blotches, scattered dark brown flecks between blotches, smaller blotches on flanks and dorsal surfaces of thighs and shanks; canthal and postorbital stripes copper with black flecks on edges; posterior surfaces of thighs beige with pale cream tubercles; iris metallic red."

La Libertad: Huamachuco, 3350 m (7 specimens): "Adult female having golden tan dorsum with two rows of darker bronze-tan blotches outlined with yellow-green; posterior surfaces of thighs uniform beige. Adult males having yellowish green or tan

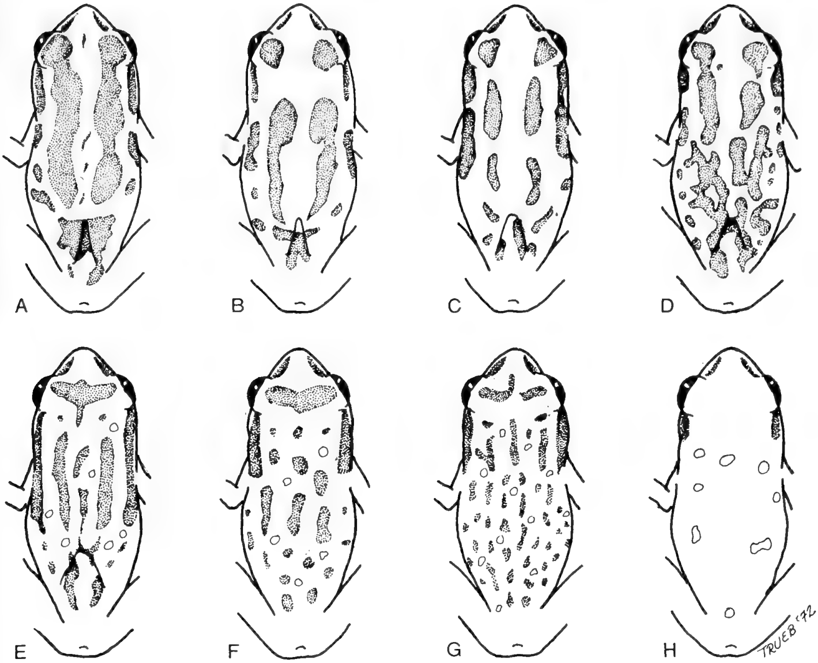

FIG. 2. Diagrammatic color patterns of *Gastrotheca peruana* (A-D) and *G. marsupiata* (E-H).

dorsum with yellow-green or dark brown blotches; posterior surfaces of thighs and inguinal region brown with red-orange blotches. Smallest juvenile having a uniform yellow green dorsum and dull bronze-beige flanks; larger juveniles gray to yellowish tan with brown blotches; iris metallic red in adults, reddish brown in juveniles."

Ancash: 5 km N Recuay, 3450 m (18 specimens): "Dorsum gray, gray-tan, or brown in adults; one female with dorsal pattern nearly obscured by yellow-green suffusion; dorsal blotches yellow-green, yellow-tan, or brown, outlined in black; four of six adults with orange tint or orange blotches on posterior surfaces of thighs, which otherwise are dark brown with beige flecks or gray with dark brown blotches; inguinal region of adults lacking orange. Juveniles gray-beige to brown with green or dark brown blotches; posterior surfaces of thighs and inguinal region dark brown with red-orange blotches; iris red-bronze."

Huánuco: 5 km NE La Unión, 3100 m (34 specimens): "Dorsum in juveniles yellow-tan, gray-beige, yellow-green, or leaf green; most are unicolor, a few have brownish bronze or yellow-green

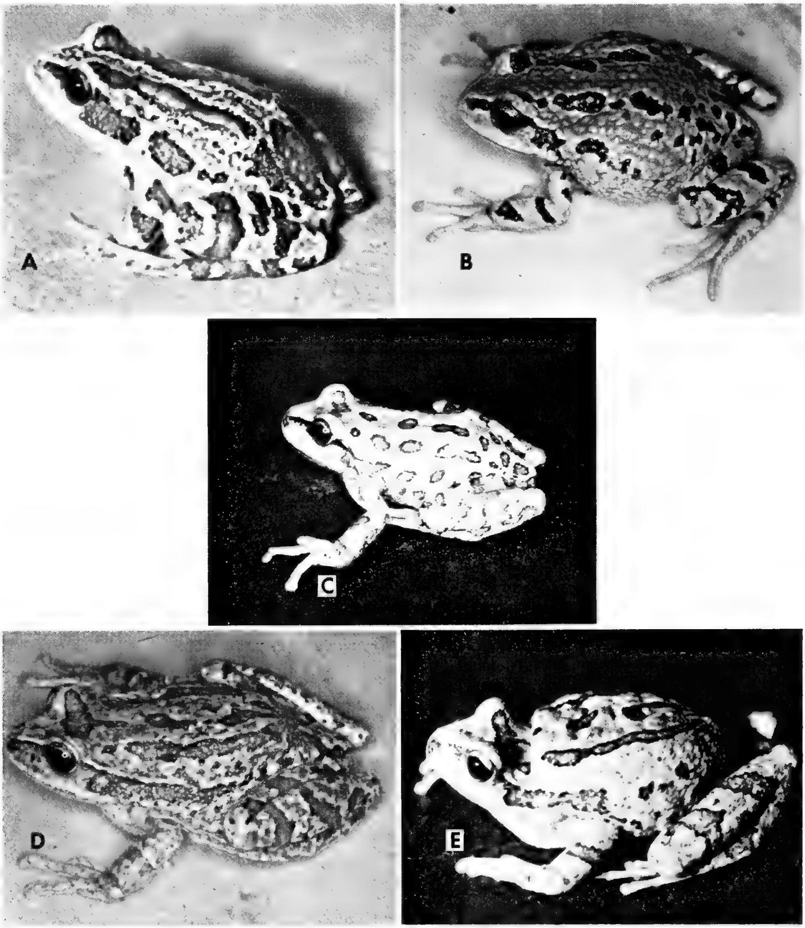

FIG. 3. A-B. *Gastrotheca peruana.* A. KU 138453, ♂ 43.0 mm in snout-vent length. B. KU 139189, ♀ 40.0 mm. C-E. *Gastrotheca marsupiata.* C. KU 139185, ♂ 33.0 mm. D. KU 139187, ♀ 43.0 mm. E. KU 138252, ♀ 43.0 mm.

blotches; smallest (<20 mm) having posterior surfaces of thighs brown with a few white flecks; those with snout-vent lengths of more than 20 mm having prominent elongate orange blotch on distal half of posterior surface of thigh and another blotch in axilla; most adults lack orange coloration; a few adults have three or four small red-orange spots on distal posterior surface of thigh; orange coloration becomes progressively fainter in larger subadults. Dorsum in adults gray, beige, or tan, all with green, tan, or brown blotches and lacking yellow spots; posterior surfaces of thighs brownish tan with white or beige flecks; iris metallic bronze."

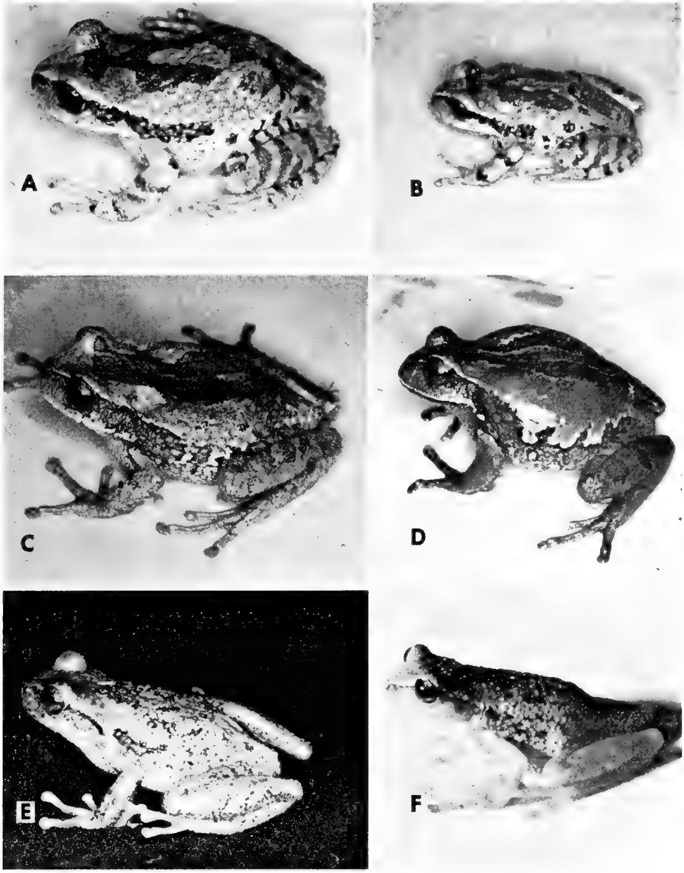

FIG. 4. A-B. *Gastrotheca griswoldi.* A. KU 139140, ♀ 37.5 mm. in snout-vent length. B. 139143, ♂ 26.5 mm. C-D. *Gastrotheca excubitor.* C. KU 139194 (holotype), ♀ 36.8 mm. D. UMMZ 131676, ♀ 41.1 mm. E-F. *Gastrotheca ochoai.* E. KU 139202 (holotype), ♀ 36.9 mm. F. KU 138666, ♀ 35.0 mm.

Junín: Between Casa Pata and Añascancha, 4050 m (2 specimens): "Dorsum tan with dark brown blotches; throat creamy yellow; belly pale gray; posterior surfaces of thighs pinkish tan; anal tubercles white; iris bronze above and copper below, with black reticulations."

It is obvious from the preceding descriptions that notable ontogenetic changes occur in color and pattern and that these changes apparently are not the same in different populations. Until the nature of the changes and the geographical limits of various populations are known, it is not feasible to recognize subspecies of *G. peruana.*

Distribution.—*Gastrotheca peruana* is wide-ranging; it extends from the Nudo de Pasco in central Perú northward to the Huancabamba Depression in northern Perú. The species occurs at elevations of 2300 to 3450 m on the Pacific slopes, in the valley of the Río Marañon at elevations of 2300 to 3350 m, and in the most northern headwaters of the Río Mantaro at elevations of 4000 to 4600 m (Fig. 5).

On the Pacific slopes of Perú the xeric conditions resulting from the effects of the Humboldt Current greatly affect the distribution of this species. The lower elevations recorded for the species on the Pacific slopes are in valleys protected from the desiccating

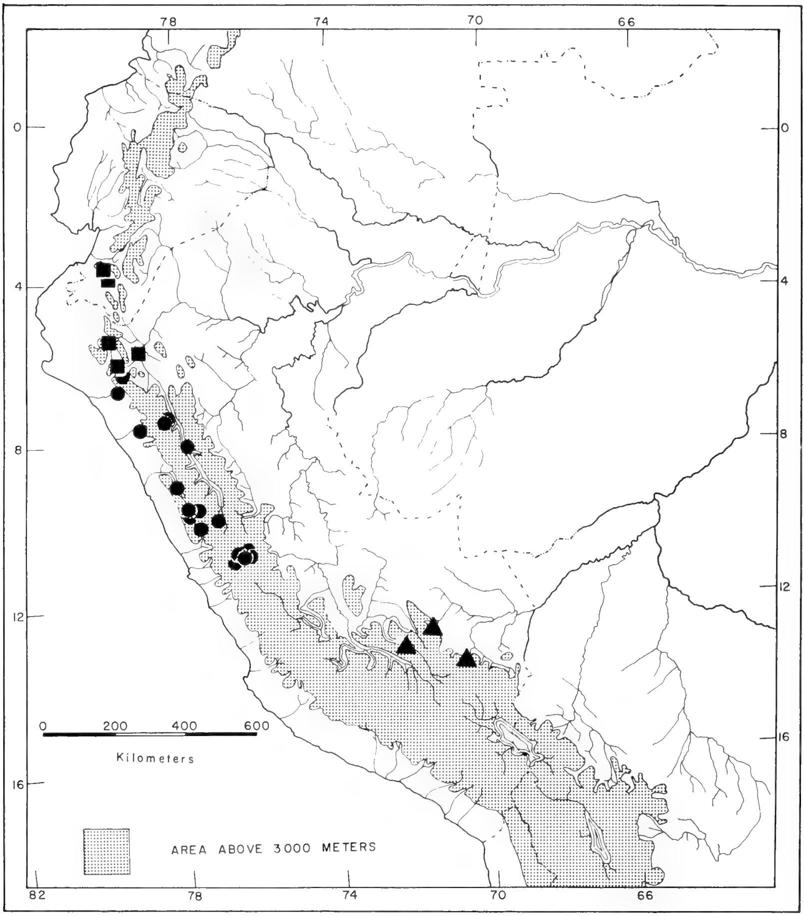

FIG. 5. Locality records for *Gastrotheca monticola* (squares), *G. ochoai* (triangles), and *G. peruana* (circles).

winds; these valleys are more moist than the exposed areas at the same elevations. The Río Chiquian near the boundary between Departamento Lima and Departamento Ancash is the southernmost Pacific valley known to be inhabited by *G. peruana.*

Gastrotheca marsupiata (Duméril and Bibron)

Hyla marsupiata Duméril and Bibron, 1841:598 [Holotype.—MNHN 4877 from Cuzco, Departamento Cuzco, Perú; Pentland collector].

Nototrema marsupiatum—Günther, 1859:116.

Chorophilus cuzcanus Cope, 1877:37 [Holotype lost, named from "Perú"; James Orton collector]. New synonymy.

Nototrema bolivianum Steindachner, 1892:840 [Lectotype.—NHMW 16490 from Puerto de San Mateo, Departamento Cochabamba, Bolivia; Standiger collector]. New synonymy.

Hylodes caeruleomaculatus Werner, 1899:482 [Syntypes.—NHMW 16496 (2 specimens) from "Bolivia"; Schlüter collector]. New synonymy.

Eleutherodactylus binghami Stejneger, 1913:542 [Holotype.—USNM 49559 from Cuzco, Departamento Cuzco, Perú; obtained by Yale-Peruvian Expedition]. New synonymy.

Eleutherodactylus footei Stejneger, 1913:543 [Holotype.—USNM 49562 from Tincochchaca, Departamento Cuzco, Perú; obtained by Yale-Peruvian Expedition]. New synonymy.

Gastrotheca boliviana—Barbour and Noble, 1920a:611 [Synonymized *Elutherodactylus binghami* Stejneger, 1913, with *Nototrema bolivianum* Steindachner, 1892].

Nototrema bolivianum—Nieden, 1923:320 [Synonymized *Hylodes caeruleomaculatus* Werner, 1899, with *Nototrema bolivianum* Steindachner, 1892].

Hylodes footei—Nieden, 1923:456.

Hylodes binghami—Nieden, 1923:456.

Gastrotheca marsupiata [*marsupiata* (by fiat)]—Parker, 1932:25.

Gastrotheca boliviana [*boliviana* (by fiat)]—Shreve, 1941:83.

Gastrotheca boliviana—Vellard, 1957:7.

Gastrotheca bifasciata vellardi Laurent, 1969a:129 [Substitute name for *Gastrotheca marsupiata marsupiata* sensu Vellard, 1957].

Diagnosis.—1) Snout-vent length attaining 41.6 mm in males, 46.5 mm in females; 2) snout acutely rounded in dorsal aspect, round in profile; 3) canthus round; 4) loreal region barely concave; 5) tympanum vertically ovoid; 6) supratympanic fold moderately heavy; 7) subarticular tubercules on hand large, round; 8) supernumerary tubercles on hand small, subconical; 9) palmar tubercle small, trifid; 10) webbing absent on hand; 11) webbing present basally on foot, extending to base of preantepenultimate phalange of fourth toe; 12) tarsal fold extending one-third length of tarsus; 13) inner metatarsal tubercle large, elliptical, visible from above; 14) outer metatarsal tubercle small, round; 15) subarticular tubercles on foot large, conical; 16) supernumerary tubercles on foot small, round, in one row on proximal segments; 17) discs slightly wider than long; 18) dorsal skin weakly granular; 19) dorsum green or brown, usually with dark green or dark brown markings consisting of interorbital bar or T-shaped mark not connected to longitudinal blotches or dashes on back, round cream spots or not; 20) facial pattern consisting of broad, dark canthal and postorbital stripes (latter continuous to point behind axilla) and narrow cream labial stripe; 21) flanks plain or marked with large dark spots; 22) dorsal surfaces of limbs plain or having irregular dark transverse bars; 23) posterior surfaces of thighs tan; 24) venter creamy white with or without grayish brown spots; 25) free-swimming tadpoles.

Gastrotheca marsupiata can be distinguished from the other species by the presence of an interorbital bar or T-shaped mark that is not connected to blotches or stripes on the back. Furthermore, it differs from *G. peruana* in snout shape, amount of webbing, and texture of the dorsal skin. *Gastrotheca excubitor* and *griswoldi* have an interorbital bar that usually is connected to a middorsal mark.

Variation.—The dorsal coloration is highly variable. In all large series that we have seen in life some individuals are brown and others are green. Some individuals have dark blotches and others lack blotches, whereas most individuals have some small, pale spots on the dorsum (Fig. 3). In most blotched specimens, a complete interorbital bar is present; the arrangement and size of the blotches on the dorsum vary from large dorsolateral, longitudinal blotches with smaller middorsal blotches to small longitudinal blotches over the entire dorsum (Fig. 2E-G).

Variation in living individuals is documented by descriptions excerpted from Fritts' field notes:

Huancavelica: Huancavelica, 3780 m (12 specimens): "One male uniform brown; one male yellowish tan with numerous yellow spots; six adults pale brown with olive-green to leaf green dorsal blotches; most of latter six with a few yellow spots on dorsum; two females and one male grayish brown with olive-green blotches; posterior surfaces of thighs pale brown to grayish brown with white flecks; dorsal and anterior surfaces of thighs pinkish beige with brown or dark green bars; iris metallic bronze, occasional specimens with yellow line over pupil. One juvenile golden brown with olive-green blotches."

Huancavelica: 10 km W Lircay, 3700 m (30 specimens): "Majority are grayish beige ground color; approximately one-third are yellow-beige; dorsal blotches olive-green to grayish brown; four juveniles uniform gray; all adults of both sexes having few to many yellow spots dorsally; posterior surfaces of thighs gray with white tubercles; all blotched individuals have a T or transverse bar between orbits; all uniform gray individuals have narrow, slightly gray bars on dorsal surfaces of thighs; iris metallic bronze."

Cuzco: 10 km E Abra Huillque, 3700 m (8 specimens): "Dorsum gray-beige to bronze-beige; all adults, except one female, have numerous yellow spots on dorsum; one male without dorsal blotches; one male with faint green dorsal blotches; one male with bronze dorsal blotches; other adults have leaf green dorsal blotches; one juvenile with uniform yellow-green dorsum."

Cuzco: 4 km NW Cuzco, 3600 m (36 specimens): "Dorsum gray-beige to medium brown; most individuals have yellow-green blotches often outlined with narrow black line; most adults and some subadults have small to large yellow spots on head, body, and thighs; approximately one-third of individuals are unicolor dorsally, except for yellow spots; unicolor adults tan, some with yellow suffusion; juveniles uniformly yellowish green; venter grayish white; posterior surfaces of thighs dark tan with white tubercles; iris metallic bronze."

Cuzco: Sicuani, 3530 m (12 specimens): "Dorsum pale to dark gray-beige with extensive bronze suffusion in adults and slight bronze suffusion in smaller individuals; all but two have yellow-green blotches outlined with narrow black line; one individual having pale green blotches and one lacking blotches; dorsal surfaces of thighs gray-beige with yellow-green bars; most larger individuals with numerous pale yellow spots on dorsum; posterior surfaces of thighs pale brown with numerous white tubercles; iris metallic bronze."

Cuzco: Granja de la Raya, 4250 m (13 specimens): "Dorsum gray, gray-beige, or medium brown; approximately one-third of individuals have intense green suffusion over entire dorsum, most prominent on anterior half of body; all have yellow-green blotches outlined with narrow black line and pale to bright yellow spots on dorsum and thighs; posterior surfaces of thighs pale greenish beige with white tubercles; iris metallic bronze."

Distribution.—Gastrotheca marsupiata is known from the Nudo de Pasco in central Perú to southern Bolivia (Fig. 6). The species is known from elevations of 2760 to 4360 m in the Peruvian river valleys of the Río Mantaro, Río Apurimac, and Río Urubamba and the altiplano of Lago Titicaca. In Bolivia it is known from the eastern slopes of Departamento La Paz southward to Departamento Chuquisaca. Little altitudinal data exists for Bolivian specimens; however, Hans Hoffman (pers. com.) observed individuals of *Gastrotheca marsupiata* at 2560 m in the city of Cochabamba. The species occurs at La Paz at an elevation of 3700 m.

Although populations of *G. marsupiata* and *G. griswoldi* are known from geographically close localities in the upper Río Mantaro valley, the two species have not been found in sympatry. *Gastrotheca marsupiata* is not known to occur above 3600 m near the Nudo de Pasco, although it is known at higher elevations in other parts of its range. Similarly, *G. griswoldi* occurs at elevations of 3200 to 3700 m in other parts of its range, but in the upper Río Mantaro valley it is known only from localities at 3700 m or higher. Present information indicates that a parapatric relationship exists between *G. marsupiata* and *G. griswoldi.*

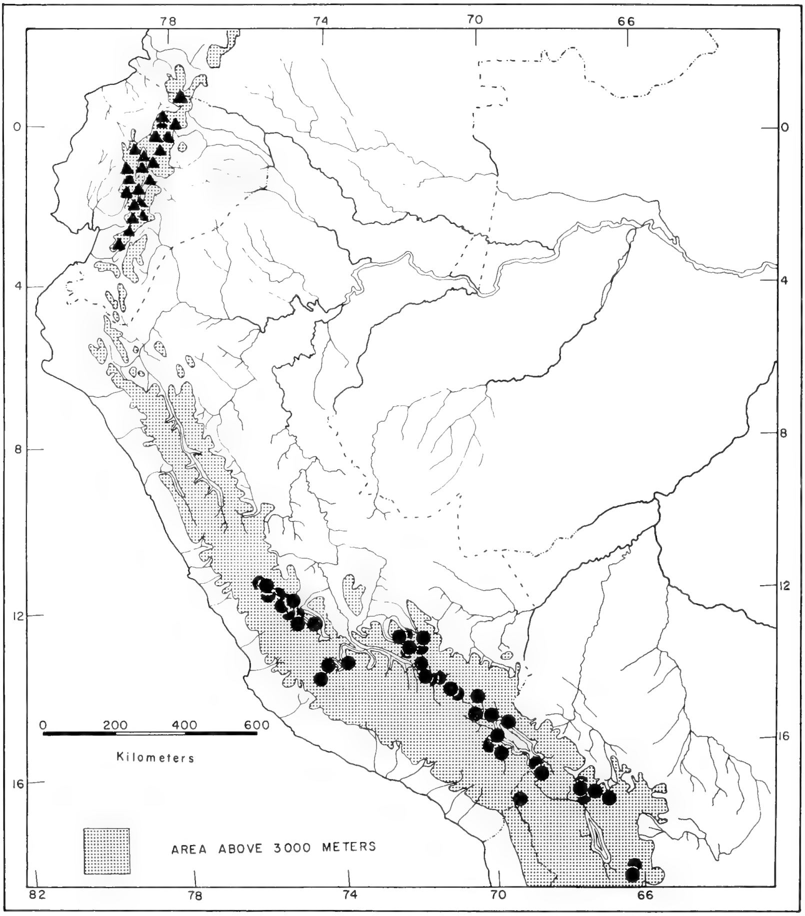

FIG. 6. Locality records for *Gastrotheca marsupiata* (circles) and *G. riobambae* (triangles).

Gastrotheca griswoldi Shreve
New Combination

Gastrotheca boliviana griswoldi Shreve, 1941:83 [Holotype.—MCZ 24102 from Maraynioc, Departamento Junín, Perú; J. A. Griswold collector].
Gastrotheca marsupiata bifasciata Vellard, 1957:23 [Syntypes.—MJP 129 (3 specimens) from Paccha, near Lo Oroya, Departamento Junín, Perú; Jehann Vellard collector]. New synonymy.
Gastrotheca bifasciata bifasciata—Laurent, 1969a:131.

Diagnosis.—1) Snout-vent length attaining 37.8 mm in males, 44.0 mm in females; 2) snout round in dorsal aspects and in profile; 3) canthus round; 4) loreal region barely concave; 5) tympanum round; 6) supratympanic fold heavy, granular; 7) subarticular tubercles on hand large, subconical; 8) supernumerary tubercles on hand large, conical; 9) palmar tubercle large, trifid; 10) webbing absent on hand; 11) webbing present basally on foot, extending to base of preantepenultimate phalange of fourth toe; 12) tarsal fold extending one-half length of tarsus; 13) inner metatarsal tubercle elongate, visible from above; 14) outer metatarsal tubercle small, conical; 15) subarticular tubercles on foot large, round; 16) supernumerary tubercles on foot large, conical, in one row on proximal and medial segments; 17) discs nearly round; 18) dorsal skin smooth to weakly granular; 19) dorsum green, gray, or tan with darker markings consisting of interorbital bar with narrow connection to diverging, irregular longitudinal marks on back; 20) facial pattern consisting of broad canthal and postorbital stripes (latter continuous to point behind axilla) and narrow cream labial stripe; 21) flanks plain or marked with few small dark spots; 22) dorsal surfaces of limbs having narrow transverse dark bars; 23) posterior surfaces of thighs pale brown; 24) venter creamy white with or without few small brown spots; 25) metamorphosis completed within maternal pouch.

Gastrotheca griswoldi differs from all other species, except *G. gracilis* and *excubitor,* in having a dark interorbital bar connected medially to the dorsal markings. In *G. griswoldi* the dorsal markings are narrow and divergent, whereas in *G. excubitor* the markings are broad, parallel, and in some individuals fused. In *G. gracilis* the interorbital bar is connected with a middorsal stripe. *Gastrotheca griswoldi* further differs from *G. excubitor* by having a heavier supratympanic fold, larger supernumerary tubercles, less webbing, and a large trifid, instead of small bifid, palmar tubercle. *Gastrotheca griswoldi* also differs from *G. gracilis* by having a broader, more rounded snout in dorsal aspect, less webbing, larger supernumerary tubercles on the foot, and round, instead of truncate, discs.

Variation.—The most noticeable variation is in dorsal color pattern (Fig. 7A-D). Of ten adults from Maraynioc, Perú, three have pattern A, six pattern B, and one pattern C. The variation in 11 adults from Paccha, Perú, is eight B and three C, whereas in 10 adults from Comas, Perú, the variation is eight B, one C, and one D. Of four adults from 14 km SW of Paucartambo, Perú, three have pattern B, and one has pattern D, but two of the individuals with pattern B have very faint patterns on a grayish tan dorsum bearing diffuse orange blotches.

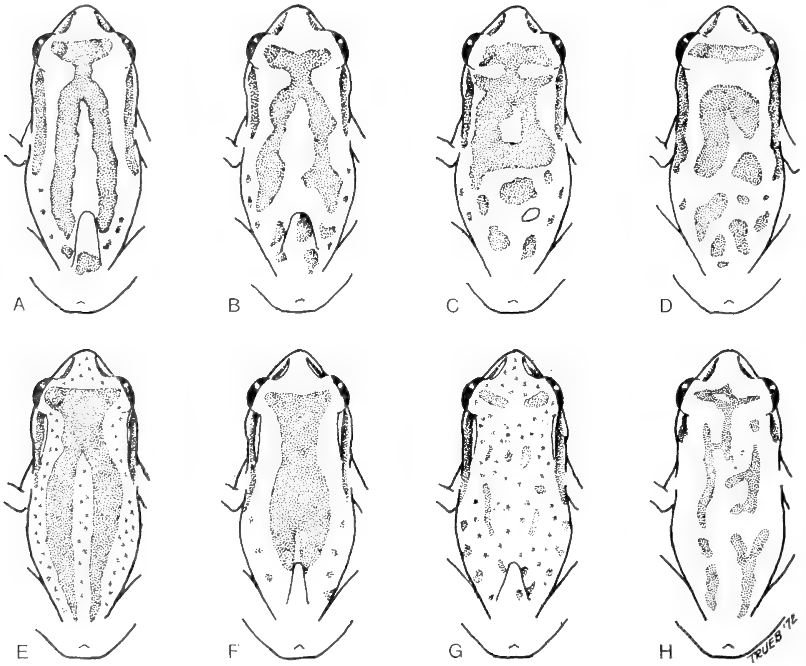

FIG. 7. Diagrammatic color patterns of *Gastrotheca griswoldi* (A-D), *G. excubitor* (E-G), and *G. gracilis* (H).

In life, individuals from Paccha were gray or tan with brown or green markings; some individuals also had yellow or orange spots on the dorsum (Fig. 4). In specimens from Comas, the spots were dull red. The venter was creamy white with or without black flecks, and the flanks were gray with black or green spots. The iris was dull bronze, darkest (nearly copper) ventrally, with a median horizontal red-brown streak and black reticulations. Two individuals from 14 km SW of Paucartambo, Perú, were colored like those from Paccha, but one individual was grayish tan with dark green markings narrowly outlined with cream. Juveniles having snout-vent lengths of less than 20 mm have uniformly green dorsal coloration in life.

Distribution.—*Gastrotheca griswoldi* is known from elevations between 3700 and 3800 m in the northern Río Mantaro valley and from elevations of 3200 to 3700 m on the eastern slopes of the Andes in central Perú in the valleys forming the headwaters of the Río Perené (Fig. 8). Vellard (1957:25) recorded eight specimens (MJP 494) from "Caina cerca de Huánuco, 3600 mts.," Departamento Huánuco, Perú. We have examined six specimens (MJP 494) bearing a locality label "Huánuco." The city of Huánuco. because of its low elevation and xeric climate, is a doubtful locality for *G. griswoldi,* but Caina at 3600 m may support a population of the species. If the locality given by Vellard is correct, these specimens represent the only population known from the northern slopes of the Nudo de Pasco or the Río Huallaga drainage.

The distribution of *G. griswoldi* on the southern slopes of the Nudo de Pasco in central Perú approaches the ranges of *G. marsupiata* and *G. peruana.* The three species occur in the short distance (less than 80 km) between Jauja and Carhuamayo. *Gastrotheca marsupiata* is known from elevations of 3400 to 3600 m near Jauja (Vellard, 1957); *G. griswoldi* occurs near La Oroya at elevations of 3700 to 3800 m, whereas *G. peruana* is known from elevations of 4000 to 4600 m near Junín and Carhuamayo. No two of the three species have been found in sympatry.

Gastrotheca excubitor new species

Holotype.—KU 139194, adult female, from the northern slope of Abra Acanacu, 31 kilometers (by road) north-northeast of Paucartambo, Departamento Cuzco, Perú, 3370 m; one of a series obtained on 16 January 1971 by William E. Duellman, Thomas H. Fritts, and Oscar Ochoa M.

Paratypes.—KU 139195-97, same data as holotype; KU 139193 from 3270 m on north slope of Abra Acanacu; KU 139198 from 3400 m on north slope of Abra Acanacu; KU 139199-201, UMMZ 131676, IML 2014 from the crest of Abra Acanacu, 3520 m.

Diagnosis.—1) Snout-vent length attaining 39.5 mm in males, 41.1 mm in females; 2) snout round in dorsal aspect and in profile; 3) canthus acutely rounded; 4) loreal region barely concave; 5) tympanum vertically ovoid; 6) supratympanic fold weak, granular; 7) subarticular tubercles on hand large, round; 8) supernumerary tubercles on hand small, subconical; 9) palmar tubercle small, bifid; 10) webbing absent on hand; 11) webbing present basally on

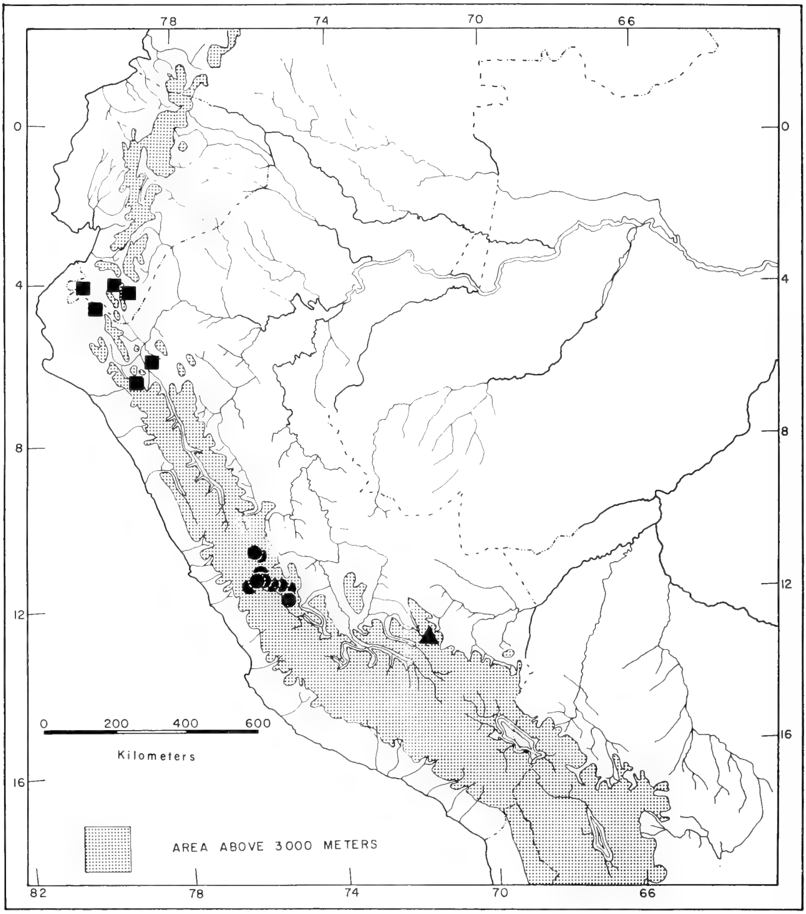

Fig. 8. Locality records for *Gastrotheca excubitor* (triangle), *G. griswoldi* (circles), and *G. lojana* (squares).

foot, extending to base of antepenultimate phalange of fourth toe; 12) tarsal fold extending one-fourth length of tarsus; 13) inner metatarsal tubercule elliptical, visible from above; 14) outer metatarsal tubercle small, round; 15) subarticular tubercles on foot large, conical; 16) supernumerary tubercles on foot small, conical, in one row on proximal segments; 17) discs nearly round; 18) dorsal skin smooth; 19) dorsum tan, gray, or green with dark brown or green markings consisting of broad interorbital bar connected to pair of broad, longitudinal stripes, partly or completely coalesced in some specimens; 20) facial pattern consisting of broad, dark canthal and postorbital stripes, bordered above by narrow light stripes, and pale labial stripe; 21) flanks tan, green, or gray with large dark spots; 22) dorsal surfaces of limbs having narrow transverse dark bars; 23) posterior surfaces of thighs dark brown; 24) venter tan with brown spots; vocal sac gray; 25) metamorphosis presumably completed in maternal pouch.

Gastrotheca excubitor has an interorbital bar connected with the dorsal markings; in this way it differs from all other species, except *G. griswoldi* and *G. gracilis.* In *G. excubitor* the dorsal markings are broad and parallel, whereas in *G. griswoldi* the markings are narrow and divergent posterolaterally, and in *G. gracilis* the interorbital bar is connected to a middorsal stripe. *Gastrotheca excubitor* further differs from both *G. griswoldi* and *gracilis* by having smaller supernumerary tubercles on the hand, a weaker supratympanic fold, and a small bifid, instead of large trifid, palmar tubercle.

Variation.—Measurements and proportions of four adult males are followed by those of five adult females (means in parentheses): snout-vent length 33.9-39.5 (36.0), 35.1-41.1 (37.1) mm; tibia/snout-vent 0.471-0.500 (0.484), 0.482-0.527 (0.510); foot/snout-vent 0.435-0.497 (0.473), 0.465-0.544 (0.491); head length/snout-vent 0.316-0.351 (0.334), 0.332-0.353 (0.342); head width/snout-vent 0.354-0.383 (0.365), 0.350-0.389 (0.378); interorbital distance/head width 0.267-0.329 (0.303), 0.266-0.335 (0.302); tympanum/eye 0.378-0.540 (0.469), 0.459-0.593 (0.503).

Although there is considerable variation in color, the dorsal pattern is rather constant in most individuals (Fig. 7E-G). Of 11 adults from Abra Acanacu, eight are pattern E, two are F, and one is G. In life, seven individuals had a tan dorsum with brown markings; three were green with dark green markings, and one was reddish brown with dark brown markings (Fig. 4). In some individuals the dorsal dark markings are narrowly outlined with bronze-tan, but all specimens have a narrow bronze-tan stripe bordering the upper edges of the canthal and postorbital stripes. In one specimen the postorbital dark stripe and bordering bronze-tan stripe are continuous to the groin, although the stripes have an irregular upper border and indistinct lower border.

In life, the flanks are bronze-tan to bluish green with dark brown and/or cream spots. The venter is tan, and in calling males the vocal sac is dark gray. The iris is copper with fine black reticulations. A juvenile having a snout-vent length of 16.3 mm was colored like the adults with a tan dorsum with dark brown markings.

Distribution.—*Gastrotheca excubitor* is known only from elevations of 3270 to 3520 m on the crest and northern slope of Abra Acanacu, Departamento Cuzco, Perú (Fig. 8). All localities are in wet páramo along the Paucartambo-Pilcopata road. Abra Acanacu is a pass in the Cadena del Paucartambo, the northwestern part of the Cordillera Carabaya. The Cadena del Paucartambo is the divide between the drainage systems of the Río Ucayali and the Río Madre de Dios. The southwestern slopes of the Cadena del Paucartambo are drained by the Río Paucartambo, which flows northward through a dry valley in the rain shadow of the cordillera, into the Río Urubamba, a southern tributary of the Río Ucayali, a large tributary of the Río Amazonas. The northeastern slopes of the Cadena del Paucartambo receive prevailing moist winds and are drained by the Río Cozñipata and Río Pilcopata, tributaries of the Río Alto Madre de Dios.

Etymology.—The specific name is Latin meaning sentinel, in reference to the outlying Cadena del Paucartambo, the type locality.

Gastrotheca gracilis Laurent

Gastrotheca gracilis Laurent, 1969b:146 [Holotype.—IML 1389 from La Banderita, Kilometer 51, Ruta Concepción-Andalgalá, Provincia Catamarca, Argentina; Roberto Cei collector].

Diagnosis.—1) Snout-vent length attaining 37.1 mm in males, 48.0 in females; 2) snout acutely rounded in dorsal aspect, round in profile; 3) canthus round; 4) loreal region barely concave; 5) tympanum round; 6) supratympanic fold moderately heavy; 7) subarticular tubercles on hand large, round; 8) supranumerary tubercles on hand large, conical; 9) palmar tubercle large, trifid; 10) webbing absent on hand; 11) webbing present basally on foot, extending to base of antepenultimate phalange of fourth toe; 12) tarsal fold extending one-fourth length of tarsus; 13) inner metatarsal tubercle elongate, visible from above; 14) outer metatarsal tubercle small, round; 15) subarticular tubercles on foot large, conical; 16) supernumerary tubercles on foot small, subconical; 17) discs broadly ovid, roundly truncate; 18) dorsal skin bearing small, low tubercles; 19) dorsum gray with green markings consisting of interorbital T-shaped mark connected to middorsal stripe, pair of dorsolateral stripes (continuous or fragmented); 20) facial pattern consisting of narrow, dark canthal and postorbital stripes and narrow tan labial stripe; 21) flanks pale gray with dark spots; 22) dorsal surfaces of limbs with broad dark transverse bars; 23) posterior surfaces of thighs gray; 24) venter creamy white with brown spots; 25) free-swimming tadpoles.

Gastrotheca gracilis has an interorbital bar connected to a middorsal stripe, bordered on either side by dorsolateral dark stripes that are continuous or fragmented. The only other species having an interorbital bar connected to dorsal markings are *G. griswoldi* and *excubitor;* in these species there is no middorsal stripe, but rather a pair of longitudinal marks. *Gastrotheca gracilis* also differs from those species by having an acutely rounded snout in dorsal aspect, instead of a broad, round snout. *Gastrotheca gracilis* further differs from *G. griswoldi* by having more webbing, smaller supernumerary tubercles on the foot, and broader, truncate discs, and from *G. excubitor* by having larger supernumerary tubercles on the hand, a heavier supratympanic fold, and a large trifid, instead of a small bifid, palmar tubercle.

Variation.—Snout-vent lengths of five adult males from the type locality are 34.9-37.1 (mean 35.8) mm; the largest adult female has a snout-vent length of 48 mm. We have not seen living individuals of this species; the following description is a free translation of Laurent (1969b:147): "Color in life gray with green lines or blotches (blotches turn blue in formalin), which form an irregular more or less reticulated pattern on the back and limbs, with a tendency to be arranged in three longitudinal lines anteriorly and a subcanthal zone that extends from the tip of the snout to the shoulder, passing below the eye and around the tympanum, which is dark brown."

In preservative, four males are brown, and one is gray. All have three rows of interrupted longitudinal marks on the back, the middorsal stripe beginning with a T-shaped mark between the eyes and extending to the sacral region. The dorsolateral stripes extend from the nape to the anus (Fig. 9). There are three dark diagonal bars on each thigh and shank and two on each forearm. A dark brown canthal-postorbital stripe is fragmented into irregular dark spots on the creamy tan flanks. The labial stripe is indistinct, narrow, and tan. The throat is brown, and the chest and belly are cream with small brown spots.

Distribution.—Gastrotheca gracilis is known from elevations of 1500 to 2000 m in the Sierra del Aronquija, an eastern spur of the Andes in northern Argentina.

Gastrotheca ochoai new species

Holotype.—KU 139202, adult female, from southwest base of Cordillera de Vilcanota, west of Río Runtumayo, about 3 kilometers north of Chilca, 10 kilometers (by road) northwest of Ollantaytambo, Departamento Cuzco, Perú, 2760 m; one of a series obtained on 9 January 1971 by William E. Duellman and Thomas H. Fritts.

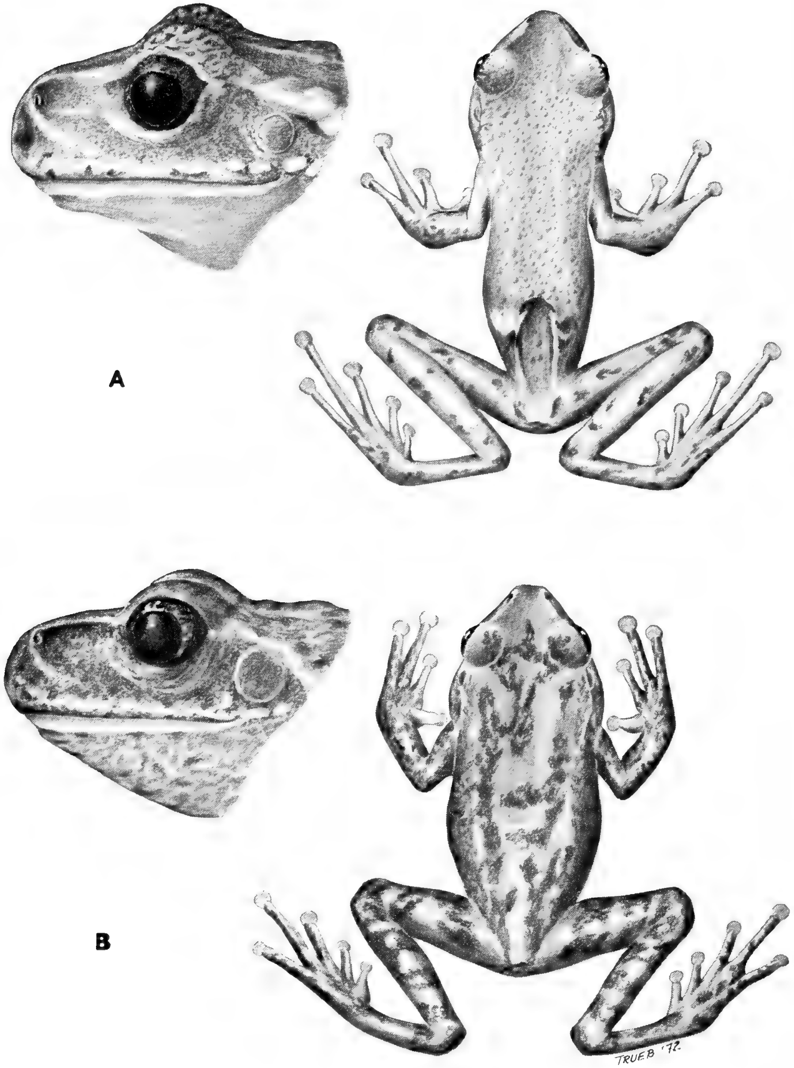

FIG. 9. A. *Gastrotheca christiani,* IML 1606, ♀ 40.0 mm in snout-vent length. B. *Gastrotheca gracilis,* IML 1530, ♂ 36.0 mm.

Paratopotypes.—IML 2012, KU 138631-35, 138645-58, 139203-09, UMMZ 131688 (9).

Diagnosis.—1) Snout-vent length attaining 32.9 mm in males, 37.9 mm in females; 2) snout pointed in dorsal aspect, round in profile; 3) canthus round; 4) loreal region barely concave; 5) tympanum round; 6) supratympanic fold weak, granular; 7) subarticular tubercules on hand large, round; 8) supernumerary tubercles on hand large, round; 9) palmar tubercle large, bifid; 10) webbing absent on hand; 11) webbing present basally on foot, extending to middle of preantepenultimate phalange of fourth toe; 12) tarsal fold absent; 13) inner metatarsal tubercle elongate, visible from above; 14) outer metatarsal tubercle large, round; 15) subarticular tubercles on foot large, subconical; 16) supernumerary tubercles on foot small, round, in one row on proximal segments; 17) discs wide, roundly truncate; 18) dorsal skin bearing small tubercles; 19) dorsum tan with dark flecks and (in some individuals) median or pair of longitudinal brown blotches; 20) facial pattern consisting of narrow, dark brown canthal and postorbital stripes and tan lips; 21) flanks tan with or without dark flecks; 22) dorsal surfaces of limbs tan with dark flecks; 23) posterior surfaces of thighs pale brown; 24) venter dusky white; 25) metamorphosis completed in maternal pouch.

Gastrotheca ochoai differs from all other species, except *G. christiani,* in having a pointed snout in dorsal aspect and round in profile, and in lacking a tarsal fold and labial stripe. *Gastrotheca ochoai* can be distinguished from *G. christiani* by the following (characters of *G. christiani* in parentheses): supratympanic fold weak (shelf-like), palmar tubercle bifid (elongate, single), no webbing on hand (fingers webbed basally), dorsal skin bearing small, round tubercles (large ovoid tubercles), no dark interorbital mark (interorbital bar or T-shaped mark), and venter dusky (spotted).

Variation.—Measurements and proportions of 12 topotypic adult males are followed by those of 10 females (means in parentheses): snout-vent length 25.9-29.2 (27.9), 30.8-36.9 (33.4) mm; tibia/snout-vent 0.490-0.580 (0.530), 0.489-0.559 (0.527); foot/snout-vent 0.430-0.495 (0.455), 0.422-0.489 (0.452); head length/snout-vent 0.330-0.355 (0.342), 0.321-0.364 (0.333); head width/snout-vent 0.344-0.381 (0.368), 0.336-0.364 (0.351); interorbital distance/head width 0.206-0.344 (0.298), 0.264-0.319 (0.303); tympanum/eye 0.355-0.640 (0.441), 0.429-0.613 (0.522).

The following coloration in life of the holotype is taken from Duellman's field notes: "Dorsum golden tan with scattered fine brown flecks; side of head bronze; canthal and postorbital stripes dark brown; flanks and dorsal surfaces of limbs bronze-tan with black flecks; venter dusky white; ventral surfaces of limbs slightly darker; tympanum dark brown; iris deep bronze with black reticulations."

In life, all adults are golden tan with black or brown markings (Fig. 4). In some individuals from Chilca there is a distinct greenish tint on the head, whereas in individuals from Ollachea, Departamento Puno, Perú, there is a rusty red tint on the head in males and subadult females. In adult females from Ollachea the flanks are brown with a greenish tint. In many preserved specimens an irregular middorsal brown blotch or a pair of blotches are present. In life, the frogs are capable of changing from golden tan to brown and can develop more intense dorsal patterns. Apparently the blotches are formed by expansion of melanophores; subsequent contraction of melanophores results in a flecked dorsal pattern.

Young removed from the pouches of females were dull gray with a black canthal stripe. The coloration of juveniles having snout-vent lengths of 13-15 mm is more like that of the adults. The dorsum is golden beige with small brown flecks; the canthus is dark brown grading ventrally to a golden tan lip. The upper arm is yellow, and the postorbital stripe is dark brown. The dorsal surfaces of the thighs are golden yellow with a few yellow spots; the posterior surfaces of the thighs are golden with small brown flecks and a few small, bright yellow spots around the anus. The axillary region is transparent, and the venter is white with a greenish blue tint. The iris is bronze.

Distribution.—*Gastrotheca ochoai* is known from three localities on the northeastern slopes of the Cordillera de Carabaya and on the southwestern slope of the Cordillera de Vilcanota in the valley of the Río Urubamba (Fig. 5). All specimens have been found in terrestrial bromeliads at elevations of 2760 to 2800 m.

Etymology.—The patronym is for Prof. Oscar Ochoa M. of the Departamento de Biología, Universidad Nacional San Antonio Abad, Cuzco, who provided facilities at his home at Hacienda Chilca and aided in collecting specimens.

Gastrotheca christiani Laurent

Gastrotheca christiani Laurent, 1967:354 [Holotype.—IML 1369 from Monumento Ruta Valle Grande, 50 kilometers northwest of Calilegua, Provincia Jujuy, Argentina; Christian Halloy collector].

Diagnosis.—1) Snout-vent length attaining 34.0 mm in males, 40 mm in females; 2) snout acutely rounded in dorsal aspect, round in profile; 3) canthus sharply rounded; 4) loreal region concave; 5) tympanum round; 6) supratympanic fold shelf-like, granular; 7) subarticular tubercles on hand large, round; 8) supernumerary tubercles on hand large, round; 9) palmar tubercle large, elongate, single; 10) webbing present basally between fingers; 11) webbing present basally on foot, extending to middle of antepenultimate phalange of fourth toe; 12) tarsal fold absent; 13) inner metatarsal tubercle large, elongate, broadly visible from above; 14) outer metatarsal tubercle small, conical; 15) subarticular tubercles on foot large, subconical; 16) supernumerary tubercles on foot small, round, in one row on proximal segments; 17) discs broad, roundly truncate; 18) dorsal skin bearing ovoid longitudinal tubercles; 19) dorsum gray or brown with darker markings consisting of interorbital bar or T-shaped mark and irregular longitudinal marks on back; 20) facial pattern consisting of narrow dark canthal and postorbital stripes and brown spots on lips; 21) flanks tan with small irregular brown spots; 22) dorsal surfaces of limbs tan with small brown spots or narrow transverse bars; 23) posterior surfaces of thighs brown; 24) venter creamy white with many small dark spots; 25) metamorphosis completed in maternal pouch.

Gastrotheca christiani resembles *G. ochoai* in having a pointed snout in dorsal aspect and round in profile, and in lacking a tarsal fold and labial stripe. In these characters *G. christiani* and *ochoai* differ from all of the other species. *Gastrotheca christiani* differs from *G. ochoai* as follows (characters of *G. ochoai* in parentheses): supratympanic fold shelf-like (weak), palmar tubercle single, elongate (bifid), fingers webbed basally (no webbing), dorsal skin bearing ovoid tubercles (small, round tubercles), interorbital bar or T-shaped mark (no interorbital mark), and venter spotted (dusky).

Variation.—We have not seen living individuals of this species, so we present a free translation of Laurent's (1969a:128) description: "Color in life gray to brown with a few darker markings. In the holotype, the paratypes, and one of the males, the blotches are large. Moreover they have a characteristic form and pattern: a transverse bar or a T between the eyelids, two dorsolateral bands separated from the interocular mark. In the other specimens the dark markings are scarce, small, and irregular. A dark band extends from the nostril to the inguinal region; in places the band has many pale vermiculations. The venter is pale with many small dark blotches, most numerous on the throat and chest."

In preservative, one adult female is brown with a dark brown postorbital stripe fragmented into irregular spots on the grayish tan flanks. A broadly interrupted dorsolateral row of small, irregular, brownish black spots extends from the inner edge of the eyelid to the anus. The lips are tan with small brown spots. The limbs are brown with small dark brown spots (Fig. 9).

Distribution.—Gastrotheca christiani is known only from 2600 m in the Serranía de Calilegua, a part of the eastern slope of the Andes in Departamento Jujuy in extreme northern Argentina.

DISCUSSION

Comparison of the ecological aspects of the species in the *Gastrotheca marsupiata* group is limited by the paucity of available data. Most of the following discussion is based on our own observations. *Gastrotheca excubitor* occupies high, moist páramo and elfin woodland on the eastern Andean crest. *Gastrotheca ochoai* has been found only in terrestrial bromeliads at intermediate elevations (2760-2800 m) in Amazonian and interandean valleys; the species occurs in a transition zone between montane páramo and low montane forest. All localities from which it is known have scattered woody shrubs and extensive grassy areas (Fig. 10). The species of bromeliad inhabited by *G. ochoai* occurs in trees and on cliffs at elevations of 2000 to 3000 m in the Río Urubamba valleys (Figs. 11-12). Possibly the range of *G. ochoai* extends down the valley into the upper montane forest.

In the Río Urubamba valley *G. ochoai* occurs in sympatry with *G. marsupiata*. In the former the young metamorphose within the maternal pouch, whereas young of *G. marsupiata* have prolonged development as free-swimming tadpoles prior to metamorphosis. The distribution of *G. excubitor* closely approaches that

FIG. 10. Valley of the Río Urubamba north of Chilca, Departamento Cuzco, Perú, with the southwestern base of the Cordillera de Vilcanota and the Nevado Verónica in the background. The type locality of *Gastrotheca ochoai* is the base of the cliff at the left of the picture; *Gastrotheca marsupiata* occurs on the valley floor in the foreground.

FIG. 11. Type locality of *Gastrotheca ochoai* showing bromeliads of the face of the cliff.

FIG. 12. Adult *Gastrotheca ochoai* in bromeliad at type locality.

of *G. marsupiata;* the dry páramo in the upper Río Paucartambo valley inhabited by *G. marsupiata* contrasts markedly with the adjacent humid crest of the Amazonian rim where *G. excubitor* is found. Adult females of *G. excubitor* have few, large ovarian eggs, indicating that prolonged development of young or completion of metamorphosis in the pouch is to be expected in this species. This reproductive mode contrasts with that of *G. marsupiata.*

Gastrotheca marsupiata, peruana, and *griswoldi* commonly occur in wet and dry páramo. Frequently they are found under rocks or near small seeps or streams. Young of *G. griswoldi* are known to complete metamorphosis within the maternal pouch, whereas in *G. peruana,* like *G. marsupiata,* development includes a free-swimming tadpole stage. *Gastrotheca griswoldi* occupies geographically and altitudinally intermediate areas between *G. marsupiata* (lower elevations) and *G. peruana* (higher elevations) in the upper Río Mantaro valley.

The geographically close populations of *G. christiani* and *G. gracilis* also differ in reproductive modes (R. F. Laurent, pers. com.). The young of the former undergo metamorphosis within the maternal pouch, whereas the latter has free-swimming tadpoles. Thus, in the *Gastrotheca marsupiata* group sympatric species or species living in geographic proximity differ from one another in reproductive mode. Selection for different reproductive strategies would result in reducing competition for limited resources, in this case aquatic situations for larval development.

The complex color polymorphism observed in populations of *G. marsupiata* and *G. peruana* (and also in *G. riobambae* in Ecuador) remain to be investigated from an evolutionary point of view. Jameson and Pequegnat (1971) showed that a similar polymorphism in *Hyla regilla* was correlated with seasonal and microecological differences in vegetation color.

RESUMEN

La revisión de las ranas del género *Gastrotheca* encontradas en los Andes al sur de la depresión de Huancabamba al norte del Perú, indica la presencia de siete especies. Catorce nombres triviales han sido aplicados a cinco de estas especies; además aquí se nombran dos especies adicionales (Table 1). *Gastrotheca peruana, G. griswoldi* y *G. marsupiata* son especies alopátricas que se encuentran en el norte del Perú, en el centro del Perú, y en el sur del Perú hasta Bolivia respectivamente. Las dos nuevas especies, *G. excubitor* y *G. ochoai,* se encuentran en la cuesta oriental andina, y en los valles amazónicos y interandinos del sur del Perú respectivamente. Dos especies, *G. gracilis* y *G. christiani* habitan las cuestas orientales andinas en el norte de Argentina.

Las poblaciones Ecuatorianas anteriormente llamadas *G. mar-*

supiata no son coespecifícas con la verdadera *G. marsupiata* del sur del Perú. *Gastrotheca riobambae* (Fowler, 1913) fué el primer nombre que se aplicó a las poblaciones Ecuatorianas; *Hyla quitoe* Fowler, 1913, *Chorophilus olivaceus* Andersson, 1945, y *Gastrotheca marsupiata ecuatoriensis* Vellard, 1957, son otros sinónimos dados más tarde.

Gastrotheca marsupiata, peruana, y *gracilis* tienen renacuajos de vida libre, mientras que en las otras especies su desarollo es completamente dentro de la bolsa maternal. Las especies que habitan en simpátria o en regiones geográficas muy cercanas difieren en las formas de reproducción.

SPECIMENS EXAMINED

Gastrotheca christiani

ARGENTINA: *Jujuy:* Alto calilegua, 2600 m, IML 1606; Río Las Lozas, KU 147306.

Gastrotheca excubitor

PERÚ: *Cuzco:* Abra Acanacu, 3520 m, IML 2014, KU 139199-201, UMMZ 131676; north slope Abra Acanacu, 3270-3400 m, KU 139193-8, 139449.

Gastrotheca gracilis

ARGENTINA: *Catamarca:* La Banderita, IML 1530 (5), KU 147307-8.

Gastrotheca griswoldi

PERÚ: *Huánuco:* ? Huánuco, MJP 494 (6). *Junín:* Casca, MCZ 22862-6, 81750-7; Comas, KU 138222-32, 138813-21; Hacienda Pucara, 8 km. E Morococha, MCZ 24400; Huasi, MCZ 24387-9, 81758-67; Huayhuay, MCZ 24390-2, 81768-72; Jachahuanca, MCZ 24418-9, 81705-49; La Oroya, AMNH 38572-6; Maraynioc, KU 137583-7, MCZ 241102-6, MNHN 8662 (5), UMMZ 90169 (3); Mayopampa, 2 km N La Oroya, KU 138221; Minas Janchiscochas, 40 km N Juajua, MCZ 22875-6; Paccha, 9.5 km NW La Oroya, IML 1702 (2), KU 139140-51, MJP 129 (3), 260 (13), 474; Pomamarca, UMMZ 122440; Tarma, MJP 205 (3). *Pasco:* Paucartambo, MJP 495 (6); 14 km SW Paucartambo, KU 139152-4, 139191-2, 139441.

Gastrotheca marsupiata

BOLIVIA: No specific locality, NHMW 16496.1-2; "Chaco," RMNH 4497. *Chuquisaca:* Sucre, MCZ 2576, 81773-4, SMF 30697. *Cochabamba:* No specific locality, UMMZ 66637 (7), 66638 (6); Cochabamba, ZSM 17/1949 (7), 24/1962 (9); Cochabamba Valley, UMMZ 68165 (2); Incachaca, AMNH 34033; Puerto de San Mateo, NHMW 16490, 16491 (5); Tarata, Yungas del Chapare, UMMZ 68164; "Yungas," BMNH 95.11.21.50; Yungas de Totora-Monte Punco, KU 125374-5. *La Paz:* Choro, AMNH 3151, 10565-8, BMNH 1902.5.29.147-54, NHMW 6486.1-3; Tiquina, MJP 177 (4), MNHN 57/864; Totara, MCZ 15334, 15581, 15585-6, UMMZ 92268. *Potosí:* Potosí, BMNH 1902.5.29.155; Tupiza, ZSM 293/1929; 25 km NE Villagren, MVZ 65531.

PERÚ: No specific locality, MCZ 4994-8; Kalinourhin, NHMW 18440 (3). *Apurimac:* Andahuaylas, CAS 84778. *Ayacucho:* Puquio, MJP 470; Querobamba, SMF 33816. *Cuzco:* 10 km E Abra Huillque, KU 138252-9; Chilca, 10 km NW Ollantaytambo, KU 138374-92, 138765-6 (tadpoles), 139186, 139446 (tadpoles), 139447 (young), UMMZ 130156; Cuzco, IML 1701 (2), 2013 (3), KU 138368-9, MCZ 4173-4, MJP 124, MNHN 4877, NHMW 6484, USNM 49559-60; 4 km NW Cuzco, KU 138334-67, 138372-3 (skeletons), 138767 (tadpoles); 3 km W Cuzco, KU 138370-1; 1 km S Cuzco, KU 139184; Granja de la Raya, KU 138319-33; Huaracondo, USNM 60766-8; La Toma, MJP 786, 788 (2); Oropeza, KU 138393-6, 138768 (tadpoles); 14.5 km SW Paucartambo, KU 139187-8; San Jerónimo, 10.7 km ESE Cuzco, KU 139155-83, 139442-5 (tadpoles); Sicuani, KU 138307-18; Tambomachay, 5 km N Cuzco, KU 139185; Tincochchaca, USNM 49561-3; Tocopoqueyu, MCZ 5059, USNM 60753-4; Tres Cruces, 18 km N Paucartambo, MVZ 57804; Urubamba, KU 138397-8, MJP 767; Uvini, Río Cosireni, MCZ 5343, USNM 60769. *Huancavelica:* Conaica, MJP 345; Churcampa, MJP 239; Lircay, KU 138260; 15 km W Lircay, KU 138291-4, 138295-6 (skeletons); 20 km W Lircay, KU 138261-90; Huancavelica, KU 138297-306, 138399-400; Pampas, KU 138243-4, 138764 (tadpoles); 20 km W Pampas, KU 138245-51. *Junín:* Acolla, MJP 397, 449 (2); "Camino a Socorro," MJP 787, 790 (2); Hacienda Yanamarca, MJP 314 (3); Huancayo, MJP 189, 201; Pachacayo, MJP 55 (2); Santa Rosa de Ocopa, KU 138242, MJP 818; Tragadiro, MJP 795. *Puno:* No specific locality, MJP 168; Capachica, BMNH 1940.4.10.21-9; Ilave, MJP 227; Moho, MJP 172, 232; Pucará, BMNH 1904.-10.26.78-9, NHMW 6486.4; Puno, MJP 167, 231, 779, 782 (11); San Antón, BMNH 1907.5.7.37-8.

Gastrotheca ochoai

PERÚ: *Cuzco:* Chilca, 10 km NW Ollantaytambo, IML 2012, KU 138628-65, 139202-9, 139210-11 (skeletons), 139448, UMMZ 131688 (9); 3 km SSW Pilahuata, MNSAA (4). *Puno:* Ollachea, 53 km N Macusani, KU 138666-718.

Gastrotheca peruana

PERÚ: Ancash: Caras, BMNH 1900.6.20.46-50; Chavin de Huantar, KU 138514-26; Chiquian, KU 138495-512, 138770 (tadpoles); Huaráz, KU 138513, MCZ 24542; 5 km N Recuay, KU 138527-44, 138771 (tadpoles). *Cajamarca:* Cajamarca, KU 138494, MJP 478 (4), MNHN 57/863; Cutervo, MJP 264 (tadpoles), 269. *Huánuco:* 5 km NE La Unión, KU 138411-52, 138772 (tadpoles). *Junín:* Añascancha, MJP 228; Casa Pata, MJP 318, 341; between Casa Pata and Añascancha, KU 139189-90; Lago Junín, BMNH 1940.2.25.30. *La Libertad:* Huamachuco, KU 138453-9, MJP 245 (47), 762 (4); Laguna Sacsacocha, 12 km E Huamachuco, IML 1703, KU 138460-90, 138492-3 (skeletons); Otuzco, KU 138545-6; Pomacocha, MJP 637 (3); Tayabamba, MJP 637 (3 + tadpoles), 759 (tadpoles). *Pasco:* Km 37 between Carhuamayo and Paucartambo, MJP 459 (2); Huayllay, MJP 758 (2); Lago de Punrún, MJP 191 (2), 195; Mina San José, Huarón, MJP 446.

LITERATURE CITED

ANDERSSON, L. G.

1945. Batrachians from east Ecuador collecter 1937, 1938 by Wm. Clarke-MacIntyre and Rolf Blomberg. Arkiv Zool., 37A (2):1-88.

BARBOUR, T. and G. K. NOBLE

1920a. Amphibians and reptiles from southern Peru collected by the Peruvian expedition of 1914-1915 under the auspices of Yale University and the National Geographic Society. Proc. U. S. Natl. Mus., 58:609-920.

1920b. Some amphibians from northwestern Peru, with a revision of the genera Phyllobates and Telmatobius. Bull. Mus. Comp. Zool., 63 (8):395-427, pls. 1-3.

BOULENGER, G. A.

1900. Descriptions of new batrachians and reptiles collected by Mr. P. O. Simons in Peru. Ann. Mag. Nat. Hist. (7)6:181-186.

COPE, E. D.
1877. Synopsis of the cold blooded Vertebrata, procured by Prof. James Orton during his exploration of Peru in 1876-77. Proc. Amer. Philos. Soc., 17:33-49.

DUMÉRIL, A. M. C. and G. BIBRON
1841. Erpétologie générale ou histoire naturelle compléte des reptiles, vol. 8. Paris, 792 pp.
1854. Erpétologie générale ou histoire naturelle compléte des reptiles, Atlas. Paris, 120 pls.

FOWLER, H. W.
1913. Amphibians and reptiles from Ecuador, Venezuela, and Yucatan. Proc. Acad. Nat. Sci. Philadelphia, 55:153-176, pls. 5-10.

GÜNTHER, A. L. C.
1859. Catalogue of the Batrachia Salientia in the collection of the British Museum. London, xvi+160 pp.

JAMESON, D. L. and S. PEQUEGNAT
1971. Estimation of relative viability and fecundity of color polymorphisms in anurans. Evolution, 25:180-194.

LAURENT, R. F.
1967. Descubrimiento del género Gastrotheca Fitzinger en Argentina. Acta Zool. Lilloana, 22:353-354.
1969a. Estudio complemetario de Gastrotheca christiani Laurent. *Ibid,* 25:123-136.
1969b. Una segunda especie del género Gastrotheca Fitzinger en Argentina. *Ibid,* 25:143-150.

MIRANDA-RIBEIRO, A. DE
1920. As hylas coelonotas do Museu Paulista. Rev. Mus. Paulista, 12: 321-328.

NIEDEN, F.
1923. Das Tierreich. Anura I. Subordo Aglossa und Phaneroglossa. Sec. 1, Arcifera. Berlin, 584 pp.

PARKER, H. W.
1932. Some new or rare reptiles and amphibians from southern Ecuador. Ann. Mag. Nat. Hist., (10)9:21-26.

SHREVE, B.
1941. Notes on Ecuadorian and Peruvian reptiles and amphibians with description of new forms. Proc. New England Zool. Club, 18: 71-83.

STEINDACHNER, F.
1892. Über zwei noch unbeschreibene Nototrema-Arten aus Ecuador und Bolivia. Sitzber. Akad. Wiss. Wien, 1892:1-6, pls. 1-2.

STEJNEGER, L.
1913. Results of the Yale Peruvian expedition of 1911. Batrachians and reptiles. Proc. U. S. Natl. Mus., 45:541-547.

VELLARD, J.
1957. Estudios sobre batracios andinos IV. El género Gastrotheca. Mem. Mus. Hist. Nat. Javier Prado, 5:1-47.

WERNER, F.
1899. Beschreibung neuer Reptilien und Batrachier. Zool. Anz., 22: 479-484.

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NEW SPECIES OF LIZARDS OF THE GENUS *STENOCERCUS* FROM PERÚ (SAURIA: IGUANIDAE)

By

THOMAS H. FRITTS[1]

In the course of an evolutionary study of the genus *Stenocercus* seven unnamed species were studied in the field and laboratory. In order to facilitate discussion of the evolutionary relationships of the genus, these new species are described in the present paper. Although several other taxonomic problems exist, the nomenclature of Etheridge (1970) is used herein. A complete taxonomic review will be presented in a paper currently in preparation.

It has become apparent that the generic status of all species in the genera *Ophryoessoides* Duméril, 1851, and *Stenocercus* Duméril and Bibron, 1837, warrants consideration. My work indicates that many of the species presently included in *Ophryoessoides* are more closely related to species of *Stenocercus* than to other *Ophryoessoides*. All species named in this paper are members of the genus *Stenocercus* as it is viewed by me.

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I am grateful to Richard E. Etheridge for information on type specimens of *Stenocercus* and *Ophryoessoides* in European museums. He has generously shared specimens in his care and given freely of his time. William E. Duellman has encouraged me in my work with *Stenocercus* and provided energies in laboratory and field aspects of the study. Many persons in South America assisted

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[1] Research Fellow, Museum of Natural History, University of Kansas. Present Address: Department of Biology, St. Edward's University, Austin, Texas 78704.

in field work; I am particularly grateful to Oscar Ochoa M., Manuel Moro, Luis Inope, James Muir, and Hugo Paz. Access to the herpetological collections of several American institutions is gratefully acknowledged.

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MATERIALS AND METHODS

The new species reported in the present report are represented in a collection of nearly 1000 specimens of the genus *Stenocercus* collected in the period of 1968-1972 and deposited in the University of Kansas Museum of Natural History (KU). Taxa are delineated on the basis of morphological and geographical discordance. The characters discussed in the diagnoses are numbered to facilitate comparison of character states between taxa; to avoid redundancy not all character states are given in each diagnosis. The ranges of characters presented in the diagnoses are based on all known specimens. The description is based on specimens from the type locality only. All other samples of the taxa are discussed in the "Remarks" section when pertinent. Geographic variation is examined through use of the Sum of Squares-Simultaneous Test Procedure (SS-STP). The SS-STP is an *a posteriori* test of significance of means (Sokal and Rohlf, 1969) and defines nonsignificant subsets of samples after significant variance is demonstrated by an overall analysis of variance. The test is used for samples of two means realizing that the probability level obtained from the analysis of variance is of an *a priori* test, not an *a posteriori* one. Significance in analyses with only two samples is therefore tentative.

TAXONOMIC ACCOUNTS

Stenocercus apurimacus new species

Figure 1B

Holotype.—KU 134273, an adult male, from Puente Pachachaca, 15 km west of Abancay, 1800 m, Departamento Apurimac, Perú, one of a series collected on 20-22 November 1969, by Thomas H. Fritts, Patricia R. Fritts, and Oscar Ochoa M.

Paratopotypes.—KU 134270-134272, 134274-134309, same data as holotype.

Diagnosis.—1) Posthumeral pocket deep; 2) postfemoral pocket absent; 4) scales posterior to tympanum equal in size to dorsal neck scales, keeled, imbricate; 5) scales on posterior thigh keeled, imbricate; 6) vertebral row continuous, forming high dorsal crest extending onto tail; 7) caudal scales equal in size to ventrals, three caudal whorls per autonomic segment; 8) antehumeral fold absent; 9) neck fold absent; 10) scales around middle of body less than 62; 11) scales across gular region between tympana less than 27; 13) venter of males gray-beige to gray with a blue hue; 17) posterior head scales large, wider than long, rounded posteriorly, a pair of large parietals in broad contact posterior to small interparietal. *Stenocercus apurimacus* is the only species of *Stenocercus* occurring in southern Perú which lacks antehumeral and neck folds. *Stenocercus apurimacus* differs from species of *Ophryoessoides* in lacking keeled ventrals and an antehumeral fold and in having enlarged scales on the posterior margin of the head.

Description.—N=35; scales of parietal and occipital regions of head large, with curved posterior margins; head scales smooth and only slightly convex; interparietal small, bordered laterally by pair of large parietal scales which meet posterior to it; scales across occipital region between angulate temporals 6-9 (7.1±0.1804); largest supraoculars nearly equal in size to scales of interorbital region; supraoculars at greatest width of semicircles 4-6 (5.4±0.094). Scales of lateral neck imbricate and keeled, slightly smaller than dorsal neck scales; antehumeral and neck folds absent; scales across gular region between tympana 18-26 (23.0±0.362).

Vertebral row continuous, forming high dorsal crest from occiput to tail; dorsal scales large, imbricate, keeled; scales around middle of the body 48-61 (52.3±0.519); lateral and ventral scales approximately equal in size to dorsals; ventrals smooth; caudal scales normal; three caudal whorls per autonomic segment. Deep posthumeral pocket present; postfemoral pocket absent; scales of ventral surface of proximal forelimb large, imbricate, keeled; scales of posterior thigh smaller, imbricate and keeled; subdigital lamellae of the fourth finger 15-22 (17.9±0.256); subdigital lamellae of fourth toe 21-28 (25.9±0.264).

Coloration of males: Dorsum red-brown to medium brown with few indistinct black chevrons; narrow black collar edged posteriorly with white across lateral and dorsal neck; labial scales near the angle of the jaw black; chin white with few gray flecks; venter beige-white with faint blue or pink tint in some specimens; ventral pelvic region, ventral base of tail and ventral thighs dull yellow.

Coloration of Females: Dorsum brown with gold-bronze tint; dorsal and lateral surfaces of the neck gold-brown; chin and gular region black posterior to level of insertion of forelimb; chin white medially in some specimens; black collar absent; dorsal chevrons less distinct than those of males; venter gray-white.

Distribution.—The species is known in Perú from elevations of

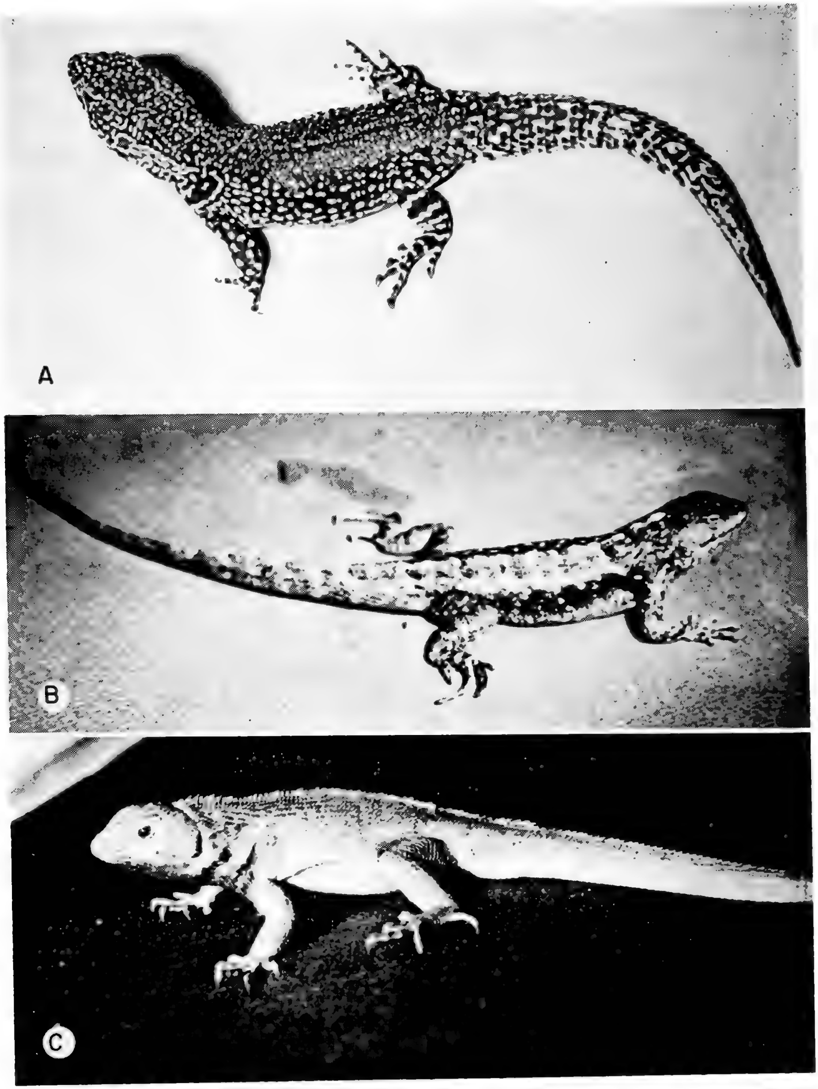

FIG. 1. A. *Stenocercus empetrus,* KU 134390, ♂ 92 mm in snout-vent length. B. *S. apurimacus,* KU 134285, ♂ 84 mm. C. *S. ochoai,* KU 133888, ♂ 95 mm.

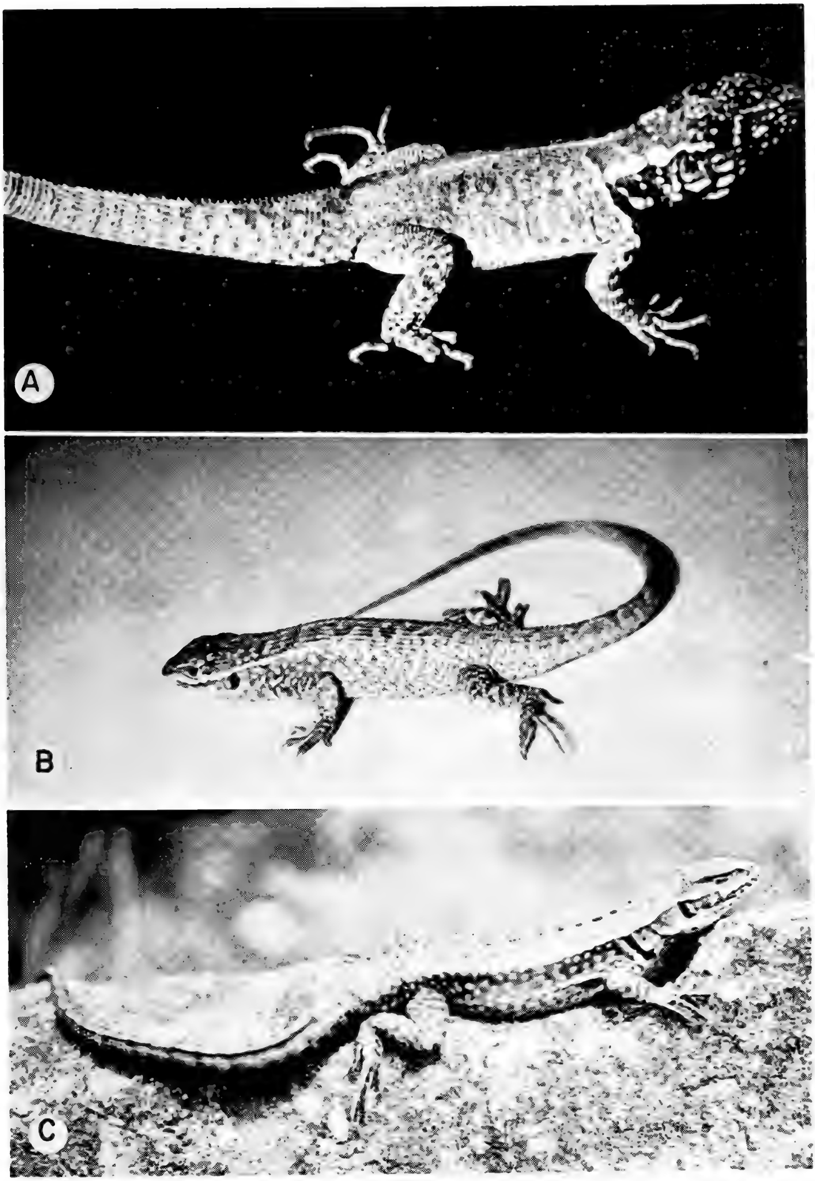

FIG. 2. A. *Stenocercus praeornatus,* cf. KU 134224-134232, ♂ approximate snout-vent length 100 mm. B. *S. orientalis,* KU 134456, ♂ 65 mm. C. *S. nubicola,* KU 134107, ♂ 72 mm.

1800 and 2700 m in the interandean valleys of the Río Apurimac and Río Pachachaca in the departments of Cuzco and Apurimac (Fig. 3). The upper valley of the Río Apurimac divides into several smaller valleys, of which the Río Pampas, Río Pachachaca and Río Apurimac valleys are the largest. Although *Stenocercus apurimacus* is known only from the last two valleys it is likely to occur in the former. Mountain ranges above 4000 m in elevation separate upper regions of the Río Pampas from the adjacent Río Mantaro drainage. The Cordillera Vilcabamba is largely above 5000 m and separates the Río Apurimac from the Río Urubamba.

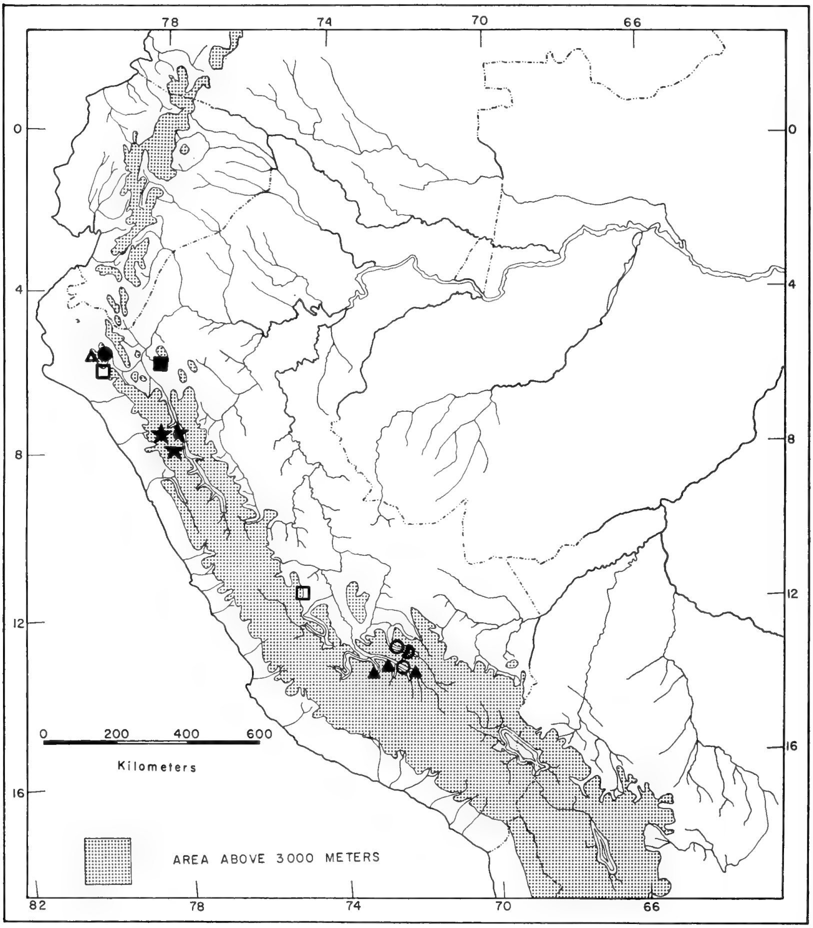

FIG. 3. Distribution in Perú of *Stenocercus apurimacus* (closed triangles), *S. ivitus* (open triangle), *S. nubicola* (closed circle), *S. ochoai* (open circles), *S. orientalis* (closed square), *S. praeornatus* (open squares), and *S. empetrus* (stars).

The Río Apurimac courses between high cordilleras until its junction with the Río Ene and Río Mantaro in central Perú.

Ecological Observations.—The species is found in xeric habitats throughout its range. At localities below 2400 m, *Acacia* and other thorn shrubs and cactus form the predominant plant cover. The lizards are active on the ground at the bases of shrubs and on rock piles. Localities at 2700 m are more mesic and have more grasses and shrubs. At these higher elevations individuals are observed in rows of *Agave. Stenocercus ochoai* occurs in sympatry with *S. apurimacus* at Curahuasi, 2700 m, Departamento Apurimac.

Etymology.—The trivial name for this lizard, which occurs throughout the drainage of the Río Apurimac, is a latinized noun from the Quecchua language, *apu* meaning the great, and *rimac* meaning the talker or one who speaks. Guardia (1967) translated the word *apurimac* as meaning "el gran hablador" or great speaker. The species is dedicated to Dr. Philip S. Humphrey, who has allowed use of the facilities of the University of Kansas Museum of Natural History.

Remarks.—Specimens from the main valley of the Río Apurimac in the Departamento Apurimac (Puente Cunyac and Curahuasi) have more scales around the middle of the body than those from the type locality. The populational means for the two main valley localities (56.8 and 56.0 respectively) are included in a nonsignificant subset significant from the mean of the type locality (52.3) in SS-STP analysis, $p<0.05$.

The extent of white coloration on the medial chin of females varies with altitude in the main valley of the Río Apurimac. Females from elevations below 2000 m have a solid black chin, whereas those from between 2000 and 2700 m on both sides of the valley have a gray-white or white region in the middle of the chin.

Stenocercus empetrus new species

Figure 1A

Holotype.—KU 134394, an adult male from Huamachuco, 3350 m, Departamento La Libertad, Perú, one of a series collected on 16-17 April 1970 by Thomas H. Fritts and Patricia R. Fritts.

Paratopotypes.—KU 134379-134393, 134395-134400, same data as the holotype.

Diagnosis.—1) Posthumeral pocket absent; 2) postfemoral pocket large; 3) dorsals imbricate, smooth or weakly keeled; 4) scales posterior to tympanum granular, smaller than dorsal neck scales; 5) scales of posterior thigh granular; 6) vertebral row discontinuous, only a few scales on neck and anterior body morphologically distinct from adjacent dorsal scales; 7) caudals spinose, enlarged, subequal, two caudal whorls per autonomic segment; 8) antehumeral fold present; 9) neck fold well developed; 10) scales around middle of body more than 86; 13) dorsal body dark brown or black, numerous yellow flecks and spots on dorsum in some populations.

Three species of *Stenocercus* have spinose caudal scutellation and lack a continuous vertebral row. *Stenocercus empetrus* differs from *S. marmoratus* (D'Orbigny, 1837) in having more than 86 scales around the middle of the body and in having more than 38 scales across gular region between tympana. *Stenocercus empetrus* differs from *S. carrioni* Parker, 1934, in having caudal whorls which are subequal in size and in having a more robust body. It differs from *S. simonsii* Boulenger, 1899, in lacking a vertebral row forming a distinct dorsal crest, in having smooth or weakly keeled dorsals, and in having a less spinose caudal scutellation.

Description.—N=21; scales of dorsal head small, subequal in size, convex; scales of posterior head similar to dorsal neck scales; posterior margin of head indistinct; temporal region bulbous; interparietal scale not distinct, parietal eye lacking; scales across occipital region between angulate temporals 14-17 (15.3±0.211); supraocular scales small, subequal in size, lacking rugosities and keels; supraoculars at greatest width of semicircle 5-7 (5.8±0.118); head scales along medial line between occiput and rostral 16-20 (17.9±0.217). Scales of lateral neck granular, smaller than dorsal neck scales; antehumeral fold present, lined with granular scales; neck folds well developed, connected to antehumeral fold by longitudinal fold in some specimens; largest neck fold extending ventrally across gular region in some specimens; scales of gular region between tympana small, 39-49 (43.1±0.599).

Vertebral row discontinuous; vertebral scales distinct from adjacent scales on neck only, forming an incomplete dorsal crest in some specimens; dorsal scales imbricate, smooth or weakly keeled, scales around middle of body 90-112 (99.9±1.140); scales of lateral body less than one-half size of dorsals, granular, meeting dorsals abruptly in dorsolateral region; caudal scales large, with heavy keels which project slightly beyond posterior margins of scales; two caudal whorls per autonomic segment; dorsomedial row of caudal scales lacking enlarged keels, not forming high crest. Posthumeral pocket absent; postfemoral pocket formed by large fold; scales of ventral surface of proximal forelimb granular; scales of posterior thigh granular; subdigital lamellae of fourth finger 19-25 (21.9±0.379); subdigital lamellae of fourth toe 25-32 (29.0±0.495).

Coloration: Little sexual dimorphism in color pattern; dorsal ground color black, heavily flecked and spotted with pale yellow; lateral neck and body black with prominent yellow spots in irregular longitudinal and transverse rows; head black with numerous yellow flecks; prominent red spots in interorbital and occipital region; venter of males orange-yellow with heavy black reticulations; chin of males orange-yellow with black or bright yellow with black reticulations; venter of females yellow with black reticulations.

Distribution.—In addition to the type locality the species is known from Laguna Sacsacocha, 12 km E Huamachuco, 3200 m, Departamento La Libertad; Otuzco, 2730 m, Departamento La Libertad; Cajamarca, 2800 m, Departamento Cajamarca; and 3 km E Celendín, 2650 m, Departamento Cajamarca (Fig. 3). All of the localities, except Otuzco, are in the drainage of the Río Crisneja and adjacent tributaries of the Río Marañón. The single locality in the Pacific drainage, Otuzco, is in the upper valley of the Río Moche.

Ecological Observations.—Individuals of both sexes are found in large rock piles and rock exposures. *Stenocercus melanopygus* Boulenger, 1900, occurs in sympatry with *S. empetrus* throughout the distribution of the latter species in the Atlantic drainage; *S. melanopygus* is common on the ground at the bases of shrubs, on solitary rocks, and at the periphery of large rock piles. *Stenocercus empetrus* is common in the mesic habitats near Huamachuco and Celendín but rare on the dry slopes near Cajamarca, despite the availability of large rocks and rock piles preferred at other localities. The black coloration of individuals from Celendín closely matches the black volcanic rocks on which the lizards occur. *Stenocercus empetrus* is also sympatric with *S. ornatissimus* (Girard, 1857) on the Pacific slopes near Otuzco. The latter species was abundant in agave rows and at the bases of shrubs; habitat partitioning between the two species similar to that observed on Atlantic slopes is probable.

Stenocercus empetrus differs from the two species with which it is sympatric in several notable aspects. It differs in lacking marked sexual dimorphism in the ventral coloration and in having enlarged and spinose caudal scutellation, a bulbous temporal region, smooth or weakly keeled dorsals, granular scales on lateral body and neck, and a larger body size.

Etymology.—The trivial name is from the Greek *empetros* meaning rock-dwelling and refers to the preferred habitat of the species.

Remarks.—Individuals of this species from Celendín, 2650 m, Departamento Cajamarca, differ from those from the type locality in having greater sexual dimorphism in coloration. Adult males are entirely black, except for a few small white flecks on the lateral body and posterior surface of the thighs. Subadult males are black to brown-black with transverse rows of small white spots extending from the dorsum to the lateral edge of venter. The antehumeral fold is black and outlined on anterior and posterior margins with white scales. The venter is white with gray reticulations whereas the chin is black with white spots. The posterior one-half of the venter has a pink suffusion. Adult females are medium gray with faint transverse rows of white flecks. The venter is gray-white with a pink suffusion on the posterior one-half. Juveniles are similar to females, except in having more prominent white flecks on lateral body.

Individuals from Cajamarca, 2800 m, Departamento Cajamarca, are somewhat similar in coloration to subadult males from Celendín, except in having equal numbers of yellow-beige and black scales on the dorsal and lateral body. The occipital region of the head is black whereas the interorbital region has a few scales which are dull red-brown. The venter is orange-yellow with prominent black spots and reticulations.

The number of paravertebral scales is higher in the specimens from Celendín than in those of other localities ($p<0.05$; SS-STP). The dorsal scales are smooth in the majority of specimens from Celendín, whereas they are smooth laterally and weakly keeled medially in specimens from other localities.

Stenocercus ivitus new species

Holotype.—KU 134654, an adult female from summit of Cordillera Huancabamba between Canchaque and Huancabamba, 3100 m, Departamento Piura, Perú, obtained on 11 May 1970, by Thomas H. Fritts and Patricia R. Fritts.

Diagnosis.—1) Posthumeral pocket absent; 2) postfemoral pocket present; 4) scales posterior to tympanum nearly equal in size to dorsal neck scales, imbricate, keeled; 5) scales of posterior thigh granular; 6) vertebral row discontinuous, vertebral scales not forming dorsal crest; 7) caudals normal, three caudal whorls per autonomic segment; 8) antehumeral fold absent; 9) neck fold absent; 10) scales around middle of body 44.

Stenocercus ivitus differs from all species of *Ophryoessoides* and *Stenocercus* in lacking antehumeral and neck folds, in lacking a continuous vertebral scale row which forms a dorsal crest, and in having granular scales on the posterior surface of the thigh.

Description.—N=1; head scales moderate in size, subequal, prominently keeled; 16 scales on middorsal line between occiput and rostral; supraoculars subequal, keeled. Interparietal scale lacking unpigmented spot of parietal eye; scales of occipital region equal in size to dorsal neck scales, posterior margin of head indistinctly demarcated from dorsal neck; a longitudinal row of angulate temporal scales from posterior margin of eye to posterior margin of head scales; 11 scales between angulate temporals across occipital region. Scales of anterior margin of tympanic opening slightly denticulate, projecting into opening; scales of lateral neck large, equal in size to dorsal neck scales, imbricate, keeled; scales posterior to tympanum imbricate, keeled; no antehumeral fold; no neck folds; 21 scales across the gular region between tympana.

Vertebral scales not in continuous row, similar to adjacent dorsals, not forming distinct dorsal crest; dorsal scales imbricate, keeled, mucronate, lanceolate; lateral scales equal in size to dorsals; ventral scales imbricate, smooth, lanceolate; 44 scales around middle of body. Scales of posterior thigh granular; scales of ventral surface of proximal forelimb imbricate, keeled; no posthumeral pocket; postfemoral pocket moderate in size; 20 subdigital lamellae on fourth fingers; 26 subdigital lamellae on fourth toe. Caudal scales normal, imbricate, keeled; three caudal whorls per autonomic segment.

Coloration of Female: Dorsum light brown with large black blotches in two longitudinal rows between yellow dorsolateral stripes; light yellow stripe on lateral neck and body from ventral margin of tympanum to base of hind limb; venter white with pinkish bronze tint; dark flecks on gular region; indistinct black lines on lateral venter.

Distribution.—*Stenocercus ivitus* is known only from the type locality at the summit of the Cordillera Huancabamba (Fig. 3). This cordillera forms the continental divide between the Río Piura (Pacific drainage) and the Río Huancabamba (Atlantic drainage).

Ecological Observations.—The adult female was observed basking on a pile of dead branches at the margin of a low shrub-forest. The moist forest at this locality is produced by moisture-saturated winds coming from the Pacific. The western side of the summit has a low cloud forest, whereas the eastern side is drier with only local patches of forest and extensive tall grasses. *Stenocercus ivitus* is known to occur in sympatry with *S. nubicola.*

Etymology.—The trivial name is a latinized acronym of the Instituto Veterinario de Investigaciones Tropicales y de la Altura, a cooperative research institute of the Universidad San Marcos and the United Nations FAO. The faculty and staff of IVITA assisted field studies through provision of facilities and logistical support.

Stenocercus nubicola new species

Figure 2C

Holotype.—KU 134107, an adult male, one of a series from summit of Cordillera Huancabama between Canchaque and Huancabamba, 3100 m, Departamento Piura, Perú, collected on 11 May 1970 by Thomas H. Fritts and Patricia R. Fritts.

Paratopotype.—KU 134108, a juvenile male with same data as the holotype.

Diagnosis.—1) Posthumeral pocket absent; 2) postfemoral pocket present; 4) scales posterior to tympanum less than one-half size of dorsal neck scales, imbricate and smooth or granular; 5) posterior thigh granular; 6) vertebral row complete, forming dorsal crest; 7) caudal scales equal in size to ventrals, keeled, three caudal whorls per autonomic segment; 8) antehumeral fold distinct; 9) neck fold present; 10) scales around middle of body more than 90; 11) scales across gular region between tympana fewer than 40; 13) black midventral stripe in males, bifurcate anteriorly, extending onto ventral thighs posteriorly.

Description.—N=2; head scales smooth, slightly convex, larger than supraoculars, subequal; scales along medial line between occiput and rostral 17; supraoculars subequal, smooth; supraoculars in transverse line at greatest width of semicircles 5-6; scales of occipital region rough, not keeled, distinct from dorsal neck scales; scales across occipital region between angulate temporals 10-12; parietal eye absent; anterior margin of auricular opening with three denticulate scales; antehumeral fold present; neck folds present; scales posterior to tympanum imbricate and smooth, smaller than dorsal neck scales; scales across gular region between tympana 38-39.

Vertebral row continuous, forming distinct dorsal crest; dorsal scales small, imbricate, keeled; laterals slightly smaller than dorsals; scales around middle of body 93-94; scales of posterior thigh granular; scales of ventral humerus imbricate, smooth; posthumeral pocket absent; postfemoral pocket distinct; subdigital lamellae of fourth finger 17-22; subdigital lamellae of fourth toe 24-28; caudal scales equal in size to ventrals, keeled; three caudal whorls per autonomic segment.

Coloration of Male: Chin, gular region and ventral pectoral region white with numerous black spots; wide charcoal-gray midventral stripe, bifurcating anteriorly to axilla, bifurcating onto ventral thighs posteriorly; lateral body and lateral venter light green with numerous red-orange spots and flecks; dorsum medium brown with small dark brown or black blotches; beige dorsolateral stripes connected with white loreal region; supralabials and infralabials black. Numerous light blue-green transverse markings on dorsum; collar fold bordered posteriorly by black bar.

Coloration of Juvenile: Dorsum gray-brown; dorsolateral stripes beige.

Distribution.—*Stenocercus nubicola* is known only from the type locality (Fig. 3). The Cordillera Huancabama forms the continental divide in extreme northern Perú and esparates the Río Huancabama Valley (Atlantic drainage) and the Río Piura Valley (Pacific drainage).

Ecological Observations.—*Stenocercus nubicola* occurs in sympatry with *Stenocercus ivitus*. The holotype was observed basking on a fallen tree limb in an open areas of the low montane shrubforest. *Stenocercus nigromaculatus* Noble, 1924, is known at lower elevations in the same region.

Etymology.—The trivial name is from the Latin *nubes* meaning cloud and *cola* meaning dweller. The name refers to the association of the species with the heavy fogs characteristic of the Pacific slopes in northern Perú.

Stenocercus ochoai new species

Figure 1C

Holotype.—KU 133888, an adult male, one of a series from Chilca, 10 km NW Ollantaytambo, 2700 m, Departamento Cuzco, Perú, collected on 30 November 1969 by Thomas H. Fritts, Patricia R. Fritts and Oscar Ochoa M.

Paratypes.—KU 133874-133887, 133889, 139263. Topoparatypes with same data as holotype, except KU 133874-133883 collected 15-16 November 1969, KU 133889 collected 17 January 1970, and KU 139263 collected 9 January 1971.

Diagnosis.—1) Posthumeral pocket absent; 2) postfemoral pocket deep; 3) dorsal scales but slightly larger than lateral scales, imbricate, keeled; 4) scales posterior to tympanum one-half size of dorsal neck scales, imbricate, usually keeled; 5) scales of posterior thigh imbricate, keeled; 6) vertebral row continuous, forming raised dorsal crest; 7) caudal scales approximately equal in size to ventrals, three caudal whorls per autonomic segment; 8) antehumeral fold present; 9) neck fold present; 10) scales around body fewer than 71; 11) scales across gular region between tympana fewer than 27; 13) venter of adult males black.

Stenocercus ochoai is most similar to *Ophryoessoides arenarium* (Tschudi, 1845) from which it differs in having larger dorsal scales, black ventral coloration in males, and only three caudal whorls per autonomic segment.

Description.—N=12; head scales convex, not keeled, subequal; scales of lateral occipital region largest of head scales; parietal eye indistinct or absent; head scales distinct from dorsal neck scales; scales across occipital region between angulate temporals 8-12 (10.3±0.333); scales on medial line between occiput and rostral 16-19 (17.1±0.285). Entire anterior margin of tympanic opening with denticulate scales; antehumeral fold prominent; neck folds present, occasionally extending onto ventral neck, not forming strong gular fold; scales posterior to tympanum approximately one-half size of dorsal neck scales, imbricate, usually keeled; scales across gular region between tympana 20-26 (22.7±0.582); dorsals imbricate, keeled; lateral scales slightly smaller than dorsals; vertebral row continuous, forming distinctly raised dorsal crest; keels of dorsal scales forming longitudinal lines which converge only slightly on posterior one-half of body; scales around middle of body 56-67 (61.7±0.882). Caudals approximately equal in size to ventrals, keeled, three caudal whorls per autonomic segment; scales of ventral surface of upper arm large, imbricate, weakly keeled; scales of posterior thigh imbricate, keeled; subdigital lamellae of fourth finger

18-21 (19.8±0.241); subdigital lamellae of fourth toe 24-31 (27.5±0.634); posthumeral pocket absent; postfemoral pocket deep.

Coloration of Males: Dorsum medium to copper brown with occasional small black blotches; lateral body, limbs and tail brown with lime-green suffusion; ventrolateral body greenish yellow; chin light yellow with extensive black suffusion; venter dull black with some yellow laterally; anal area, ventral base of tail and ventral thighs dull yellow, occasionally with black suffiusion.

Coloration of Females: Dorsum gray-brown to charcoal with occasional beige or light gray scales; lateral body light brown; ventrolateral body gray-brown with bronze or light red-orange suffusion; venter beige-white; chin beige-white with gray suffusion; lateral neck same as dorsal ground color. Juveniles similar with dark brown blotches on dorsum.

Distribution.—Stenocercus ochoai (Fig. 3) is known between 2000 and 3000 m in the valleys of the Río Urubamba (Burt and Burt, 1930) and Río Apurimac (Mertens, 1952). The two rivers are separated by the Cordillera Vilcabamba in excess of 4000 m elevation.

Ecological Observations.—Stenocercus ochoai occurs in sympatry with *Stenocercus crassicaudatus* (Tschudi, 1845) between 2000 m and 2600 m in the Río Urubamba Valley. It occurs in sympatry with *Stenocercus apurimacus* at Curahuasi, 2700 m, Departamento Apurimac, in the Río Apurimac Valley. In areas of allopatry, individuals can be observed using the ground substrate, bases of shrubs, isolated rocks and rock piles for feeding and basking activity. Males tend to occupy rocks whereas females are more frequently found on the ground. In sympatry with the rock-dwelling *Stenocercus crassicaudatus, S. ochoai* is confined to the ground, isolated rocks and small rock piles.

Etymology.—The trivial name is a patronym for Dr. Oscar Ochoa M., who generously provided assistance and support with field work in southern Perú.

Remarks.—Specimens of *Stenocercus ochoai* have been erroneously reported by Barbour and Noble (1920) and Burt and Burt (1930) under the names *Liocephalus ervingi* (Stejneger, 1913) and *Liocephalus arenarius* (Tschudi, 1845), respectively.

Stenocercus orientalis new species

Figure 2B

Holotype.—KU 134466, an adult male, one of a series from Chachapoyas, 2340 m, Departamento Amazonas, Perú, collected on 2 May 1970, by Thomas H. Fritts and Patricia R. Fritts.

Paratopotypes.—KU 134447-134465, 134467-134473 collected 1-2 May 1970.

Diagnosis.—1) Posthumeral pocket absent; 2) postfemoral pocket present; 4) scales posterior to tympanum half size of dorsal neck scales, imbricate, keeled; 5) scales of posterior thigh granular; 6) vertebral row continuous, not forming dorsal crest; 7) caudal scales approximately equal in size to ventrals, keeled, three caudal whorls per autonomic segment; 8) antehumeral fold present; 9) neck fold present; 10) scales around the middle of the body 47-58; 15) head scales prominently keeled.

Stenocercus orientalis, S. ornatissimus (Girard, 1857), *S. moestus* Boulenger, 1885, *S. chrysopygus* Boulenger, 1900, and *Ophryoessoides haenschi* (Werner, 1901) differ from other species of *Stenocercus* and *Ophryoessoides* in lacking a dorsal crest and spinose caudal scutellation, and in having antehumeral and neck folds. *Stenocercus orientalis* is uniquely characterized by prominently keeled scales on the snout and interorbital region. It differs from S. *ornatissimus* in having a well-developed postfemoral pocket, and from S. *moestus* in having more than 47 scales around the middle of the body. *Stenocercus orientalis* is distinguished from S. *haenschi* by the absence of green dorsal coloration and presence of fewer than 30 scales across the gular region. It differs from S. *chrysopygus* in having imbricate scales posterior to the tympanum and keels of dorsals in continuous longitudinal series.

Description.—N=27; head scales subequal, keeled; supraoculars subequal, keeled; parietal eye only occasionally visible as unpigmented spot on small interparietal scales; head scales distinct from those of dorsal neck; 10-13 (12.0±0.173) scales across occipital region between angulate temporals; 14-18 (16.3±0.267) scales on middorsal line between occiput and rostral. Anterior margin of auricular opening with 1-2 denticulate scales projecting into opening; antehumeral fold prominent; neck fold present; scales posterior to dorsal one-half of tympanum imbricate, keeled, nearly granular, less than one-half size of dorsal neck scales. Scales on edges of antehumeral and neck fold larger than adjacent scales, keeled, imbricate; 23-38 (25.4±0.289) scales across gular region between tympana. Dorsals imbricate, keeled; vertebral row continuous, not forming dorsal crest; keels of dorsal scales forming longitudinal lines converging slightly posteriorly; 47-58 (51.9±0.552) scales around middle of body. Caudals approximately equal in size to ventrals, keeled; three caudal whorls per automatic segment. Scales of ventral humerus keeled, imbricate; scales of posterior thigh granular; 17-22 (19.7±0.275) subdigital lamellae on fourth finger; 25-31 (27.7±0.287) subdigital lamellae on fourth toe; posthumeral pocket absent; postfemoral pocket deep.

Coloration of Males: Head brown with a few light spots; light stripe from under eye to dorsolateral region of shoulder; dorsum brown with irregular dark brown or black blotches; blotches occasionally forming chevrons; ventral pelvic region and ventral thighs yellow; chin and gular region beige, similar to venter.

Coloration of Females: Dorsum brown; gray-white stripe from under eye extending posteriorly dorsal to tympanum and onto dorsolateral body; two rows of irregular dark blotches on dorsum; vertebral stripe absent; chin and venter gray-beige.

Distribution.—The species is known in Perú only from the type locality in the valley of the Río Utcubama (Fig. 3). The Río Marañón Valley has an elevation of less than 1000 m at this latitude and bounds this range of the Andes on the west and north. The most eastern ridge of the Andes, reaching above 3000 m at this latitude, is immediately east of Chachapoyas. The extremely xeric valley of the Río Marañón is in extreme contrast with the moist eastern slopes.

Ecological Observations.—In the vicinity of Chachapoyas patches of open chaparral are intermixed with low montane forest. The species was collected in open areas at the bases of shrubs. There are few exposed rocks in the immediate area; lizards seek refuge in holes at the bases of shrubs and in tall grasses. No other iguanid species is known in the area.

Etymology.—The trivial name is from the Latin *oriens* meaning east and refers to the distribution of the species east of the Río Marañón valley.

Stenocercus praeornatus new species

Figure 2A

Holotype.—KU 134231, an adult male, one of a series from Comas 3220 m, Departamento Junín, Perú, collected on 26-27 September 1969, by Thomas H. Fritts and Patricia R. Fritts.

Paratopotypes.—KU 134224-134230, 134232, same data as holotype.

Diagnosis.—1) Posthumeral pocket consisting of weak fold; 2) postfemoral pocket large; 4) scales posterior to tympanum granular, less than one-half size of dorsal neck scales; 5) scales of posterior thigh granular; 6) vertebral row continuous, forming high dorsal crest; 7) caudals approximately equal in size to ventrals, keeled, three caudal whorls per autonomic segment; 8) antehumeral fold present; 9) neck fold present; 10) scales around middle of body more than 88; 13) ventral coloration of males rose pink; 14) gular region of males black.

Of the species having a black ventral collar in males, *Stenocercus praeornatus* is the only one having more than 88 scales around the middle of the body and having pink ventral coloration in males.

Description.—N=9; scales of head subequal, convex, not keeled; supraoculars smooth, not greatly enlarged; supraoculars at greatest width of semicircles 5-7 (6.3±0.236); scales of medial region of occipital area granular, smaller than more lateral scales, scales across occipital region between angulate temporals 12-14 (13.3±

0.236); parietal eye absent, interparietal indistinct; scales of dorsal snout slightly larger than other head scales; scales along midline between occiput and rostral 17-20 (18.8±0.324). Scales of anterior margin of auricular opening only weakly projecting into ear; antehumeral fold prominent; neck folds often connected with antehumeral fold; scales posterior to tympanum granular, less than one-half size of dorsal neck scales; neck fold continuing ventrally, meeting its fellow, forming a weak gular fold in some specimens; scales across gular region between tympana 40-57 (48.2±1.786).

Vertebral row continuous; vertebral scales forming distinct raised dorsal crest; skin of lateral neck folded, forming slight dorsolateral fold from dorsal margin of tympanum to point posterior to scapular region; dorsal scales imbricate, keeled; scales around middle of body 100-121 (106.8±2.29); lateral scales less than one-half size of dorsal scales, granular or slightly imbricate; lateral scales sharply meeting dorsals at dorsolateral region; shallow fold in axillary region forming shallow posthumeral pocket; postfemoral pocket large; dorsal crest continuing onto tail; caudal scales approximately equal in size to ventrals, imbricate, keeled; three caudal whorls per autonomic segment. Scales of ventral humerus imbricate, keeled or smooth; scales of posterior thigh granular; subdigital lamellae of fourth finger 20-22 (20.8±0.324); subdigital lamellae of fourth toe 28-31 (29.4±0.324).

Coloration of Males: Head dull chocolate brown with scattered yellow-beige spots; nape dull brown posterior to level of shoulders with diagonal yellow markings and spots; dorsum gray-brown with faint irregular darker brown diamond blotches; lateral areas light yellow-brown with dull yellow spots; chin gray-brown peripherally; central chin blue-green with yellow spots; gular region rose pink with faint gray reticulation; chest anterior to pectoral girdle jet black; ventral pectoral region, ventral fore- and hindlimbs and narrow midventral line pale yellow; lateral venter rose pink; base of tail yellow with orange tint.

Coloration of Females: Dorsum gray-beige with middorsal brown blotches; dorsal blotches paired, nearly connecting medially; venter gray-white; ventral thighs with slight yellow tint; chin beige with gray-brown spots or reticulations.

Distribution.—The species is known in central Perú from the higher elevations of the Río Tulumayo in Departamento Junín (Fig. 3). Additional specimens of this species are known from northern Perú, Abra Porculla, 2144 m, Departamento Piura. Although both localities from which the species is known are Amazonian, the major river valleys of the Río Marañón and Río Huallaga are between them. A similar distribution is exhibited by *Stenocercus boettgeri* Boulenger, 1911.

Ecological Observations.—No other iguanid species is known to occur in sympatry with S. *praeornatus*. Populations of S. *variabilis* Boulenger, 1901, and S. *boettgeri* are known from geographically close areas of Departamento Junín. *Stenocercus praeornatus* was collected in large rock piles and in terraces made of rocks. Because S. *variabilis* is largely confined to terrestrial habitats and small rocks, sympatry with S. *praeornatus* is more probable than with the rock-dwelling species, S. *boettgeri*.

Etymology.—The trivial name is from the Latin *prae* meaning front or anterior part and *ornatus* meaning ornate; it refers to the ornate coloration of the head and shoulders in contrast to that of the remainder of the body.

Remarks.—Five specimens from Abra Porculla in northern Perú have fewer scales across the gular region between tympana, 32-35 (33.0±0.632), than topotypic specimens 40-57 (48.2±1.786). The scales around the body in specimens from the former locality range from 89 to 112 (97.8±3.219). Females from Abra Porculla lack dark blotches on the chin. Although differences in scutellation between the two populations are suggested by the small samples available, acquisition of more material is necessary to assess geographic variation. The close similarity in most scutellational aspects, as well as in coloration, is the basis for assignment of the northern population to this species.

RESUMEN

Mientras un estudio evoluciónario del género *Stenocercus* corriente, siete especies nuevas estaban siendo estudiadas. Las especies nuevas que están siendo descritas son de zonas poco conocidas en los Andes Peruanos. Discordancia de dato morfológicos, geográficos, y ecológicos es la base de la delimitación taxonómica. El presente conocimiento necesita consideración de la posición génerica de todas las especies en *Ophryoessoides* y *Stenocercus* con motivo de formación de grupos naturales que conformen con relaciónes evoluciónarias. Algunas especies de *Ophryoessoides* son más afines con *Stenocercus* que otras especies de *Ophryoessoides*. La variación morfológica, distribución geográfica, y preferencias ecológicas son presentados para cada especie.

SPECIMENS EXAMINED

The following abbreviations are used to indicate the museums housing specimens examined in this study: AMNH, American Museum of Natural History; FMNH, Field Museum of Natural History; KU, University of Kansas Museum of Natural History; MCZ, Museum of Comparative Zoology; MVZ, Museum of Vertebrate Zoology—Berkeley; SM, Senckenbergische Natur-Museum; UMMZ, University of Michigan Museum of Zoology; USNM, United States

National Museum. Specimens are listed alphabetically by species, country, state and locality.

Stenocercus apurimacus

PERÚ: *Apurimac*: Curahuasi, 2700 m, KU 134240, 134242-134249, 134251-134252; Hacienda Matara, Dist. Matara, MCZ 62253; Puente Pachachaca, 1800 m, KU 134270-134309; Río Apurimac, Puente Cunyac, 1830 m, KU 134235-134239, 134253-134257. *Cuzco*: Limatambo, 2700 m, KU 134263-134269; 3 km E Puente Cunyac, 1830 m, KU 134258; 8 km E Puente Cunyac, 2300 m, KU 134259-134262.

Stenocercus empetrus

PERÚ: *Cajamarca*: Baños, MCZ 8084; Cajamarca, 2800 m, FMNH 3941-3942, 5710-5711, KU 134411-134413; 3 km E Celendín, 2650 m, KU 134414-134427; Hacienda Huagac, UMMZ 60094-60095. *La Libertad*: Huamachuco, 3350 m, KU 134379-134400; Laguna Sacsacocha, 12 km E Huamachuco, 3200 m, KU 134401-134410; Otuzco, FMNH 5708.

Stenocercus ivitus

PERÚ: *Piura*: Summit Cordillera between Canchaque and Huancabamba, 3100 m, KU 134653.

Stenocercus nubicola

PERÚ: *Piura*: Summit of Cordillera between Canchaque and Huancabamba, 3100 m, KU 134107-134108.

Stenocercus ochoai

PERÚ: *Apurimac*: Curahuasi, 2700 m, KU 134241, 134250. *Cuzco*: Chilca, 10 km N Ollantaytambo, 2760 m, KU 133874-133889, 139263; Chospyoc, Río Huarocondo, USNM 60705-60706; Ruinas de Machu Picchu, 2400-2450 m, KU 117108, 134233-134234, 139267-139268; Ollantaytambo, USNM 60810, MCZ 41984; Río Huaracondo, 3048 m, MCZ 12410; Torontoy, USNM 60811.

Stenocercus orientalis

PERÚ: *Amazonas*: Chachapoyas, 2340 m, KU 134447-134473.

Stenocercus praeornatus

PERÚ: *Junín*: Comas, 3220 m, KU 134224-134232. *Piura*: Abra Porculla, 2144 m, SM 65252, 65254, 65257-65259, MVZ 82370.

LITERATURE CITED

BARBOUR, T. and G. K. NOBLE

1920. Amphibians and reptiles from southern Peru collected by the Peruvian expedition of 1914-1915 under the auspices of Yale University and the National Geographic Society. Proc. U.S. Natl. Mus., 58:609-620.

BOULENGER, G. A.

1885. Catalogue of the lizards in the British Museum (Natural History). 2nd Ed. London, 2:xiii+497 pp.

1899. Descriptions of new reptiles and batrachians collected by Mr. P. O. Simons in the Andes of Ecuador. Ann. Mag. Nat. Hist., (7) 4:454-457.

1900. Descriptions of new batrachians and reptiles collected by Mr. P. O. Simons in Peru. *Ibid.*, (7) 6:181-186.

1901. Further descriptions of new reptiles collected by Mr. P. O. Simons in Peru and Bolivia. *Ibid.*, (7) 7:546-549.

1911. Descriptions of new reptiles from the Andes of South America, preserved in the British Museum. *Ibid.*, (8) 7:19-25.

BURT, C. E. and M. D. BURT

1930. The South American lizards in the collection of the United States National Museum. Proc. U.S. Natl. Mus., 78(6):1-52.

D'ORBIGNY, A. D.

1837. 350-353, 356-359 pp. *In* Duméril, A. M. C. and G. Bibron, 1837. Erpetológie génèrale. Vol. 4, 572 pp.

DUMÉRIL, A. M. C. and G. BIBRON

1837. Erptológie génèrale. Vol. 4, 572 pp.

DUMÉRIL, M. A.

1851. Catalogue methodique de la collection des reptiles. Museum D'Histoire Naturelle de Paris. Liv. 1, 128 pp.

ETHERIDGE, R. E.

1970. *Stenocercus.* pp. 254-257. *In* Peters, J. A. and R. Donoso-Barros, Catalogue of neotropical Squamata: Part II. Lizards and amphisbaenians. Bull. Smithsonian Inst., 297:1-293.

GIRARD, C.

1857. Descriptions of some new reptiles collected by the United States exploring expedition, under the command of Capt. Charles Wilkes, U.S.N. Fourth part including the species of saurians exotic to North America. Proc. Acad. Nat. Sci. Philadelphia, 1857:195-198.

GUARDIA MAYORGA, C.

1967. Diccionario Kechwa-Castellano, Castellano-Kechwa. Editora Los Andes, Lima, Perú. 219 pp.

MERTENS, R.

1952. Amphibien und Reptilien I. pp. 257-266. *In* Titschack, E. Beitrage zur Fauna Perus. Verlag Gustav Fischer, Jena. Bd. III.

NOBLE, G. K.

1924. New lizards from northwestern Peru. Occas. Papers Boston Soc. Nat. Hist., 5:107-113.

PARKER, H. W.

1934. Reptiles and amphibians from southern Ecuador. Ann. Mag. Nat. Hist., (10) 14:264-273.

SOKAL, R. R. and F. J. ROHLF

1969. Biometry. W. H. Freeman and Company, San Francisco. 776 pp.

STEJNEGER, L.

1913. Results of the Yale Peruvian expedition of 1911. Batracians and reptiles. Proc. U.S. Natl. Mus., 45:541-547.

TSCHUDI, J. J.
1845. Reptilium conspectum quae in republica Peruana reperiuntur et pleraque observata vel collecta sunt in itinere. Arch. Naturg., 11 (1):150-170.

WERNER, F.
1901. Ueber Reptilien und Batrachier aus Ecuador und Neu-Guinea. Verh. Zool.-Bot. Gesell. Wien, 51:593-614.

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A REVIEW OF THE NEOTROPICAL FROGS OF THE *HYLA BOGOTENSIS* GROUP

By

WILLIAM E. DUELLMAN[1]

By comparison with the highlands of Central America, which are inhabited by a diversity of stream-breeding hylid frogs, the Andes in northwestern South America are characterized by a paucity of stream-breeding hylids. Duellman (1970:327) pointed out that one stream-breeder, *Hyla colymba,* in the highlands of Costa Rica and Panamá seemed to be related to the Colombian *Hyla bogotensis,* and he tentatively referred specimens from Ecuador to *Hyla colymba.* Recent field work in northwestern South America has resulted in the accumulation of series of specimens from many localities, tadpoles, and recordings of mating calls. Thus, it is now possible to review systematically six species that seem to form a natural unit—the *Hyla bogotensis* group.

The purposes of the present paper are to: 1) define the *Hyla bogotensis* group, 2) present the results of a multivariate analysis of characters, 3) diagnose the species, and 4) present the accumulated data on the biology of the species.

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[1] Curator, Division of Herpetology, Museum of Natural History, University of Kansas.

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MATERIALS AND METHODS

This investigation was based on the study of 149 preserved frogs (including the type specimens of all nominal taxa), 17 lots of tadpoles, two skeletons, nine radiographs, and eight tape recordings. For purposes of statistical analyses, 14 characters were recorded for 114 adult frogs. Of these characters, three are morphometric, eight are structural, and three are coloration. These data were subjected to a stepwise discriminant analysis by use of the BMDO7M Program (Dixon, 1971), which performs a multiple discriminant analysis in a stepwise manner, entering one variable at a time into a set of discriminating variables. The program computes canonical correlations and coefficients for canonical variables and plots the first two canonical variables in a two-dimensional matrix.

Individuals were grouped on the basis of geography and sex, as follows: Central America 6♂, 3♀; Pacific slopes of Ecuador 13♂, 15♀; Amazonian slopes of Ecuador and Perú 13♂, 3♀; Andes of central and southern Colombia 7♂, 4♀; Andes of western Venezuela 37♂, 11♀. One male and one female from northern Colombia were each treated as a group. Thus, the matrix for the discriminant analysis consisted of 14 variables and 12 groups.

Subsequently, the sexes were pooled, and each of the six groups was treated as an OTU in the NT-SYS Phenogram Program (Rohlf and Kishpaugh, 1966); in this program unweighted arithmetic character states were analyzed and plotted as a distance phenogram. For purposes of the Phenogram Program, 11 coded characters were used (see following definition of characters). Five coded characters of tadpoles were analyzed by the Phenogram Program; again, groups (taxa) were treated as OTUs. Finally, the adult and tadpole characters were analyzed together by the Phenogram Program. All computations were done on a Honeywell 635 computer.

Recordings of the mating calls of three species are available. The calls of eight individuals were analyzed for seven characters: 1) notes per call group, 2) note repetition rate, 3) duration, 4) pulse rate, 5) number of harmonics, 6) fundamental frequency, and 7) dominant frequency (see Duellman, 1970, for methodology and terminology).

Definition of Characters

In the list of characters, those marked with an asterisk were used in the Phenogram Program; all characters of adults were used in the BMDO7M Program.

*Snout-vent Length (SVL)**.—Measurement to nearest 0.1 mm of straight line distance from tip of snout to posterior edge of body; for NT-SYS coded: 1) ♂ <44 mm, ♀ <50 mm, 2) ♂ >44 mm, ♀ >50 mm.

Tibia Length (TL).—Measurement of length of tibia to nearest 0.1 mm; used as a ratio of snout-vent length.

Head Width (HW).—Measurement of greatest width to nearest 0.1 mm; used as a ratio of snout-vent length.

*Webbing on Hand (WEB)**.—The extent of webbing on the inner edge of the fourth finger coded with respect to the point of termination of the webbing with respect to the distal subarticular tubercle: 1) proximal to tubercle, 2) at tubercle, 3) distal to tubercle.

*Subarticular Tubercles (TUB)**.—The structure of the distal subarticular tubercles on the third and fourth fingers was coded: 1) conical, single, 2) conical, bifid, 3) flat, bifid.

*Ulnar Fold (ULN)**.—A dermal fold on the ventrolateral edge of the forearm was coded: 1) absent, 2) present.

*Tarsal Fold (TAR)**.—A dermal fold on the ventrolateral surface of the foot was coded: 1) absent, 2) present.

*Calcar (CAL)**.—A triangular dermal appendage projecting posteriorly from the upper edge of the heel was coded: 1) absent, 2) small, 3) large.

Snout Profile (SNO)*.—The shape of the snout in lateral view coded: 1) round, 2) truncate, 3) anteriorly inclined.

*Tympanum (TYM)**.—The upper edge of the tympanum is covered by a supratympanic fold, but the tympanic ring below the fold coded: 1) distinct, 2) covered with undifferentiated skin.

Mental Gland (MEN).—A round glandular structure at the apex of the jaw was coded: 1) absent, 2) present.

Dorsolateral Stripe (DST)*.—A pale stripe extending from the edge of the eyelid to a point on the side of the body was coded: 1) absent, 2) present.

*Tarsal Stripe (TST)**.—Longitudinal stripes on the outer edge of the foot were coded: 1) absent, 2) white, 3) white above and brown below.

Anal Stripe (AST)*.—Transverse stripes above the anus were coded: 1) absent, 2) white, 3) white above and brown below.

*Tooth Rows (TOO)**.—The number of upper/lower rows of teeth in tadpoles was coded: 1) 4/5, 2) 5/7, 3) 6/9, 4) 7-8/10.

*Labial Papillae (LAB)**.—Labial papillae are continuous around the mouth in the tadpoles; the number of rows of papillae was coded: 1) one, 2) two.

*Serrations on Beak (SER)**.—The serrations on the cutting edge of the upper beak in tadpoles were coded: 1) none, 2) small, 3) medium, 4) large.

*Shape of Body (SHA)**.—The shape of the body of tadpoles in dorsal view was coded: 1) narrowly ovoid, 2) broadly ovoid, 3) narrow anteriorly and widening abruptly just anterior to eyes.

Caudal Musculature (CAU)*.—The proportionate depth of the caudal musculature was coded: 1) $<65\%$, 2) $>65\%$.

RESULTS

For ease in discussion the nomenclature adopted in the following section on taxonomy is used throughout. The results of the discriminant analysis are discussed first, followed by the Phenogram Program and finally the mating calls.

Multiple Discriminant Analysis

Within-group Variation.—The amount of variation in snout-vent length is approximately the same in all species except *H. bogotensis* and *H. platydactyla* in which it is somewhat greater (Table 1). However, the amount of variation in the ratios of tibia length and head width to snout-vent length is no greater in these two species than in the others.

Variation of all structural features, except presence or absence of ulnar and tarsal folds, occurs within groups; likewise, color pattern characters show within-group variation (Table 2). Tarsal and anal stripes are either present or absent within a group; if present, there may be one or two stripes *(Hyla phyllognatha).* The presence of a mental gland is the most variable structural feature, displaying variation in five of the 12 groups. The amount of webbing is the next most variable character; variation occurs in four groups.

The variation within groups is not highly correlated with respect to the following characters—size, proportions, subarticular tubercles, snout shape, tympanum, and mental gland. Absolute positive cor-

TABLE 1.—Measurements and proportions of species in the *Hyla bogotensis* group.

(Mean and one standard deviation given below observed range.)

Species	Sex	*N*	Snout-vent Length	Tibia Length/ SVL	Head Width/ SVL
H. alytolylax	♂	13	32.1—37.0 34.85±1.51	0.443—0.525 0.474±0.024	0.298—0.331 0.316±0.010
	♀	15	37.2—43.9 40.38±2.23	0.462—0.532 0.496±0.021	0.296—0.331 0.310±0.010
H. bogotensis	♂	7	29.4—43.0 35.20±5.58	0.491—0.514 0.502±0.010	0.329—0.365 0.345±0.012
	♀	4	29.4—48.1 41.43	0.449—0.506 0.483	0.313—0.380 0.347
H. colymba	♂	6	31.9—37.0 34.65±2.29	0.452—0.514 0.481±0.023	0.302—0.327 0.318±0.010
	♀	3	31.4—39.1 36.23	0.486—0.493 0.490	0.310—0.340 0.325
H. denticulenta	♂	1	44.2	0.493	0.303
	♀	1	52.2	0.513	0.308
H. phyllognatha	♂	13	31.5—34.0 32.96±0.69	0.443—0.524 0.488±0.028	0.301—0.348 0.319±0.013
	♀	3	33.0—39.3 36.87	0.488—0.506 0.495	0.326—0.331 0.329
H. platydactyla	♂	37	26.5—39.4 34.36±3.05	0.464—0.540 0.488±0.016	0.323—0.383 0.347±0.014
	♀	11	30.6—42.3 38.41±3.64	0.457—0.506 0.491±0.016	0.333—0.356 0.342±0.009

relation exists between presence or absence of ulnar and tarsal folds, between tarsal folds and tarsal stripes, and between tarsal and anal stripes. Webbing is the most extensive and calcars are the largest in the species, *H. denticulenta*.

Sexual Dimorphism.—No sexual dimorphism is evident in proportions, amount of webbing, nature of folds or calcars, snout shape, or nature of tarsal and anal stripes. Minor sexual dimorphism occurs in the nature of the subarticular tubercles in *H. platydactyla*, in the tympanum in *H. bogotensis*, and in the dorsolateral stripe in *H. colymba* (Table 2). Snout-vent length is greater in females than in males; snout-vent lengths of 77 males is 26.5-44.2 ($\bar{x}$=34.43) mm, and of 37 females is 29.4-52.2 ($\bar{x}$=39.63) mm.

As noted above, the nature of the mental gland is highly variable. The gland is present in 44 of 77 (57.1%) males and in nine of 37 (24.3%) females. The structure and function of the mental gland are unknown; its development may be seasonal and associated with reproductive activity. Thus, its usefulness as a taxonomic character within the *Hyla bogotensis* group is questionable.

Interpopulational Variation.—The combination of the sexes in

TABLE 2.—Variation in structural characters and coloration in the *Hyla bogotensis* group.
(See Definition of Characters for abbreviations and coding; mean and one standard deviation given below observed range.)

Species	Sex	*N*	WEB	TUB	ULN	TAB	CAL	SNO	TYM	MEN	DST	TST	AST
H. alytolylax	♂	13	2–3 2.538 0.519	1 — —	2 — —	2 — —	1 — —	1 — —	1 — —	2 — —	2 — —	2 — —	2 — —
	♀	15	2–3 2.867 0.352	1 — —	2 — —	2 — —	1–2 1.067 0.258	2 — —	1 — —	1 — —	2 — —	2 — —	2 — —
H. bogotensis	♂	7	2 — —	2 — —	1 — —	1 — —	1 — —	2 — —	1–2 1.571 0.535	1–2 1.143 0.378	1 — —	1 — —	1 — —
	♀	4	2	2	1	1	1	2	2	1	1	1	1
H. columba	♂	6	2	1	2	2	1	1	1	2	2	2	2
	♀	3	2 — —	1 — —	2 — —	2 — —	1 — —	1 — —	1 — —	1–2 1.667 0.577	1–2 1.667 0.577	2 — —	2 — —
H. denticulenta	♂	1	3	3	2	2	3	3	1	1	1	3	3
	♀	1	3	3	2	2	3	3	1	1	1	3	3
H. phyllognatha	♂	13	1–2 1.077 0.277	1 — —	2 — —	2 — —	1–2 1.308 0.480	1–2 1.077 0.277	1 — —	2 — —	1 — —	2–3 2.538 0.877	2–3 2.538 0.877
	♀	3	1–2 1.667 0.577	1 — —	2 — —	2 — —	1–2 1.667 0.577	1–2 1.333 0.577	1 — —	1–2 1.333 0.577	1 — —	2–3 2.333 1.155	2–3 2.333 1.155
H. platydactyla	♂	37	1 — —	1–2 1.892 0.315	1 — —	1 — —	1 — —	2 — —	1–2 1.162 0.374	1–2 1.297 0.463	1–2 1.162 0.374	1 — —	1 — —
	♀	11	1 — —	2 — —	1 — —	1 — —	1 — —	2 — —	1–2 1.091 0.302	1–2 1.545 0.522	1–2 1.091 0.302	1 — —	1 — —

the geographic samples provides an assessment of populational differences for taxonomic distinction. Each of the 14 characters, in combination with others, serves to distinguish one population from another, but, with the exception of snout-vent length in *H. denticulenta,* no one character distinguishes one population from all of the others. The stepwise discriminant analysis provided a multivariate analysis of 14 characters in the 12 groups (males and females were treated separately in each of the geographic samples) and produced a two-dimensional plot of the first and second canonical variables (Fig. 1). The first canonical variable is weighted primarily on webbing, secondly on subarticular tubercles, and lastly on ulnar and tarsal folds, whereas the second canonical variable is weighted on snout-vent length, calcar, and dorsolateral stripe, in descending order. The plot clearly shows the clustering of samples and the overlap (in most cases) of the sexes within the samples. Thus, on the basis of adult morphology, the samples can be treated as different taxa.

Distance Phenograms

In an attempt to determine the phenetic relationships of the six geographic samples, each of the six was treated as an OTU. Mean values for each of 11 characters (sexes pooled) were used. Body ratios and the nature of the mental gland were excluded from the analysis. The resultant distance phenogram (Fig. 2A) shows the separation of the phenetically similar *H. bogotensis* and *H. platydactyla* from the other taxa. *Hyla denticulenta* is separated from the remaining three species clumped in the middle of the phenogram. The arrangement of the taxa is compatible with the plot of the canonical variables (Fig. 1). Thus, the results of the Phenogram Program supports the results of the multiple discriminant analysis.

The previous analyses were based on characters of the adult frogs. Tadpoles are available for all six geographic samples; these have been associated with adults on the basis of morphological characteristics of the metamorphosing young. The most obvious interpopulational differences are evident in the structures of the mouths (Fig. 3). The distribution of character states of five characters is shown in table 3. For purposes of analysis, the mean ratio of depth of caudal musculature to total caudal depth was used; the other characters are constant within populations and were coded. The phenogram of populations as OTUs differs only slightly from the arrangement based on adults (Fig. 2B). The major difference is that *H. alytolylax* is clustered with *H. denticulenta,* whereas in the phenogram based on adults *H. alytolylax* is grouped with *H. colymba* and *H. phyllognatha.*

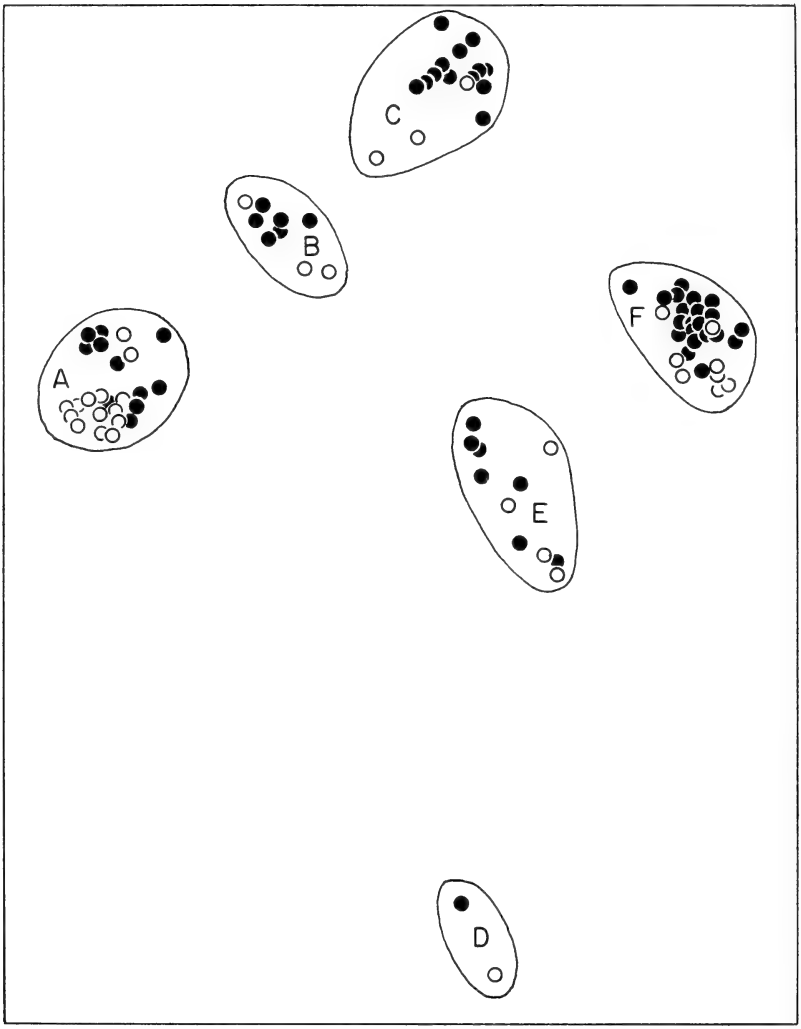

FIG. 1.—Plot of first (horizontal axis) and second (vertical axis) canonical variables; solid dots are males and open circles are females. A. *Hyla alytolylax.* B. *H. columba.* C. *H. phyllognatha.* D. *H. denticulenta.* E. *H. bogotensis.* F. *H. platydactyla.*

A final analysis of both adult and larval characters produced a phenogram somewhat intermediate between the first two (Fig. 2C). Here it can be seen that *H. bogotensis* and *H. platydactyla* are divergent from the other taxa and that *H. colymba* and *H. phyllognatha* are close to *H. alytolylax,* whereas *H. denticulenta* is more distant.

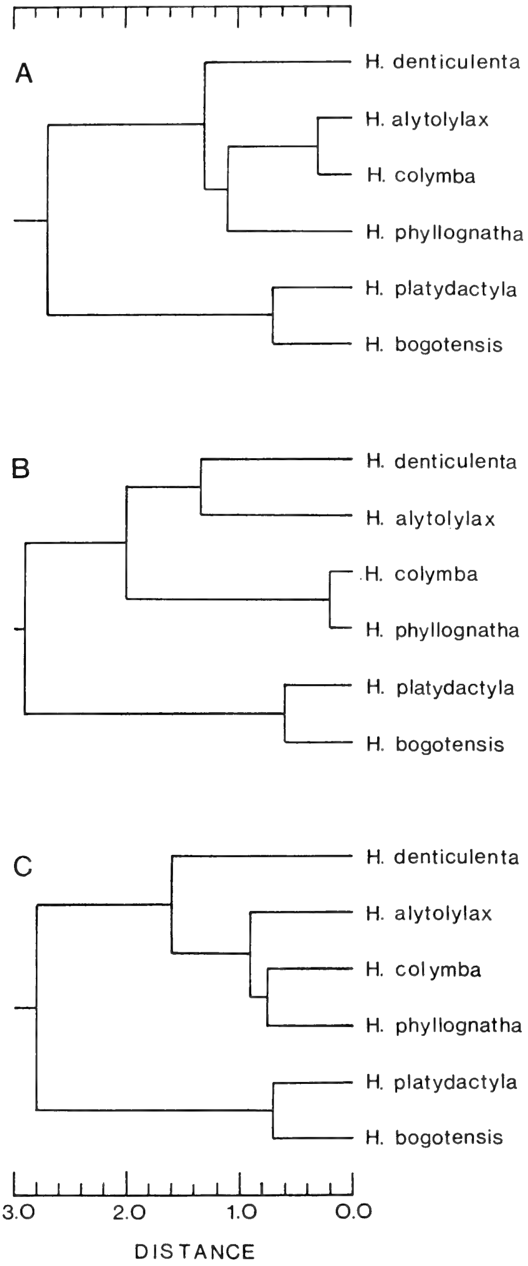

FIG. 2.—Distance phenogram of *Hyla bogotensis* group based on unweighted analysis of 11 adult and five larval characters. A. Adult characters. B. Larval characters. C. Adult and larval characters.

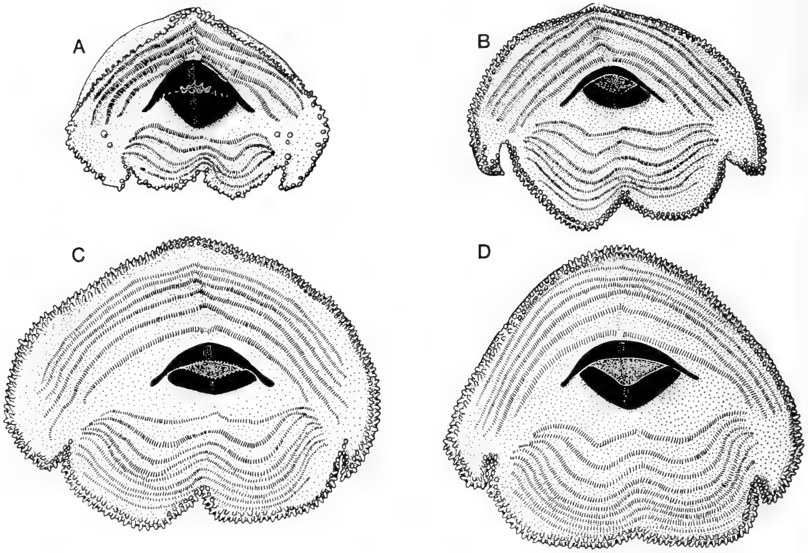

FIG. 3.—Mouths of tadpoles of *Hyla bogotensis* group. A. *H. platydactyla,* KU 139521. B. *H. alytolylax,* KU 112358. C. *H. phyllognatha,* KU 143542. D. *H. denticulenta,* KU 139531. ×8. The mouth of the tadpole of *H. bogotensis* is like that of *H. platydactyla* except that the former has much smaller serrations on the beaks; the mouth of the tadpole of *H. colymba* is like that of *H. phyllognatha* (see Duellman, 1970:330).

Mating Calls

The mating calls are known for all species, except *H. bogotensis* and *H. denticulenta;* the calls consist of a series of short, loud peeps. Analysis of tape recordings of calls of three species reveals noticeable differences in several parameters of the calls (Table 4, Fig. 4). *Hyla colymba* has the most distinctive call, differing from the others in notes per call group, duration of notes, pulse rate, and pitch; the second harmonic is dominant. The calls of *H. phyllognatha* and *H. platydactyla* are more nearly alike in having only one har-

TABLE 3.—Characteristics of tadpoles of *Hyla bogotensis* group.

Species	Tooth Rows	Labial Papillae	Serrations on Beak	Total Length/ Body length	Caudal Musculature/ Caudal Depth
H. alytolylax	5/7	2	small	30.2%	63.1%
H. bogotensis	4/5	1	medium	32.3%	66.7%
H. colymba	6/9	2	small	35.6%	61.1%
H. denticulenta	7-8/10	2	none	35.3%	57.2%
H. phyllognatha	6/9	2	small	35.2%	60.0%
H. platydactyla	4/5	1	large	39.5%	80.0%

monic and fewer, but longer, notes per call group. However, their calls differ in note repetition rate, pulse rate, and pitch. The absence of analyzable recordings of the other three species precludes a complete biosonic analysis of the group. Nevertheless, the differences in the parameters of the calls of the three sepcies are of the magnitude separating both sympatric and allopatric species in other Neotropical hylids [see Duellman (1963), Duellman and Trueb (1966), Duellman and Fouquette (1968), and Duellman (1972) for examples].

TABLE 4.—Comparison of mating calls of species in the *Hyla bogotensis* group.

Character *N*[a]	*H. colymba* 3/9	*H. phyllognatha* 4/13	*H. platydactyla* 1/16
Notes per Call Group	12–104 (40.3)	2–12 (5.5)	7–10 (8.8)
Note Repetition Rate (min)	123–236 (179)	120–360 (210)	540 ------
Duration (sec)	0.05 ------	0.11–0.13 (0.12)	0.09–0.17 (0.14)
Pulses per Second	120–160 (138)	260–280 (279)	170–180 (177)
Harmonics	4	1	1
Fundamental Frequency (Htz)	1760–1820 (1796)	2550–2620 (2588)	2700–2860 (2790)
Dominant Frequency (Htz)	3520–3640 (3592)	2550–2620 (2588)	2700–2860 (2790)

[a] *N*=individuals/notes.

DISCUSSION

The grouping of specimens into geographic samples provided an *a priori* assumption that the groups represented different taxa. This assumption was tested by discriminant analysis of 14 characters in adults. The results were re-tested by subsequent independent and combined analyses of 11 characters of adults and five of tadpoles by means of the distance phenogram program. The conclusions are supported by data on mating calls. Although it is possible that some of the taxa (*H. bogotensis* and *H. platydactyla; H. colymba* and *H. alytolylax*) might be geographical variants (subspecies), there exists no evidence for gene flow between populations. Consequently, the six recognized taxa are treated as species.

The distributions of the species are broadly allopatric (Fig. 5). Two species, *H. bogotensis* and *H. platydactyla,* occur in the Andes at elevations of 2500-2900 m and 1600-2700 m, respectively. *Hyla colymba* inhabits both Caribbean and Pacific slopes at elevations of 560-1410 m in Costa Rica and Panamá. The other species occur on Andean slopes: *H. alytolylax* at 800-1460 m on Pacific slopes,

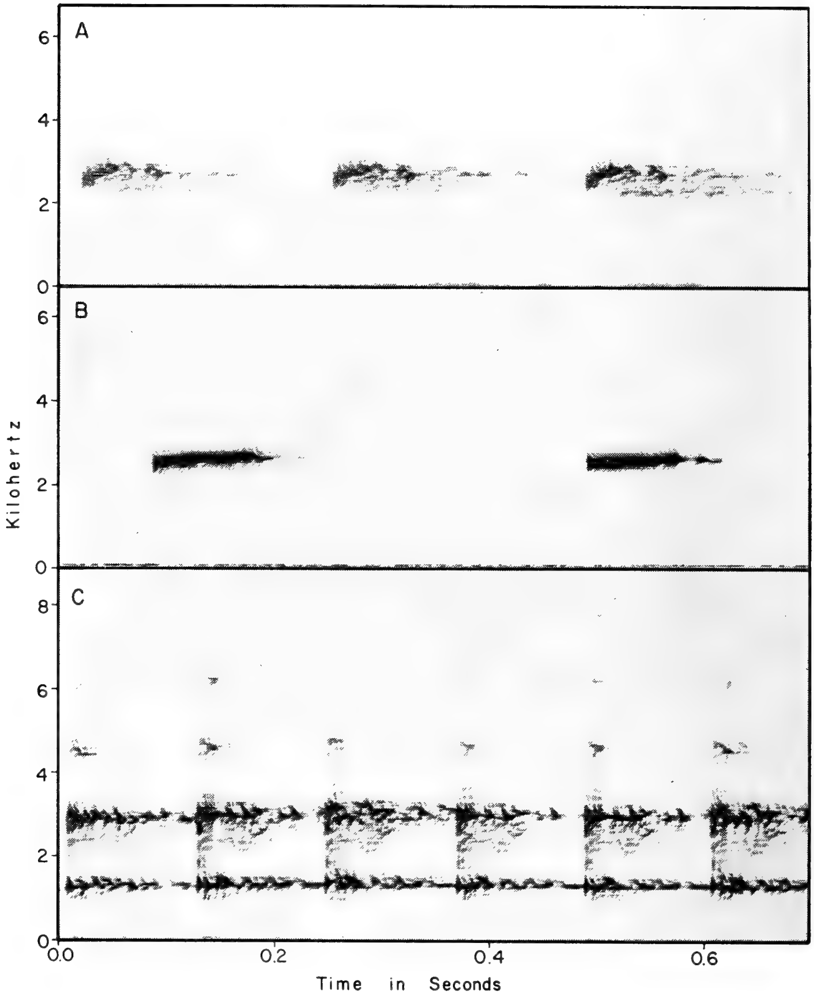

FIG. 4.—Audiospectrograms of mating calls. A. *Hyla platydactyla,* KU Tape 1029; 15-20 km NW Mérida, Mérida, Venezuela; temperature unknown B. *H. phyllognatha,* KU Tape 1166; Río Azuela, Napo, Ecuador; 18° C. C. *H. columba,* KU Tape 599; ridge between Río Jaqué and Río Imamadó, Darién, Panamá; 19° C. Band width 20 Htz.

H. phyllognatha at 610-1740 m on Amazonian slopes, and *H. denticulenta* at 1400-2400 m on Caribbean slopes. The principal habitat requirement seems to be cool, rocky streams for development of the tadpoles.

Due to lack of substantive information on direction of evolutionary change in many of the characters utilized, no quantitative phyletic analysis (Kluge and Farris, 1969) was attempted. The

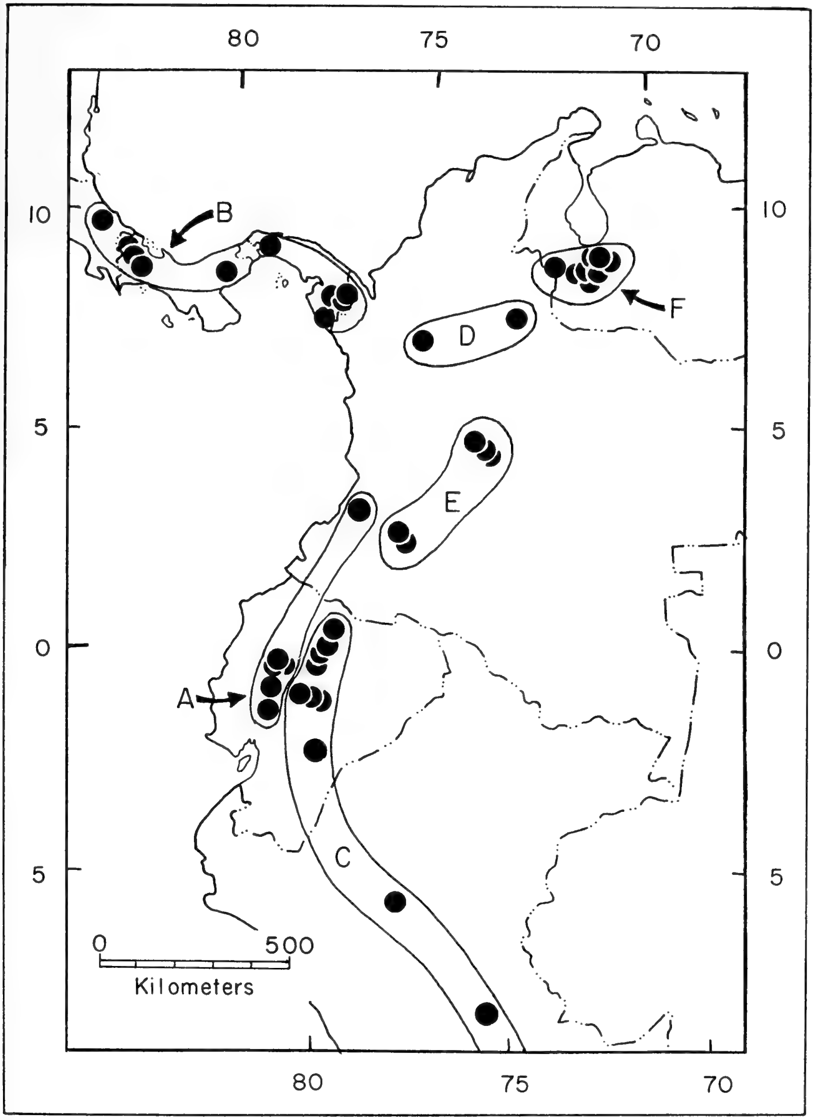

FIG. 5.—Distributions of the species in the *Hyla bogotensis* group. A. *H. alytolylax*. B. *H. columba*. C. *H. phyllognatha*. D. *H. denticulenta*. E. *H. bogotensis*. F. *H. platydactyla*. Lines enclose approximate known ranges, within which specific localities are indicated by dots; the range of *H. phyllognatha* extends to southern Perú.

presence of dermal folds and calcars in adults and proliferation of tooth rows in tadpoles are certainly derived states (Duellman, 1970). The occurrence of extensive webbing and bifid subarticular tubercles are probably derived character states. Furthermore, it seems that the presence of two tarsal stripes may have evolved from a condition in which one stripe was present. Other characters of structure and coloration remain evolutionarily enigmatic. All evidence points to *H. bogotensis* and *H. platydactyla* being the most generalized species, that is, having fewest derived character states. *Hyla denticulenta* possesses an array of derived states in both larvae and adults and seems to be the most advanced species in the group. The remaining three species seem to be closely related and phylogenetically intermediate between the primitive *H. bogotensis* and *H. platydactyla* and the advanced *H. denticulenta.*

Evidence from a variety of sources points to considerable Pleistocene climatic fluctuation and concomitant shifts in vegetation in the northern Andes (see Vuilleumier, 1971, for summary). This climatic fluctuation, together with orogenic changes in the Andes during the Pleistocene and volcanic activity to the Present, provided ample opportunity for isolation of populations on different slopes of the Andes (*H. alytolylax, H. denticulenta,* and *H. phyllognatha*), in disjunct interandean basins (*H. bogotensis* and *H. platydactyla*), and dispersal across presently uninhabited lowlands *(H. colymba).*

TAXONOMY

The inclusion of six species in the *Hyla bogotensis* group necessitates a modification of the definition of the group as given by Duellman (1970:327). The group can now be defined: 1) moderate-sized, stream-breeding frogs with males attaining snout-vent lengths of 45 mm and females 53 mm; 2) dorsum pale green or brown with or without dark flecks; 3) digits bearing small discs; 4) toes about three-fourths webbed; 5) axillary membrane absent; 6) quadratojugal articulating with maxillary; 7) sphenethmoid broad, not ossified anteriorly; 8) nasals small, widely separated medially; 9) frontoparietal fontanelle large; 10) tadpoles having long muscular tails, low fins, ventral mouths completely bordered by papillae, and 4/5—8/10 tooth rows; 11) mating calls consisting of series of short, loud peeps.

Distribution.—The combined distributions of the six species include the Andes and interandean valleys of western Venezuela and central and southern Colombia, Pacific and Amazonian slopes of Andes in Ecuador, Amazonian slopes in Perú, Caribbean slopes in northern Colombia, and Caribbean and Pacific slopes of highlands in Costa Rica and Panamá, with an elevational range of 560 to 2900 m (Fig. 5).

Remarks.—Members of the *Hyla bogotensis* group superficially resemble another group of species inhabiting lower Andean slopes in Ecuador, Colombia, and Venezuela (*H. palmeri* Boulenger, *H. albopunctata* Boulenger, and *H. lascinia* Rivero). These frogs lack mental glands; the mating calls and tadpoles are unknown.

Key to the Species in the Hyla bogotensis Group

1. Tarsal and ulnar folds and tarsal and anal stripes present; distal subarticular tubercle on fourth finger single, conical (if bifid, flat, not conical) 2

   Tarsal and ulnar folds and tarsal and anal stripes absent; distal subarticular tubercle on fourth finger bifid, conical 5

2. Distal subarticular tubercle on fourth finger single, conical; calcar, if present, small; snout round or truncate; tarsal and anal stripes single or double 3

   Distal subarticular tubercle on fourth finger bifid, flat; calcar large; snout anteriorly inclined; tarsal and anal stripes double, light above, dark below .... *H. denticulenta*

3. Dorsolateral stripe absent; webbing in males not extending to distal subarticular tubercle on fourth finger, reaching tubercle in females .... *H. phyllognatha*

   Dorsolateral stripe usually present; webbing in both sexes extending to or beyond subarticular tubercle on fourth finger 4

4. Dark pigment fine, scattered on dorsum; webbing usually extending beyond distal subarticular tubercle on fourth finger .... *H. alytolylax*

   Dark pigment coarse, dense on dorsum; webbing extending to distal subarticular tubercle on fourth finger .... *H. colymba*

5. Webbing extending to distal subarticular tubercle on fourth finger; dorsolateral stripe absent; dark pigment usually fine and scattered on dorsum .... *H. bogotensis*

   Webbing not extending to distal subarticular tubercle on fourth finger; dorsolateral stripe present or absent; dark pigment on dorsum forming discrete spots in adults .... *H. platydactyla*

Hyla alytolylax new species

Figure 6A

Holotype.—KU 111903 from Tandapi, Provincia Pichincha, Ecuador, 1460 m, obtained on 22 July 1967, by John D. Lynch.

Paratopotypes.—KU 111892-6, 111898-902, 111906, John D. and Marsha Lynch, 15-24 July 1967; KU 117982-4, John D. Lynch, 1-3 March 1968; KU 120851-60, John D. Lynch and Gerald R. Smith, 27-28 July 1968; KU 132425-6, John D. Lynch, 6 August 1970.

Diagnosis.—1) Webbing extending to or beyond distal subarticular tubercle on fourth finger; 2) distal subarticular tubercles on fingers single, conical; 3) ulnar and tarsal folds present; 4) calcar absent in males, absent or small in females; 5) snout in profile round in males, truncate in females; 6) tympanum distinct; 7)

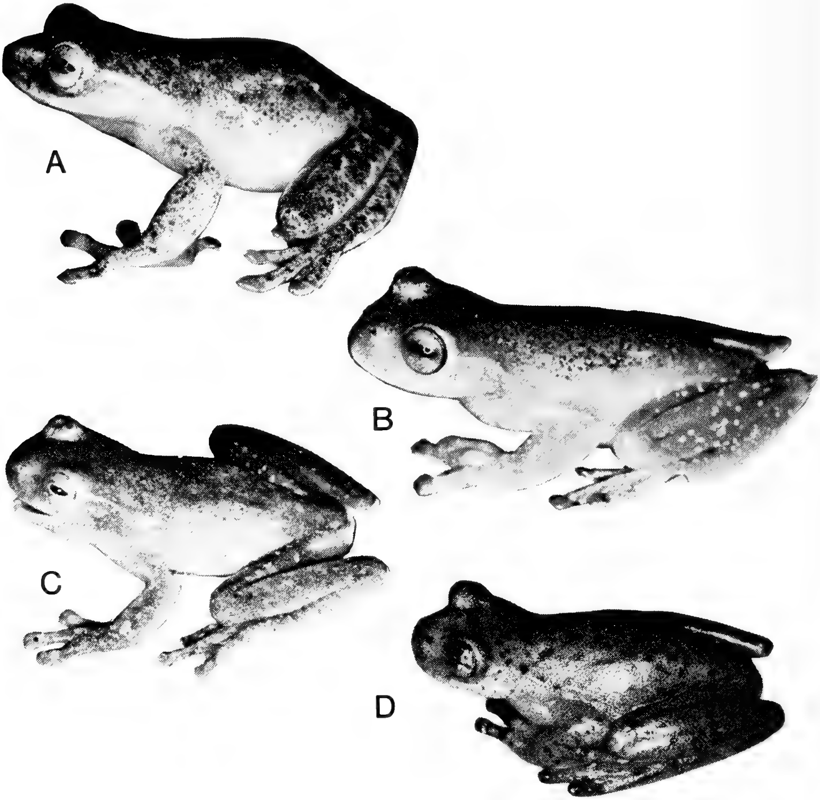

FIG. 6.—Frogs of the *Hyla bogotensis* group. A. *H. alytolylax,* KU 111900, ♀, 39.6 mm SVL. B. *H. denticulenta,* KU 133451, ♂, 44.2 mm SVL. C. *H. phyllognatha,* KU 143197, ♂, 33.3 mm SVL. D. *H. platydactyla,* KU 133433, ♂, 36.5 mm SVL.

mental gland present in males, absent in females; 8) dorsolateral light stripe present; 9) tarsal and anal stripes white; 10) tadpoles having 5/7 tooth rows, two rows of labial papillae, and small serrations on beaks.

Hyla alytolylax most closely resembles *H. colymba,* from which it differs by having slightly more webbing and less dense flecking on the dorsum; furthermore, the tadpoles of *H. alytolylax* have fewer tooth rows and a narrower snout. *Hyla alytolylax* also resembles *H. phyllognatha,* from which it differs by having more webbing, no or smaller calcars, and a dorsolateral light stripe; furthermore, the tadpoles of *H. phyllognatha* have more tooth rows and a broader snout.

Description.—N=13 ♂ ♂, 15 ♀ ♀; pertinent measurements and proportions given in table 1. Head slightly narrower than body; snout moderately short, round in dorsal aspect, round in profile in males, truncate in females; nostrils four-fifths distance from eye to tip of snout, not protuberant; internarial area slightly depressed; canthus round; loreal region concave; lips thin, round; top of head flat; eyes not greatly protuberant; supratympanic fold weak, curved downward toward angle of jaw, obscuring upper edge of tympanum; tympanic ring evident ventrally; tympanum slightly less than one-half diameter of eye (0.382-0.484, $\bar{x}=0.434$, N=13 ♂♂; 0.425-0.500, $\bar{x}=0.457$, N=15 ♀♀), separated from eye by distance slightly greater than diameter of tympanum.

Axillary membrane absent; forearm robust, bearing ulnar fold; prepollical tubercle large, elliptical; palmar tubercle large, bifid; distal subarticular tubercle on fourth finger conical, single; supernumerary tubercles small, indistinct; fingers short, bearing small discs (that on third finger slightly larger than tympanum); length of fingers from shortest to longest 1-2-4-3; webbing vestigial between first and second fingers, extending from base of penultimate phalange of second finger to middle of antepenultimate phalange of third, from base of penultimate phalange of third to base or middle of penultimate phalange of fourth finger. Hind limb moderately robust; dermal fold on knee; calcar usually absent; inner tarsal fold absent; outer tarsal fold extending entire length of tarsus; inner metatarsal tubercle elliptical, barely visible from above; outer tarsal tubercle absent; subarticular tubercles small, round; supernumerary tubercles minute, present proximally; toes long; length of toes from shortest to longest 1-2-3-5-4; discs slightly smaller than those of fingers; webbing extending to base of penultimate phalange of fourth toe, to discs on other toes.

Anal opening directed posteriorly at upper level of thighs in both sexes; skin on belly and proximal posteroventral surfaces of thighs weakly granular; skin on other surfaces smooth; mental gland present in males. Tongue cordiform, shallowly notched posteriorly, barely free behind; dentigerous processes of prevomers anteromedially inclined posterior to small ovoid choanae; total number of prevomerine teeth 15-22 ($\bar{x}=18.8$, N=13 ♂♂), 20-24 ($\bar{x}=21.8$, N=15 ♀♀); vocal slit extending from midlateral base of tongue to angle of jaw; vocal sac bilobate, subgular.

Coloration.—In life, adults have a greenish dorsum varying from pale green to greenish yellow, greenish gray, or greenish brown. In some individuals the anterior part of the dorsum is darker than the posterior part, and the loreal region usually is dark green. A cream line extends along the canthus, edge of eyelid, and supratympanic fold; a narrow white tarsal stripe and white anal stripe are present. The dorsal surfaces of the body and limbs have small scattered brown or black flecks and, in some individuals, minute white flecks. In some specimens faint cream reticulations are present on the dorsal surfaces of the body and thighs. The groin and concealed surfaces of the limbs are not pigmented. The venter is white, and in males the vocal sac is bluish green. The iris is creamy white.

In preservative, the dorsum is creamy tan with black flecks, varying from few to many, scattered over the dorsum. Dorsolateral, tarsal, and anal white stripes are evident. The groin, hidden surfaces of thighs, and all ventral surfaces are cream. Pale reticulations are evident posteriorly in some specimens.

Tadpoles.—A typical tadpole in developmental stage 27 from Tandapi, Ecuador, has a body length of 15.2 mm and a total length of 42.6 mm. Body ovoid, widening abruptly just anterior to eyes, three-fourths as deep as wide; nostrils about midway between eyes and tip of snout; spiracle sinistral; spiracular opening directed posteriorly at a point just below midline about two-thirds length of body; cloacal tube dextral; caudal fin not extending onto body; caudal musculature robust, tapering gradually, extending nearly to tip of pointed tail; depth of caudal musculature at one-third length of tail 63 percent of total depth of tail. Mouth moderately large; lips indented posterolaterally, completely bordered by two rows of small labial papillae; five upper and seven lower rows of teeth; fifth upper row narrowly interrupted medially; beaks slender; lateral processes not expanded distally; upper beak bearing small peglike serrations; lower beak having small pointed serrations (Fig. 3B).

In preservative, the body is dark brown above and dull gray below; the caudal musculature is cream with brown flecks or reticulations laterally. The dorsal musculature is cream with transverse brown bars. The fins are transparent, except for a few brown flecks on the outer edge of the dorsal fin. In life, the body is pale brown above and dark brown below; the caudal musculature is pale cream with brown mottling laterally and blotches dorsally. The iris is silvery cream.

Etymology.—The specific name is derived from the Greek *alytos* meaning continuous, and the Greek *lylax* meaning babbler; the name is applied in reference to the long continuous calls of the species.

Distribution.—Hyla alytolylax is definitely known from elevations of 800 to 1460 m on the Pacific slopes of the Cordillera Occidental in Ecuador and southeastern Colombia. The northern localities in Ecuador are along the Río Pilatón, a tributary of the Río Toachi, and the southern localities are in the Río Playas drainage.

Remarks.—At Tandapi, Ecuador, males were calling from vegetation over, and boulders in, cascading mountain streams in cloud forest in July 1967 and in March and July 1968. Gravid females were found on bushes along streams. Tadpoles were obtained from gravel-bottomed pools in fast-flowing streams. Metamorphosing young were found on low vegetation along streams in July 1967, and two metamorphosed on 14 September from tadpoles obtained on 17 July 1967. Five young have snout-vent lengths of

17.6-20.4 ($\bar{x}$=18.4) mm. In life, the dorsal surfaces were pale green with a middorsal brown streak, expanded anteriorly into an interorbital bar in one individual.

The mating call consists of a long series of short, loud whistles, reminiscent of the call of *Hyla colymba.* Analyzable recordings are not available.

Two specimens (LACM 73000-1) from Camino de Yupe, Chocó, Colombia (420 m), possibly are referable to *Hyla alytolylax,* but because of certain differences, they have not been included in the analysis nor in the description. Both are males having snout-vent lengths of 39.0 mm and large mental glands. The dorsolateral stripe is absent, but tarsal and anal stripes are present; on either side of the anus is a triangular dermal flap, larger than the calcar. Perhaps these specimens represent an undescribed species that is intermediate in certain characters between *H. alytolylax* and *H. denticulenta.*

Duellman (1970:331) referred specimens of *H. alytolylax* to *H. colymba.*

Hyla bogotensis (Peters)

Hylonomus bogotensis Peters, 1882a:107 [Holotype.—ZMB 10209 from Bogotá, Departamento Cundinamarca, Colombia; Möschler collector].
Hyloscirtus bogotensis Peters, 1882b:127.
Hyla bogotensis—Duellman, 1970:327.

Diagnosis.—1) Webbing extending to distal subarticular tubercle on fourth finger; 2) distal subarticular tubercles on fingers bifid, conical; 3) ulnar and tarsal folds absent; 4) calcar absent; 5) snout in profile truncate; 6) tympanum distinct or covered in males, covered in females; 7) mental gland present or absent in males, absent in females; 8) dorsolateral light stripe absent; 9) tarsal and anal stripes absent; 10) tadpoles having 4/5 tooth rows, one row of labial papillae, and medium-sized serrations on beaks.

Hyla bogotensis is like *H. platydactyla* in having bifid, conical subarticular tubercles, no ulnar and tarsal folds, no tarsal and anal stripes, and tadpoles with 4/5 tooth rows and one row of labial papillae; these characters distinguish these two species from other members of the group. *Hyla bogotensis* can be distinguished from *H. platydactyla* by the presence of more webbing and finer dorsal flecking in the former; moreover, the tadpoles of *H. bogotensis* have smaller serrations on the beaks than do those of *H. platydactyla.*

Coloration.—I have not seen living individuals of this species, so I must rely upon descriptions given by others. Cochran and Goin (1970:315) noted that a specimen from Bogotá, Colombia, was ". . . a yellowish brown with a definite pattern of more or less uniformly distributed pencil-like black spots on all the dorsal surfaces. All ventral surfaces were a dirty gray without pattern, except for faint pepper-like flecks under the throat and a yellowish tinge to the under-margin of the jaws." Philip A. Silverstone (field notes, 6 January 1966) described a specimen (LACM 50562) from Páramo de Puracé, Colombia, as "Green all over; yellowish tinge on flanks and ventral surfaces of thighs. Blue on ankle and sole; web orange." Juan A. Rivero (pers. com.) stated that a specimen (UPR-M 1800) from Páramo de Palacio was solid brown above in life, but that the freshly preserved specimen was chartreuse above with dark brown dots; there was some yellow on the throat and ventral surfaces of the thighs.

In preservative, most specimens are creamy tan with or without scattered dark flecks on the dorsum. Two individuals (FMNH 81916 and UPR-M 1800) have many larger black dots on the dorsum.

Tadpoles.—A single tadpole (CAS-SU 22971) in developmental stage 37 has a body length of 21.0 mm and a total length of 68.0 mm. Body ovoid, two thirds as deep as wide; nostrils slightly closer to eye than to tip of snout; spiracle sinistral; spiracular opening directed posterodorsally on midline at about midlength of body; cloacal tube dextral; caudal fin not extending onto body; caudal musculature robust, tapering gradually; extending nearly to tip of pointed tail; depth of caudal musculature at one-third length of tail 66.7 percent of total depth of tail. Mouth moderately large; lips indented posterolaterally, completely bordered by single row of labial papillae; four upper and five lower rows of teeth; fourth upper row narrowly interrupted medially; beaks massive; lateral processes expanded distally; beaks bearing medium-sized serrations.

In preservative the body is pale brown above and cream below. The caudal musculature is pale brown with a dorsolateral dark brown stripe on the proximal half of the tail.

Distribution.—This species is known from subpáramo regions in the Bogotá Valley in the Cordillera Oriental and in the highlands east of Popoyán in the Cordillera Central in Colombia. All recorded elevations are between 2500 and 2900 m.

Remarks.—For many years this species was regarded as being generically distinct from *Hyla* on the basis of having rounded, instead of dilated, sacral diapophyses. Duellman (1970:328) noted that the type (ZMB 10209) actually had expanded sacral diapophyses. Subsequent examination of additional specimens supports the contention that the sacral diapophyses are not round in this species.

The mating call is unknown. Dunn (1944:79) noted that a specimen was found in a bromeliad at Boquerón, Colombia. Philip A. Silverstone (field notes, 6 January 1966) found one individual on a leaf near a stream in subpáramo by day. Notes by Anne Funkhouser accompanying a tadpole and partially metamorphosed young (CAS-SU 22970-1) state: "Fast mountain stream on road to Choachí from Bogotá. Fairly common in area collected. Adults were never found, but young kept for several months were bright grass green above with random dark spots; turquoise shading to yellow ventrally; iris gold." The metamorphosing young (CAS-SU 22970) has a snout-vent length of 22.0 mm and a tail stub of 7.2 mm; in preservative, it is creamy tan with scattered brown flecks on the dorsum.

Hyla colymba Dunn

Hyla colymba Dunn, 1931:400 [Holotype.—MCZ 10234 from La Loma, Provincia Bocas del Toro, Panamá; Chester Duryea and Emmett R. Dunn collectors].

Hyla alvaradoi Taylor, 1952:882 [Holotype.—KU 30886 from Moravia, Provincia Cartago, Costa Rica; Edward H. Taylor collector]. Synonymy fide Duellman (1966:267).

Diagnosis.—1) Webbing extending to distal subarticular tubercle on fourth finger; 2) distal subarticular tubercles on fingers single, conical; 3) ulnar and tarsal folds present; 4) calcar absent; 5) snout in profile round; 6) tympanum distinct; 7) mental gland present in males, present or absent in females; 8) dorsolateral light stripe present in males, present or absent in females; 9) tarsal and anal stripes white; 10) tadpoles having 6/9 tooth rows, two rows of labial papillae, and small serrations on beaks.

Hyla colymba most closely resembles *H. alytolylax*, from which it differs by having slightly less webbing and more dense flecking on the dorsum; furthermore, the tadpoles of *H. colymba* have more tooth rows and a broader snout. *Hyla colymba* differs from *H. phyllognatha* by having more webbing and usually a dorsolateral light stripe; the structure of the tadpoles of the two species is identical, but dark transverse blotches are present on the dorsum of the tail in *H. phyllognatha,* whereas the tail in *H. colymba* is nearly uniform brown.

Coloration.—In life, most individuals are pale green with faint yellow flecks or scattered brown flecks on the dorsum. A faint creamy yellow stripe extends from the canthus, along the edge of the eyelid and on the supratympanic fold to a point above the arm. The anal, ulnar, and tarsal stripes are pale creamy yellow. The ventral surfaces of the limbs are pale green, and the throat is pale bluish green. The belly and chest are white, and the mental gland is white or creamy yellow. Some individuals are pale tan with brown flecks. The iris is pale brown.

In preservative, the dorsum is pale creamy white, creamy tan, or pale brown. Minute dark flecks are present dorsally; usually these are most numerous on the head and middorsally on the body. The stripes are white, and the venter is creamy white.

Tadpoles.—A typical individual in developmental stage 25 from Darién, Panamá, has a body length of 15.1 mm and a total length of 37.3 mm. Body ovoid, four-fifths as deep as wide; nostrils midway between eyes and tip of snout; spiracle sinistral; spiracular opening directed posteriorly just below midline at midlength of body; cloacal tube dextral; caudal fin not extending onto body; caudal musculature robust, tapering gradually, extending nearly to tip of pointed tail; depth of caudal musculature at one-third length of tail 61 percent of total depth of tail. Mouth large, ventrals; lips deeply indented posterolaterally, completely bordered by two rows of labial papillae; six upper and nine lower rows of teeth; sixth upper and first lower rows narrowly interrupted medially; outermost three lower rows shorter than others; upper beak broadly arched, bearing long slender lateral processes; lower beak broadly V-shaped; both beaks bearing small, blunt serrations.

In preservative, the body is brown with faint white flecks. The caudal musculature is creamy tan; brown flecks are present on the musculature and dorsal fin. In life, the dorsum of the body is bronze-tan with golden lichenous flecks; the sides of the body are brown with gold flecks. The caudal musculature is tan; dark brown spots are present on the musculature and dorsal fin. This iris is dull bronze.

Distribution.—This species occurs in cloud forest and lower humid montane forest at elevations of 610-1200 m on the Caribbean slopes of the Cordillera Talamanca in Costa Rica and Western Panamá and 560-1410 m on the Pacific slopes of the highlands in central and eastern Panamá.

Remarks.—Duellman (1970:328) gave a detailed account of *H. colymba* and discussed the nomenclatural history of the species; his reference to the occurrence of the species in Ecuador was based on material herein assigned to *H. alytolylax.*

The mating call consists of a series of short high-pitched, cricket-like chirps. Calls have as many as 104 notes produced at a rate of 123-236 notes per minute. The second harmonic at about 3600 Hertz is dominant (Fig. 4C).

Adults have been found on vegetation along streams, and males were found calling beneath boulders in streams. Tadpoles have been found in quiet pools in small rocky streams.

Hyla denticulenta new species

Figure 6B

Holotype.—KU 133451 from Charta, Departamento Santander, Colombia, 2400 m, obtained on 15 July 1970, by Stephen R. Edwards.

Paratype.—KU 133452 from Valdivia, Departamento Antioquia, Colombia, obtained on 3 August 1970, by Stephen R. Edwards.

Diagnosis.—1) Webbing extending beyond distal subarticular tubercle on fourth finger; 2) distal subarticular tubercles on fingers bifid, flat; 3) ulnar and tarsal folds present; 4) calcar large; 5) snout in profile anteriorly inclined; 6) tympanum distinct; 7) mental gland absent; 8) dorsolateral stripe absent; 9) tarsal and anal stripes white above, brown below; 10) tadpoles having 7-8/10 tooth rows, two rows of labial papillae, and no serrations on beaks.

Hyla denticulenta differs from all other members of the group by its large size, bifid and flat subarticular tubercles, large calcars, and anteriorly inclined snout; also, the presence of 7-8/10 tooth rows and absence of serrations on the beaks distinguish the tadpoles from all others.

Description.—N=1 ♂ (holotype), 1 ♀ (paratype); pertinent measurements and proportions given in table 1. Head as wide as body; snout moderately short, round in dorsal aspect, anteriorly inclined in profile (especially in female); nostrils three-fourths distance from eye to tip of snout, not protuberant; internarial area flat; canthus round; loreal region concave; lips thin, round; top of head flat; eyes not greatly protuberant; supratympanic fold weak, curved downward toward angle of jaw, obscuring upper part of tympanum; tympanic ring distinct; tympanum one-half diameter of eye, separated from eye by distance equal to half again diameter of tympanum.

Axillary membrane absent; forearm robust, bearing ulnar fold; prepollical tubercle large, elliptical; palmar tubercle large, bifid; distal subarticular tubercle on fourth finger flat, bifid; others round; supernumerary tubercles small, indistinct; fingers short, bearing small discs (that on third finger slightly larger than tympanum); length of fingers from shortest to longest 1-2-4-3; webbing vestigial between first and second fingers, extending from base of penultimate phalange of second to distal end of antepenultimate phalange of third, from base of penultimate phalange of third to base (male) or middle (female) of penultimate phalange of fourth finger. Hind limb moderately robust; dermal fold on knee; calcar prominent, triangular; inner tarsal fold absent; outer tarsal fold extending length of tarsus; inner metatarsal tubercle elliptical, visible from above; outer tarsal tubercle absent; subarticular and supernumerary tubercles about equal in size, small, round; toes long; length of toes from shortest to longest 1-2-3-5-4; discs slightly smaller than those on fingers; webbing extending to base of penultimate phalange of fourth toe, to discs on other toes.

Anal opening directed posteroventrally at midlevel of thighs (male), posteriorly at upper level of thighs (female); skin on belly and proximal posteroventral surfaces of thighs weakly granular; skin on other surfaces smooth. Tongue broadly cordiform, shallowly notched posteriorly, barely free behind; dentigerous processes of prevomers slightly anteromedially inclined posterior to small ovoid choanae, bearing 21 (male), 20 (female) teeth; vocal slit extending from posterolateral base of tongue to angle of jaw; vocal sac subgular, possibly bilobate.

Coloration.—In life, the male holotype had a pale green dorsum covered with many small white flecks; black flecks were present on the head and back. The flanks were creamy yellow; the throat, chest, groin, anterior surfaces of the thighs, and ventral surfaces of the shanks were bluish green. The belly was creamy yellow, and the iris was reddish gold. The female had a green dorsum with a white margin to the lips and white anal, ulnar, and tarsal stripes. The axilla, groin, and ventral surfaces of the thighs were blue-green; the flanks were yellow-orange. The throat and belly were greenish white, and the iris was dark gold with black reticulations.

In preservative, all pigment is lost, except for many small brown flecks on the head and anterior two-thirds of the back in the male and a few scattered flecks on the eyelids, head, and middorsum of the female. Also, white flecks are apparent dorsolaterally in the male. In both specimens narrow white anal, ulnar, and tarsal stripes are bordered below by a narrow line of brown pigment, which is expanded on the palm and sole.

Tadpoles.—Five tadpoles (KU 139531) are from the type locality. The smallest individual is in developmental stage 25 and has a body length of 17.5 mm and a total length of 51.5 mm; the largest is in stage 38 and has measurements of 22.0 and 65.5 mm. Body ovoid, four-fifths as deep as wide, widening and deepening abruptly just anterior to the eyes; nostrils midway between eyes and tip of snout; spiracle sinistral; spiracular opening directed posteriorly just below midline at about midlength of body; cloacal tube dextral; caudal fin not extending onto body; caudal musculature robust, gradually tapering, extending nearly to tip of pointed tail; depth of musculature at one-third length of tail 57 percent of total depth of tail. Mouth large, ventral; lips deeply indented posteriolaterally, completely bordered by two rows of small papillae; seven or eight upper and ten lower rows of teeth; proximal upper row narrowly interrupted medially; upper beak slender with long, tapering lateral processes; lower beak broadly V-shaped; both beaks smooth or bearing minute serrations (Fig. 3D).

In preservative, the body is dark brown above and dull gray below; the caudal musculature is cream with dense brown pigment laterally, forming distinct transverse bars, separated by narrow cream interspaces, dorsally. The fins are transparent, except for a few flecks on the dorsal fin. In life, the body is pale gray; the tail is distinctly mottled black, gray, and white, and the fins are transparent.

Etymology.—The specific name is derived from the Latin *denticulus* meaning with small teeth, and the Latin *lentus* meaning full of; the name refers to the many rows of teeth in the tadpoles.

Distribution.—This species is known from only two localities: Charta at an elevation of 2400 m on the northern slope of the Cordillera Central, and Valdivia at an elevation of 1400 m on the northern slope of the Cordillera Central. These localities are separated by the low Río Magdalena Valley. It is unlikely that gene flow exists between the populations; thus, it is possible that additional material will reveal differences between the populations.

Remarks.—At Charta the frogs were found along a shallow river south of the village. The river, a tributary of the Río Suratá, flows through pasture land with a few scattered trees. Tadpoles and a metamorphosing young having a snout-vent length of 24.6 mm and a tail stub of 10.4 mm were found in pools in the river bed. The holotype was found by day under a large rock in a small stream cascading into the river bed. The adult female was found in the town of Valdivia, where it was perched on a leaf of a large herb 2 m above the ground on a steep bank at night. The mating call is unknown.

Hyla phyllognatha Melin

Figure 6C

Hyla phyllognatha Melin, 1941:30 [Holotype.—NHMG 474 from Roque, Departamento San Martín, Perú; Douglas Melin collector].

Diagnosis.—1) Webbing not extending to, or just extending to, distal subarticular tubercle on fourth finger; 2) distal subarticular tubercles on fingers single, conical; 3) ulnar and tarsal folds present; 4) calcar absent or small; 5) snout in profile round or truncate; 6) tympanum distinct; 7) mental gland present in males, present or absent in females; 8) dorsolateral light stripe absent; 9) tarsal and anal stripes absent or white; 10) tadpoles having 6/9 tooth rows, two rows of labial papillae, and small serrations on beaks.

Hyla phyllognatha is like *H. colymba* and *H. alytolylax* but has less webbing and no dorsolateral stripe. In some specimens of *H. phyllognatha* a calcar is present, but this is smaller than the calcars in *H. denticulenta,* which further differs by having bifid subarticular tubercles, anteriorly inclined snout, and more webbing. The tadpoles of *H. phyllognatha* have 6/9 tooth rows, a character shared with *H. colymba,* the tadpoles of which differ from those of *H. phyllognatha* by not having transverse brown blotches on the dorsal caudal musculature.

Coloration.—In life, the dorsum is olive-green anteriorly changing to olive-tan posteriorly; the dorsal surfaces of the limbs are green. Minute black flecks are present on the head and middorsal part of the body, and small white flecks are scattered on the body and limbs. The margin of the lip is yellow, and the anal and tarsal stripes are pinkish white. The hidden surfaces of the limbs are dull green. The belly is creamy yellow, and the webbing is dull yellow. The vocal sac is green, and the lining of the mouth is bluish green. The iris is dull bronze with black reticulations. One female found by day was bright green with bluish white flecks.

In preservative, the dorsum is cream to grayish brown with scattered dark flecks apparent in paler specimens. The venter and hidden surfaces of the thighs are cream.

Tadpoles.—A typical tadpole in developmental stage 27 from 16.5 km NNE of Santa Rosa, Ecuador, has a body length of 16.5 mm and a total length of 50.3 mm. Body ovoid, slightly wider than deep; nostrils slightly closer to tip of snout than to eyes; spiracle sinistral; spiracular opening directed posteriorly just below midline about two-thirds length of body; cloacal tube dextral; caudal fin not extending onto body; caudal musculature robust, tapering gradually, extending nearly to tip of pointed tail; depth of musculature at one-third length of tail 60 percent of total depth of tail. Mouth large, lips indented posterolaterally, completely bordered by two rows of small labial papillae; six upper and nine lower rows of teeth; sixth upper row narrowly interrupted medially; beaks moderately slender, bearing small, blunt serrations; upper beak arched with lateral processes barely expanded distally; lower beak broadly V-shaped (Fig. 3C).

In preservative, the body is dark brown above and gray below; the caudal musculature is cream with dense brown flecking laterally and dark brown transverse bars anterodorsally. The fins are transparent with brown flecks, except anteriorly on ventral fin. In life, the body is dark brown with small green, lichenous flecks. The caudal musculature is tan with brown blotches; the fins are clear with orange spots. The iris is dark bronze.

Distribution.—*Hyla phyllognatha* is known from elevations of 610-1740 m on the Amazonian slopes of the Cordillera Oriental of the Andes and associated ranges, such as the Cordillera del Dué and Cordillera Carabaya, from northern Ecuador to southern Perú.

Remarks.—Males call from low bushes over torrential mountain streams; calling males have been found in April, July, August, and October. Gravid females have been found in October. The tadpoles live in gravel-bottomed pools in the streams. Recently metamorphosed young have been found on vegetation along streams at night and in bromeliads by day. Four young have snout-vent lengths of 18.4-20.3 ($\bar{x}=19.5$) mm; in life, the dorsum is green with black flecks middorsally.

The mating call consists of a series of short, loud whistles, repeated at a rate of about 210 notes per minute. The notes have about 280 pulses per second; the fundamental frequency at about 2560 Hertz is dominant (Fig. 4B).

No information has been published on *Hyla phyllognatha* since Melin's (1941) original description. The holotype (NHMG 474) is an adult male having a snout-vent length of 32.3 mm and a mental gland. The specimen compares favorably with series of fresh specimens from Equador and three individuals from southern and central Perú.

Hyla platydactyla Boulenger

Figure 6D

Hyla platydactyla Boulenger, 1905:183 [Holotype.—BMNH 1904.6.30.17 (RR 1947.2.13.14) from Mérida, Estado Mérida, Venezuela; Briceño collector].

Hyla paramica Rivero, 1961:112 [Holotype.—UMMZ 59016 from Escorial, Estado Mérida, Venezuela; received from W. F. H. Rosenberg]. New synonymy.

Hyla jahni Rivero, 1961:113 [Holotype.—UMMZ 46465 from Escorial, Estado Mérida, Venezuela; presented by A. G. Ruthven]. New synonymy.

Diagnosis.—1) Webbing not extending to distal subarticular tubercle on fourth finger; 2) distal subarticular tubercles on fingers single or bifid in males, bifid and conical in females; 3) ulnar and tarsal folds absent; 4) calcar absent; 5) snout in profile truncate; 6) tympanum distinct or covered; 7) mental gland present or absent in both sexes; 8) dorsolateral stripe present or absent; 9) tarsal and anal stripes absent; 10) tadpoles having 4/5 tooth rows, one row of labial papillae, and large serrations on beaks.

Hyla platydactyla is like *H. bogotensis* in having bifid, conical subarticular tubercles, no tarsal or anal stripes, no ulnar or tarsal folds, and tadpoles with 4/5 tooth rows and one row of labial papillae; these characters distinguish these two species from other members of the group. *Hyla platydactyla* can be distinguished from *H. bogotensis* by having less webbing and, in large adults, discrete dark spots dorsally. Also, the tadpoles of *H. platydactyla* have larger serrations on the beaks than do those of *H. bogotensis.*

Coloration.—In life, specimens from a locality 15-20 km NW of Mérida, Venezuela, had reddish brown dorsal surfaces with many small black spots on the back. The throat was greenish tan, and the belly was white. The iris was copper with fine black reticulations. Through the courtesy of Juan A. Rivero, I have seen colored photographs of individuals having olive-tan dorsal coloration and creamy yellow dorsolateral stripes. Rivero stated (pers. com.) that some individuals are dark brown above and that in most specimens the anterior and posterior surfaces of the thighs are orange.

In preservative, in adults the dorsal surfaces of the head, body, forearms, and shanks are tan to brown with small dark brown to black spots present in most specimens. The dorsolateral stripe, thighs, and ventral surfaces are cream.

Tadpoles.—In a series from 15-20 km NW of Mérida, Venezuela, the smallest tadpole is in developmental stage 25 and has a body length of 8.5 mm and a total length of 26.5 mm; the largest tadpole (stage 37) has measurements of 23.0 and 60.5 mm. Body ovoid, three-fourths as deep as wide; nostrils slightly closer to eyes than to tip of snout; spiracle sinistral; spiracular opening directed posteriorly on midline about midlength of body; cloacal tube dextral; caudal fin not extending onto body; caudal musculature robust, tapering gradually, extending nearly to tip of pointed tail; depth of caudal musculature at one-third length of tail 80 percent of total depth of tail. Mouth moderately large; lips deeply indented posterolaterally, completely bordered by one row of labial papillae; four upper and five lower rows of teeth; fourth upper row narrowly interrupted medially; fifth lower row short; upper beak moderately massive, arched, with robust lateral processes and large, pointed serrations; lower beak massive, broadly V-shaped, bearing large blunt serrations (Fig. 3A).

In preservative, the body is dark brown above and paler brown below; the caudal musculature is creamy tan with a heavy suffusion of brown laterally and two or three distinct longitudinally rectangular blotches on the dorsum, separated by narrow cream interspaces. The dorsal fin and posterior one-third of ventral fin are heavily flecked with brown.

Distribution.—This species is known only from the Mérida Andes in western Venezuela, where it occurs at elevations from 1600 to at least 2500 m, inhabiting subtropical and temperate areas.

Remarks,—Rivero (1961:115) diagnosed *Hyla paramica* from *H. jahni* by the former having a ". . . rounded snout, less defined canthus and in lacking supratympanic fold, canthal, palpebral, and supratympanic lines and closely set dark dots above." He (1961: 116) stated that *Hyla platydactyla* differed from *H. jahni* ". . . in the shorter snout and less defined canthus, absence of a light canthal and supratympanic line, narrower interorbital space, more vertical loreal region and different coloration [no dorsal spots]." Rivero based his descriptions of *H. paramica* on five specimens and of *H. jahni* on seven, all of which are rather poorly preserved; he examined no specimens of *H. platydactyla.*

I have examined all of the specimens studied by Rivero and the holotype of *H. platydactyla,* together with several series from western Venezuela (total of 59 adults and subadults). I find no consistent structural differences, such as snout shape, definition of canthal ridge, or inclination of loreal region, by which to distinguish more than one taxon in western Venezuela. The dorsolateral stripe (canthal, palpebral, and supratympanic lines of Rivero) is variable; a stripe is evident in the supratympanic region in slightly more than half of the specimens; in some of these it extends posteriorly to the axilla. Also, in some of these specimens no stripe is evident on the canthus. On the basis of preserved specimens alone, there seems to be a continuum from well-defined to no stripes. Thus, only one species, *H. platydactyla,* can be recognized.

The mating call consists of a series of short notes repeated at a rate of 540 notes per minute; the pulse rate is about 177 pulses per second, and the fundamental frequency at about 2790 Hertz is dominant (Fig. 4A).

At a locality 15-20 km NW of Mérida, Venezuela, adults were found at night on leaves of herbs on a steep bank over a roadside ditch. Tadpoles were found in quiet pools in a cascading stream. Juan A. Rivero stated (pers. com.) that adults are found in bromeliads by day and that males call from bushes over streams at night. He also noted that the frogs produce a smelly exudate when handled.

Cochran and Goin (1970:256) proposed the name combination *Hyla labialis platydactyla;* the name was used for the population of frogs in the eastern Andes of Colombia that is referable to the highly variable *Hyla labialis,* a species quite distinct from *H. platydactyla.*

RESUMEN

Las ranas del grupo *Hyla bogotensis* se crian en los arroyos de las vertientes de los Andes en el occidente de Venezuela, Colombia, Ecuador, y Perú, y en las sierras de Costa Rica y Panamá. Las ranas de este grupo se caracterizan por: 1) su tamaño moderado (longitud de cabeza-cuerpo de los machos hasta 45 mm, en las hembras hasta 53 mm); 2) el dorso de color verde opaco o carmelita con manchas pequeñas oscuras espacidas en el; 3) los dedos con tres cuarta partes cubiertos por la membrana interdigital; 4) la glándula del mentón en el ápice de éste; 5) membrana axilar ausente; 6) el cuadratoyugal articulado con el maxilar; 7) los nasales pequeños, separados ampliamente en el medio; 8) la fontanela frontoparietal grande; 9) renacuajos con colas musculares, largas, la boca ventral grande, completamente bordeada por papilas labiales, con 4/5—8/10 hileras de dientes.

Se analizaron 14 caracteres de ranas adultas por medio del programa de computación de análisis discriminante multiple; los seis grupos resultantes fueron tratados como OTUs en los programas de NT-SYS, en el cual 11 caracteres de adultos y cinco de los renacuajos constituyeron los datos básicos para la construcción de los fenogramas. Los resultados de estos análisis son sostenidos por el análisis de las llamadas de reclamo de tres especies.

Se reconocen seis especies en el grupo: 1) *H. alytolylax* especie nueva, laderas del Pacífico de los Andes en Ecuador; 2) *H. bogotensis* (Peters, 1882), Andes del centro y sur de Colombia; 3) *H. colymba* Dunn, 1931, sierras de Costa Rica y Panamá; 4) *H. denticulenta* especie nueva, laderas del Caribe de los Andes en el norte de Colombia; 5) *H. phyllognatha* Melin, 1941, laderas amazónicas de los Andes en Ecuador y Perú; 6) *H. platydactyla* Boulenger, 1905, Andes del occidente de Venezuela. *Hyla paramica* Rivero, 1961, y *Hyla jahni* Rivero, 1961, son colocadas en sinónimia de *Hyla platydactyla* Boulenger, 1905.

SPECIMENS EXAMINED

Hyla alytolylax.—COLOMBIA: *Chocó:* Camino de Yupe, 420 m, LACM 73000-1. *Valle:* Anchicayá, KU 148703-4. ECUADOR: *Bolivar:* Balsabamba, 800 m, KU 132432, 132545 (tadpoles). *Cotopaxi:* 20.3 km W Pilaló, 830 m, KU 142857 (tadpoles). *Pichincha:* 3.7 km E. Dos Ríos, 1190 m, KU 142856 (tadpoles); Las Palmas, 920 m, KU 132427; Tandapi, KU 111892-903, 111904 (skeleton), 111905-10, 112357-8 (tadpoles), 112359 (young), 117982-4, 118123 (tadpoles), 120851-60, 132425-6.

Hyla bogotensis.—COLOMBIA: *Cauca:* Moscopán, 2500 m, UMMZ 121032. *Cundinamarca:* Bogotá, 2630 m, CAS-SU 22970 (tadpole), 22971 (young), KU 125363, UMMZ 123946-8, ZMB 10209; Boquerón, 2900 m, FMNH 81916; Páramo de Palacio, Siberia, UPR-M 1800. *Huila:* east of Páramo de Puracé, 2500 m, LACM 50562.

Hyla colymba.—COSTA RICA: *Cartago:* Moravia, 1200 m, KU 30886, 31864, 31865 (skeleton). PANAMÁ: *Bocas del Toro:* La Loma, 610 m, MCZ 10234-5; Río Changena, 650 m, KU 104237 (young); Río Changena, 830 m, KU 104236 (tadpoles). *Coclé:* El Valle, 560 m, AMNH 59606. *Darién:* Cerro Cituro, Serranía de Pirre, 1100 m, KU 116357; Cerro Malí, 1410 m, GML 4-00426; Laguna, 820 m, KU 77414; ridge between Río Jaqué and Río Imamadó, 730 m, KU 116779 (tadpoles), 116780-1 (young). *Panamá:* Altos de Pacora, 740 m, KU 95979.

Hyla denticulenta.—COLOMBIA: *Antioquia:* Valdivia, 1400 m, KU 133452. *Santander:* Charta, 2400 m, KU 133450-1, 139531 (tadpoles).

Hyla phyllognatha.—ECUADOR: *Morona-Santiago:* Macas, AMNH 33911. *Napo:* Bermejo No. 4 (oil well site), 15 km ENE Umbaquí, 720 m, KU 123130-2; Río Azuela, 1740 m, KU 143199-204, 143543 (young), USNM 193349-50; Río Salado, 1 km upstream from Río Coca, 1410 m, KU 146794 (tadpoles); Salto de Agua, 2.5 km NNE Río Reventador, 1660 m, KU 143205, 143544 (young), 146793 (tadpoles); San José, AMNH 22164; 16.5 km NNE Santa Rosa, 1700 m, KU 143197-8, 143542 (tadpoles). *Pastaza:* Mera, 1140 m, KU 121418 (tadpoles), 121419 (young); Puyo, 960 m, FMNH 172632; Río Alpayacu, 1 km E Mera, 1100 m, KU 121040. *Tungurahua:* 18.5 km E Baños, 1600 m, KU 141596 (young). PERÚ: *Junín:* Perene, AMNH 17260, 17277. *Puno:* La Unión, Río Huacamayo, Carabaya, 610 m, BMNH 1907.5.7.36. *San Martín:* Roque, NHMG 471.

Hyla platydactyla.—VENEZUELA: *Mérida:* Camino de La Culata, UPR-M 2763, 2765; Carretera La Azulita, PUR-M 2762; Escorial, 2500+ m, FMNH 3567-8, NHMW 6397 (4), 6398, UMMZ 46465, 59016, 105439, UPR-M 3158-62; La Culata, 2700 m, AMNH 10636-40, BMNH 1905.5.31.83-87, NHMW 6396 (3), UPR-M 3150-2, 3932-5, 4330; La Mucuy, 2500 m, UPR-M 4321-2; Mérida, 1620 m, BMNH 1909.4.30.81-83, 1912.11.1.83, 1947.2.13.14, MCZ 2523; 15-20 km NW Mérida, road to La Azulita, 1700 m, KU 133430-3, 139521 (tadpoles); 32 km NW Mérida, road to La Azulita, 2010 m, KU 139522 (tadpoles); Río Albarregas, 2400 m, UPR-M 2767-70; Río Chama, Mérida, 1620 m, UMMZ 95310 (tadpoles). *Tachira:* 15 km from Delicias, to Rubio, 1800 m, UPR-M 2249-50, 2766; Guacharaquita, near La Grita, UPR-M 4858.

LITERATURE CITED

Boulenger, G. A.

1905. Descriptions of new tailless batrachians in the collection of the British Museum. Ann. Mag. Nat. Hist., (7)16:180-184.

Cochran, D. M. and C. J. Goin

1970. Frogs of Colombia. Bull. U.S. Natl. Mus., 288:xii+655 pp.

Dixon, W. J. (Ed.)

1971. BMD Biomedical computer programs. Univ. California Publ. Auto. Comp., 2, ed. 2:x+600 pp.

Duellman, W. E.

1963. A review of the Middle American tree frogs of the genus Ptychohyla. Univ. Kansas Publ. Mus. Nat. Hist., 15:297-349.

1966. Taxonomic notes on some Mexican and Central American hylid frogs. *Ibid.*, 17:263-279.

1970. The hylid frogs of Middle America. Monog. Mus. Nat. Hist. Univ. Kansas 1:xi+753 pp.

1972. South American frogs of the *Hyla rostrata* group (Amphibia, Anura, Hylidae). Zool. Meded. Leiden, 47:177-192.

Duellman, W. E. and M. J. Fouquette, Jr.

1968. Middle American hylid frogs of the Hyla microcephala group. Univ. Kansas Publ. Mus. Nat. Hist., 17:517-577.

Duellman, W. E. and L. Trueb

1966. Neotropical hylid frogs, genus Smilisca. *Ibid.*, 17:281-375.

Dunn, E. R.

1931. New frogs from Panama and Costa Rica. Occas. Papers Boston Soc. Nat. Hist., 5:385-401.

1944. Herpetology of the Bogotá area. Rev. Acad. Colombiana Cien. Exact. Físicas y Nat., 6:68-81.

Kluge, A. G. and J. S. Farris

1969. Quantitative phyletics and the evolution of Anurans. Syst. Zool., 18:1-32.

Melin, D.

1941. Contribution to the knowledge of Amphibia of South America. Göteborgs Kungl. Vetensk.-och Vitterh.-Sam. Handl., Ser. B, 1(4):1-71.

Peters, W.

1882a. Eine neue Gattung von Batrachiern, *Hylonomus,* aus Bogotá. Sitzber. Gesell. Naturfors. Fr. Berlin, 1882(7):107-109.

1882b. Der Namen der Batrachiergattung *Hylonomus* in *Hyloscirtus* zu ändern und legte zwei neue Arten von Schlangen, *Microsoma notatum* und *Liophis Ygraecum. Ibid.,* 1882(8):127-129.

Rivero, J. A.

1961. Salientia of Venezuela. Bull. Mus. Comp. Zool., 126:1-207.

Rohlf, F. J. and J. Kishpaugh

1966. NT-SYS, a system of multivariate statistical programs for use in numerical taxonomy. Dept. Entomology, Univ. Kansas.

Taylor, Edward H.

1952. A review of the frogs and toads of Costa Rica. Univ. Kansas Sci. Bull., 35(1):577-942.

Vuillermier, B. S.

1971. Pleistocene changes in the fauna and flora of South America. Science, 173(3999):771-780.

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MORPHOMETRIC VARIATION AND LIFE HISTORY OF THE CYPRINID FISH *NOTROPIS STRAMINEUS* (COPE)

By

JÜLIDE TANYOLAÇ[1]

The sand shiner, *Notropis stramineus* (Cope) is a common inhabitant of shallow, sandy streams from Quebec and New York westward to Saskatchewan and Montana, and southward to México. Sand shiners occupy streams of diverse sizes, from springs discharging only a few cubic feet per second to the largest rivers in the Mississippi system. As its vernacular name implies, *N. stramineus* is usually associated with sandy stream bottoms; the species has rarely been found in upland areas (Ouachita, Ozark, Cumberland, and Appalachian regions) within its otherwise extensive range.

The purposes of this paper are: 1) to indicate the extent and degree of geographic correlation of variation in several morphological features of *N. stramineus,* and 2) to describe some aspects of its life history, with primary reference to populations in the Kansas River at Lawrence, Kansas.

Problems relating to the nomenclature of the sand shiner have been resolved by Suttkus (1958) and Bailey and Allum (1962:64-68). Suttkus demonstrated that the name *Moniana (= Notropis) deliciosa* (Girard, 1856) is applicable not to the sand shiner but instead to the weed shiner, *Notropis texanus* (Girard, 1856). Suttkus concluded that the oldest name available for the sand shiner is

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[1] Department of Zoology, University of Ankara, Ankara, Turkey. This paper is based on research accomplished while the author was a Research Associate at the Museum of Natural History at the University of Kansas, supported by a Fellowship from the American Association of University Women and a grant from the University of Ankara.

Hybognathus stramineus Cope, 1864; he considered *Minnilus microstomus* Rafinesque, 1820, and *Alburnus lineolatus* Agassiz, 1863, to be *nomina dubia.* The following names were listed as chronological synonyms of *stramineus* by Suttkus (type localities in parentheses): *Hybopsis missuriensis* Cope (Missouri River at St. Joseph, Missouri); *H. scylla* Cope (Red Cloud Creek, tributary to Platte River); *Cliola chlora* Jordan (upper Missouri region); *Notropis phenacobius* Forbes (Peoria, Illinois); and *N. reticulatus* Eigenmann and Eigenmann (Qu'Appelle, Assiniboia [Assiniboine River in Saskatchewan, Canada]).

Bailey and Allum (1962:64-68) reported that sand shiners in South Dakota "fall into two sharply defined morphotypes" that they recognized as subspecies (*N. s. stramineus* and *N. s. missuriensis*), distinguished by differences in number of circumference scale-rows. Bailey and Allum allocated *H. scylla, C. chlora,* and *Hybopsis montana* Meek, 1884, to the synonymy of *N. s. missuriensis.* Metcalf (1966:124-131) supported the opinion of Bailey and Allum, on the basis of his counts of circumferential and predorsal scale-rows. Previously, Hubbs and Lagler (1958:37, 43) and several other authors had indicated the existence of a third subspecies, southwestern in occurrence. The southwestern populations are those with which the name *deliciosa* was improperly associated.

GEOGRAPHIC VARIATION

Methods

In my analysis of geographic variation in the sand shiner, nine characters were examined on 896 specimens from 61 localities, following procedures defined by Hubbs and Lagler (1958:19-26). Meristic characters used were number of lateral-line scales, predorsal-scale rows, and circumference scale-rows. Morphometric characters used were predorsal length, length of caudal peduncle, head length, head width, length of orbit, and postorbital length of head, all measured to the nearest 0.1 mm and expressed as thousandths of standard length.

Values obtained for each character were compared, among localities, by application of a program entitled Sum of Squares Simultaneous Test Procedures (SS-STP), adapted to an IBM 7090/94 computer. The analysis indicates which of the locality means, for each character, fail to differ from one another at the 95 percent confidence level. On the distribution maps that accompany the discussion of each character, the results have been coded as follows:

solid circles indicate localities where mean values are not significantly different from the lowest mean obtained at any locality; solid triangles indicate localities where means are not significantly different from the highest mean value obtained at any locality; and open circles designate the remaining localities (those having intermediate values significantly different from means of the extreme groups).

The 61 localities include three in the Great Lakes drainage, 58 in the Mississippi basin, one in the Guadalupe River in Texas, and one in the Rio Grande system. All are within the presumed native range of the species. In the Mississippi basin, seven series are from the Ohio River system; 13 are from upper Mississippi system (upstream from the mouth of the Missouri River, excepting one collection from the Meramec River immediately south of the Missouri River); 26 are from the Missouri River system; six are from the Arkansas River system; and two are from the upper Red River system.

Results

Circumference scale-rows (Fig. 1).—The SS-STP results indicate that the distinctive sets of sample means fall into eastern and western groups that correspond to the two subspecies (*stramineus* and *missuriensis,* respectively) recognized by Bailey and Allum (1962:64-68), Metcalf (1966:124-131), and others; their interpretations were based primarily on this character. In my samples, the range of non-significant low mean numbers of circumference scales is 22.2-24.6, the range of non-significant high mean numbers 27.7-30.0. These two sets include 72 percent of the localities. Intermediate numbers of scale-rows around the body were found at 17 localities, in the Platte River system, in the Missouri River and its smaller tributaries from the mouth of the Platte eastward to the Chariton River in northern Missouri, in the upper Neosho River (Arkansas River drainage), and in the Red River system in western Oklahoma.

Postorbital length of head (Fig. 2).—This character differentiates approximately the same samples that were separated by circumference scale-counts (Fig. 1). Low mean values (0.1101-0.1202, as a proportion of standard length) are mainly eastern, and high mean values (0.1316-0.1401) mainly western. The two sets include 57 percent of the 56 samples in which data are available for this character. Intermediate lengths of the postorbital part of the head are found mainly in the Platte and lower Missouri rivers, the upper Neosho River in Kansas, and the upper Red River. Intermediate values in the Rio Grande and in the Osage, Meramec, and Gasconade rivers of the Missouri system in Missouri are discordant with results

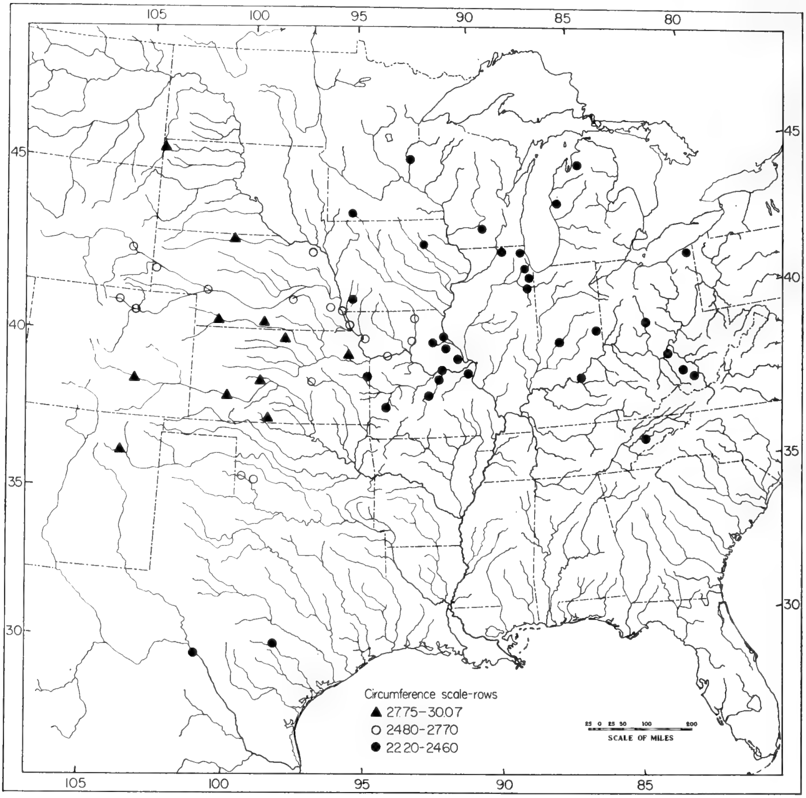

FIG. 1. Geographic trends in numbers of circumference scale-rows in *Notropis stramineus*. Triangles represent sample-means not significantly different from the highest mean value at any locality (.05 level); solid circles indicate means not significantly different from the lowest mean value of any locality; open circles represent locality means intermediate between those extreme sets.

based on circumference scales, in which these localities were a part of the eastern group.

Length of orbit (Fig. 3).—Geographic variation in the orbital diameter of sand shiners is great, but individual variation within local populations is small. Therefore, the SS-STP discriminated numerous (31) combinations of localities having means not significantly different—a greater number of small sets of localities than emerged for any other character. As a result, few localities are included in either the "low" or the "high" groups, whose ranges of values were 0.6210-0.6980 and 0.9088-1.0030, respectively. The mean orbital diameters at most localities lie between these extreme sets, in the group designated by open circles as "intermediate" in

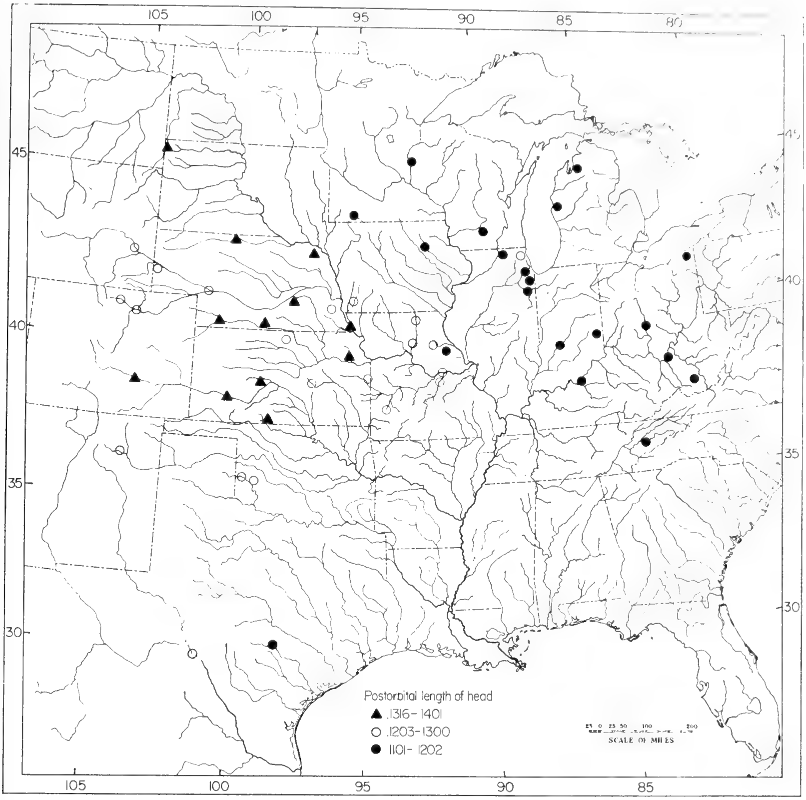

FIG. 2. Geographic trends in postorbital length of head in *Notropis stramineus.* Symbols as in figure 1.

figure 3. The orbit is smallest in the westernmost populations, and largest (relative to standard length) in populations near the center of the range of the species (eastern Missouri and Iowa). The large-eyed populations fall within the "eastern" set as defined by scale counts. In terms of absolute values, most "intermediates" located northeastward from Iowa and Missouri have relatively large eyes, as do specimens from the Rio Grande and Guadalupe in Texas. It is noteworthy that the results using orbital diameter and postorbital length of head are not entirely complementary; populations having the largest orbits do not have minimal postorbital lengths.

Predorsal scale-rows (Fig. 4).—The total extent of variation in number of predorsal scale-rows is small, relative to local (individual) variation in sand shiners. Therefore, the SS-STP did not yield discrete sets of localities having distinctively "low" and "high" mean values; the range of "low" means, not significantly different from

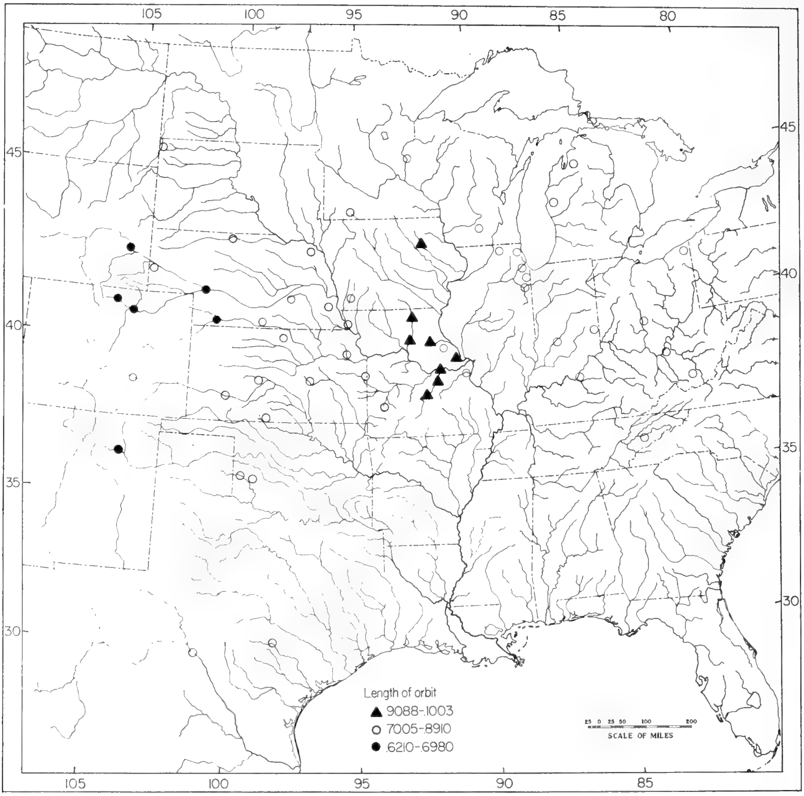

FIG. 3. Geographic trends in length of orbit in *Notropis stramineus*. Symbols as in figure 1.

one another, extended from 13.86 to 15.13 scales, and the range of "high" means from 14.93 to 16.53 scales. Therefore, in figure 4, the localities plotted as having "intermediate" values (open circles) are ones that are a part of both sets, rather than ones excluded from both sets. These five localities are scattered across the range of the species, at about the same latitude. Values at other localities are geographically correlated, forming a pattern generally like that shown by the characters previously discussed. Two departures are notable: 1) greater westward extent of the "eastern" group into areas that yielded intermediate values for other characters; and 2) exceptionally high numbers of predorsal scales at the northernmost localities, causing their populations to be associated with the western rather than the eastern group in this character. The mean numbers of predorsal scale-rows at the three northeastern localities in question (Ohio, Michigan, and Minnesota) are 15.14, 15.80, and 15.20, respectively.

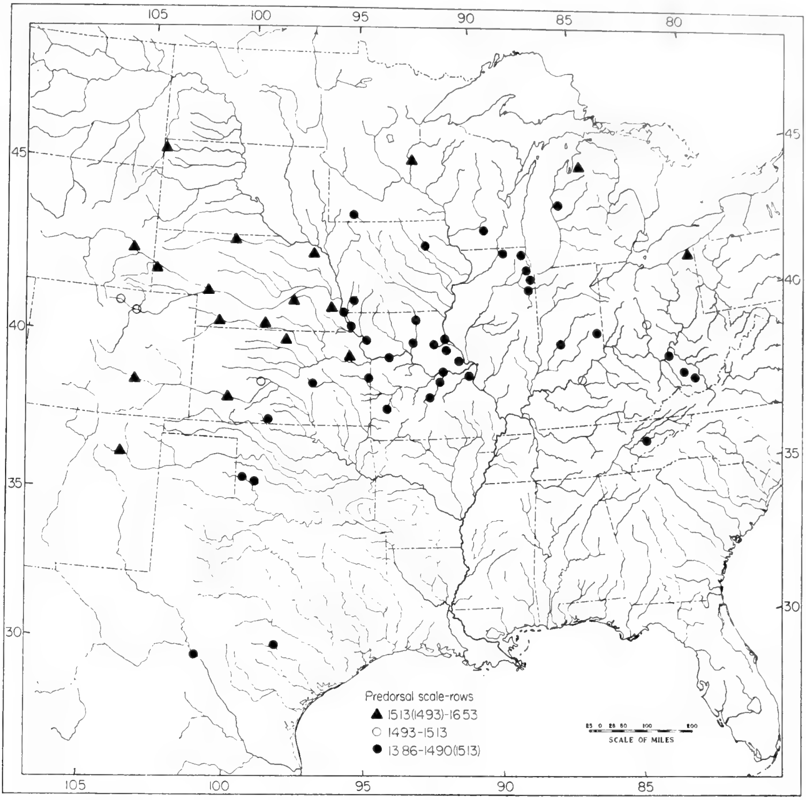

FIG. 4. Geographic trends in number of predorsal scale-rows in *Notropis stramineus*. Symbols as in figure 1.

Predorsal length (Fig. 5).—Western populations of sand shiners have the shortest predorsal lengths, in relation to their standard lengths. However, the geographic pattern shown by this character does not conform well to an east-west clinal trend, because "high" and "low" values are found at adjacent localities in several parts of the range: upper Red River, Kansas River, lower Missouri River, upper Illinois River, and upper Ohio River.

Predorsal length and the number of predorsal scale-rows are not positively correlated. Rather, the opposite tendency exists; those populations having the shortest bodies anterior to the dorsal fin usually have the largest number of scales along the nape. Most such populations are western or northern. As in predorsal scale-counts, local variation is so great compared to inter-locality variation that no wholly distinctive sets of localities emerged from the SS-STP analysis. The "low" (0.5077-0.5201) and "high" (0.5201-0.5480)

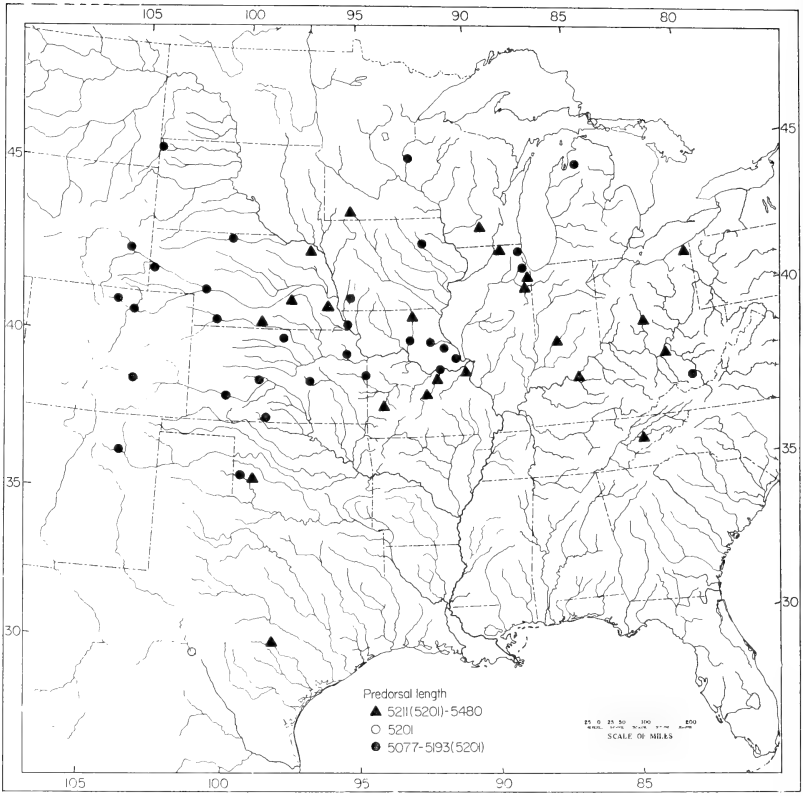

FIG. 5. Geographic trends in predorsal length in *Notropis stramineus.* Symbols as in figure 1.

sets overlapped by one locality. That locality, in the Rio Grande drainage, is therefore the only one shown as "intermediate" by an open circle in figure 5.

Head length (Fig. 6).—Although variation in head length has only limited relation to geographic region, most northern and eastern populations have shorter heads than do southwestern populations. The analysis separated localities into numerous (27) sets for this character; hence, the "high" and "low" sets contain only 23 localities, 41 percent of the total from which data were taken. The ranges of mean values within these two sets are well separated (low=0.2494-0.2596; high=0.2711-0.2857). All localities belonging to the low group lie along or east of the Mississippi River or in the Platte River system, with the exception of one locality in the Kansas River basin. All localities having high mean values lie west of the

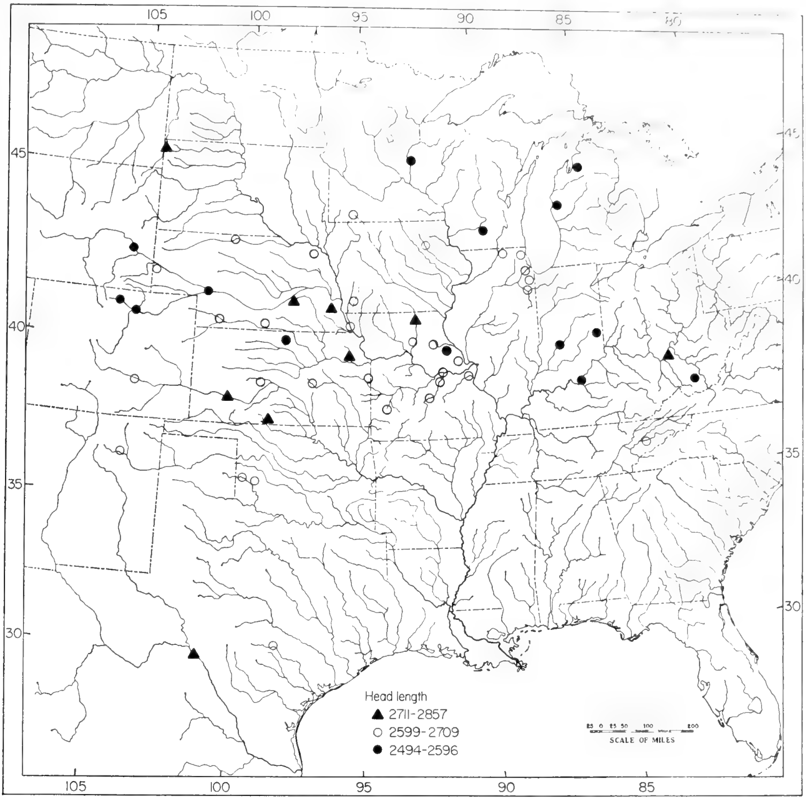

FIG. 6. Geographic variation in head length in *Notropis stramineus*. Symbols as in figure 1.

Mississippi, except for one locality in the upper Ohio basin. Intermediate head-lengths are found at widely scattered localities.

Head width (Fig. 7).—In general, northeastern sand shiners have relatively narrow heads, whereas southwestern sand shiners have broad heads. The distribution of high and low mean values for this character resembles that for head length, demonstrating that the total size of the head increases westward, and especially southwestward. At the 18 localities included in the "low" group in figure 7, mean head-widths varied from 0.1293 to 0.1439; mean head-widths at the 13 localities in the "high" group varied from 0.1556 to 0.1698.

Length of caudal peduncle (Fig. 8).—Geographic pattern is scarcely evident in the distribution of distinctively high and low mean values for this character. The longest caudal peduncles tend to occur at high latitudes and high elevations, hence at peripheral localities. Caudal peduncles are usually shortest in the central, and

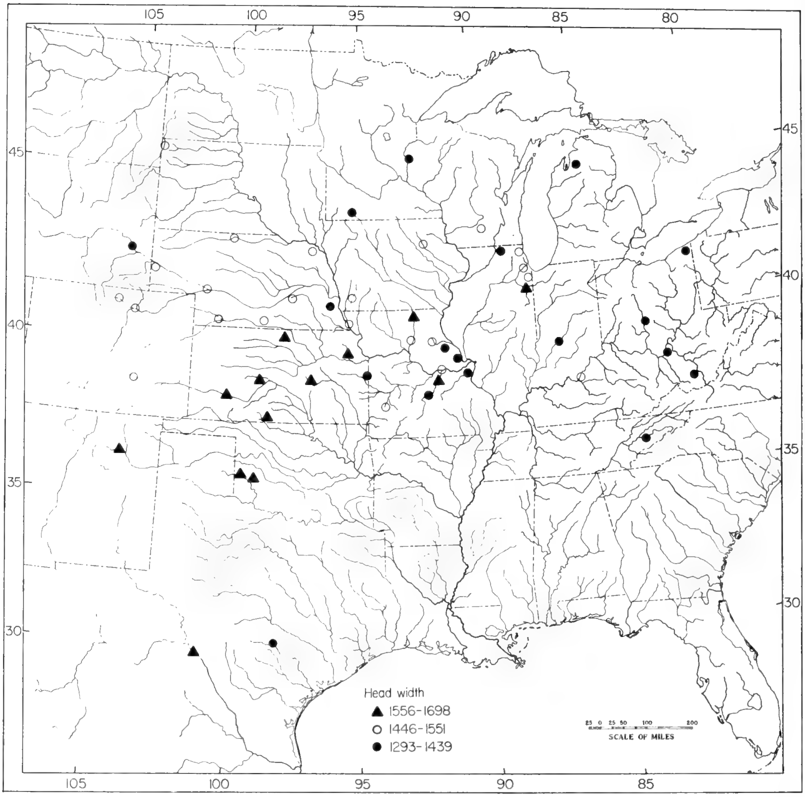

FIG. 7. Geographic variation in head width in *Notropis stramineus.* Symbols as in figure 1.

especially the west-central, part of the range of the sand shiner. Individual (local) variation accounts for a large part of the total variation in length of the caudal peduncle. The group of low means (0.2152-0.2348) includes 27 localities, and the group of high means (0.2360-0.2512) 21 localities; only seven localities (13%) fall into the intermediate group.

Lateral-line scales (Fig. 9).—Low numbers of lateral-line scales characterize sand shiners in the central and southern parts of the range of the species. Lateral scale-rows are more numerous at peripheral localities in the east, north, and west. Therefore, lateral-line scales vary independently of circumference scales and predorsal scales, and tend to be most numerous at high latitudes or high elevations. The group of low mean values (32.61-34.00) includes 25 localities, and the group of high values (34.53-36.25) includes 17 localities, leaving 18 localities (30%) in the intermediate group.

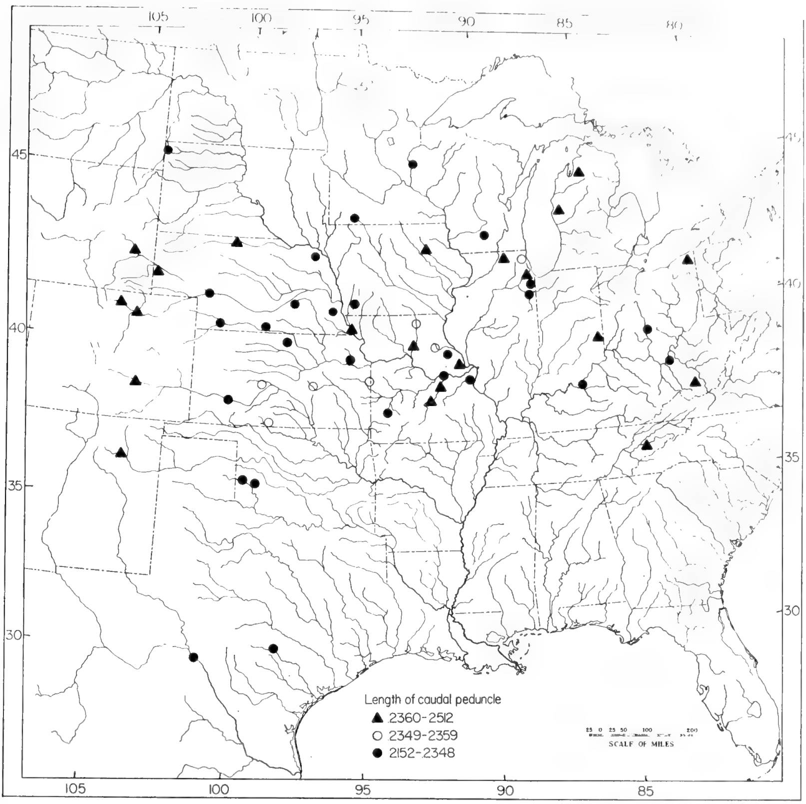

FIG. 8. Geographic variation in length of caudal peduncle in *Notropis stramineus*. Symbols as in figure 1.

Character Summary and Taxonomic Conclusions

The SS-STP analysis disclosed similar geographic trends in three of the nine characters. Circumference scale-rows, predorsal scale-rows, and postorbital length of head have extreme values in essentially the same sets of eastern and western populations. The populations are segregated somewhat differently by the SS-STP results in the remaining six characters. Orbital size is smallest in the westernmost populations, but largest near the center of the range of the species; populations having the largest orbits are among the eastern set distinguished by the three characters mentioned above. Predorsal length diminishes from east to west, but local variation in this character is great and members of the two extreme sets are intermixed broadly through the central part of the range. Head width sorts, principally, southwestern populations from those elsewhere. Head length, caudal peduncle length, and the number of lateral line scales

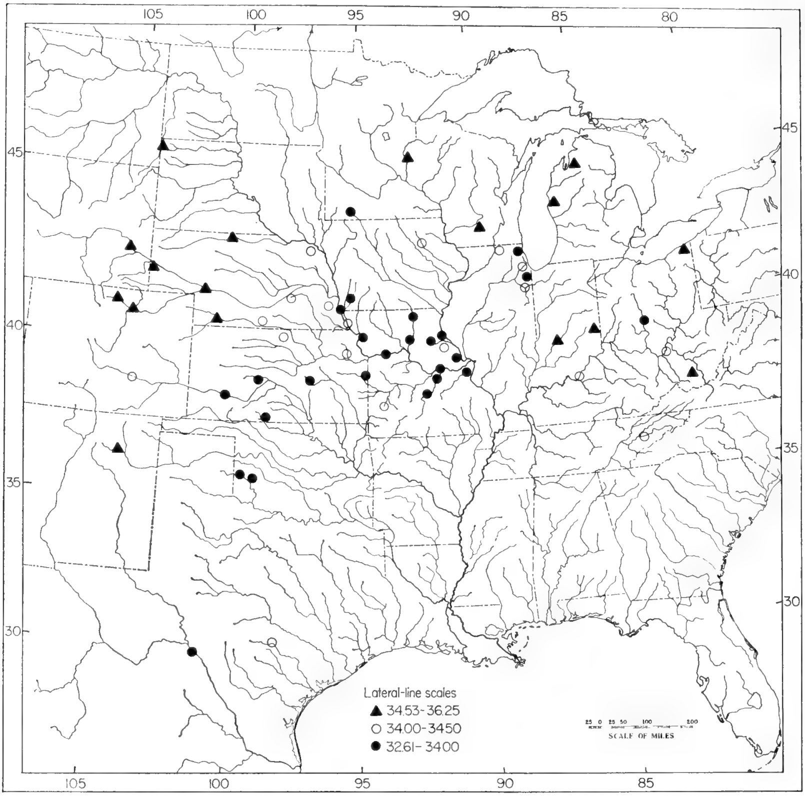

FIG. 9. Geographic variation in lateral-line scales in *Notropis stramineus.* Symbols as in figure 1.

vary without clear geographic pattern, although the highest values for the last two characters tend to occur at peripheral localities.

In view of nonconformities in the variational patterns of these characters, recognition of subspecies may seem to be unwarranted in *Notropis stramineus.* However, I believe the results are sufficiently in accord with one another, in five traits having well-defined geographic patterns, to justify continued recognition of two taxa. Their distinguishing features, synonymies, and ranges are stated below.

Notropis stramineus stramineus (Cope)

Diagnosis.—Circumference scales 22-25; postorbital length of head 11-12 percent of standard length; orbital diameter more than 8 percent of standard length; head width less than 15 percent of standard length; predorsal scale-rows usually 13-15.

Range.—Southern Saskatchewan to Quebec (Slastenenko, 1958), southward through Great Lakes drainage and Ohio River basin; upper Mississippi basin westward to eastern Iowa, southern Missouri and southeastern Kansas (including Osage River system); Red River in eastern Oklahoma and Texas; southwestward in Gulf-coastal streams to Rio Grande.

Remarks.—On geographic grounds, the names *N. phenacobius* Forbes, 1885, and *N. reticulatus* Eigenmann and Eigenmann, 1893, apply to this subspecies.

Notropis stramineus missuriensis (Cope)

Diagnosis.—Circumference scales usually 27-30; postorbital length of head 13-14 percent of standard length; orbital diameter less than 8 percent of standard length; head width more than 14 percent of standard length; predorsal scale rows 15-17.

Range.—Missouri and Arkansas River systems; intergrades with *N. s. stramineus* in eastern South Dakota and Nebraska (including Platte River system), small tributaries of Missouri River in northeastern Kansas and northwestern Missouri, Neosho River in Kansas and upper Red River system in western Oklahoma.

Remarks.—On geographic grounds, the names *Hybopsis scylla* Cope, 1870, *Cliola chlora* Jordan, 1878, and (according to Bailey and Allum, 1962:68) *Hybopsis montanus* Meek, 1884, apply to the subspecies *missuriensis.*

LIFE HISTORY

A study of some aspects of the life history of the sand shiner in the Kansas River at Lawrence was based on 3632 specimens, collected biweekly or monthly in 1967 (March 24, May 2, June 8 and 24, July 6, 13, and 24, August 9, September 1, and October 18). The study area extended along the north shore of the Kansas River for a distance of several hundred yards downstream from a low-flow dam in Lawrence.

The Kansas River is a turbid stream having variable flow. At the gauging station nearest to my study area, discharge has varied from 185 cubic feet per second (cfs) to 483,000 cfs within the 30-year period of record. In 1967, minimum and maximum rates of discharge were 220 and 88,900 cfs. Flow on dates when sand shiners were collected increased from 468 cfs (March 24) to 41,700 cfs (June 24), and diminished to approximately 2,000 cfs in September.

Sand shiners were collected by means of seines 6 to 15 feet long, having 1/8 to 3/16-inch woven nylon mesh. The fish were preserved in 10 percent formalin for three or more days, washed in water, and transferred to 70 percent ethyl alcohol, where they remained for at least one week before data were taken from them.

The accounts of age- and size-composition and of reproduction that follow are based mainly on the collections from the Kansas River at Lawrence; observations on other populations are appended to these accounts. The latter observations are based on series of specimens deposited in the University of Kansas Museum of Natural History. The series selected are representative of the western subspecies, commonly recorded as *N. s. missuriensis* (from South Dakota, Wyoming, Colorado, Nebraska, Kansas, and New Mexico), and eastern subspecies, commonly recorded as *N. s. stramineus* (from Kentucky, Wisconsin, Minnesota, Illinois, Iowa, Missouri, Kansas, Oklahoma [Red River], Texas, and Mexico). Series of "intergrades" from eastern Kansas, southeastern Nebraska, southwestern Iowa, and Missouri were examined also. These collections were obtained in spring or summer in various years.

Age- and Size-composition

Most samples of sand shiners from the Kansas River consisted of three age-groups, based on evidence obtained from opercles, scales, and length-frequency distributions. For 233 sand shiners of selected sizes, opercles and scales were removed, cleaned, and examined under magnification using transmitted light. Annuli were discernible on both structures, but usually were most obvious on the opercle, where they appeared as fine opaque lines parallel to the posterior margin of the bone. The 1967-annulus had not formed on fish taken March 24, and only a few yearlings caught on May 2 had completed that annulus. All age-I fish had an annulus by June 8, but the 1967 year-mark was not apparent on all age-II and age-III specimens until mid-July. Thus, prior to July 24, ages of individual fish were inferred from the positions of annuli (extent of growth beyond the outermost annulus), as well as the number of annuli observed on their opercles and scales.

The age- and size-distributions of the 10 samples of sand shiners obtained from March 24 to October 18 are shown in figure 10. The number of fish in the samples varies greatly; on figure 10, differences in the numerical scale (vertical scale) on various dates should be noted. Age-III fish were present, but in diminishing numbers, from March 24 through July 6; none was found thereafter. Age-II fish were numerous on March 24 and May 2, but diminished in abun-

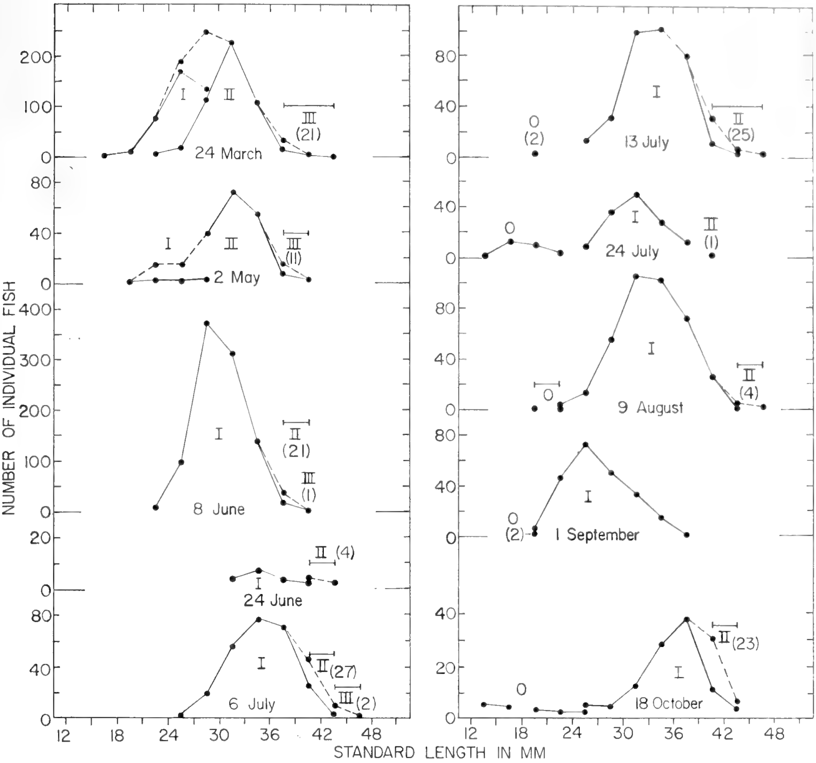

FIG. 10. Length-frequency distribution in samples of *Notropis stramineus* from the Kansas River at Lawrence, obtained on various dates in 1967. Roman numerals indicate the age-groups represented in the samples, arabic numerals the number of individuals assigned to each age-group.

dance later. Age-I fish dominated all samples from June through October.

Nearly all growth in length by age-groups I and II was accomplished before July 13. From that date onward, the size-range and average size of the fish in my samples remained almost constant, except for the sample obtained September 1 (Fig. 10). That sample consisted of surprisingly small fish judged to be age-I by examination of opercles and scales. One possible reason for the disparate size-range in the September sample can be suggested. Deep, swift flow at the study-site made seining unusually difficult, and all specimens were caught from one small pool, only a few inches deep, that extended into a slight depression on a large sandbar. On other dates samples were taken from more extensive areas, and greater range of depths, in the mainstream as well as in pools along sandbars.

The size-ranges of different age-groups overlapped in all samples. The smallest age-III fish found was 38 mm in standard length (March 24), the largest 47 mm (July 6). The size-range in age-II was 21 mm (March 24) to 45 mm (October 18), and of age-I fish 15 mm (March 24) to 43 mm (October 18). Young-of-the-year first appeared in my collections on July 13, following disappearance of age-III fish from the samples. Special efforts to obtain young, using 1/8 inch-mesh netting as well as 3/16 inch-mesh seines, were made only on July 24 and October 18. Young as small as 12 mm in standard length following preservation were present on both of these dates.

Populations of *N. s. missuriensis* and *N. s. stramineus* from other localities in Kansas and Missouri consisted of age-III and younger fish. Three-year-old sand shiners occurred as late as August, but no four-year-old fish were found among specimens from these states. The largest specimen of *N. s. missuriensis* in collections from 30 localities is 64.2 mm in standard length, and was obtained in the Cache la Poudre River, Colorado, in September. The largest *N. s. stramineus* in collections from 52 localities is 61.5 mm long; it was obtained in Black Earth Creek, Wisconsin, in June.

No differences in age-composition, average size, or maximum size distinguish the two subspecies. In both, northern populations seem larger in average size (standard length) than southern populations.

Reproduction

Sex-ratio.—Male and female gonads are distinguishable by gross inspection in sand shiners more than 25 mm in standard length. For this and later analyses, the fish in each sample were grouped by 3-mm intervals of length; my discussion concerns specimens larger than 26 mm (groups 27-30 mm and longer). Sex was ascertained for 2101 sand shiners from the Kansas River, of which 1128 (53%) were males (Table 1). Males were more numerous than females in all samples except those on July 13 and 24—dates on which I think spawning was in progress. On some other dates, females outnumbered males in the smaller size-groups (Table 1), indicating that the average size attained by males slightly exceeded that of females. Nevertheless, the maximum size attained by females (46.0 mm on July 13) was as great as that of males (46.6 mm on August 9) in my samples from the Kansas River.

In *N. s. missuriensis* from 22 other localities, males were more numerous than females in 13 cases. Males outnumbered females in 17 of 26 collections of *N. s. stramineus* for which sexes were deter-

TABLE 1. Sex-ratio in samples of *Notropis stramineus missuriensis* obtained in the Kansas River at Lawrence from March 24 through October 18, 1967.

Standard Length (mm)	24 March		2 May		8 June		24 June		6 July		13 July		24 July		9 August		1 Sept.		18 Oct.		Total	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
27 - 30	–	–	–	–	–	–	–	–	–	–	9	18	9	20	13	13	37	13	2	1	70	65
30 - 33	87	100	24	24	133	117	3	1	23	32	42	56	18	22	50	53	21	12	6	5	407	432
33 - 36	63	36	28	25	87	44	4	2	41	36	51	45	13	14	49	50	11	4	10	18	357	274
36 - 39	10	10	10	3	27	10	1	3	34	30	27	37	6	6	36	25	1	–	18	20	170	144
39 - 42	6	–	3	1	4	1	3	1	28	19	19	11	1	–	21	5	–	–	20	10	105	48
42 - 45	1	–	–	–	–	–	1	1	6	2	3	2	–	–	3	1	–	–	3	2	17	8
45 - 48	–	–	–	–	–	–	–	–	–	1	1	1	–	–	1	–	–	–	–	–	2	2
	167	156	65	53	251	172	12	8	132	120	152	170	47	62	173	147	70	29	59	56	1128	973
TOTALS	323		118		423		20		252		322		109		320		99		115		2101	

mined. The largest individuals were males in 17 of 22 series of *missuriensis* and in 19 of 26 series of *stramineus.*

Reproductive period.—In males, readiness for spawning was inferred from the presence of nuptial tubercles on the head and pectoral fins. No males smaller than 28 mm in standard length bore tubercles in the Kansas River population. Most males larger than 32 mm were tuberculate in all samples from May 2 through September 1. Most males smaller than 32 mm were tuberculate only in samples taken from July 13 through September 1. No tuberculate males were found on March 24 or October 18.

In females, readiness for reproduction was inferred from the size (weight) of the ovaries, and the size and number of eggs therein. The weight of ovaries in individual fish, and the *average* diameter of the ten *largest* ova (or oocytes) in the same fish, are shown for various dates in figures 11 and 12. Ovaries and eggs were uniformly small in March and May, but they enlarged rapidly thereafter. I doubt that spawning occurred before June 24, when ovary-weights and egg-sizes in the largest fish still were maximal. Most fish still had not spawned by July 6, although some must have done so, judging from reduced weights of ovaries in five relatively large fish (Fig. 11). By July 13, most fish larger than 36 mm in standard length had spawned, as indicated by the smaller size of the ovaries and eggs in these large fish on that date, as compared with earlier dates (Fig. 12). In females smaller than 36 mm, enlargement of ovaries and eggs continued through July and August. I think many of these small fish spawned in late summer. Therefore, I conclude that the spawning season extended from early July until September, but that progressively smaller fish comprised the spawning population after July 6. Age-II fish contributed importantly to the spawning population through mid-July. After July 24, only one age-II female (a spent fish) occurred in my samples. Probably, the entire spawning population in the latter part of the season consisted of yearlings.

At localities other than the Kansas River at Lawrence, periods of sexual development and reproductive activity are as follows:

Males of *N. s. missuriensis* usually are tuberculate from April to September. All samples taken in May, June, and July from South Dakota, Wyoming, Nebraska, and Kansas had tuberculate specimens. Samples taken in August and early September from Wyoming, Colorado, Nebraska, Kansas, and New Mexico still contained some tuberculate specimens. The smallest tuberculate male of *N. s. missuriensis,* 26.1 mm in standard length, was found on June 12 in the Medicine River, a tributary of the Arkansas River in Kansas.

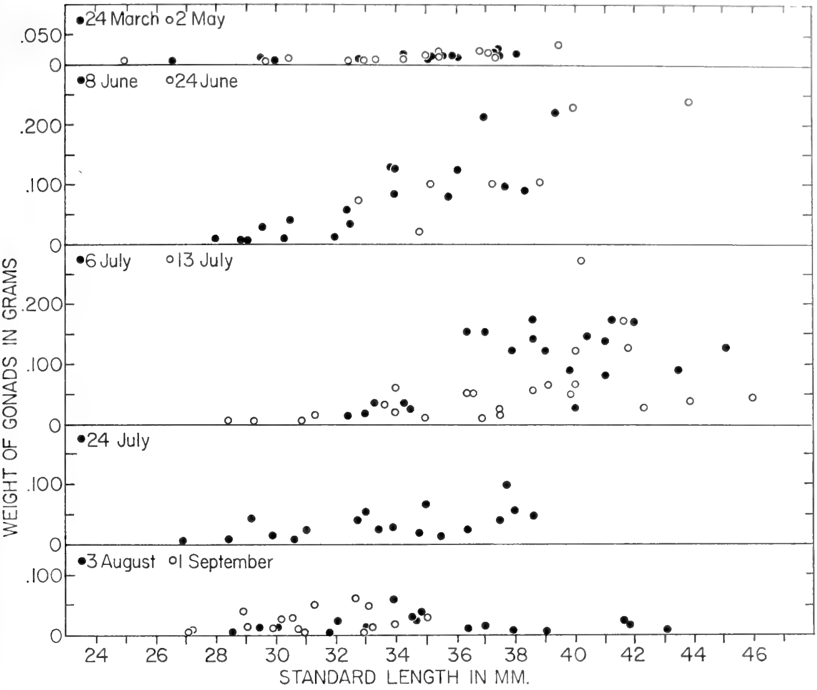

Fig. 11. Gonosomatic index (ovary weight/total fish weight) in female *Notropis stramineus* obtained from the Kansas River at Lawrence in 1967, as a function of date of capture and standard length of specimens.

Males of *N. s. stramineus* are tuberculate from April (Oklahoma and Texas) to July (Illinois and Wisconsin) and August (Iowa, Kansas, Missouri). Specimens taken on August 25 (Minnesota) and September 1 (Missouri) had no tubercles.

In populations regarded as intergrades (eastern Kansas, southeastern Nebraska, southwestern Iowa, and northern Missouri), tuberculate males were found from May through August.

Females of *N. s. missuriensis* usually had maximal ovary weights in June. However, a population from Gypsum Creek, McPherson Co., Kansas, had large gonads at the end of April; also, the smallest mature female, 24.5 mm in standard length, with large eggs was found in that collection. The largest individuals in a sample from Spring Creek, Smith Co., Kansas, seemingly had spawned by June 24; smaller fish probably had not spawned by that date. In the Arkansas system in southwestern Kansas, most sand shiners may complete spawning in June, but a population from Crooked Creek, Meade Co., had ovaries heavier than 0.200 g on July 4. No females

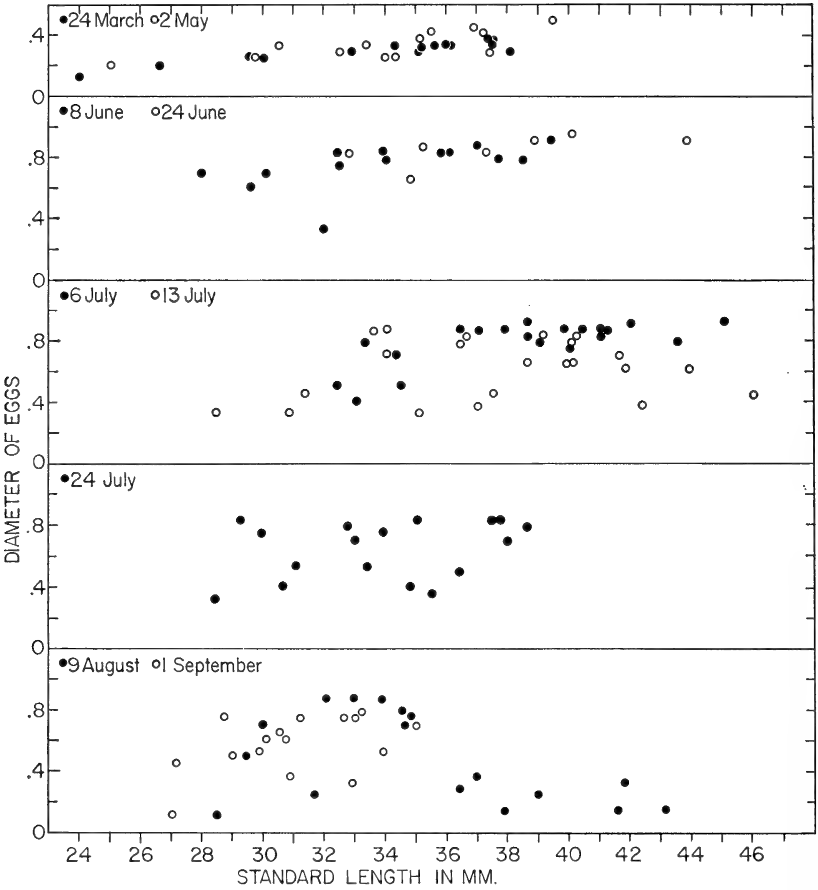

FIG. 12. Size of ova in female *Notropis stramineus* from the Kansas River at Lawrence, 1967. Vertical scale in mm. Each point plotted represents the average diameter of 10 of the largest eggs found in an individual fish.

had ova exceeding 0.79 mm diameter later than August 29 in Kansas. One specimen from Wyoming, 46.0 mm in standard length, 24 June, had not spawned and had the largest ovaries (0.735 g) of any fish examined in my study.

In a separate study of sand shiners in the Smoky Hill River in western Kansas, Summerfelt and Minckley (1969:447) reported that "Spawning probably occurred several times between June and August, but apparently most fish spawned in late July and August in both 1965 and 1966." Those authors noted a striking year-round correlation between water temperature and egg size; mid-summer temperatures were between 20°C and 25°C in 1965 and 27-33°C in 1966 when eggs were largest.

Females of *N. s. stramineus* in series that I examined had maximal ovary weights in May (Kansas and Missouri) to July (Michigan and Wisconsin). A population from Middle Creek, Miami Co., Kansas, probably had completed spawning by June 28, while one from Floyds Fork Creek, Jefferson Co., Kentucky, and one from the Loutre R., Montgomery Co., Missouri, had ovaries heavier than 0.200 g on June 2 and 6. None had ova exceeding 0.79 mm in diameter later than August 30 in Missouri. Ovary weight and maximum egg-size (0.95 mm) in *stramineus* are about the same as in *missuriensis.*

Females in series identified as intergrades had maximal ovary weights and egg-size in May, as in the case of *N. s. stramineus* from the same latitude. The smallest female, 29.6 mm, with large eggs was found in May (North Fork Cottonwood River, Marion Co., Kansas.)

Seemingly, the spawning period for *N. s. stramineus* varies latitudinally (May in South to July in North), but is mainly earlier and shorter in duration than the spawning season of *N. s. missuriensis* in Kansas and Missouri.

Fecundity.—Ovaries were categorized as 1) undeveloped—gray ovaries containing nucleated cells (oocytes) and small eggs (ova) with diameters not more than 0.33 mm; 2) developed—yellow ovaries having eggs from 0.33 mm to 0.95 mm in diameter; 3) spent—gray ovaries flaccid and containing few eggs.

Fecundity was determined from females that appeared to be well developed but not to have spawned. Ordinarily eggs were counted in one of the ovaries, because the two lobes appeared to be the same size; this number was doubled to determine the total egg complement. When the two lobes appeared to differ in size, the eggs were counted in both lobes. The "diameter of ova," as shown in table 2, represents the average diameter of the ten largest eggs in each fish; egg-diameters were determined by means of an ocular micrometer at constant magnification, and converted to mm by calibration to a stage micrometer. All contained eggs of varied sizes during the spawning season. Egg diameters of mature fish as given by Summerfelt and Minckley (1969:447) are smaller than those I report, because their measurements were taken from the total egg complement of each ovary.

Females of *N. s. missuriensis* from the Kansas River had maximal egg counts from June 8 to July 6, as shown in table 2. Seven females, from 32.8 mm to 43.9 mm in standard length, contained 550 to 1533 eggs.

TABLE 2. Fecundity and related data for 10 females of *Notropis stramineus missuriensis* from the Missouri River Basin in Kansas and seven *Notropis stramineus stramineus* from the same basin in Missouri

Date	Age	Standard Length (mm)	Weight of Fish (g)	Weight of Gonads (g)	Gonosomatic Index	Largest Ova (mm)	Number of Ova
			Notropis stramineus missuriensis				
24 June	I	32.8	0.713	0.072	0.10	0.83	550
24 June	I	35.2	0.899	0.100	0.11	0.87	574
6 July	I	37.0	0.949	0.154	0.16	0.87	817
6 July	I	38.6	1.279	0.175	0.13	0.91	1165
8 July	II	39.4	1.330	0.222	0.16	0.91	1401
24 June	II	40.1	1.643	0.227	0.13	0.95	1138
24 June	II	43.9	1.628	0.237	0.14	0.91	1533
9 June	II	41.5	---	0.285	--	0.87	2162
9 June	II	45.5	---	0.383	--	0.95	2390
9 June	III	49.9	---	0.405	--	0.95	2508
			Notropis stramineus stramineus				
6 June	I	35.4	---	0.073	--	0.83	626
6 June	I	38.3	---	0.118	--	0.83	1076
10 May	II	41.8	---	0.295	--	0.91	2314
10 May	II	42.4	---	0.228	--	0.95	1916
10 May	II	43.5	---	0.163	--	0.79	1394
10 May	II	44.9	---	0.232	--	0.87	2536
10 May	III	47.4	---	0.325	--	0.91	2660

Fecundity ranged from 2162 to 2508 eggs for three *N. s. missuriensis* females from North Fork Prairie Dog Creek, Decatur Co., Kansas; their lengths were 41.5 to 49.9 mm (Table 2).

N. s. stramineus females from the Loutre and the Pomme de Terre rivers, Missouri, 35.4 mm to 47.4 mm in standard length, had 626 to 2660 eggs (Table 2). The range in egg-complement observed in *N. stramineus* was 550-2660.

The results indicate considerable individual variation in fecundity but little or no difference of fecundity between the subspecies. Fecundity increased with standard length (or age) of the fish.

Discussion of Life-cycle

The population of sand shiners in the Kansas river, followed through the spring and summer of 1967, consisted of three age-groups. Many fish two or three years old were found in spring, but these became scarce in late summer, when the population was dominated by yearlings. After June 24 there was little or no increase in the modal length of individuals representing age-groups I and II. Modal lengths of each of these age-groups on June 24 exceeded the modal length of the next older age-group at the beginning of the growing season (24 March and 2 May). Either growth ceased by the end of June or the larger fish in both age-groups were depleted by mortality thereafter. Age-III fish disappeared from samples in early July. Attainment of maximal size of each age-group coincided with the onset of reproduction. Thus, the life cycle of this population of *N. s. missuriensis* can be summarized as shown in table 3.

I think that growth by older individuals occurs in spring, but terminates as these fish reproduce and disappear in July. Growth by small yearlings continues until they too spawn, later in summer. Many of them may fail to spawn, but survive to become spawners (the two-year-old component) in the following year.

This cycle has some attributes of an "annual" life-cycle, modified to provide a protracted reproductive period and consequent variation in size and age of individuals belonging to the same year-class. That variation tends to protract the period during which maturity is attained by different individuals, and thereby sustains a prolonged reproductive season. Such a cycle may have survival advantage in streams with erratic variation in flow. Abrupt changes in waterlevel are unlikely to destroy the entire year's production, regardless of when the changes occur. Yet the longevity of the sand shiner is short, enabling a rate of turnover in the population only slightly less rapid than that characterizing annual life cycles.

TABLE 3. Mean standard lengths (mm) of sand shiners from the Kansas River on various dates in 1967.

Date	Age-groups			
	I	II	III	
24 March	26	32	40	
2 May	26	32	40	Period of growth: increasing biomass age-groups I-III
8 June	29	38	41	
24 June	35	42	--	
6 July	35	42	45	
13 July	35	44	--	Period of reproduction: decreasing biomass age-groups I-III
24 July	32	41	--	
9 Aug.	33	45	--	
1 Sept.	26	--	--	
18 Oct.	38	42	--	

I am uncertain whether the hypothesis above can be extended to include *N. s. stramineus.* There is some evidence that the period of spawning by the eastern subspecies is brief at specific localities, compared to that of *N. s. missuriensis.* Maturation occurs earlier in *N. s. stramineus* than in *N. s. missuriensis* in Missouri and Kansas. Northern populations of *N. s. stramineus* mature and spawn later than do southern populations of that subspecies, but latitudinal variation in the spawning time of *N. s. missuriensis* seemed slight in the samples I examined.

SUMMARY

Although geographic agreement among characters is imperfect, the sand shiner, *Notropis stramineus,* seems logically divisible into eastern and western subspecies (*N. s. stramineus* and *N. s. missuriensis,* respectively). The range of the nominate subspecies extends from the Rio Grande and Guadalupe rivers northeastward across the lower Red River and the southernmost tributaries of the Missouri River to the Mississippi River, eastward and northward to the headwaters of the Ohio River basin and the Great Lakes basin. The western subspecies occurs in rivers of the Arkansas and Missouri systems that extend westward across the plains to the slopes of the Rocky Mountains. Intergradation occurs in the Platte and lower Missouri river systems, the upper Neosho River of the Arkansas system, and the upper Red River.

The two subspecies do not differ demonstrably in size attained (*ca.* 60 mm), age attained (3 years), total reproductive period (May or June through August), or egg-complement (range 550-2660). At single localities, however, the reproductive period probably is longer in *N. s. missuriensis* than in *N. s. stramineus*, and latitudinal variation in the time of spawning is more pronounced in *N. s. stramineus*. At similar latitude in Kansas and Missouri, females of *N. s. stramineus* mature earlier (May) than females of *N. s. missuriensis* (June-July).

A population of western sand shiners from the Kansas River at Lawrence contained both yearling and older individuals in March, 1967, but most two- and three-year-old fish disappeared before autumn. Growth in length by the larger fish was nearly confined to spring, terminating when they spawned early in July. Small yearlings matured later in summer. Males seemed slightly more numerous and slightly larger than females, and appeared to be sexually active for a longer term in spring and summer. Most individuals larger than 28 mm (standard length of alcoholic specimens) were mature.

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I thank Dr. Frank B. Cross of the Museum of Natural History, University of Kansas, for his suggestions and advice throughout the course of my work, for use of specimens and facilities in that museum, and especially for assistance in preparation of this manuscript. I am grateful to several graduate students in ichthyology at the museum for obtaining sand shiners from the Kansas River in 1967. Mr. T. H. Swearingen prepared final drawings of the graphs and maps. Computer time was made available by the Computation Center of the University of Kansas; Dr. A. C. Echternacht and Miss Linda Flatten aided me greatly in obtaining the SS-STP analysis of my data. My study was partly supported by a grant from the fellowship fund of the American Association of University Women, Educational Foundation.

SPECIMENS EXAMINED

Forty-eight of 61 collections examined in this study are deposited in the Museum of Natural History, University of Kansas (KU), 6 in the United States National Museum (USNM), 2 in the University of Michigan Museum of Zoology (UMMZ), and 5 were borrowed from the Field Museum of Natural History (FMNH), Chicago.

Some data from collections in USNM and UMMZ were obtained from an unpublished manuscript by Bernard C. Nelson. Specimens from USNM were measured and counted by Dr. Frank B. Cross of the University of Kansas in the United States National Museum.

Specimens examined are listed below, together with museum catalogue number, number of individuals examined (in parentheses), range of standard length (mm), locality of capture, and year of collection. Collections are arranged by State, alphabetically; series from México (Rio Grandé drainage) conclude the list.

COLORADO: KU 4751 (20), 36.5-48.5 mm, *Pueblo Co.:* Arkansas R. at Pueblo, 1959; KU 4797 (20), 48.3-56.4 mm, *Weld Co.:* South Fork Platte R., 7 mi E Greeley, 1959; KU 5566 (20), 47.2-64.2 mm, *Larimer Co.:* Cache la Poudre R. 2 mi S, 4 mi E Ft. Collins, 1960.

ILLINOIS: FMNH 43398 (15), 42.2-54.7 mm, *McHenry Co.:* Conf. Rush Cr. and Kishwaukee R., 2 mi W Marengo, 1941; FMNH 60754 (15), *Will Co.:* N branch Hickory Cr., 2 mi NE Frankfort, 1950; FMNH 90949 (15), 41.5-54.0 mm, *Will Co.:* Marley Cr., below trestle at 108th Rd. above Alpine, 1954; FMNH 61053 (15), 43.5-48.5 mm, *Lake Co.:* Des Plaines R. 1/2 mi upstream from Deerfield Rd., 1953; FMNH 61241 (15), 42.9-55.6 mm, *Kankakee Co.:* Kankakee R. 4 mi downstream from Kankakee, 1955.

INDIANA: UMMZ 106607 (15), 40.0-51.8 mm, *Wayne Co.:* E Fork Whitewater R.; USNM 36499 (15), 43.8-50.4 mm, White River, Gosport.

IOWA: KU 8629 (15), 38.7-46.9 mm, *Buchanan Co.:* Wapsipinicon R. at Park 4.5 mi N Jesup, 1964; KU 8669 (15), 40.4-55.9 mm, *Montgomery Co.,* Little Tarkio Cr., 1964.

KANSAS: KU 3943 (15), 40.6-49.0 mm, *Ford Co.:* Arkansas R., 1958; KU 3973 (15), 38.0-48.5 mm, *Rush Co.:* Walnut Cr., Sec. 27, T18S, R18W, 1958; KU 4058 (20), 36.9-49.9 mm, *Smith Co.:* Spring Cr., Sec. 10, T4S, R13W, 1958; KU 4700 (20), 41.2-50.0 mm, *Miami Co.:* Little Wea Cr., Sec. 10, T17S, R24E (Kay Ranch), 1959; KU 7316 (20), 35.9-51.1 mm, *Jefferson Co.:* Honey Cr., Sec. 28, T9S, R19E, 1963; KU 8140 (15), 39.5-46.3 mm, *Marion Co.:* Cottonwood R., 1964; KU 8586 (15), 37.5-44.3 mm, *Comanche Co.:* Salt Fork Arkansas R., 1964.

KENTUCKY: KU 4083 (15), 41.5-49.5 mm, *Jefferson Co.:* Floyds Fork Cr. 1 1/2 mi NE Wood, 1858.

MICHIGAN: UMMZ 110283 (15), 41.0-49.2 mm, *Mason Co.:* Bass Lake outlet, 1932; USNM 193163 (10), 39.9-47.5 mm, *Antrim-Kalkoska Co's.:* Torch Lake, 1952.

MINNESOTA: KU 3422 (5), 31.2-43.6 mm, *Jackson Co.:* Des Moines R., 1954.

MISSOURI: KU 5162 (15), 37.4-48.4 mm, *Osage Co.:* Gasconade R. on Mo. 89, Sec. 16, T42N, R8W, 1960; KU 7815 (20), 39.5-48.4 mm, *Hickory Co.:* Pomme de Terre R. below dam at Pomme de Terre Reservoir, 1963; KU 7962 (10), 36.1-38.8 mm, *Lincoln Co.:* Cuivre R. 2.5 mi N Troy, 1962; KU 9134 (10), 40.8-45.3 mm, *Marion Co.:* South R. 3 mi S Palmyra, 1964; KU 9190 (10), 35.0-43.8 mm, *Marion Co.:* South Fabius R. 7 1/4 mi NW Palmyra, 1964; KU 9625 (7), 34.4-43.1 mm, *Gasconade Co.:* Missouri R. at Gasconade, 1963; KU 9764 (15), *Atchison Co.:* Missouri R. at mouth Nishnabotna R., 1963; KU 9774 (15), 26.9-34.9 mm, *Buchanan Co.:* Missouri R. at St. Joseph, 1963; KU 9788 (15), 27.6-34.8 mm, *Lafayette Co.:* Missouri R. at Lexington, 1963; KU 10054 (10), *Marion Co.:* Mississippi R. near West Quincy, 1963; KU 10601 (15), 38.5-46.1 mm, *Franklin Co.:* Meramec R., 1963; KU 10638 (9) 41.3-50.6 mm, *Phelps Co.:* Dry Fork Cr., 7.5 mi SE Rolla, 1963; KU 10994 (10), 39.0-45.0 mm, *Adair Co.:* stream below lake 5 mi W Kirksville, 1963; KU 11058 (15), 37.4-45.9 mm, *Chariton Co.:* Mussel Fork Chariton R. 6 mi N Keytesville, 1963; KU 11074 (15), 39.9-53.9 mm, *Atchison Co.:* Tarkio Cr. 4 mi S Tarkio, 1963.

NEBRASKA: KU 4829 (20), 46.0-60.2 mm, *Banner Co.:* Pumpkin Cr. on

Nebr. 29, 1959; KU 4847 (20), 48.9-55.4 mm, *Keith Co.:* North Platte R. at Keystone, 1959; KU 7043 (20), 41.0-54.0 mm, *Franklin Co.:* Thompson Cr., Sec. 28, T2N, R13W, 1961; KU 7100 (20), 42.0-52.4 mm, *Cherry Co.:* North Minnechaduza Cr. 4 mi E Valentine, 1961; KU 7130 (15), 44.3-50.3 mm, *Dundy Co.:* South Republican R 1/2 mi N Kan./Nebr. border on Nebr. 61, 1961; KU 7148 (20), 40.8-48.5 mm, *Otea Co.:* trib. North Fk. Little Nemaha R. 4.8 mi S Jct. Nebr. 50 and US 34, 1961; KU 7157 (20), 38.4-56.8 mm, *Dixon/Cedar Co's.:* 1/2 mi W Concord, 1961; KU 8228 (20), 35.5-47.1 mm, *Adams Co.:* Little Blue R. 3.6 mi S Roseland, 1961.

NEW MEXICO: KU 4231 (17), 42.0-48.4 mm, *Mora Co.:* Mora R. 1 mi SE Valmora, 1957.

OHIO: KU 2790 (7), 31.8-46.8 mm, *Ashtabula Co.:* Grand R. at Mechanicsville, 1944-1945; KU 11378 (5), 36.7-43.6 mm, *Pickaway Co.:* Big Daddy Dr., 1966.

OKLAHOMA: KU 8054 (20), 37.4-49.1 mm, *Beckham Co.:* Timber Cr. 3.2 mi E Sayre, 1964; KU 8098 (15), 41.0-46.2 mm, *Beckham Co.:* N Fk. Red River at Sayre, 1964.

SOUTH DAKOTA: KU 10175 (20), 39.5-46.5 mm, *Harding Co.:* Little Missouri R. 4 mi S, 7 mi W Ladner, 1961.

TENNESSEE: USNM 190885 (15), 39.3-45.3 mm, *Sevier Co.:* Waldens Cr., T59-19 on Sevierville-Wear Valley Road, 2 1/2 mi S of US 441, 1959.

TEXAS: KU 5996 (8), 32.5-40.9 mm, *Hays Co.:* Blanco R. at Wimberley on T-12, 1961.

WEST VIRGINIA: USNM uncatalogued (8), 38.2-44.7 mm, Price Hill, Pond Fork, Rd. 23-55, 1955; USNM uncatalogued (10), 39.8-49.5 mm, Trace Fk. Mud R. 200 yds above mouth (Coal R. System), 1956; USNM uncatalogued (7), Low Gap, Swinging Bridge and RR trestle section, Rd. 19-56, 1956.

WISCONSIN: KU 4923 (10), 43.5-52.6 mm, *Polk Co.:* St. Croix R., 1959; KU 7276 (8), 50.0-61.5 mm, *Dane Co.:* Black Earth Cr. 1 mi SE Mazomanie, 1962.

MÉXICO

COAHUILA: KU 2982 (3), 40.2-44.8 mm, unnamed river 1 mi NW Elmoral, 1952; KU 3006 (3), 28.9-38.5 mm, 2 mi W Jiménez, 1952; KU 3020 (4) and KU 3034 (8), 36.0-41.7 mm, 2 mi W Jiménez, Río San Diego, 1952.

LITERATURE CITED

BAILEY, R. M., AND ALLUM, M. O.
1962. Fishes of South Dakota. Univ. Michigan Mus. Zool., Misc. Publ. 119:65-68. June 5.

HUBBS, C. L., AND LAGLER, K. F.
1958. Fishes of the Great Lakes Region (revised edition). Cranbrook Inst. Sci., Bull. 26. xiii + 213 pp., 44 pls.

METCALF, A. L.
1966. Fishes of the Kansas River System in relation to zoogeography of the Great Plains. Univ. Kansas Publ., Mus. Nat. Hist., 17:124-132. March 24.

SLASTENENKO, E. P.
1958. The distribution of freshwater fishes in the provinces and main water basins of Canada. Bull. Shevchenko Sci. Soc., 1(6):1-11. February.

SUMMERFELT, R. C. AND MINCKLEY, C. O.
1969. Aspects of the life history of the sand shiner, *Notropis stramineus* (Cope), in the Smoky Hill River, Kansas. Trans. Amer. Fish Soc., 98(3):444-453.

SUTTKUS, R. D.
1958. Status of the nominal cyprinid species *Moniana deliciosa* Girard and *Cyprinella texana* Girard. Copeia, 4:307-318. December 22.

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LIFE HISTORY AND ECOLOGY OF THE HYLID FROG *OSTEOCEPHALUS TAURINUS*, WITH OBSERVATIONS ON LARVAL BEHAVIOR

By

WILLIAM E. DUELLMAN[1] AND JEAN LESCURE[2]

The large hylid frog *Osteocephalus taurinus* Steindachner is widely distributed in the Amazon Basin and the Guianas in South America. Despite the abundance of specimens of this species and its four congeners (*O. buckleyi, leprieurii, pearsoni,* and *verrucigerus*) in museum collections, little information is available concerning the life history and behavior of *Osteocephalus.* Bokermann (1964) remarked on the calling behavior and deposition site of *O. taurinus.* Trueb and Duellman (1970) presented data on the mating call and life history of *O. verrucigerus* (Werner) and provided the only description of a tadpole of the genus. Field observations on four species of *Osteocephalus* in Amazonian Ecuador were summarized by Trueb and Duellman (1971).

Independently, data were gathered on tadpoles of *Osteocephalus taurinus* by Duellman and his associates in Brasil and Ecuador, and by Lescure in French Guiana. As a result, the larval development of the species is described, together with some aspects of larval behavior observed experimentally and in the field. In addition, the mating call of *O. taurinus* is described for the first time. Tadpoles have been deposited in the collections of Museum National d'Histoire Naturelle (MNHN), Université de Paris (UP), and the University of Kansas Museum of Natural History (KU).

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[1] Curator, Division of Herpetology, Museum of Natural History, University of Kansas.

[2] Reptiles et Poissons, Museum National d'Histoire Naturelle, 57 Rue Cuvier, Paris, and Laboratoire Arago, 66650 Banyuls-sur-Mer, France.

LARVAL DEVELOPMENT

The only record of egg deposition by *Osteocephalus taurinus* was by Bokermann (1964), who observed that this species deposits its eggs in a film on the surface of flooded depressions in the forest. Larvae were transformed in the laboratory by Lescure. The post-metamorphic frogs clearly could be associated with adult *O. taurinus,* thus substantiating the identification of these and other larvae.

Description.—A typical tadpole in development stage 37 (Gosner, 1960) from Kérenroch, French Guiana, has a body length of 18.3 mm and a total length of 48.5 mm. Body two-thirds as deep as wide, deepest posteriorly; in dorsal view elongately elliptical with round snout; in profile snout narrow, round. Eyes small, widely separated, directed laterally; nostrils directed anterolaterally about midway between eyes and tip of snout. Spiracle sinistral; spiracular opening directed posterodorsally just below midline at about midlength of body. Cloacal tube short, dextral. Caudal musculature moderately slender, curved upward terminally, extending nearly to tip of narrowly rounded tail; caudal fins about equal in depth, deepest at about two-fifths length of tail; depth of caudal musculature at midlength of tail slightly less than depth of either fin; dorsal fin not extending onto body (Fig. 1).

Mouth moderately small, directed ventrally; median third of upper lip bare; rest of mouth bordered by two rows of small labial papillae; lips indented posterolaterally. Beaks slender, bearing small, blunt serrations; upper beak forming a broad arch with long, slender lateral processes; lower beak broadly V-shaped. Three upper and five lower rows of teeth; first row composed of small teeth and broadly interrupted medially; third upper row narrowly interrupted medially; fifth lower row composed of small teeth and not extending so far laterally as other rows (Fig. 2).

In life and in preservative, the tadpoles are entirely black.

Ontogenetic Change.—Small tadpoles in developmental stage with total lengths of 13.0-14.2 mm ($\bar{x}=13.6$, $N=10$) have less pigment in the fins than do larger tadpoles. Otherwise, there is no change in pigmentation during development; all tadpoles beyond

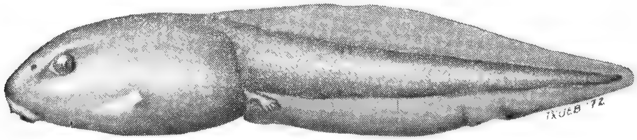

Fig. 1. Tadpole of *Osteocephalus taurinus,* KU 148706, total length 48.5 mm.

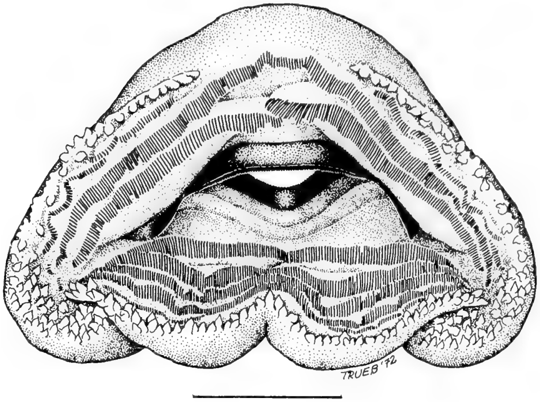

FIG. 2. Mouthparts of tadpole of *Osteocephalus taurinus,* KU 148706; line equals 1 mm.

stage 25 are entirely black. The sizes of tadpoles at Kérenroch, as correlated with development stages, are shown in figure 3.

The most obvious changes during larval development are in the

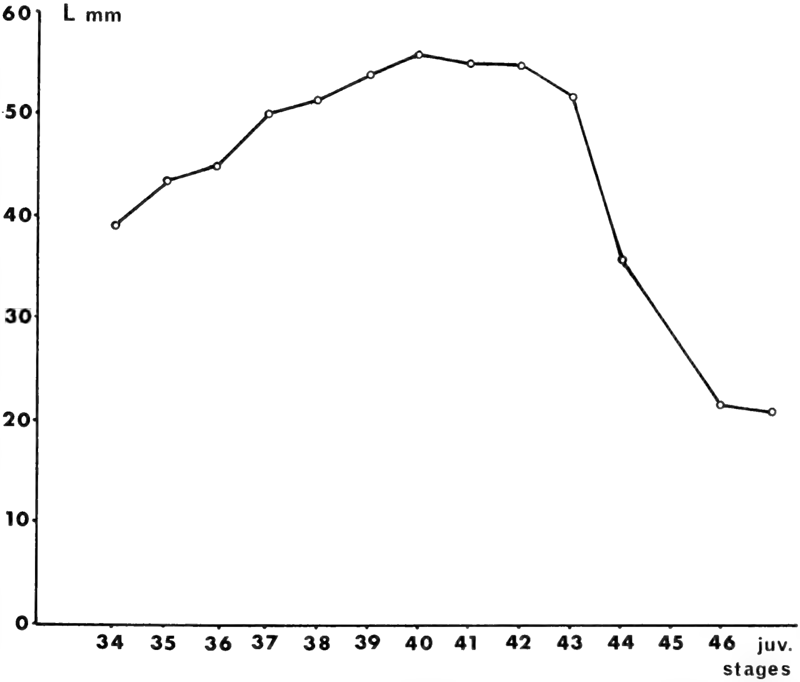

FIG. 3. Sizes (total length) of 79 tadpoles as correlated with developmental stages. Each point is the mean total length for a sample in a given developmental stage.

mouthparts. The smallest tadpoles available are in stage 25 and have only two upper and three lower rows of teeth. The third lower row is weakly developed; the outermost upper row and the two outer lower rows are absent. Larger tadpoles in stage 25 have a full complement of tooth rows. During metamorphosis the outer tooth rows are the first to degenerate. Small tadpoles in stage 25 have a few small labial papillae arranged in one row. Most tadpoles in stages 27-36 have one row of labial papillae; beginning at stage 37 the papillae become more numerous and tend to form two rows in the larger tadpoles. These ontogenetic changes are like those described for *Triprion petasatus* by Duellman and Klaas (1964) and for *Smilisca phaeota* by Duellman and Trueb (1966).

Recently metamorphosed young have snout-vent lengths of 19.5-20.5 ($\bar{x}=19.7$, $N=3$). In life, the dorsum is gray with clusters of melanophores; the anterior and posterior surfaces of the thighs, flanks, and venter are black. In larger individuals the limbs and flanks become gray, and in still larger specimens the flanks and thighs become tan, the belly cream, and the dorsum tan with brown markings.

Comparisons.—The tadpoles of *Osteocephalus taurinus* differ from those of *O. verrucigerus* by having three (instead of two) upper rows of teeth and in having fewer labial papillae; two rows of papillae are present in all *O. verrucigerus,* except hatchlings. Furthermore, the tadpoles of *O. verrucigerus* are not uniform black; they have a pale transverse, crescent-shaped mark ventrally on the body. Superficially, the tadpoles of *O. taurinus* resemble those of *Hyla geographica,* which also are uniform black, but which have two upper and four lower rows of teeth and deeper caudal fins (Bokermann, 1963).

LARVAL ECOLOGY

Lescure observed tadpoles of *Osteocephalus taurinus* in French Guiana near an ORSTOM hydrological research station at Kérenroch (5° 5′ N, 53° 2′ W, 5 m elev.), on the left bank of the Sinnamary River, 45 km upstream (south) from its mouth. Behind the station two rivers, of which the Crique Grégoire is the largest, flow into the Sinnamary at the same point. The soil of the granite basin crossed by these rivers is a clayish sand with coarse sand dominant. During heavy rains the rivers rise rapidly and overflow, so as to form one wide expanse of water flooding the forest for a width of several hundred meters. The current is very strong near the Sinnamary.

The vegetation consists of tropical rainforest having an abundance of large lianas.

On three occasions (February 1969, February and June 1971) large aggregations of tadpoles of *O. taurinus* were found in flooded areas of the forest where the current was weak and the depth of the water was 0.5 to 1 m. The tadpoles swam along the new banks amongst dead leaves or grazed on moss on logs in the water. Each aggregation probably contained more than 1,000 tadpoles. One catch consisted of 296 tadpoles after many had escaped. Within the aggregations most tadpoles were in stages 36 and 37 of development; six were in stages 29 and 30, and one was in stage 25 (Fig. 4). Others were more advanced, for shortly after the capture eight individuals left the water to complete their metamorphosis. Of 79 tadpoles collected on the same day, more than half were in stages 37-39.

The tadpoles in a given aggregation do not metamorphose at the same time. Those in stages 44 and 45 leave the water one at a time and climb onto vegetation, whereas those in stage 43 remain swimming with the group. Thus, there is no metamorphic aggregation as there is in *Scaphiopus* (Bragg, 1950) or in *Bufo marinus* (Lescure,

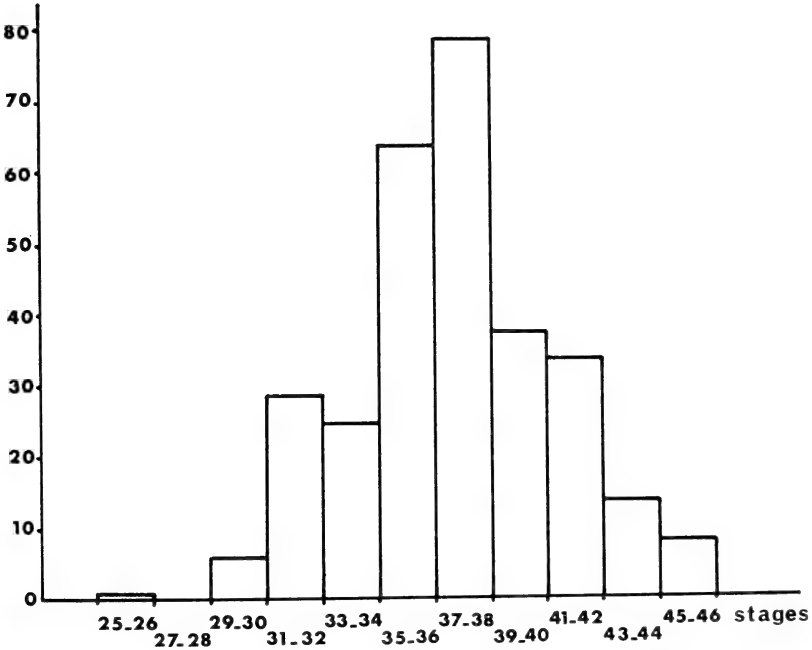

FIG. 4. Population structure (number of individuals in different developmental stages) with respect to developmental stages of 296 tadpoles removed from one aggregation.

per. obser.) where tadpoles in advanced stages aggregate and remain immobile in shallow water.

On 18 June 1970, Martha L. Crump observed five aggregations of tadpoles of *O. taurinus* in a shallow stream on the Ducke Reserve near Manáus, Amazonas, Brasil. The stream, about 1 m wide and no more than 25 cm deep, flowed slowly through young second-growth rainforest. Parts of the stream were in direct sunlight, but tadpoles were observed only in shaded areas along about 20 m of the stream. Four aggregations containing about 100 small tadpoles each; a sample of one of these consisted only of individuals in stage 25. A fifth aggregation contained an estimated 500 tadpoles; a sample consisted of individuals in stages 33-36.

A small series of tadpoles in stages 35-39 was seined from a swampy pool with no current at Veracruz, Pastaza Province, Ecuador, 950 m, on 4 July 1968, by John D. Lynch. These were part of an aggregation of "several hundred" tadpoles. On 6 July 1968, Lynch obtained one tadpole in stage 42 in quiet water at the edge of the Río Puyo, 3 km S Puyo, Pastaza Province, Ecuador, 980 m.

LARVAL BEHAVIOR

Observations made at Kérenroch, Veracruz, and at the Ducke Reserve indicate that tadpoles of *Osteocephalus taurinus* form large aggregations and that this behavior occurs throughout larval development. The following observations and experiments were made by Lescure at Kérenroch, French Guiana.

Observations.—The tadpoles in an aggregation are close together and frequently touch one another. When the group is stationary, it assumes a spherical shape. Tadpoles in the middle of the mass are immobile and not oriented in any particular direction; those on the periphery typically wriggle and seem to push towards the middle.

As a group moves along the margin of a bank or log, the tadpoles along the leading edge of the group and those in the middle slow their movements, apparently in order to feed. The tadpoles in the rear of the group bump into those ahead of them but continue to advance by moving along the outer edge of the group. Apparently they cannot penetrate the middle of the group, so they move to the front, where they graze or move back along the log towards the middle. This circulation of tadpoles within the group continues with the result that tadpoles from the rear keep moving around the periphery to the front even though food remains behind. Thus, the entire aggregation progresses forward in a manner analagous to a slowly rolling ball (Fig. 5).

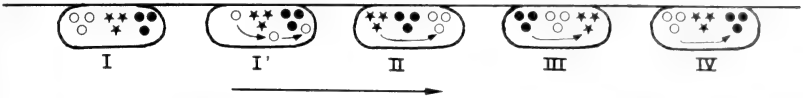

FIG. 5. Schematic diagram of movement of a group of tadpoles along a log; solid dots = A, stars = B, open circles = C. I. Disposition of tadpoles within group at position one. I^1. Tadpoles C advance by moving along edge of group. II. Tadpoles C are in front of the group; tadpoles B begin to advance. III. Tadpoles B are in front; tadpoles A begin to advance. IV. Tadpoles A are in front (same disposition as in position one). The arrow indicates direction of movement of the aggregation; small arrows within ellipses indicate movements of tadpoles within the aggregation.

Occasionally the group branches out in another direction, but either the tadpoles soon return to the aggregation, or the entire group follows the new direction. When an individual tadpole leaves the group, it does not wander far and soon returns to the group.

Experiments.—Two hundred tadpoles were removed from an aggregation and placed in a rectangular tank, 8 x 1 m with water 20-30 cm deep. During the several days that the tadpoles were kept in the tank they demonstrated no gregarious behavior. However, when they were replaced in the river, they formed aggregations.

The tadpoles were released in three groups at 5 m intervals in the river. Forty minutes later the group that was close to the bank stopped at a submerged twig. Immediately the tadpoles began to feed voraciously with their heads down and tails quivering. The two other groups, which were several meters away, immediately began to swim faster. In a few moments they reached the feeding group and joined to form one active mass of tadpoles around the twig. Several minutes later the excitement subsided, and the whole aggregation moved slowly along the bank.

Discussion.—The method of progression of aggregations and the general lack of orientation of tadpoles within aggregations of tadpoles of *Osteocephalus taurinus* differ from schooling behavior in fishes. The tadpoles do not swim in parallel formations, and instead of maintaining a constant distance from one another, the tadpoles tend only to remain close together. However, a certain coordination of movement exists when a group swims in one direction. The tight grouping probably is maintained by the continual contact among individuals. The lack of contact on the edges of the group may provoke the movements toward the middle when the group is stationary or the lateral movements when the group is in motion. Possibly the need for oxygen or food initiated the movement of tadpoles from below to swim around the edge of the group to the surface.

Movements upward through the middle, as observed in *Rana temporaria* by Savage (1961), were not observed.

Feeding activity seems to be an important factor in the gregariousness of the tadpoles of *O. taurinus*. Living in temporarily flooded areas, the tadpoles do not have permanent grazing grounds. Thus, the discovery of a supply of food by one group of tadpoles may normally result in frenzied feeding activity which attracts other groups of tadpoles. The grouping seems to be a lasting one, because the group moves as a whole even when not feeding.

The presence of one unlimited dimension in the water may be a requirement for the maintenance of an aggregation. No gregariousness was observed in tadpoles kept in a rectangular tank. The same phenomenon occurs in fish that normally live in schools; Schaffer (1955) noted that schools of young herring broke up in quadrangular tanks but remained aligned in annular ones.

Obviously, neither tactile nor visual stimuli can account for the regrouping witnessed in the second experiment. Possibly chemical sensations were involved, but because of the frantic movements of the tadpoles that discovered the food, it may be assumed that the resulting vibrations in the water attracted the distance groups. Nevertheless, visual stimuli are involved in some movements by the tadpoles. The shadow cast by the observer on a group of tadpoles near the surface results in the group plunging downward. This collective reaction is not the only kind of protective reaction by a group. If an object is dropped or pushed into a group, the tadpoles scatter in small groups, but in the absence of further disturbance, they regroup within 15 min. Wassersug and Hessler (1971) demonstrated that the stimulus for aggregation is visual in *Xenopus laevis* (Daudin).

The presence of a current in the water may affect the aggregational behavior of the tadpoles, but one aggregation has been observed in a swampy pond. Furthermore, tadpoles in the quiet water in the tank did not aggregate.

Bragg (1968) defined two kinds of aggregations in tadpoles: 1) social, in which the stimulus for aggregation is generated by the tadpoles, and 2) asocial, in which the stimulus is from environmental factors. Bragg concluded that aggregations of plankton-feeding tadpoles were social aggregations, but that groups that formed at concentrations of food were asocial aggregations. Tadpoles of *O. taurinus* aggregate at concentrations of food but also are gregarious when not feeding. The aggregations have a social aspect, because when moving the tadpoles remain close together and react defensively as a group. These are not chance aggregations. They are elementary groups, as defined by Lescure (1968). The accumulated observations and results of the experiments suggest that tactile stimuli may be the primary factor for maintenance of aggregations in tadpoles of *O. taurinus,* but the vibrations caused by tadpoles that find concentrations of food may initiate the formation of an aggregation. Chemo-stimuli remain an unstudied possibility. We have no data on temperature responses of the tadpoles; Brattstrom (1962) demonstrated that tadpoles of *Hyla regilla* Baird and Girard aggregated in response to thermal gradients.

MATING CALL

We have one lengthy recording of *Osteocephalus taurinus* recorded at Limoncocha, Napo Province, Ecuador, on 30 June 1971, by W. Ronald Heyer, who informed us that the call was typical of others that he heard at the same locality.

This individual produced two kinds of notes—short melodious notes (herein termed type A) and longer, poorly modulated tones (type B). In a two-minute sequence, type B notes were always preceded by two or three type A notes, but in other cases the latter were produced without subsequent type B notes. Thus, any given call group might consist of *N* A or *N* B. The number of type A notes per call group is 2 or 3 ($\bar{x}=2.4$, $N=37$), and the number of type B notes per call group is 0-4 ($\bar{x}=0.46$, $N=37$). In a given sequence of calls the frequency of notes and combinations of types of notes in individual call groups was (frequency of occurrence in parentheses; not sequential as produced): 2A (18), 2A + 1B (4), 3A (9), 3A + 1B (2), 3A + 2B (2), 3A + 3B (1), 3A + 4B (1).

The rate at which call groups are produced is 27.5 per min, and note repetition rate is 83.5 notes per min. Pulse rates of type A and B notes are about 160 and 95 pulses per sec, respectively. In sequences of type A notes, the first and third (if present) notes have an equal harmonic arrangement, whereas the harmonics are higher pitched in the second note (Fig. 6A-B). The first harmonic is dominant, and each successive higher harmonic has less energy. The first harmonic is at 570-625 ($\bar{x}=598$, $N=10$) Hertz in the first note in a sequence, and in the second note the first harmonic is at 770-805 ($\bar{x}=788$, $N=10$) Hertz. The duration of type A notes is 0.03-0.05 ($\bar{x}=0.042$, $N=10$) sec; the duration of type B notes is 0.36-0.65 ($\bar{x}=0.47$, $N=5$) sec. Type B notes generally have poor modulation (Fig. 6C).

The call of *Osteocephalus taurinus* can be described as "boop-boop-boop," followed or not by "worrr." The call differs notably

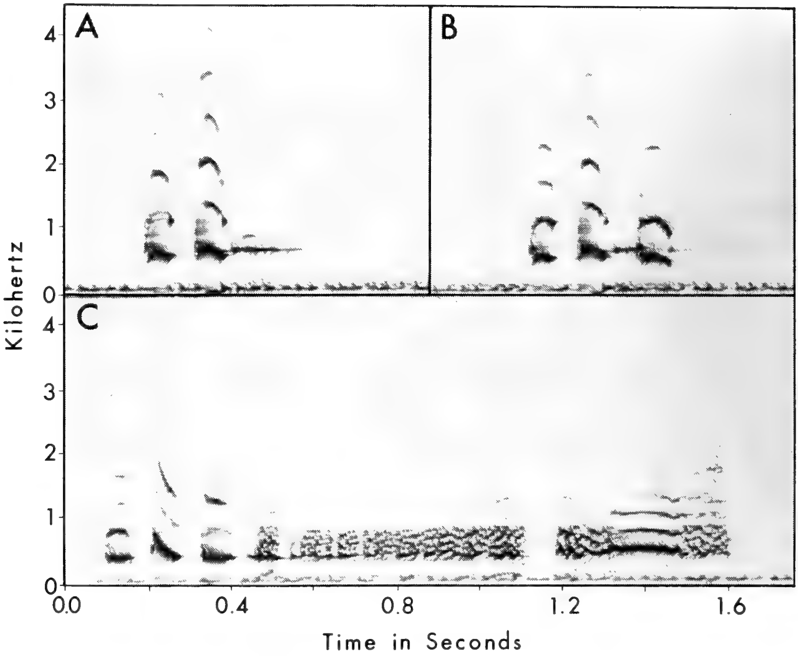

FIG. 6. Mating call of *Osteocephalus taurinus* showing different sequences of notes. A. Two type A notes. B. Three type A notes. C. Three type A notes followed by two type B notes. KU Tape 1204; Limoncocha, Napo Province, Ecuador; 30 June 1971; 24.6° C; effective band width 40 Hz.

from that of *O. verrucigerus,* which consists of a series of well-pulsed, low, guttural notes (Trueb and Duellman, 1970).

The mating call of *Osteocephalus taurinus* is highly complex by comparison with known calls of other hylids. The type A and B notes are not comparable to the primary and secondary notes produced by many small hylids; in these notes the acoustical differences are in duration and phase (Duellman, 1970), whereas the type A and B notes differ in several acoustical parameters and apparently differ in information content.

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We express our gratitude to Mr. Brugiere, Director of the Central Offce de la Recherche Scientifique et Technique Outre-Mer of Cayenne for his hospitality extended to Lescure at the hydrological station ORSTOM at Kerenroch and to Duellman's field associates, Martha L. Crump and John D. Lynch, for providing specimens and field observations. We are indebted to W. Ronald Heyer for the tape

recording of *O. taurinus* and to Linda Trueb for the illustrations depicted in figures 1 and 2.

RÉSUMÉ

Le têtard d'*Osteocephalus taurinus* (Hylidae) est entièrement noir, il a une petite bouche ventrale avec trois rangées supérieures de dents et cinq rangées inférieures. Les lèvres ont une rangée de papilles excepté dans la partie médiane de la lèvre supérieure; chez les plus grands individus, les papilles plus nombreuses sont disposées en deux rangées.

Des groupements d'environ 1000 têtards furent observés dans des parties inondées de la forêt ou le courant est faible. Les observations et les résultats des expériences suggèrent que les contacts entre les têtards sont le principal stimulus de ce comportement grégaire. Le stimulus déclencheur de la formation du groupe serait les vibrations de l'eau provoquées par l'agitation des têtards découvrant de la nourriture.

L'appel sexuel d'*O. taurinus* est complexe et consiste en deux catégories de notes. La production d'une longue note à peine modulée paraît dépendre d'une première série de deux ou trois notes courtes et plus modulées.

RESUMEN

El renacuajo del hílido, *Osteocephalus taurinus,* es completamente negro, tiene boca ventral moderademente pequeña, con tres hileras de dientes en el labio superior y cinco en el inferior. La parte media del labio superior carece de papilas, el resto de los labios posee una sola hilera; sin embargo, en los individuos de mayor tamaño hay proliferación de las papilas en dos hileras.

Se encontraron renacuajos en todos los estadios de desarrollo en agregaciones hasta 1000 individuos colectados en las partes anegadas con agua en movimiento, cercanas a los ríos. Las observaciones y los resultados experimentales realizados sugieren que el estímulo principal en la formación de las agregaciones es tactil, aunque el estímulo inicial tal vez sea la presencia de comida.

El complejo canto nupcial de *O. taurinus* consiste de dos tipos distintos de notas; la producción de una nota larga, poco modulada aparentemente depende de la produción previa de dos o tres notas melodiosas cortas.

LITERATURE CITED

Bokermann, W. C. A.

1963. Girinos de anfíbios brasileiros—1. (Amphibia-Salientia). An Acad. Brasileira Cien., 35:465-474.

1964. Field observations on the hylid frog *Osteocephalus taurinus* Fitz. Herpetologica, 20:252-255.

Bragg, A. N.

1950. Mass movement at metamorphosis in the savannah spadefoot, *Scaphiopus hurterii* Strecker. Proc. Oklahoma Acad. Sci., 31:26-27.

1968. The formation of feeding schools in tadpoles of spadefoots. Wasmann Jour. Sci., 26(1):11-16.

Brattstrom, B. H.

1962. Thermal control of aggregational behavior in tadpoles. Herpetologica, 18:38-40.

Duellman, W. E.

1970. The hylid frogs of Middle America. Monog. Mus. Nat. Hist. Univ. Kansas, 1: xi+753 pp.

Duellman, W. E. and L. T. Klaas

1964. The biology of the hylid frog *Triprion petasatus*. Copeia, (3):308-321.

Duellman, W. E. and L. Trueb

1966. Neotropical hylid frogs, genus Smilisca. Univ. Kansas Publ. Mus. Nat. Hist., 17:281-375.

Gosner, K. L.

1960. A simplified table for staging anuran embryos and larvae, with notes on identification. Herpetologica, 16:183-190.

Lescure, J.

1968. Le comportement social des batraciens. Rev. Comportement Anim., 2(4):1-33.

Savage, M. R.

1961. The ecology and life history of the common frog *Rana temporaria*. Pitman, London, 221 pp.

Schaffer, W.

1955. Über das Verhalten von Jungerheringsschwarmen in Aquarium. Arch. Fischereiwiss., 6:276-287.

Trueb, L. and W. E. Duellman

1970. The systematic status and life history of *Hyla verrucigera* Werner. Copeia, (4):601-610.

1971. A synopsis of Neotropical hylid frogs, genus *Osteocephalus*. Occas. Papers Mus. Nat. Hist. Univ. Kansas, 1:1-47.

Wassersug, R. and C. M. Hessler

1971. Tadpole behaviour: Aggregation in larval *Xenopus laevis*. Anim. Behav., 19:386-389.

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A PENNSYLVANIAN DISSOROPHID AMPHIBIAN FROM KANSAS

By

THEODORE H. EATON[1]

Among rhachitomous labyrinthodont Amphibia of the Late Paleozoic, the Dissorophidae and Trematopsidae currently are considered to be separate but closely related families. They are generalized in most features but show trends toward terrestrial life. Commonly recognized distinctions between the two families include the great enlargement of the external nares in the trematopsids, whereas the dissorophids have: 1) transverse plates of bony armor along the back usually attached to the neural spines; 2) broad, rounded interpterygoid vacuities; and 3) palatine bone forming part of the lower rim of the orbit.

Apart from the limitations imposed by incomplete specimens, these features are neither consistently present in the appropriate group nor mutually exclusive between the two. For instance, DeMar (1966a) described a Permian genus *Longiscitula* with enlarged nares; yet because of other characters such as dorsal armor, he placed it in the Dissorophidae. Vaughn (1969) showed that another Permian genus, *Ecolsonia,* has broad, rounded interpterygoid fenestrae such as characterize the dissorophids, but because of the presence of large nasal openings, Vaughn referred the genus to the Trematopsidae. It is not known whether or not armor was present in *Ecolsonia.*

Amphibamus from the Middle Pennsylvanian Allegheny beds of

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[1] Curator, Vertebrate Paleontology, Museum of Natural History, University of Kansas.

Linton, Ohio, is the oldest dissorophid; fortunately it can be studied from a number of specimens (Carroll, 1964). Watson (1940), who investigated *Amphibamus* in reference to the origin of frogs, noted that it is probably more aquatic and more primitive in some ways (e.g., exclusion of the frontal from the rim of the orbit by the prefrontal and postfrontal) than any other dissorophid.

The genus described here from Kansas is from the Late Pennsylvanian. Although in most respects it is an unspecialized dissorophid, it does have an enlarged nasal opening. The other known genera are variably characterized by small or large nostrils, presence or absence of armor, and wide or narrow palatine fenestrae; all are of Permian age. It is a part of the thesis of this paper that we should no longer recognize two families in this group, but only one, for which the older name, Dissorophidae, would be used. Two other valid families can be included in a superfamily, Dissorophoidea; these are the Zatracheidae and Doleserpetontidae. Both are closely related to dissorophids. *Doleserpeton* is a minute amphibian, probably terrestrial, from the Lower Permian fissure deposits at Fort Sill, Oklahoma. This animal was described by Bolt (1969) as a possible "protolissamphibian." Its structure, apart from the pedicellate, bicuspid teeth and large pleurocentra, differs remarkably little from that of *Amphibamus*.

The specimen named and described here is a nearly complete skull and skeleton of a small labyrinthodont amphibian, order Temnospondyli, suborder Rhachitomi, family Dissorophidae, taken from the Rock Lake Shale member of the Stanton Limestone, Missourian series, Upper Pennsylvanian, approximately 6 mi NW of Garnett, Kansas. The locality is that from which *Petrolacosaurus, Hesperoherpeton, Edaphosaurus ecordi,* and other members of the Garnett fauna were obtained. The dissorophid is in a limy shale bed containing plant fragments and numerous bones of the primitive pelycosaur *Clepsydrops.*

Actiobates new genus

Type species.—**Actiobates peabodyi** new species.

Holotype.—University of Kansas Museum of Natural History (VP) 17941; locality, age, and formation as given in preceding paragraph.

Diagnosis.—Skull broad, shallow, comparable to *Amphibamus* and *Ecolsonia;* cranial roofing bones thin, with pit-and-ridge ornamentation externally; basipterygoid joint moveable; frontals entering margin of orbits; otic notch moderate, its posterior opening slightly narrowed; marginal teeth uneven, those of anterior end of maxillary large.

Actiobates differs from *Amphibamus* in having a greatly enlarged nasal opening and from *Ecolsonia* in having the frontal and parietals of nearly equal size, and the postparietals narrow and elongate laterally. Diagnosis of the species is the same as that of the genus. This specimen is mentioned by Estes (1965) and Estes and Reig (1973).

Etymology.—The generic name is derived from the Greek *actios* meaning shore, and *bates* meaning one who walks. The specific patronym is in remembrance of Frank E. Peabody, who initiated the extensive study of the Garnett fauna.

DESCRIPTION AND DISCUSSION

The skull is flattened by pressure, but has sustained little damage and slight displacement of bones (Fig. 1). Its medial length is 59 mm, but the lateral edges have been pressed out a few millimeters, making the skull a little broader than it was in life. At the same time the nasal and premaxillary parts were spread laterally, leaving a gap between. In addition there is a small round fenestra between the tips of the nasals, which is commonly present in dissorophids. Ventrally, the mandibles were pressed against the lateral parts of the palate and upper jaw; a full description of this area must await further preparation. The pterygoid, parasphenoid and otic parts are remarkably well preserved. In the ventral view (Fig. 1b) the stapes and opisthotic are shown on the left side of the drawing as they are in the specimen; on the right, they are placed in their original positions relative to one another and the fenestra ovalis.

The postcranial skeleton and details of the skull not yet available will be described in a subsequent paper. The vertebral column is nearly complete, but scattered, because of the rhachitomous division of each vertebra. The forelimbs, including the girdle and feet, are complete; similarly, most of one hind limb is complete. A few scattered chevron bones and part of the pelvis are present. Four small bones are present anteriorly that look like double-ended paddles; these are probably units of the dorsal armor, but they lack attachment to the neural spines.

One curious feature is the presence of an occipital (one basi- and two exoccipitals in one unit) of a small individual of *Clepsydrops* inside the mouth cavity and pressed up into the orbit. A few other associated fragments suggest that this was not a chance relationship, but instead, that the amphibian was feeding on the pelycosaur.

Figure 1 shows most of the visible features of the skull, but some

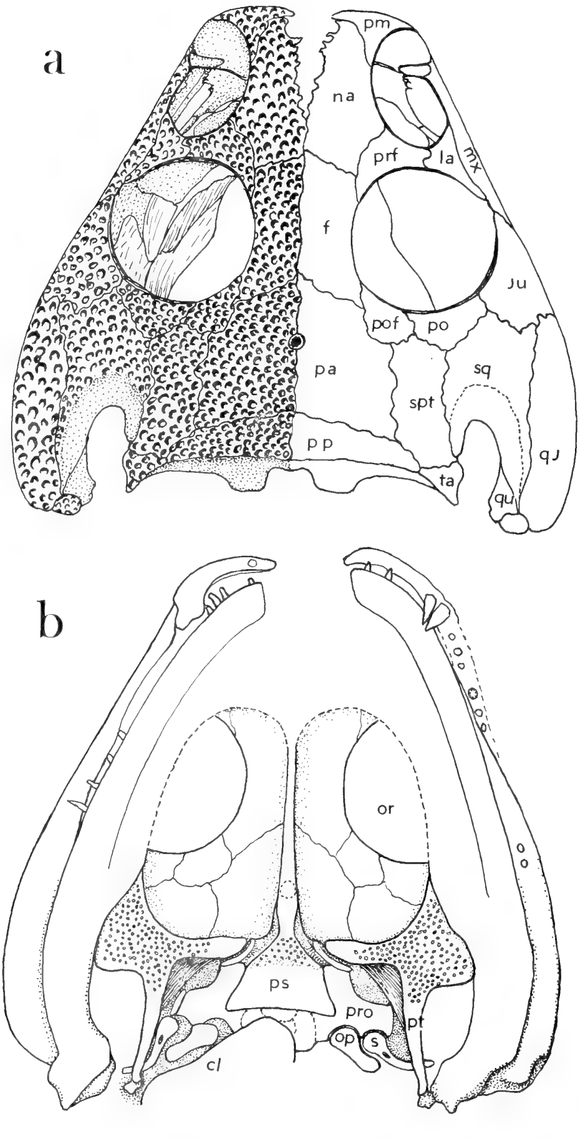

FIG. 1. Skull of *Actiobates peabodyi*, KU (VP) 17941, actual size. A. Dorsal view. B. Ventral view. Abbreviations: *cl*, edge of clavicle; *f*, frontal; *ju*, jugal; *la*, lacrimal; *mx*, maxillary; *na*, nasal; *op*, opisthotic; *or*, orbit; *pa*, parietal; *pm*, premaxillary; *po*, postorbital; *pp*, postparietal; *pof*, postfrontal; *prf*, prefrontal; *pro*, prootic; *ps*, parasphenoid; *pt*, pterygoid; *qj*, quadratojugal; *qu*, quadrate; *spt*, supratemporal; *sq*, squamosal; *st*, stapes; *ta*, tabular.

items need to be discussed. Comparison of the expanded nasal opening with those of most dissorophids and other labyrinthodonts shows that the anterior part (one-third) has not been changed by the enlargement, but that the posterior two-thirds resulted from recession of the edges of the lacrimal and prefrontal bones and some of the lateral edge of the nasal. The lacrimal and prefrontal are left as little more than a cross-bar separating the orbit and nostril. Whatever the reason for this expansion may have been, it need not have affected the original function of the anterior portion, which was for the passage of air.

The more lateral and anterior parts of the palate are concealed beneath by the lower jaws which are crushed against them; it may be possible to reveal these parts of the palate by further preparation while reconstructing the lower jaw at the same time. Much of the pterygoid is visible; its joint with the basisphenoid was evidently moveable. The expanded ventral surface of the pterygoid and that part of the parasphenoid which is between the basipterygoid processes are closely scattered with minute (0.25 mm diameter or less), round, flattened, dome-like teeth. Each tooth occupies, but may not fill, a round, shallow alveolus. Some of the teeth are much smaller than the alveolar opening and deeply placed in it; these are apparently in early stages of eruption. Other teeth nearly fill the alveolus to the rim, and the largest appear to have fused with the margin. A few have their rounded peaks worn off exposing the inner cavity.

The basisphenoid is exposed on either side of the converging, ventralmost part of the parasphenoid; the bone bears grooves for the interal carotids. The medial edges of these grooves are bounded by the parasphenoid except in their anterior parts, where the basipterygoid processes project laterally. The cultriform process of the parasphenoid is slender and crushed against the skull roof; thus, it is not possible to see a cranial cavity or foramina. There is no indication of a sphenethmoid.

No palatine, ectopterygoid, or vomerine teeth can be seen, because these bones are covered. The few visible teeth of the jaws are shown in figure 1b. There appears to be space for about 30 teeth in each jaw. Apparently, the largest teeth are two located on the forward end of the maxilla.

Morphologically, the otic region is most interesting. The otic capsule is represented mainly by the prootic, and is bounded laterally by the quadrate process of the pterygoid, anteriorly by the basal process, medially by the parasphenoid plate, and posteriorly by the anterior edge of the clavicle. At the posterolateral corner of the otic capsule is the fenestra ovalis, with the stapes slightly displaced, as seen on the left side of figure 1b. Beyond its rounded footplate, the stapes has a foramen in its shaft; distal to the foramen, the shaft curves laterally. The shaft lies dorsal to the quadrate process of the pterygoid, beyond which its tip shows. Posterior to the foot of the stapes, lies a short bone which evidently forms a portion of the wall of the fenestra ovalis. I assume that this bone is the opisthotic, which is considerably reduced and bears a short paroccipital process laterally. On the right side of figure 1b, the stapes and opisthotic are shown in their proper positions relative to the fenestra ovalis.

The resemblance of this apparatus to those of frogs and salamanders is at once obvious. If we allow a little more reduction of the opisthotic until it is a small, flat plate, and eliminate its ossification (as is usual for the otic region among modern amphibians), the opisthotic becomes quite precisely the operculum of the otic capsule. Primitively, the paroccipital process was for muscle attachment. When the bone was reduced, the muscle (opercularis) remained inserted on the operculum; it extends back to the anterior edge of the scapula in the modern Amphibia. It may have done so in dissorophids in the early stages of terrestrial life. This alone is not enough to demonstrate conclusively that *Actiobates* is directly ancestral to Lissamphibia, because we do not yet know the relationship of the expanded nasal opening to the reduction of the skull in frogs, salamanders, and caecilians. On the other hand, the condition of the ear in *Actiobates* approaches that of the modern Amphibia remarkably closely.

Elements of the hyobranchial apparatus, although not figured, are present. They are somewhat displaced against the otic region of the left side of the skull.

SKULL CHARACTERS AND RELATIONSHIPS

The question whether dissorophids and trematopsids represent one family or two depends on the occurrence of differential characters or combination thereof. But interpretation of these, in turn, requires viewing a given character, or characters, as a stage or "state" in the evolution of certain morphological features. For instance, among the Rhachitomi a moveable basipterygoid articulation is clearly more primitive than a fixed articulation. The moveable articulation occurs in the two Pennsylvanian genera, but not, so far as is known, in those of the Permian. On the other hand, union in a fixed joint could have occurred more than once; if it did, then possession of a fixed joint is not, by itself, evidence of a direct relationship among genera.

Likewise, there is no doubt that the small external nares characteristic of most labyrinthodonts are primitive with respect to large external nares. The former occur in *Amphibamus, Dissorophus* and most other genera in the Dissorophidae, but not in *Actiobates, Ecolsonia, Longiscitula,* or the genera usually placed in the Trematopsidae. Again, the enlarged condition, being specialized, could have originated more than once. The size of the external nares is not a simple character, and the modification of at least three bones in a particular area of the skull in the same way in more than one evolutionary line seems improbable. Such an interpretation would require independent evidence from other characters that genera having enlarged nares represent separate phyletic lines.

Morphologically it is not possible to determine the relative primitiveness of wide, rounded interpterygoid vacuities as compared with narrow or small interpterygoid vacuities. However, within the scope of dissorophids and trematopsids, we can suppose that the wide, rounded state is primitive because it is present in *Amphibamus* and *Actiobates* of the Pennsylvanian in addition to other dissorophid genera. The fenestrae are narrow and relatively small in several trematopsids. If these taxa are closely related and form a natural group (whether one family or two), then there is a high probability that the narrowed condition is secondary. In spite of the fact that the most primitive labyrinthodonts had no interpterygoid vacuities, it is reasonable to suppose that rounded interpterygoid vacuities were present in primitive dissorophids, because they are known in *Amphibamus.*

None of the features of the skull that has been discussed, nor the occurrence of dorsal armor, seem to be suitable to distinguish the two families. In the case of each character there is at least one taxon for which a character state cannot be determined. Furthermore, the distribution of known characters is discordant. Thus, any arrangement of the genera in separate groups requires that some inconsistency in overlapping or contradictory characters be introduced in their diagnosis. It seems more satisfactory, therefore, to recognize only one family, the Dissorophidae, for all the animals hitherto placed in this and the Trematopsidae.

SUMMARY

A virtually complete skeleton of a new dissorophid labyrinthodont, *Actiobates peabodyi,* is reported from the Rock Lake Shale member of the Stanton Limestone, Missourian Series, near Garnett, Kansas. The skull is characterized by an expanded narial opening, characteristic of Permian trematopsids and seen here for the first time in a Pennsylvanian amphibian. In other respects, the skull is that of a generalized dissorophid. The distribution of characters among dissorophids and trematopsids no longer seems to warrant recognition of more than one family, the Dissorophidae, for both.

LITERATURE CITED

Bolt, J. R.

1969. Lissamphibian origins: possible Protolissamphibian from the Lower Permian of Oklahoma. Science, 166:888-891.

Carroll, R. L.

1964. Early evolution of the dissorophid amphibians. Bull. Mus. Comp. Zool., Harvard, 131(7):163-250.

DeMar, R. E.

1966a. *Longiscitula houghae,* a new genus of Dissorophid Amphibian from the Permian of Texas. Fieldiana Geology, 16(2):45-53.

1966b. The phylogenetic and functional implications of the armor of the Dissorophidae. Fieldiana Geology, 16(3):55-88.

Estes, Richard

1965. Fossil salamanders and salamander origins. Amer. Zool., 5:319-334.

Estes, Richard and Osvaldo Reig

1973. The early fossil record of frogs: a review of the evidence. *In* J. L. Vial, Evolutionary biology of the Anurans. University of Missouri Press, Columbia (in press).

Vaughn, P. P.

1969. Further evidence of close relationship of the Trematopsid and Dissorophid Amphibians with a description of a new genus and species. Bull. So. Calif. Acad. Sci., 68(3):121-130.

Watson, D. M. S.

1940. The origin of frogs. Trans. Roy. Soc. Edinburgh, 60:195-231.

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POPULATION STUDIES OF THE CAVE BAT *(MYOTIS VELIFER)*: REPRODUCTION, GROWTH, AND DEVELOPMENT

By

THOMAS H. KUNZ[1]

An integral part of the ecology of an animal is the manner in which it successfully adapts to its environment. Under conditions of thermal seasonality in the temperate zones, insectivorous bats have evolved strategies that compress reproduction and development into a relatively short time period in the warm season, when food is abundant and temperature conditions are optimal for rapid growth of young.

Seasonal reproductive patterns of temperate insectivorous bats (including autumn copulation, spring ovulation and gestation, and summer parturition) have been documented for several species. Much of the available information on reproduction has been summarized by Asdell (1964), Barbour and Davis (1969), and Carter (1970). Wimsatt (1945, 1960a) gave a thorough account of breeding behavior, pregnancy, and parturition of several vespertilionids and also discussed aspects of reproduction relating to hibernation (Wimsatt, 1960b, 1969). Orr (1970) summarized studies on growth and development.

There are a number of important studies detailing aspects of natural history, population dynamics and behavior of *Myotis velifer* (J. A. Allen) (Twente, 1955a, 1955b; Tinkle and Milstead, 1960; Tinkle and Patterson, 1965; Dunnigan and Fitch, 1967; and Hayward, 1970). Other important contributions are those of Vaughan

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[1] Assistant Professor, Department of Biology, Boston University, Boston Massachusetts 02215. This paper represents part of a Ph.D. dissertation submitted to the Department of Systematics and Ecology, University of Kansas.

(1959) on functional morphology and Constantine (1957) on pelage and molt. However, these studies do not assess an entire seasonal cycle, and little is known with respect to the reproduction, growth and development of *M. velifer.* In this study I have considered the seasonal chronology of reproduction and examined factors relating to growth and development in two populations occupying physically and thermally contrasting nurseries in Kansas.

The ecological and geographic distribution of *M. velifer* typically is patchy and extends northward from Honduras into the central Great Plains. The study area lies within the Gypsum Hills and adjacent areas of south-central Kansas. A complete discussion of the study area was given by Kunz (1973). See the appendix for place names, coordinates, and counties of each locality mentioned in text. Of the four races of *M. velifer* currently recognized, the northernmost race is now known as *Myotis velifer grandis* Hayward (1970) and occurs in parts of Texas, Oklahoma and in south-central Kansas. Previously, the name *Myotis velifer incautus* (J. A. Allen) was used for these bats (Miller and Allen, 1928).

Climatically, the study area is typical of the southwestern plains. Most of the area falls within the O° C January isotherm and above the 26° C July isotherm (U.S. Department of Commerce, Climatological Data). The length of the average frost-free period varies from 180 to 190 days. The last vernal frost occurs in April and the earliest frost in autumn usually is in late September or early October. The summers are long, hot, and dry; it is not uncommon for temperatures of 39° C to prevail for several days. The warmest months are July and August. Winters generally are mild, although temperatures may remain below freezing for short periods. The coldest period usually occurs in February and early March, although this may vary considerably from year to year. Precipitation varies locally and seasonally and months may pass with little measurable amounts recorded. Mean annual precipitation is 16-28 in. (406-711 mm).

Acknowledgments

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Appreciation is extended to Frank B. Cross, Robert S. Hoffman, and J. Knox Jones, Jr., who read and criticized an earlier version of this manuscript. I am also grateful to M. Brock Fenton and Stephen R. Humphrey who offered several helpful suggestions. I am particularly indebted to Frank B. Cross who made available financial and travel support, both for field and laboratory studies, through the State Biological Survey of Kansas. Computer time was secured through the Department of Systematics and Ecology and University of Kansas Computation Center.

METHODS AND MATERIALS

Field studies were begun in March 1968 and continued through January 1971. Data for mark-recovery analyses include all recoveries through June 1970. All bats were marked using size 2b, lipped, aluminum bat bands (U.S. Fish and Wildlife Service, Washington, D.C.). Some bands were color-anodized (blue, green, and red) for marking juveniles occupying different nurseries. Four "seasons," corresponding to Summer (June-August), Autumn (September-October), Winter (November-March), and Spring (April-May), were selected to best represent the seasonal changes in population behavior. Although this scheme does not correspond exactly to the seasonal activity of the entire population, it does represent a general pattern and probably includes most populations in the study area.

Environmental Measurements

Lost Colony and Wilmore were selected for intensive study in order to assess the influence of ambient temperature and relative humidity on reproduction, growth and development. These two nursery roosts, a cave and a barn respectively, were selected mostly because populations of approximately the same size occupy them in the summer. Also, the roosts invite comparative study because their environments contrast sharply with respect to physical and thermal properties.

Temperature and relative humidity recordings were taken in roost areas using seven-day recording hygrothermographs and a Bendix Psychron. Twenty-four hour recordings of micro-roost temperatures (including body-surface temperatures), were obtained using a 12 channel, Model 44, YSI telethermometer with general purpose thermister probes positioned in roost areas at the Wilmore barn. Periodic recordings were made from April through October (Kunz, 1973). Similar attempts were made to measure micro-roost temperatures and body-surface temperatures of bats occupying Lost Colony but these efforts were unsuccessful. Whenever thermisters were positioned in an area that had been occupied by bats they would either abandon that specific site or would move to a different part of the cave. Temperature and relative humidity measurements also were taken at other roosts.

Population Estimates, Age, Sex, and Reproductive Condition

Methods used to estimate population size of active bats depended on the number and size of entrances used by the bats. Where single entrances to caves or buildings were used, flight counts were employed (see Dwyer, 1966; Humphrey, 1971) and this method probably provided the most accurate estimate. Flight counts were not practical at sites with multiple-use entrances; in such situations, estimates were often based on the size of the stained area in a roost, the quantity of the accumulated guano, or number of neonates present after adults had departed. In a few instances, estimates were based on observations of clusters occupying ceiling areas.

Sex ratios were determined mostly from trap samples (Tuttle, ms.) taken at entrances during emergence and return activity, over streams, or by taking hoop-net or hand samples within a roost. The two latter methods were avoided during the nursery period (June-July) in order to reduce disturbance, and were used selectively at other times.

Young bats born in summer could be distinguished from adults at least through August. Generally, after this time, closure of the epiphyseal region of the phalanges occurred and many young bats developed adult-like pelage, and some were nearly equivalent to adults in body weight (Kunz, 1971). After August, age determination was based on the condition of teats in females and size of testes in males. Young females usually have smaller, non-pendulant teats in contrast to those of post-lactating adults, and young males have smaller testes than adults. However, this aging criterion for males becomes less reliable in late September and October when testicular regression occurs in adults.

Reproductive condition of females (pregnancy, lactation, and post-lactation) was determined by palpation. In April and early May pregnant females can not be distinguished from those that may be non-reproductive. In summer, non-pregnant females were considered to be lactating if milk could be extruded from the mammary tissue, or white areas were notably visible beneath the skin. When milk no longer could be obtained, or mammary tissue was visibly pink and undergoing regression, individuals were considered to be post-lactating. Judgments of reproductive activity were based solely on the presence or absence of a discernible fetus in the latter two or three weeks of gestation and the presence of milk in the first week of lactation. When all individuals have given birth, the difficulty of estimating the proportion of reproductive females in the population was compounded by the fact that some females may have aborted in late term or lost their offspring in early days following parturition. These individuals may appear to be non-reproductive upon gross examination so the category is probably appropriate for them. Reliable estimates of non-reproductive females in a population also are contingent on the fact that they, too, reside in nurseries.

Establishment of a seasonal reproductive pattern for adult males was based mostly on linear measurements of testes and the cauda epididymides from preserved samples. Field observations on the changes in the size and position of testes and epididymides provide a general measure of seasonal activity; however, I think that temporal aspects of the reproductive pattern of adult males can be extrapolated from the pattern observed in preserved specimens.

Growth and Development

Studies of prenatal growth were based on preserved fetuses, which were removed from autopsied females and weighed to the nearest 0.01 gram using a Mettler top-loading analytical balance. Linear measurements of the width and length of the uterine horns and crown-rump length were taken from preserved specimens.

The field methods utilized in studies of post-natal growth were selected primarily to minimize disturbance to nursery colonies. Data obtained from any one nursery were limited by the location and type of structure, the size of the resident colony, and its relative susceptibility to disturbance. Studies at Lost Colony were conducted mostly for the assessment of morphological growth, whereas those at Wilmore were conducted for the purpose of recording behavioral observations.

Preliminary observations at Lost Colony and at other nurseries suggested that an interval from one to one and a half hours was permissible to capture, process, and return young to their roosts before adults returned from foraging. During this period some behavioral observations were made on social organization and age distribution of young within the roost. The procedure of sampling and observing young while adults were foraging was advantageous in reducing disturbance to the colony. However, the recovery rate of known age individuals was low once young became volant. In spite of this disadvantage, the procedure was preferable to sampling bats in the daytime when excessive disturbance to adults may result in high mortality and/or abandonment.

Captures of newborn (or very young) bats were essential for a complete analysis of post-natal growth. Young bats having attached umbilical cords were assumed to be approximately one day old. This assumption has been used by others (see Pearson *et al.*, 1952; Davis, 1969b), although it may not always be valid. When the relative humidity of roosts is high, the umbilical cord may remain attached to a neonate longer than one day. Young bats were sexed, banded, weighed, and measurements of the forearm and fifth finger were taken. Color-anodized bands were used in roost areas for distinguishing young from adults once the former were fully grown.

At approximately 10-day intervals, newly captured neonates and young that had been previously marked were captured and processed. By the beginning of the fourth week, several young that had been marked in the first period had become volant. Throughout the summer unmarked samples of young bats that were trapped at colony entrances or in roost areas were processed as described above.

Periodic samples of unmarked young corresponding to sizes of known-age bats, were collected from several different colonies. These bats were killed and preserved in 10 percent formalin for studies of pelage, dentition, and food consumption. Drawings of wing areas were made before preservation for the purpose of studying age-related changes in wing-loading. Wing areas were traced on paper in the field and surface area determinations were made following the methods described by Davis (1969a). Linear and wing-area measurements, were taken using a metric dial caliper (0.1 mm) and a polar planimeter (0.1^2 inches), respectively; the latter measures were converted to metric units (cm^2).

Binoculars (7 x 35) were used for making observations at Wilmore. At this site ambient light conditions were usually sufficient for making diurnal observations from a distance of approximately five meters without noticeably disturbing the colony.

On periodic visits to each nursery, I examined areas beneath roosts for evidence of juvenile mortality. However, this search was hindered at Lost Colony because small young became buried in the wet guano after falling to the cave floor. This problem was not encountered at building nurseries where guano usually dried rapidly under conditions of low relative humidity.

Growth Analysis

A FORTRAN program, fitting properties of the von Bertalanffy growth model applicable to mark-recovery data (Fabens, 1965), was used in the analysis of post-natal growth. The only basic input requirements of this program are sets of linear or weight data (arranged as paired measurements, and corresponding capture intervals that need not be equal) and a separate input that includes linear size or weight of some known-age individuals (preferably those taken at or near birth). In the analysis that follows, linear growth is expressed by the general formula $X=a(1\text{-}be^{-kt})$ and weight by the formula $W=[a(1\text{-}be^{-kt})]^3$, where X represents the computed length of the forearm or fifth finger, and W is the 2/3 power of the body weight. The quantities *a*, *b*, and *k* in both equations are parameters: *a* is a measure of the asymptotic size; *b* is a measure related to the size of the animal at birth; and *k* is a measure of the intrinsic rate of growth. The values *e* and *t* represent the base of the natural logarithm and the number of days of growth, respectively.

A thorough account of the mathematical and physiological theory of the model was presented by von Bertalanffy (1960); he cautioned that at present quantitative analysis of growth in mammals must be considered provisional. Laird *et al.* (1965) and Laird (1966) used models based on the Gompertz equation for studying growth of body weight in mammals. However, von Bertalanffy argued that models based on this equation are not only unsuitable for analyses of linear measurements but also lack a physiological basis for application to study of growth.

Curve-fitting of growth data is useful to summarize data for descriptive purposes. If a growth curve is derived from a theoretical model, so that parameters have some additional meaning, independent investigations then can be conducted to test the theory on which the model is based. The von Bertalanffy growth curve of the decaying exponential type (von Bertalanffy, 1960) has been derived from a model that has physiological significance and provides parameters that are useful for independent testing. The underlying assumption of this model is that growth, in the biological sense, is intimately related to metabolism and is characterized by the highest rates in the early stages of development, decreasing exponentially with time.

RESULTS

Nursery Roost Environments

Nursery "caves" seldom showed significant daily fluctuations in temperature or relative humidity. Hygrothermograph recordings taken at Lost Colony in late spring and summer 1969 revealed little daily change in ambient temperature or relative humidity. A representative record in the second week of July showed that the cave temperature remained near 20° C and the relative humidity near 100 percent (Fig. 1). Periodic measurements of temperature and relative humidity in the nursery area at the National Gypsum Mine suggest a similar pattern. Much of the gypsum substrate becomes saturated with ground-water following spring and early summer rains at these sites. The accumulation of this water, the presence of seasonally intermittent streams or standing water, and the relatively low air circulation in summer reduce evaporative conditions and contribute to the high relative humidity.

Building nurseries, in contrast to cave nurseries showed marked daily variations of temperature and relative humidity. A comparison of temperature recordings and relative humidity at Lost Colony and Wilmore in the second week of July (Fig. 1) demonstrates these striking differences. In this period temperatures at Wilmore varied from 25-35° C, and relative humidity ranged from 40-100 percent. Because Wilmore was occupied by spring transient and a resident summer population, the recordings shown in figure 2 were selected to depict the roost conditions during this period. It is clear that bats

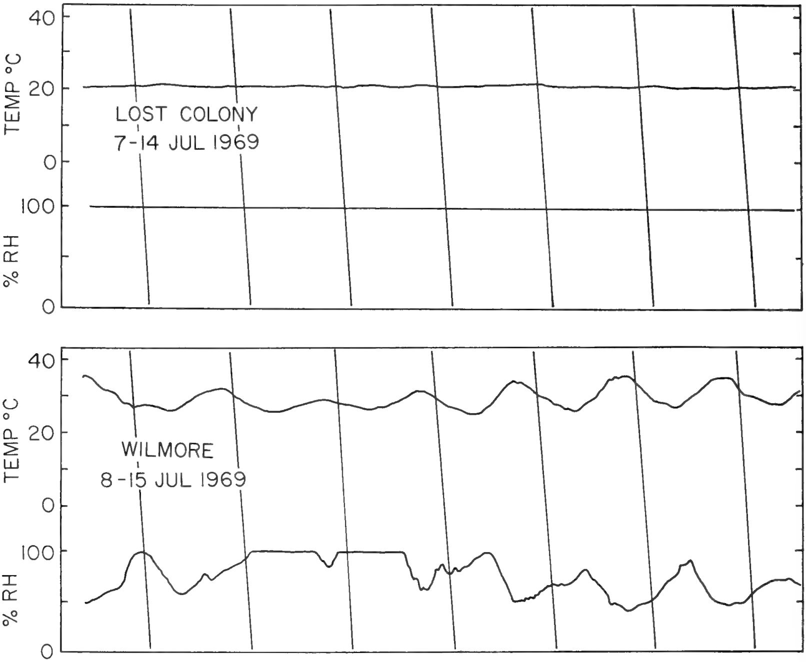

FIG. 1. A comparison of hygrothermograph records during the nursery period (second week of July) at Lost Colony and Wilmore. On both records the temperature measurements (upper) and relative humidity measurements (lower) represent ambient conditions in the colony irrespective of the thermal influence or vapor pressure changes brought about by the presence of the bats. The diagonal lines indicate the 2400 hour (midnight) of each day.

occupying this roost potentially were exposed to widely fluctuating conditions. There is a general seasonal pattern of increasing mean ambient temperatures and decreasing relative humidity from early spring to late summer.

Environmental fluctuations may vary considerably depending on the physical structure of the roost, the location of the building or cave with respect to topography, surrounding vegetation, and the facing direction of the entrance. Ambient temperature in small buildings usually fluctuated more than in large structures. Nursery sites in caves, in contrast to those in buildings, were usually located in areas where little, if any, light penetrated beyond the entrance area. In most buildings, however, light was sufficiently bright during parts of the day to permit observation without the use of artificial sources. At Lost Colony and the National Gypsum Mine no light was evident in the nursery areas but at Wilmore bats occupied dimly lighted areas and the darkest areas were not occupied.

Clustered bats modify the microclimate of their nursery roosts. Tendencies of bats to cluster, coupled with the physical features of

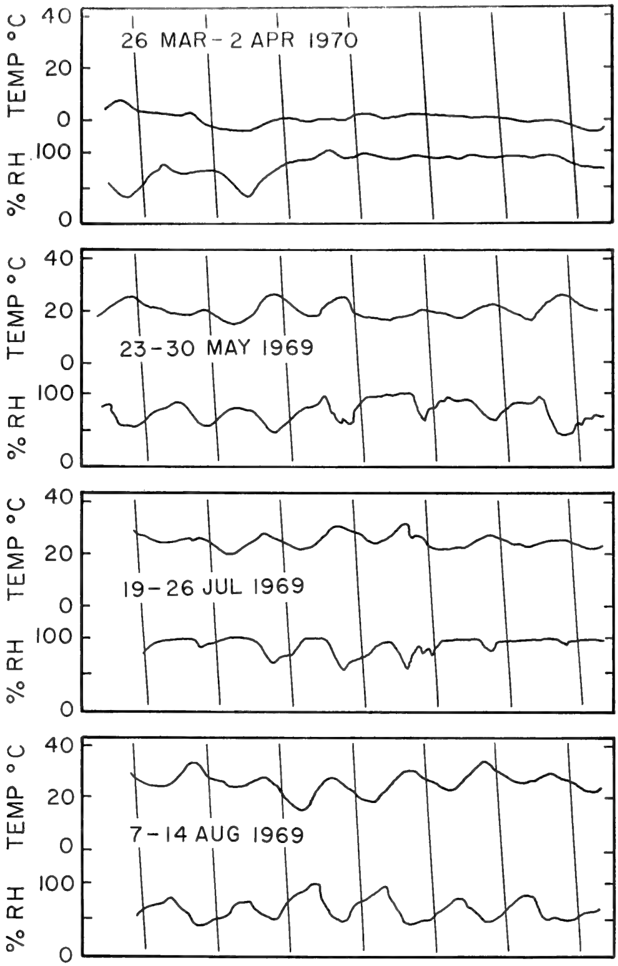

FIG. 2. Hygrothermograph records showing seasonal patterns of ambient temperature and relative humidity at a barn occupied by transient and nursery populations of *M. velifer*. The diagonal lines indicate the 2400 hour (midnight) of each day.

the roost, combine as important factors in maintaining high roost temperatures. Microenvironmental temperatures recorded in roosts at Wilmore in late June often reached daytime levels exceeding 35° C (Fig. 3). To assess the effect of bats on their roost microclimate, temperature differentials between test probes and control probes were determined (see insert Fig. 3). I have assumed that these differences represent the thermal influence that bats had on their roost microclimate. On 29-30 June these differences varied from 4-

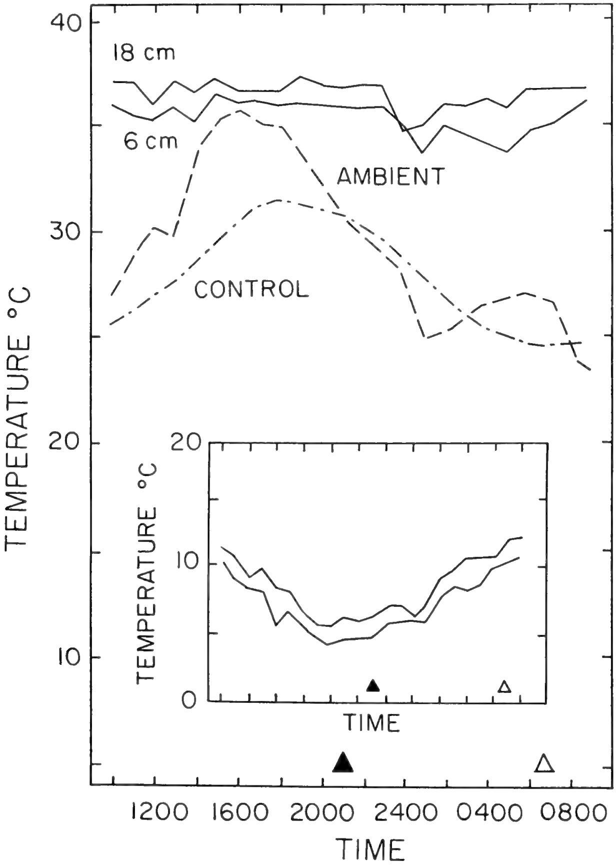

FIG. 3. Microenvironmental temperatures recorded at the Wilmore nursery on 29-30 June 1969 (after most females had given birth). Data are based on hourly temperatures recorded along a vertical gradient in a joist crevice from thermisters positioned at 6 and 18 cm from the ceiling (see Kunz, 1973 for further explanation). One daily record of a control probe (6 cm) and the outdoor ambient temperature are shown for comparison. The insert shows temperature differentials between control sites (bats absent) and test sites (bats present). The solid and open triangles at the bottom of the figure denote sunset and sunrise time, respectively.

12° C depending on the time of day and the number of bats present at any one time. Much of the loft floor at Wilmore was covered with loose straw and broken hay bales to a depth ranging from two to 40 centimeters. The accumulated litter may have been important in providing insulation by trapping heat that was generated by bats roosting on the joists supporting the loft floor.

The daily and seasonal fluctuations of relative humidity in building roosts also were subject to modification by bats. In spite of the pattern of relative humidity recorded in the Wilmore barn (Figs. 1 and 2), the presence of clustered bats in the daytime tends to modify the vapor pressure in roosts when, otherwise, it is low. In June and July 1969 and 1970, roosts were examined periodically after adults had departed to feed. These observations revealed that the wood substrate of joists on which the bats roosted was saturated with urine. Instruments were not available that would permit remote micro-determinations, but measurements of relative humidity using a Bendix Psychron positioned at the opening of joist crevices revealed substantially higher readings than from the hygrothermograph recordings taken in open areas near the joist crevice. It is quite probable that as these wood joists become saturated during periods of occupancy, increases in vapor pressure become comparable to the 100 percent saturation recorded in cave nurseries.

In early spring, the thermal environment at Lost Colony appeared to be unsuitable for occupancy; temperatures varied from a low of 8° C in mid-April to 13° C in mid-May, and little daily variation was evident. These temperatures were considerably lower than those recorded at other spring roosts and that were occupied by transient populations (Kunz, 1971). When individuals first arrived at Lost Colony in early May, they usually selected the warmest sections available. In contrast, Wilmore was subjected to the environmental fluctuations of the outside environment. In early spring, roost temperatures occasionally dropped below 0° C but by May daily highs reached 30° C (Fig. 2).

Adult Sex Composition of Nursery Roosts

Adult male *M. velifer* accompany females to nursery roosts; this phenomenon is apparently uncommon in other members of the genus. The sexes occur in nearly equal numbers in spring transient roosts and in nurseries until parturition begins (Table 1). Monthly comparisons of the proportion of adult sexes occupying Lost Colony and Wilmore showed that the males occupying these two sites declined measurably in May and June. Proportionately fewer males remained in the barn at Wilmore from May through August than occupied Lost Colony during the same period.

Samples of bats taken at the National Gypsum Mine in July and August, 1969, revealed that a comparatively large proportion of males occupied this site. Here, many males occupied cool caves and were solitary or roosted in small groups. On 19 August several bats were found scattered throughout the mine at considerable distances from the nursery area; of 39 individuals captured, 38 were adult males. A trap sample on the same date during emergence activity yielded 406 bats, of which 296 were males.

TABLE 1. Seasonal comparisons of adult male *Myotis velifer* occupying nurseries at Lost Colony (cave) and Wilmore (barn).

	Lost Colony				Wilmore			
Month	Number of samples	Pooled *N*	Males	Percent males	Number of samples	Pooled *N*	Males	Percent males
Mar	--	----	----	----	1	49	23	47.0
Apr	1	4	2	50.0	1	112	51	45.6
May	2	216	106	49.0	4	304	87	28.6
Jun	4	696	106	15.2	2	343	28	8.2
Jul	3	574	194	33.8	5	305	24	7.9
Aug	4	687	137	20.0	4	93	10	10.7
Sep	3	241	48	20.0	2	15	2	13.3
Oct.	1	68	65	95.4	1	20	20	100.0

Reproduction

MALES

Testes and Epididymides.—Seasonal changes in size of testes and epididymides of adults show that testes increase in size following departure from hibernacula with maximum hypertrophy occurring in late August (Fig. 4). These observations concur with those of Krutzsch (1961) and Hayward (1970) based on samples from Texas and Arizona, respectively. Increase in the size of testes corresponds to the period of spermatogenesis in summer reported for other vespertilionids (Wimsatt, 1960b, 1969). In early autumn when testes decrease in size, the epididymides become distended with spermatozoa. Maximum engorgement of the cauda epididymides occurs in October and is followed by a decrease in size throughout the winter. Testes are abdominal throughout hibernation and early spring, but in mid-summer (July) they descend into the pigmented sheaths adjacent to the tail in the uropatagium.

FEMALES

Age at Sexual Maturity.—Female *M. velifer* apparently reach sexual maturity in their first year of life. Thirty-nine females were recovered from 21 May through 21 June 1970, that had been marked as juveniles in the preceding summer; all were either pregnant or lactating. It was not determined whether or not yearling females are inseminated in spring or at other times.

Ovulation and Fertilization.—Wimsatt (1944, 1945) suggested that ovulation in *M. lucifugus* probably occurs between the time of departure from hibernation and arrival at nurseries in spring. If fertilization in *M. velifer* occurs at this time, then this would include the period from late March to late April for populations in this study. In 1970, some females had already departed from hiber-

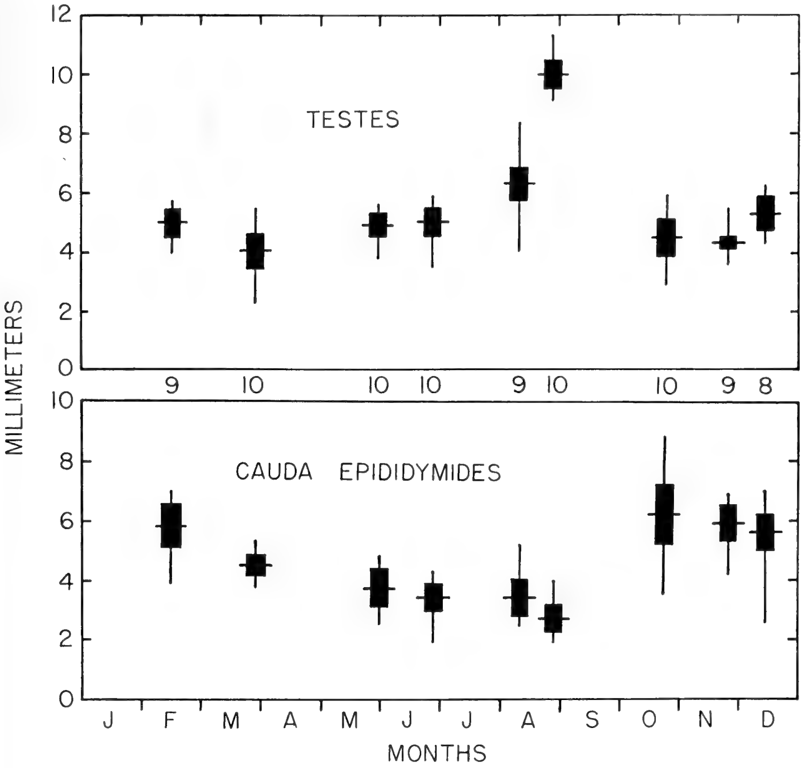

FIG. 4. Seasonal changes in size of testes and cauda epididymides of adult male *M. velifer.* Dice grams indicate mean, range and 2 SE. Sample sizes are shown between the two graphs.

nacula and had arrived at spring roosts by 25 March, although the median departure date from hibernacula was estimated to be mid-April (Kunz, 1971).

Gestation and Prenatal Development.—The means for length and width of the right uterine horn (Table 2) are plotted to portray the general period of gestation and pattern of prenatal growth (Fig. 5). Prenatal growth follows a sigmoidal pattern with a characteristic lag phase in the early stages. Throughout this early period of growth, the length and width of the uterine horn were nearly proportional. Most of the growth up to this time mainly reflected the increase in the size of the uterus, the placenta, and extraembryonic membranes. Once these tissues are well developed, embryos grow rapidly as evidenced by their elongation, change in the relative proportions of the linear dimensions of the uterine horn, and increase in embryo size and weight. Mean weight of the fetus at birth was approximately 3.0 grams; on 29 May, about three weeks before

TABLE 2. Prenatal growth of *Myotis velifer,* where growth is expressed as the length and width (± 0.1 mm) of the right uterine horn, weight (± 0.01 gm) and crown-rump length (± 0.1 mm) of the fetus (means ± SE and ranges are given).

		Length of right uterine horn (mm)			Width of right uterine horn (mm)		
Date	*N*	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range
24 Apr	12	2.6	0.14	(1.9– 4.0)	1.9	0.09	(1.5– 2.7)
8 May	12	4.0	0.25	(2.9– 6.3)	3.6	0.29	(2.3– 6.1)
29 May	9	12.8	0.99	(9.1–17.4)	10.1	0.89	(6.4–14.4)
11 Jun	15	21.4	0.41	(18.8–24.1)	13.6	0.18	(12.5–14.8)
16 Jun	11	23.9	1.92	(16.3–26.4)	15.8	0.61	(14.5–16.9)
20 Jun	8	23.7	0.94	(20.4–28.0)	16.1	0.51	(14.0–18.2)

		Weight of embryo (gm)			Crown-rump length (mm)		
Date	*N*	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range
24 Apr	12	----	----	----	----	----	----
8 May	12	----	----	----	----	----	----
29 May	9	0.43	0.073	(0.05–0.73)	10.3	0.98	(6.2–15.9)
11 Jun	15	1.66	0.068	(1.20–2.25)	20.7	0.43	(17.9–23.5)
16 Jun	11	2.31	0.176	(1.10–3.30)	23.6	0.78	(16.4–27.1)
20 Jun	8	2.80	0.251	(1.90–3.92)	23.1	0.72	(20.4–26.0)

parturition, mean embryo weight was 0.43 grams, representing only 14.3 percent of the fetal weight at birth. It is clear from these data that most of the prenatal growth occurs in the last three weeks of gestation.

The sex ratio of fetuses did not differ significantly from unity. Before late May sex determination was not possible by external macroscopic examination of the fetus. Sex determinations made on and following 29 May revealed 26 males and 22 females (Chi-square, 0.31, $P > 0.05$). The sexes of five fetuses taken on 29 May could not be determined owing to their exceedingly small size and relatively underdeveloped condition.

Samples from various nurseries were taken from late May through August to assess the reproductive condition of females. The data summarized in table 3 represent the number and percentage of pregnant, lactating, and post-lactating females captured in this interval. Data for Lost Colony and Wilmore are plotted separately (Fig. 6) and form the basis for the following discussion. A median parturition date was estimated when 50 percent of the reproductive females sampled at each location had produced young. In 1969 this date was estimated to be on 21 June both at Lost Colony and Wilmore.

If one assumes that 15 April was the median date for fertilization and 21 June for the median parturition date, then the gestation period for *M. velifer* is approximately 67 days. If individuals that

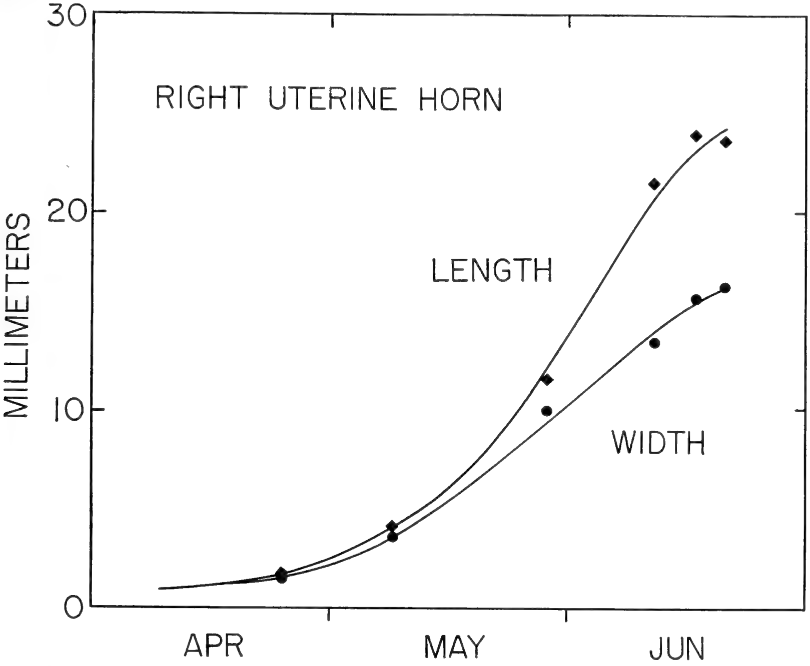

FIG. 5. Period of gestation and pattern of prenatal growth of *M. velifer* expressed as the mean increase in length and width of the right uterine horn (also see table 2).

arrived at Wilmore on 26 March were indeed pregnant and parturition began soon after 11 June, this would suggest a gestation period of approximately 77 days, assuming that these individuals were the first to give birth. Based on the available data, the most reliable estimate probably lies somewhere between 60 and 70 days. Wimsatt (1945) estimated that the gestation period in *M. lucifugus* ranged from 50 to 60 days and Pearson *et al.* (1952) reported the gestation period for *Plecotus townsendii* in California as 56 to 100 days.

Parturition.—The parturition period at Lost Colony and Wilmore extended over a period approximating four weeks in 1969 and corresponded closely to the range of departure dates from hibernacula. Periodic examination of the number of young occupying these two nurseries in June and July supported the contention that most of the young are born within a short period. Nearly 80 percent of the births occurred in a two-week period from 14 to 28 June. On 8 June 1969 no young were present in the nursery at Lost Colony, although approximately 100 and 400 neonates were present on 16 and 17 June, respectively. These data indicate that approximately 300 young were born within a 24-hour period between the nights of 16 and 17 June. Ten days later, on 27 June, there were nearly 4500

TABLE 3. Seasonal changes in the reproductive condition of adult female *Myotis velifer* occupying nursery colonies in Kansas.[a]

	Pregnant		Lactating		Post-lactating		
Date	*N*	Percent	*N*	Percent	*N*	Percent	Location
22-23 May 1970	48	100.0					Wilmore
28 May 1969	230	100.0					Englewood[b]
28-29 May 1969	69	100.0					Wilmore
30-31 May 1969	96	100.0					Lost Colony
8-9 Jun 1969	124	100.0					Lost Colony
9-10 Jun 1969	10	91.0	1	9.0			Nat'l Gypsum Mine
10-11 Jun 1970	42	100.0					Wilmore
16-17 Jun 1969	83	84.7	15	15.3			Lost Colony
18 Jun 1969	56	96.5	2	3.5			Nat'l Gypsum Mine[b]
18-19 Jun 1969	51	76.2	16	23.8			Belvidere
19-20 Jun 1970	147	66.6	68	33.4			Wilmore
21 Jun 1970	266	74.7	90	25.3			Lost Colony[b]
21-22 Jun 1970	45	50.0	45	50.0			Nat'l Gypsum Mine
27-28 Jun 1969	13	12.0	95	88.0			Lost Colony
28-29 Jun 1969	7	7.0	92	93.0			Wilmore
29-30 Jun 1969			210	100.0			Wilmore
7-8 Jul 1969			122	100.0			Lost Colony
8-9 Jul 1969			107	100.0			Wilmore
9-10 Jul 1969			27	100.0			Wilmore
18-19 Jul 1969			153	100.0			Lost Colony
19-20 Jul 1969			10	100.0			Wilmore
27-28 Jul 1969			78	74.2	27	25.8	Lost Colony
28-29 Jul 1969			5	83.4	1	16.6	Wilmore
31 Jul 1969			101	60.4	66	39.6	Double Entrance S[b]
31 Jul — 1 Aug 1969			196	77.5	57	22.5	Protection
6-7 Aug 1969			42	37.5	70	62.5	Lost Colony
7-8 Aug 1969			3	15.7	16	84.3	Wilmore
8-9 Aug 1969			6	10.9	49	89.1	Wilmore
10 Aug 1969			31	14.9	177	85.1	Lost Colony[b]
16-17 Aug 1969					93	100.0	Lost Colony
17-18 Aug 1969					18	100.0	Wilmore
19 Aug 1969			1	0.4	210	99.6	Nat'l Gypsum Mine
20 Aug 1969					189	100.0	Protection[b]
27-28 Aug 1969					11	100.0	Wilmore
31 Aug — 1 Sep 1969					136	100.0	Lost Colony

[a] Non-reproductive females were excluded because they usually represented less than one per cent of any sample.

[b] Roost sample.

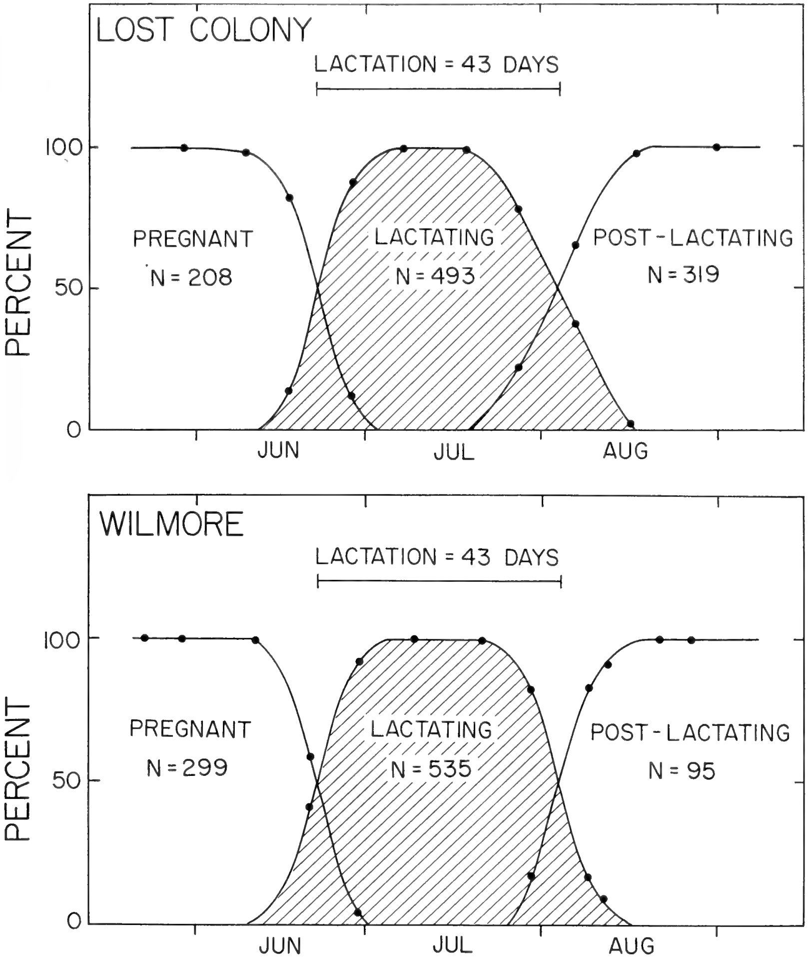

FIG. 6. A comparison of the summer reproductive patterns of female *M. velifer* expressed as the percentage of pregnant, lactating, and post-lactating individuals sampled at Lost Colony and Wilmore. The median parturition date is indicated when 50 percent of the reproductive females had already produced young. The interval between the median parturition date and the median cessation date of lactation represents an estimated individual lactation period.

young ranging from one day to nearly two weeks of age. If 50 percent of the young were born by 21 June this would mean that in the four-day period from 18 to 21 June, an average of more than 500 young were born per day. Similar observations were made at Wilmore. A trap sample taken at an entrance to the National Gypsum Mine on the night of 22 June 1970 (45 pregnant and 45 lactating females) revealed a comparable median parturition date.

Some authors have suggested that yearling females of some species give birth later in the season than older bats (see Griffin, 1940; Pearson *et al.*, 1952; Davis and Hitchcock, 1965). To test the null hypothesis that there was no difference in parturition dates of yearling or adult *M. velifer*, I examined females that had been marked at Lost Colony and Wilmore in 1969 and recovered there between 19 and 21 June 1970. Of 22 adults and 28 yearlings recovered in this period, six adults (27.2%) had already given birth or were lactating and only four yearlings (14.8%) had given birth. A *t* test for the equality of these two percentages was non-significant ($t=1.14$, $P>0.05$) thereby supporting the null hypothesis.

Actual parturition was not observed in the field, although studies conducted in captivity (unpublished observations) concur with those of Twente (1955b) and Wimsatt (1945, 1960a) for *M. velifer* and *M. lucifugus*, respectively. Fresh paper was placed beneath nursery areas at Wilmore in an attempt to determine if the placentae were dropped or eaten. The fact that few were found beneath roosts occupied by several hundred young is circumstantial evidence that placentaphagia is practiced by *M. velifer*.

Nursing.—Soon after parturition, females begin to nurse their young. A noticeable decrease in the intensity of audible vocalizations was observed between 0800 and 1000 and again between 1500 and 1800 in the Wilmore barn. I have interpreted this to indicate two nursing periods; one follows the return of females in morning and another occurs in late afternoon. The evidence is circumstantial, but it seems reasonable that a reduction in vocalization would occur when young are nursing. Also, between 1100 and 1300 hours I observed a large proportion of adult females occupying open-faced joists adjacent to the areas mostly occupied by both young and adults at other times. Based on samples of young and the amount of milk found in their stomachs during the daytime, Davis *et al.* (1962) suggested that female *Tadarida brasiliensis* have two daily nursing periods.

In the first weeks following parturition, many female *M. velifer* return to their young within an hour or two after emergence; whether or not nursing takes place at this time was not established. When females departed in the evening, little milk could be expressed from the mammary tissue, whereas females returning to the roost after 0400 appeared to have fully distended mammary glands.

Little is known concerning the length of time females nurse their offspring. The lactation period may be approximately 43 days (or six weeks) if one assumes that the time interval between the estimated median parturition date and the median cessation date of lactation represents the average for an individual (Fig. 6). Most young begin to forage well before the age of six weeks (see section on Growth and Development). And, evidence based on captures of

TABLE 4. Annual reproductive effort of female *Myotis velifer.*

Date	Females	Reproductive females[a]	Percentage of reproductive females
20-31 May	443	443	100.0
1-10 Jun	180	177	98.4
11-20 Jun	242	240	99.2
21-30 Jun	861	861	100.0
Total	1,726	1,721	99.9

[a] Pregnant and lactating females (table 3) sampled from late May through June; reproductive activity (pregnancy and lactation) was determined by palpation.

foraging young suggests that they continue to nurse after they have become volant.

Reproductive effort.—Yearling and adult females captured at all nurseries were pooled at 10-day intervals from 20 May through 30 June for an analysis of annual reproductive effort (Table 4). These data, coupled with the fact that only a few barren females were found, indicate that most adult female *M. velifer* in the population are reproductive and also that females reach sexual maturity in their first year. If non-reproductive females remain solitary or occupy other sites separate from nurseries then the annual reproductive effort of 99.9 percent may be an overestimate. Some pregnant females, which had aborted or lost their offspring at birth, may have been considered as non-reproductive individuals upon external examination. If these individuals were counted as non-reproductives, but in reality had been parous, then the overestimate resulting from the possibility of a greater proportion of non-reproductives at other locations is offset.

Growth and Development

GROWTH PATTERNS

Growth curves and descriptive parameters based on 90 paired records for body weight, forearm, and fifth finger are shown in figure 7. Relative growth is expressed as the percentage of body weight and size of adults from samples taken in mid-August (Fig. 9). For linear measures (forearm and fifth finger), relative growth is based on curves shown in figure 7. Relative changes in body weight were based on sample means shown in figure 8 and tables 5 and 6. Data for both sexes were combined in the analysis because there were no significant differences in weight or linear measures in the early stages of post-natal development. Unless otherwise indicated, linear measurements are based on values extrapolated from the computed curves. It should be understood that these curves repre-

TABLE 5. Body weight, wing size, and wing-loading of known age, pre-volant juvenile *Myotis velifer* (means and standard errors).[a]

Age (days)	N[b]	Forearm (mm) $\bar{x}$	SE	Fifth finger (mm) $\bar{x}$	SE	Weight (gm) $\bar{x}$	SE	Wing area (cm^2) $\bar{x}$	SE	$\bar{x}$ wing loading (gm/cm^2)
1-2	89	17.0	0.09	19.0	0.11	3.2	0.03	10.75	0.53	.298
11-12	26	30.5	0.21	32.5	0.26	7.6	0.12	31.09	0.89	.245
21-22	26	41.3	0.29	48.5	0.39	10.6	0.21	82.58	1.38	.128

[a] Samples are based on recaptured individuals that were initially marked when approximately one to two days old.

[b] Each sample size for wing area was 10.

sent best fit approximations to the observed data, and that variation due to errors in measurement and stochastic properties are inherent.

Bats that had been marked as neonates seldom were recovered in the roost area more than twice. Of 175 neonates marked at Lost Colony in 1969, 90 recoveries of 64 individuals were made. Loss of bands may account for a low recovery owing to the fact that bands may slip over the wrist of neonates before wing dimensions reach sufficient size to hold them in place. However, only two lost bands later were found beneath the roost. Apparent "loss of bands" may occur if mothers move their young following disturbance (see Roer, 1968; Fenton, 1969a; Davis, 1970), and account for a low recovery of non-volant young. After young became volant, the probability of recovering them (while foraging or at entrances) is even lower.

On the day of birth the calculated lengths of the forearm and fifth finger were 16.0 and 18.0 mm, respectively. (The forearm measured approximately 34% of the adult size, whereas the fifth finger was only 29%.) By three weeks of age the forearm exceeded 80 percent of the adult size and by the fourth week, when most of the young had begun to forage, the forearm (43.0 mm) had reached 90

TABLE 6. Seasonal changes in body weight of volant, juvenile *Myotis velifer* (means and standard errors).

Date	Males N	Males Body weight $\bar{x}$	Males Body weight SE	Females N	Females Body weight $\bar{x}$	Females Body weight SE
18 Jul 1969	17	10.4	0.26	16	10.4	0.34
27 Jul 1969	49	10.7	0.12	58	10.7	0.11
6 Aug 1969	59	9.8	0.11	40	10.2	0.15
16 Aug 1969	34	10.2	0.13	38	10.4	0.14
31 Aug 1969	36	11.8	0.11	53	11.9	0.09
7 Sep 1969	35	12.0	0.11	52	12.4	0.07
18 Oct 1969[a]	55	14.7	0.17	----	----	----
18 Oct 1969	30	15.3	0.25	----	----	----

[a] Taken in a hibernaculum.

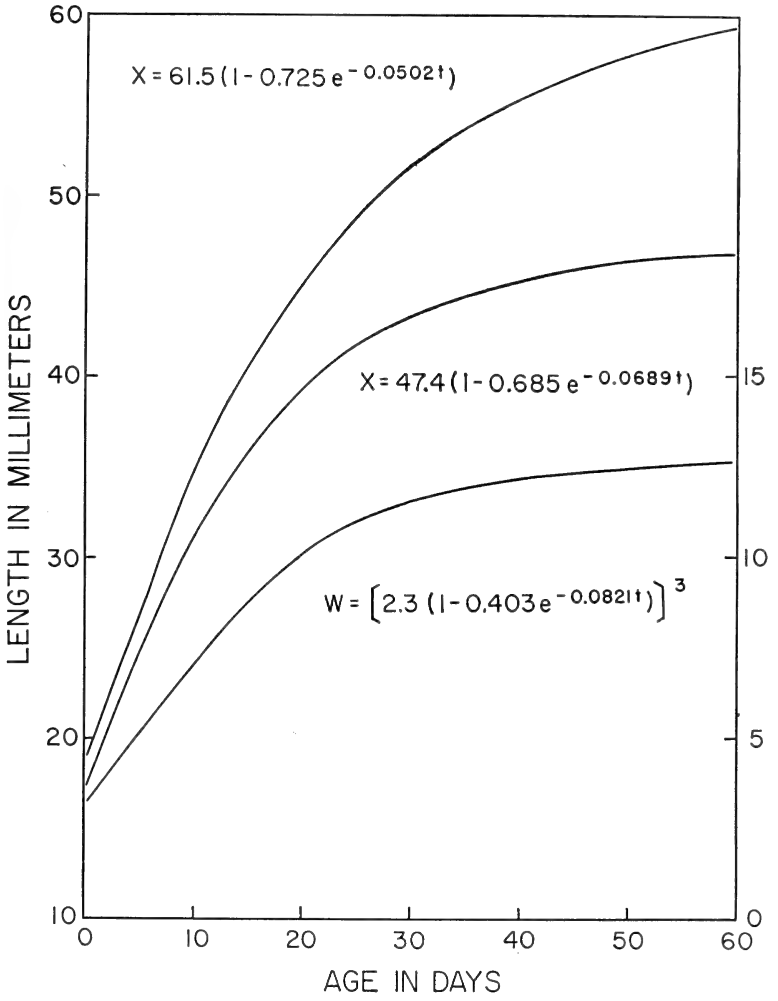

FIG. 7. Growth of juvenile *M. velifer*. The growth curves from top to bottom are fifth finger, forearm, and body weight, respectively. The growth equation for linear measures is expressed by the general formula $X=a(1-be^{-kt})$ where X is the length in millimeters and t is the number of days of growth. The growth equation for body weight is expressed by the general formula $W=[a(1-be^{-kt})]^3$, where W is the 2/3 power of body weight, and t is the number of days of growth. The quantities a, b, and k in both equations are parameters—a, a measure of the asymptotic size; b, a measure related to the size of the animal at birth; k, a measure of the intrinsic rate of growth, and e, the base of natural logarithms.

percent of adult size. In contrast, the fifth finger did not reach an equivalent proportion until the fifth or sixth week. By the time young were 60 days old (approximately mid-August for most) the forearm and fifth finger had reached 98 and 96 percent of adult size, respectively. The fifth finger, as well as other digits, probably continues to grow at least until late August or early September. This corresponds to the time that closure of the phalangeal epiphyses becomes evident in field examinations. The asymptotic size for the forearm (47.4 mm) and fifth finger (61.5 mm) was reached in approximately 70 days. These calculated values for asymptotic size may be slightly larger than adult means although they do fall within the ranges for the forearm (43.6-48.6) and fifth finger (57.3-62.5) recorded from recently killed and live specimens. Linear measurements based on live individuals are slightly larger than those recorded from dried specimens; for comparison see measurements of *Myotis velifer* recorded for preserved specimens from Kansas by Hayward (1970).

Absolute growth rates for the forearm and fifth finger are shown in table 7. Ten-day intervals were selected to depict relative changes in growth over the 60-day period. In the first 10 days, growth of the forearm and fifth finger was nearly linear. Average increases of 1.56 and 1.71 millimeters per day for the forearm and fifth finger, respectively, can be noted; growth rates in the subsequent 10-day intervals were measurably less.

The computed growth curve for weight was compared with samples of body weights taken at intervals throughout the growth period (Fig. 8). It is evident that the computed curve only represents a general trend and that actual changes in weight after young became volant were obscured in the process of curve fitting. For this reason, relative changes in body weight (Fig. 9) were based on data presented in figure 8. The estimated weight of young at birth is 3.0 grams, approximately 25.8 percent of the weight of post-parturiant females. This value differs slightly from the mean (3.2 gm) shown in table 5, although the discrepancy can be accounted for by the fact that this sample included some individuals that may have been older than one day. By the time individuals were one week old they had reached 50 percent of their adult weight; at three weeks of age they exceeded 85 percent of adult weight. Increases in body weight

TABLE 7. Absolute growth rates of the forearm and fifth finger of *Myotis velifer* expressed in mm/day at ten-day intervals.[a]

Age interval (days)	Forearm (mm)	Fifth finger (mm)
1-10	1.56	1.71
11-20	0.81	1.07
21-30	0.34	0.64
31-40	0.21	0.39
41-50	0.10	0.23
51-60	0.05	0.14

[a] Rates were computed from data on growth curves shown in figure 7.

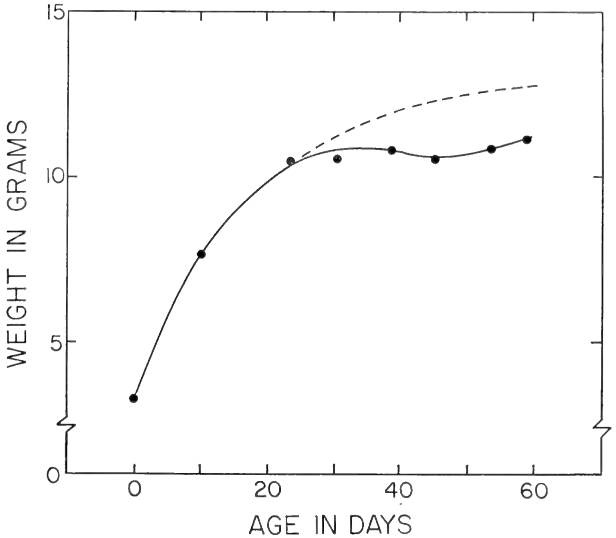

FIG. 8. A comparison of the calculated and realized increase in body weight of juvenile *M. velifer.* The realized increase in body weight is shown by the solid line (closed circles) and represents an eye-fit construction based on sample means (see table 6). The predicted pattern (which includes the dotted line in addition to the early phase of the realized increase) was computed from mark-recapture data using the von Bertalanffy growth analysis. See figure 7 and text.

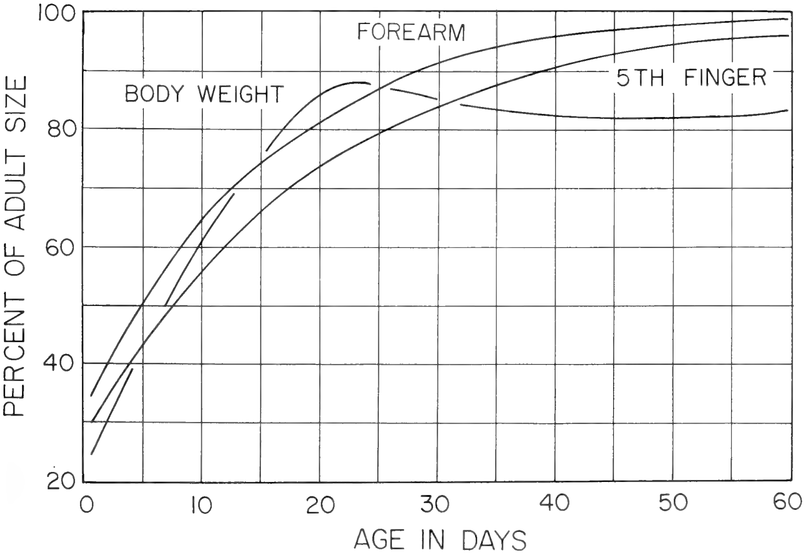

FIG. 9. Growth of juvenile *M. velifer* expressed as the percentage of mean body weight, forearm, and fifth finger of adults taken in mid-August.

were nearly linear for the first three weeks. Based on data in table 5, absolute increase in body weight in this period was 0.36 grams per day. By the fourth week, when most young were foraging, body weight decreased and then stabilized between 82 and 86 percent of the adult weight; subsequent increases were not evident until fat deposition began in late August.

Physical Development

Skin and Pelage.—At birth the body is pink, but the wings, interfemoral membrane, distal portion of the ears, and the anterior facial regions are pigmented (pale to dark brown). Short, whitish hairs are scattered over the dorsum, but the most densely haired region is at the base of the interfemoral membrane. Short scattered hairs also are present on the venter but are comparatively shorter and less dense than those on the dorsum. The facial vibrissae and hairs on the feet are relatively well developed.

At the age of one week the hairs on the dorsum have increased in length and density and are brownish gray in color; the longest and densest hairs still are located at the base of the interfemoral membrane. Hairs on the venter are whitish-gray, although still relatively short and sparse. Although skin on the venter remains pink, some areas on the dorsum are lightly pigmented and appear brownish. The vibrissae and hairs on the feet have become increasingly long and stiffened.

By two weeks of age the dorsum is almost completely covered with short, dense, brownish-gray pelage; the hair on the venter also has increased in length and density. Little change is evident in the amount of pigmentation of the membranes, although the skin on the forearm is paler and more adult-like in appearance. The skin on the venter remains pink, but the dorsal skin has become increasingly pigmented and now appears bluish-gray.

At the age of three weeks the hair on the dorsum has become distinctly bi-colored, characterized by a dark brown basal portion and pale brown terminal part. The hairs on the venter are whitish-gray and the skin has darkened. By four weeks the skin on the dorsum is again pink in color, and the pelage is plumbeous in appearance and characterized by a dense, dark undercoat and longer overhairs. The hairs of the venter also are bi-colored, with a dark gray base and a whitish-gray terminal portion; the skin of the venter remains darkly pigmented.

Between the ages of three and four weeks the pelage of some individuals becomes faded. By late July or early August the bicolored appearance is no longer recognizable and the pelage also appeared to be less dense than when individuals first became volant.

By the time juveniles have become nutritionally independent (at approximately six weeks), a juvenile molt is initiated. Although this molt extends from early August through late September, only a few individuals have actually begun to molt by the first week of August. The initiation of molt is characterized by a darkening of the skin. Darkening occurs first on the dorsum and then on the venter; replacement of dorsal pelage usually was well underway before the ventral skin darkened. Of 288 individuals examined in mid-August, 130 (45%) showed some sign of molt; by late August some had nearly completed molt, but others had only begun. By the third week of September the pelage of many juveniles was indistinguishable from that of adults.

Dentition.—At birth, *M. velifer* may or may not have a full complement of deciduous dentition. Maximum development of deciduous teeth usually was reached in the first week. Loss of these teeth began at the age of 10 to 12 days; concurrently, some permanent teeth began to erupt lingual to the deciduous dentition. The general description, sequence of loss, and eruption in *M. velifer* generally follow that reported by Fenton (1970) for *M. lucifugus*. By the time individuals were four weeks old all permanent teeth had erupted, although teeth were not well developed until the age of seven to eight weeks.

INFANT SOCIAL BEHAVIOR

The social organization of neonates apparently is influenced by their physical development, motor coordination, and sensory capacity. Young *M. velifer* have relatively poor motor coordination in the first few days after birth and movements in the roost are restricted. Observations made after adults had departed suggest that the smallest young (presumably the youngest) do not move from areas where they apparently have been left by their mothers. By the time young were approximately two days old, their motor coordination had improved considerably inasmuch as most could crawl rapidly over the roost substrate.

Following evening departure of the mothers, young (those older than two days) usually formed dense clusters along natural crevices comprising the roost substrate. In contrast, the smallest (youngest) bats remained scattered, and made little apparent effort to join the clusters of older bats. As an experiment to test the mobility and social instinct of young bats, a number of individuals judged to be more than two days old were moved from clusters which they occupied. Within a few minutes most of these bats returned to a nearby cluster (not necessarily the one from which they had been removed). In contrast, bats that were approximately one day old and displaced from their site of occupancy made little or no attempt to move except to establish a firmer grip on the substrate.

Maternal-Infant Relationship

Apparently the maternal-infant bond is closely maintained in the first few hours after birth. Mothers may not depart to feed on the day of parturition, especially if birth has only taken place within a few hours of the emergence period. Observations made at Wilmore indicated that some mothers, having recently given birth, remained with their young until all other females had departed. Females may not depart until their newly-born offspring have been thoroughly groomed and the placenta has been discharged. This behavior also may reduce the chances of neonates being dislodged from roosts during emergence activity (Kunz, 1973).

I found no evidence that female *M. velifer* carried their newborn young while foraging, despite the fact that Twente (1955b) suggested that they may do so for the first few days. Of more than 1000 post-parturiant females trapped at colony entrances in the course of this study, only 12 were carrying young. In each instance, the circumstance could be accounted for by some previous disturbance (entry into the nursery area, banding, or handling young).

From birth until the age of six weeks, young bats undergo marked changes in behavior from a complete maternal dependence in the first day to complete independence at the age of six weeks. The curved, reticulated milk teeth, the well-developed claws on the hind feet and the first finger of newborn facilitate a tenacious attachment to their mother. In the first week, young usually occupy a place beneath their mother's wing. Because pelage of infants is still sparse and poorly developed, this behavior may be important in heat transfer from mother to infant. By the time young have become more densely furred (at the age of one to two weeks) they may hang beside their mothers or on her back.

Initiation of Flight

Young *M. velifer* initiated flights within the confines of their roost at the age of three weeks. Simulated flight motions prior to this were made when individuals extended their wings laterally, forcing them in a down-stroke, and simultaneously lifting their bodies upward. Repetitive movements of this type were observed rather frequently. Young bats would hold a "stretch-and-push" position for nearly five seconds and repeat it up to six times within a period of a few minutes; concurrently they lifted their heads and opened their mouths as if they were echolocating. Gould (1971) observed this head-lifting behavior and sound emission and suggested that this motor pattern probably permitted young bats to test their physical surroundings before initiating flight.

Few young bats emerged on evening foraging flights before mid-

July, although a number of individuals began making short flights within the roost in the first week of July (Kunz, 1973). This preflight behavior was common prior to the time that young bats actually departed to feed and was characterized by straight-line flights (from two to five meters in distance). Individuals often shifted from one roost to another regaining altitude after initially dropping from their roost. Several days after straight-line flights were initiated some individuals began to make turning maneuvers and sustained flight for extended periods.

Flight not only depends on sufficient behavorial readiness but also on physical development. Because camber of the wing is produced by the flexion of the phalanges and particularly that of the fifth finger (Vaughan, 1959), flight efficiency and maneuverability would be expected to improve with physical maturation. One requirement of flight is the development of a wing surface that can be held rigidly against the force of an air stream (Vaughan, 1959, 1970). Therefore, until the fifth finger can be held in a stabilized position, the development of camber probably is one factor limiting early flight activity.

Wing-loading.—The fact that low wing-loading permits bats to fly at relatively low speeds is clearly advantageous to young in early stages of flight. The wing area of one to two-day old *M. velifer* is 10.75 cm^2, which is approximately 10 percent of the adult wing area (Kunz, 1971). By the time young are three weeks of age the wing area is nearly 76 percent of adult size, and corresponds to the proportion of 76.6 percent given for *M. myotis* when flight was initiated at the age of three weeks (Krátky, 1970). By comparing wing-loading of pre-volant young with maximum adult wing-loading, it is evident that juveniles reach adult-like loading near the time they initiated flights within the roost (Fig. 10).

Although changes in body weight remain negligible from four to five weeks (Fig. 8), wing elements continue to increase in size after flight has been initiated (Fig. 7). This suggests that wing-loading will remain low, at least until fat deposition begins in late August. Because the wing area is directly correlated with the dimensions of the wing elements, the wing area would approach 96 to 98 percent of adult size at the age of 60 days. By selecting an average of 97 percent for the adult wing area (104 cm^2), and a mean body weight of juveniles at the age of 60 days (10.2 gm), juvenile wing-loading at this time would be approximately 0.97 gm/cm^2. This value is considerably less than measures for pre-volant bats (Table 5) but closely approximates the wing-loading of adults taken in spring roosts (Kunz, 1971). Low wing-loading values up until this time, when young are developing flight proficiency and beginning to secure resources, would have an obvious selective advantage.

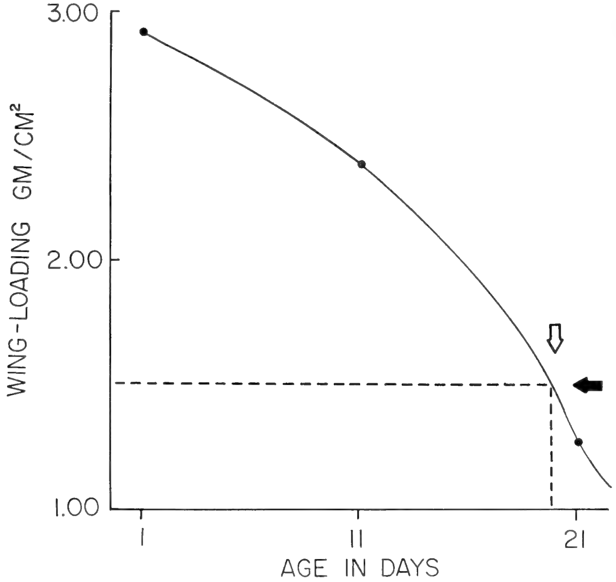

FIG. 10. Wing-loading of juvenile *M. velifer*. Maximum adult wing-loading is shown by the solid arrow, and the age at which adult-like wing-loading is achieved by juveniles is shown by the open arrow. The graph is based on data in table 5 and data for wing-loading computed for adults (Kunz, 1971).

INFANT MORTALITY

Infant mortality may be high during the first few days after birth. Before young have well developed motor coordination, some individuals may fall or be dislodged from their roost by older bats. Several dead and dehydrated young were found beneath the roost at Wilmore in the summer of 1969. Whether these individuals had died on impact, were stillborn, or were abandoned after unsuccessful attempts to retrieve them could not be determined; all appeared to be physically well formed.

Young that fall from their roosts may be susceptible to predation, drowning, or abandonment. At sites where nursery roosts are located over water (National Gypsum Mine), young that fall from the ceiling probably succumb. Young bats that fall into wet guano also may die before being retrieved. Only when areas beneath roosts are relatively dry, do neonates have a good chance of being recovered. In June 1970, I observed a neonate that had fallen to the floor at Wilmore from a height of approximately three meters. Soon afterward, an adult bat (presumed to be its mother) made several low, sweeping flights around the fallen young. She landed over it with her wings outstretched and after approximately three minutes flew from the ground, returning the neonate to the roost above. Successful retrieval may depend in part on the size of infants and on their relative physical condition. Females may not be able to carry large young or those that are weak or injured and unable to assist in a retrieval.

Infant mortality is difficult to assess because an undetermined loss may result from predation. In the summers of 1969 and 1970, rat snakes *(Elaphe guttata)* were encountered in the nursery area at Lost Colony. Only in 1970 were snakes found that had actually eaten neonates that apparently had fallen to the floor of the cave. In each instance these observations were made soon after adults had departed to feed; perhaps these young were dislodged from their roost at the time of emergence activity.

DISCUSSION

Reproduction

MALES.—Judging from the changes in size of the epididymides and testes (Fig. 1), and observations in the field, copulation occurs mostly in September and October. Evidence that copulation had occurred by mid-October was based on the occurrence of a wet vaginal region or the occurrence of dried semen on the venter of females. Krutzsch (1961) noted that copulation in this species also may occur during wakeful periods in winter and it has been suggested that the intermittent activity in "warm rooms" of hibernacula (Twente, 1955b) may serve a reproductive function. The decrease in size of the epididymides throughout the winter supports these observations. Sperm resorption and tubular involution may account for some of the decrease in size in this period. Observations in spring suggest that some copulation occurs at this time. Guthrie (1933) observed copulations of *Myotis lucifugus* in spring, and Rice (1957) suggested that spring copulations in *Myotis austroriparius* may function to ensure the insemination of yearling females. Further studies are needed to detail the reproductive activity of male *M. velifer* and other species, especially upon arousal from hibernation.

The time required for the development of sexual maturity in males has not been widely studied. Apparently, *M. velifer* does not produce mature spermatozoa in their first autumn (Krutzsch, 1961). Christian (1956) indicated that male *Eptesicus fuscus* are sexually active in their first autumn although in other species, including *M. lucifugus* and *M. grisescens* (Miller, 1939), *Plecotus townsendii* (Pearson, *et al.*, 1952), *M. myotis* (Sluiter, 1961), individuals apparently do not become sexually mature until their second autumn. Fenton (1969b) observed young *M. lucifugus* copulating in autumn, but whether or not these copulations resulted in pregnancies was undetermined. Studies where young bats can be marked soon after birth and later recovered and compared histologically are needed to detail sexual maturation in males.

The seasonal differences in sex ratios and the observed shift in the proportion of males at Lost Colony and Wilmore (Table 1) may be correlated with the onset of gonadal development in summer. It has been documented in other mammalian groups that spermatogenesis is retarded at high temperatures where a breakdown in important enzyme systems has been implicated (Glover and Young, 1963). Detrimental effects from exposure to high environmental temperatures in summer could interfere with spermatogenesis. Because spermatogenesis is sensitive to localized increases in temperature, solitary behavior and occupation of cooler caves could be an important reproductive strategy for males.

Data from the National Gypsum Mine indicate that adult males are less gregarious than females in summer, and furthermore, that most occupy relatively cooler roost sites than females. Body temperatures of males thus could potentially remain cooler than if they occupied active clusters or roosted in areas that were susceptible to high ambient temperatures. It is of interest that comparatively few males occupied the Wilmore barn which was subject to higher temperatures than at Lost Colony. Perhaps the existence of higher temperatures at Wilmore explains why proportionately more males departed from this site before they did from Lost Colony. If yearling males do not become sexually mature until their second autumn (Krutzsch, 1961) this might be explained, in part, by the fact that they do remain at nursery roosts throughout their first summer and are therefore exposed to higher temperatures.

Females.—The absence of differences in parturition dates or duration of lactation at Lost Colony and Wilmore (Fig. 6) suggests that factors influencing the timing of reproductive activity for these two nurseries in 1969 were similar. Both nurseries were occupied by approximately the same number of adult females in 1969, but the population at Lost Colony in late May and early June was larger than at Wilmore owing to the greater number of males (Table 1). Although this difference may only reflect the behavior of males in response to different thermal environments at this time of year, the presence of the larger total population at Lost Colony also may contribute to a greater increase in temperature at the cave than otherwise may be possible in the absence of males. Perhaps the presence of males is important initially to the successful occupation of a relatively cool cave in spring.

It has been demonstrated that low temperatures are capable of retarding embryonic development and extending the gestation period in bats (Eisentraut, 1937; Racey, 1969). Wimsatt (1969) noted that females may be more susceptible to cold depression in early stages of pregnancy, and that lengthening of gestation may involve arresting early stages of embryonic development, rather than later when complex placental relationships have become established.

To assess the possible influence of environmental factors on gestation, I compared median parturition dates at Lost Colony and Wilmore in two different years. In 1969, the median parturition date at both nurseries was estimated to be 21 June (Fig. 6). Between 19 and 22 June 1970, samples again were taken at these two nurseries to compare with estimates for these dates in 1969. Of 356 females taken at Lost Colony on 21 June, only 90 (25.2%) were lactating, whereas at Wilmore on 19-20 June, only 68 (33.4%) of 215 females had given birth, revealing that gestation likely was longer at both sites in 1970 than in 1969 or that it began later in the spring.

When mean minimum ambient temperatures in April and May were compared for the two years, it was found that temperatures in early spring 1970 were slightly cooler than those in 1969. In April and May 1969, the mean minimum temperatures were 7.2° C and 13.2° C, respectively, and in April only one day was recorded as having a temperature below freezing. In spring 1970, the mean minimum temperatures for April and May, respectively, were 6.2° C and 13.4° C, and five days in April were recorded as having temperatures below freezing. The differences recorded in April were small but they may have been enough to account for the difference in gestation periods in the two years. The fact that there were five days in April 1970 where temperatures were recorded below 0° C may be the most important consideration.

When the 1970 percentages of post-parturiant females at Lost Colony and Wilmore are compared, the proportion of lactating females at the former (25.2%) is less than the proportion at Wilmore (33.4%). The fact that the sample at Lost Colony was taken a day later than that for Wilmore suggests that even fewer lactating females would have been found there had samples been taken on the same dates. Although the null hypothesis that there was no difference between these two percentages was accepted ($t=1.64$, $P>0.05$), the above data suggest that gestation may have been further delayed at Lost Colony. It is of interest that the population densities at each nursery in 1970 were reduced from their 1969 levels; the estimated population at Lost Colony in June 1970 was approximately 2000 adult females, compared to approximately 5000 in 1969 (Kunz, 1971). At Wilmore, the 1970 population also was lower than in 1969 but the reduction was less than at Lost Colony. Considering the fact that bats can increase the micro-temperature of their own roost and that populations in 1970 were reduced from the previous year, the size of the resident population may influence the duration of gestation.

Smith (1956) reported significant differences in the weight gains of pregnant *Myotis lucifugus* in two different years. The fact that she found no correlation between ambient temperature and weight gain in the two years suggests that the observed difference in weight gain may be accounted for by the difference in population size in the two years of study (see Smith, 1954). Clustering behavior and maintenance of high metabolic levels usually are characteristic of females late in pregnancy (Smith, 1956; Stones and Wiebers, 1967). Herreid (1967) has shown that energy cost is less among individuals of *Tadarida brasiliensis* occupying large clusters than those in small clusters or singles. Perhaps when a nursery colony is reduced in size, and fewer bats are present to cluster, more energy is expended in maintaining homeothermy, and proportionately less is available for development. Additional studies involving examination of pregnant females in spring are needed to fully assess the influence of clustering behavior, population size, and ambient temperature on rates of gestation.

Daily production of milk probably reaches maximal levels in the second or third week following parturition and corresponds to the increasing size of the young and the increased food consumption at this time (Kunz, 1973). Davis *et al.* (1962) suggested that female *Tadarida brasiliensis* may produce an amount of milk equivalent to 16 per cent of their lactating body weight within a 24-hour period. Based on the 12 gram average weight of lactating *Tadarida* (Short, 1961), daily milk production per female should be in excess of 1.9 grams. Since Davis *et al.* (1962) also reported an average weight increase from daily food consumption of only one gram, there is little doubt that their estimation of milk production was too high or, alternatively, that their evaluation of food consumption was too low. Although I have no comparable data on milk production for *M. velifer,* my estimates on daily food consumption for lactating females (Kunz, 1973) suggest that their estimate of food consumption for *Tadarida* (a bat comparable in size to *M. velifer*) was much too low.

Growth and Development

Few studies provide data on growth of known-age bats under natural conditions. Because the forearm has been the most consistently measured element in growth studies, comparisons of the relative stages of development of several species were made at birth and at the age of six weeks to illustrate the similarity in growth. The forearm of *M. velifer* at birth and at six weeks are 34 and 96 percent, respectively, of adult size. Proportions based on data given for *Antrozous pallidus* (Davis, 1969) at birth and at six weeks are 32 and 96 percent, respectively. Corresponding values for *Plecotus townsendii* are 38 percent at birth and 98 percent at the age of six weeks (Pearson *et al.,* 1952). Similar proportions based on data presented by Krátky (1970) for *M. myotis* are 37 percent at birth and 98 percent at six weeks. This evidence illustrates the similarity of developmental stages at the time of birth and at the time when young bats probably are weaned.

Pearson *et al.* (1952) reported an absolute growth rate of 0.85 mm per day for the forearm of *Plecotus townsendii* in the first 16 days of growth, and Davis *et al.* (1968) reported that some individual *Eptesicus fuscus* showed increases in forearm length in early stages of growth up to 2.6 mm per day. Based on data extrapolated from growth curves presented by the above authors, I have computed for comparison absolute growth rates for the forearm in the first 10 days. Rates of 1.20 mm per day for *Plecotus townsendii* and 1.45 for *Eptesicus fuscus* generally are comparable to the value of 1.56 determined for *M. velifer.*

At birth, the proportion of body weight of young to the weight of post-parturiant female *M. velifer* (25.8%) closely approximates the proportions for *M. lucifugus* (24.6%) and *M. nigricans* (25.6%) recorded by Wimsatt (1960b) and Wilson (1971), respectively.

In the first two months of post-natal life, maximum body weight of *M. velifer* is attained at the age of three to four weeks. Loss of weight after this time seems to be common as it has been observed both in field and laboratory studies (Short, 1961; Kleiman, 1969; Davis, 1969; Krátky, 1970). Short suggested that this decrease may be accounted for by loss of body fats after young have become volant. The fact that similar decreases have been observed under conditions of laboratory confinement (Kleiman, 1969) suggests that nutritional conditions at time of weaning are important. Thus weight loss under natural conditions in this period may be accounted for by a combination of factors related to the weaning period and early flight activity, including reduced milk consumption, expenditure of accumulated fats, and inefficient insect capture (Kunz, 1973). Perhaps the deposition of fat in early developmental stages, and prior to the initiation of flight, is an important strategy that helps sustain juveniles through the weaning period.

Davis and Hitchcock (1965) observed that juvenile *M. lucifugus* continued to nurse after they had become volant and similar observations have been reported for *M. mysticinus* and *M. daubentoni* (Nyholm, 1965). The fact that volant young *M. velifer* contained both milk and the remains of insects (Kunz, 1973) suggests that weaning does not take place abruptly at the time young initiate foraging activity. Vocalizations that Gould (1971) recorded suggest that weaning may be initiated by the withdrawal behavior of young (weaning in *M. lucifugus* and *Eptesicus fuscus* apparently took place at the age of three weeks under conditions of laboratory confinement). Kleiman (1969) observed that weaning of *Eptesicus serotinus* and *Pipistrellus pipistrellus* in captivity began in the third or fourth week but was not completed until two to three weeks later.

Unusually long nursing periods have been reported for some bats reared in captivity (Eisentraut, 1936; Kleiman, 1969; and others). Differences in weaning time between captive bats and those under natural conditions may be due to artifacts resulting from nutritional deficiences existing under laboratory confinement.

Juvenile *M. velifer* began feeding on insects near the time when permanent teeth were fully erupted (approximately 3-4 weeks); however, adult-like feeding behavior and success (Kunz, 1973) was not achieved until permanent teeth were fully developed (approximately 7-8 weeks). These observations are in contrast to those of Krátky (1970) who reported that permanent teeth in *M. myotis* were fully erupted in 30 days and that they did not begin to feed on insects until the age of 40 days (approximately 7 weeks). Continued linear growth and stabilization of body weight soon after foraging is initiated in *M. velifer*, results in a low wing-loading, and probably is important in leading to the development of successful feeding behavior.

Two generations of hair in the juvenile pelage were evident—over-hair, that began development in the prenatal period, and under-hair which appeared at approximately one week. A second generation apparently began as early as seven days as evidenced by darkening of the skin (melanin deposition).

A juvenile molt was initiated at approximately six weeks (when young bats had become nutritionally independent) and was not completed until September (10 weeks). These observations correspond to those reported by Mazák (1963) who noted that termination of hair growth in juvenile *M. myotis* coincided with the time that external measurements reached adult size.

Although parturition in this study occurred over a period of four weeks, there was no evidence of age segregation beyond the fact that the young less than two days old did not join older bats in forming clusters. The fact that juveniles less than two days of age were found scattered in peripheral areas suggests that either females intentionally deposit newborn young away from the densest part of the colony, or that the older young are more mobile and have a strong tendency to cluster. It seems likely that mothers would be able to locate their newborn easily if the latter were solitary, especially before the young have developed a reciprocal vocal response to their mothers' calls. Dwyer (1963) suggested that the behavior of females to deposit young on the periphery of nursery clusters may reduce the mortality of neonates by decreasing the probability of being dislodged by larger, more active individuals. Gould (1971) theorized that if bats remained organized into different age groups corresponding to the time of their birth, such behavior also may facilitate mothers recognizing their young as they returned from feeding.

Environment and Growth

Nursery sites that can be maintained at temperatures near thermal neutrality probably are important to the promotion of rapid growth in young. Also, less energy would be required for the maintenance of homeothermy at such temperatures. The selection of warm nursery roosts along with clustering behavior probably contribute measurably to a reduction in energy cost to individuals (Herreid, 1963, 1967). Cluster formation in nurseries not only provides a potential avenue for conductive and convective heat exchange for the enhancement of growth (Dwyer and Hamilton-Smith, 1965) but also in promoting efficient digestion and assimilation of food (Twente, 1955b; Davis *et al.*, 1962).

One of the initial designs of this study was to examine the relationships between growth and roost microclimate at Lost Colony and Wilmore. Efforts to obtain comparative temperature data at Lost Colony, however, were not completely successful. Measurements that were comparable are those from hygrothermograph records (Fig. 2). These data demonstrate that cave temperatures at Lost Colony remained near 20° C. Because bats at Lost Colony maintained high activity levels in daytime, I assumed that cluster temperatures (body surface temperatures), at least during and subsequent to parturition, would be similar to those recorded at Wilmore. If this assumption is valid, and individuals at Lost Colony had body temperatures in daytime between 32 and 37° C, body temperature-ambient temperature differentials would be expected to vary from 12-17° C. At Wilmore daytime differentials ranged from 5-12° C in the nursery period (see insert Fig. 3). If, on the average, higher temperature differentials are needed to maintain cluster temperatures at Lost Colony, then the energy cost of occupying Lost Colony would be greater than for occupying Wilmore. And, any difference in energy cost in occupying these two sites may be reflected in different growth rates, reproductive periods, or quantities of daily food consumption.

In spite of the apparent thermal differences at Lost Colony and Wilmore a seasonal comparison of reproductive parameters at these two sites (Fig. 6) suggests that there were no differences in reproductive chronology. The fact that parturition began at approximately the same time, the median parturition dates were the same and the lactation periods were comparable further suggests that post-natal growth rates may have been similar.

If early flight of young bats can be used as a measure of comparable growth, then I would suggest that there was no measurable difference in growth rates at these two nurseries in 1969. On 7-8 July and 8-9 July 1969, when young bats were first captured while departing to forage, approximately the same number of individuals was trapped at entrances in a comparable period or time; five were taken at Lost Colony and six at Wilmore. Because both nurseries were occupied initially by the same number of young (approximately 5000), these data suggest that the same proportion of individuals in these two colonies reached flight stage at the same time. Mean forearm lengths of the earliest volant young trapped at Lost Colony (43.6 ± 0.56) and Wilmore (43.2 ± 0.70) are not significantly different ($t=0.54$, $P > 0.05$).

Based on observations of Pearson *et al.* (1952) that *Plecotus townsendii* grew more rapidly at warmer temperatures, and the fact that Herreid (1963) recorded increases in cave temperatures throughout the nursery period, Herreid (1967) postulated that bats born in the early part of the parturition period would grow more slowly than those born later. To test this hypothesis groups of neonates that were born at Lost Colony both in the early and late stages of the parturition period were individually marked. One group consisted of individuals taken on 17 June, when approximately 300 (16% of the total juvenile population) had been delivered. The second group was taken on 27 June, after approximately 4500 (more than 90%) young were present. If growth rates differed according to the time of birth, I expected to find differences in the first three weeks since the most rapid growth occurs during this period (Fig. 8). Individuals marked as neonates on the above dates were recovered at intervals of 10 and 20 days after initial marking. Of all paired comparisons made (using a *t* test) no significant differences in linear size or weight were found ($P > 0.05$). Although differences in growth may be evident in later periods, sample sizes (less than five on any one capture date) at these times were inadequate for making valid comparisons. Although these data fail to support the hypothesis presented by Herreid (1967), they do not disprove the premise that temperature may have a measurable effect on development.

Additional studies are needed to examine the influence of environmental factors and roost temperatures on growth and development of bats. Studies using the von Bertalanffy growth analysis (Fabens, 1965) may be useful for comparing growth patterns at different environmental temperatures. According to von Bertalanffy (1960), growth occurs most rapidly where protein turnover is high. Interspecific and intraspecific growth comparisons could be made by comparing catabolic constants in roosts subject to different thermal environments—the higher the catabolic constant, the faster the growth rate. The catabolic constant is determined as $3k$, where k is the intrinsic rate of growth (see Methods and Materials). An anabolic constant also may be computed (Fabens, 1965), but because it is a function of body weight, and computed curves may not correspond to observed measures, this determination may be less useful.

Geographic Variation

Bats occurring at northern latitudes and higher altitudes usually give birth later than do those in more southerly areas and at lower elevations. Differences in temperature, abundance of resources, and variation in periods of hibernation all have been implicated as influencing factors. Few studies on *M. velifer* are available that permit a broad geographic comparison of reproduction. Hayward (1970) assumed that the average birth date of populations in Arizona was 17 June, although he presented little evidence to substantiate his assumption. Davis *et al.* (1962), however, reported that parturition in *M. velifer* occurred several weeks before parturition of *Tadarida brasiliensis* in southern Texas. Examination of dates recorded for *Tadarida* would suggest that most of the births for *M. velifer* occurred in early June. This and the fact that young reportedly were flying in Texas by late June suggest that the average parturition period for that latitude was two to three weeks sooner than in Kansas. Owing to the wide distribution of *M. velifer* it would be of interest to compare reproduction in the northern populations with those occurring at lower latitudes, especially in areas where the availability of resources may be less influenced by thermal seasonality.

SUMMARY

A study detailing reproduction, growth and development of the cave bat, *Myotis velifer,* was conducted in south-central Kansas from March 1968 through January 1971. Reproductive and growth patterns were examined at two physically and thermally contrasting nurseries (barn and cave) that included a temporal analysis of gestation, parturition and lactation. Post-natal growth was determined from mark-recapture data. Reproductive activity of males was examined throughout an annual cycle.

Adult males and females occurred in approximately equal numbers at transient and nursery roosts in spring. By early June the adult sex composition at the nursery sites was predominantly female. A comparison of the sex composition of adults occupying a cave and a building revealed that proportionately fewer males occupied the building. These differences may be related to the intolerance of males for high roost temperatures in buildings.

Testes began increasing in size in June and reached maximum hypertrophy in late August. After late August and early September the testes decreased in size and remained in an arrested state until the following summer. In early autumn the epididymides increased in size and became maximally distended with spermatozoa by mid-October. Most copulations occurred in October.

Ovulation probably occurs in April when bats depart from hiber-

nacula. The gestation period was 60 to 70 days and most of the prenatal growth occurs in the latter three weeks of gestation. In 1969, parturition began in the second week of June and extended for approximately four weeks with a median parturition date of 21 June. Nearly 80 percent of all young were born in a two week period from mid to late June. Females apparently are reproductive in their first year with no significant tendency for them to give birth later than older females. No apparent differences in growth rates were evident in bats occupying a cave and a building nursery. A comparison of reproductive parameters at two sites in 1969 and 1970 revealed that parturition in 1970 was later than in 1969 suggesting that cooler temperatures and a reduced population size may have contributed to this observed difference.

Post-natal growth followed a decaying exponential model. The forearm and fifth finger lengths at birth were 34 and 29 percent of adult size, respectively. Growth occurred rapidly in the first three weeks in which time the above linear dimensions exceeded 80 percent of adult size. By the fourth week when young bats began to forage, the forearm had reached 90 percent of adult size. The fifth finger did not reach equivalent proportions until the fifth or sixth week. Adult linear size was achieved at the age of 9 to 10 weeks (late August and early September). Young bats at birth weighed 3.0 grams (25.8% of adults); by the time they were three weeks of age they exceeded 85 percent of adult weight. By the fourth week their weight stabilized between 82 and 86 percent of adult weight until fat deposition began in late August.

Flight was initiated within the confines of the nursery roost at the age of three weeks. When bats began to forage permanent teeth were fully erupted. Weaning occurred at approximately six weeks when linear dimensions had reached 90 percent of adult size. Juvenile pelage increased in density until the age of three to four weeks. A juvenile molt was initiated at the age of six weeks (when young became nutritionally independent) and was completed near the time that external measurements reached adult size.

The importance of clustering behavior and the maintenance of roost temperatures were discussed with respect to successful reproduction and growth.

APPENDIX

Name	*Coordinate (N, W)*	*County*
Belvidere (Barn)	37°30′35″, 99°03′56″	Kiowa
Double Entrance S Cave	37°04′37″, 99°02′25″	Comanche
Englewood (Barn)	37°07′30″, 100°03′03″	Clark
Lost Colony Cave	37°01′46″, 98°59′06″	Barber
National Gypsum Mine	37°21′46″, 98°56′47″	Barber
Protection (Barn)	37°03′28″, 99°28′53″	Comanche
Wilmore (Barn)	37°19′37″, 99°09′16″	Comanche

LITERATURE CITED

Asdell, S. A.

1964. Patterns of mammalian reproduction. Cornell Univ. Press, Ithaca, New York, 2nd ed., 670 pp.

Barbour, R. W., and W. H. Davis

1969. Bats of America. Univ. Press of Kentucky, Lexington, 286 pp.

Carter, D. C.

1970. Chiropteran reproduction. Pp. 233-246, *in* About bats (B. H. Slaughter and D. H. Walton, eds.), Southern Methodist Univ. Press, Dallas.

Christian, J. J.

1956. The natural history of a summer aggregation of the big brown bat, Eptesicus fuscus fuscus. Amer. Midland Nat., 55:66-95.

Constantine, D. G.

1957. Color variation and molt in *Tadarida brasiliensis* and *Myotis velifer.* J. Mamm., 38:461-466.

Davis, R.

1969. Growth and development of young pallid bats, *Antrozous pallidus.* J. Mamm., 50:729-736.

1970. Carrying of young by flying female North American bats. Amer. Midland Nat., 83:186-196.

Davis, R. B., C. F. Herreid, II, and H. L. Short

1962. Mexican free-tailed bats in Texas. Ecol. Monogr., 32:311-346.

Davis, W. H., and H. B. Hitchcock

1965. Biology and migration of the bat, *Myotis lucifugus,* in New England. J. Mamm., 46:296-313.

Davis, W. H., R. W. Barbour, and M. D. Hassell

1968. Colonial behavior of *Eptesicus fuscus.* J. Mamm., 49:44-50.

Dunnigan, P. B., and J. H. Fitch

1967. Seasonal movements and population fluctuations of the cave bat (Myotis velifer) in south-central Kansas. Trans. Kansas Acad. Sci., 70:210-218.

Dwyer, P. D.

1963. The breeding biology of *Miniopterus schreibersi blepotis* (Temminck) (Chiroptera) in northeastern New South Wales. Australian J. Zool., 11:219-240.

1966. The population pattern of *Miniopterus schreibersii* (Chiroptera) in north-eastern New South Wales. Australian J. Zool., 14:1073-1137.

Dwyer, P. D., and E. Hamilton-Smith

1965. Breeding caves and maternity colonies of the bent-winged bat in south-eastern Australia. Helictite, 4:3-21.

Eisentraut, M.

1936. Zur Fortpflanzungsbiologie der Fledermause. Zeit. Morph. Okol. Tiere, 31:27-63.

1937. Die Wirkung niedriger temperaturen auf die Embryonalent Wiklung bei Fledermausen. Biol. Sentralblatt. Leipzig, 57:59-74.

Fabens, A. J.

1965. Properties and fitting of the von Bertalanffy growth curve. Growth, 29:265-289.

Fenton, M. B.

1969a. The carrying of young by females of three species of bats. Canadian J. Zool., 47:158-159.

1969b. Summer activity of *Myotis lucifugus* (Chiroptera: Vespertilionidae) at hibernacula in Ontario and Quebec. Canadian J. Zool. 47:597-602.

1970. The deciduous dentition and its replacement in *Myotis lucifugus* (Chiroptera: Vespertilionidae). Canadian J. Zool., 48:817-820.

GLOVER, T. D., and D. H. YOUNG

1963. Temperature and the production of spermatozoa. Fertil. Steril., 14:441-450.

GOULD, E.

1971. Studies of maternal-infant communication and development of vocalizations in the bats *Myotis* and *Eptesicus*. Comm. Behav. Biol. (Part A), 5:263-313.

GRIFFIN, D. R.

1940. Notes on the life history of New England bats. J. Mamm., 21:181-187.

GUTHRIE, M. J.

1933. The reproductive cycle of some cave bats. J. Mamm., 14:199-216.

HAYWARD, B. J.

1970. The natural history of the cave bat *Myotis velifer*. Res. Sci., Western New Mexico Univ., 1:1-74.

HERREID, C. F., II

1963. Temperature regulation of Mexican free-tailed bats in cave habitats. J. Mamm., 44:560-573.

1967. Temperature regulation, temperature preference and tolerance, and metabolism of young and adult free-tailed bats. Physiol. Zool., 40:1-22.

HUMPHREY, S. R.

1971. Population ecology of the little brown bat *Myotis lucifugus*, in Indiana and north-central Kentucky. Ph.D. dissertation, Oklahoma State Univ., 138 pp.

KLEIMAN, D. G.

1969. Maternal care, growth rate and development in the noctule *(Nyctalus noctula)*, pipistrelle *(Pipistrellus pipistrellus)* and serotine *(Eptesicus serotinus)* bats. J. Zool., 157:187-211.

KRÁTKY, J.

1970. Postnatale Entwicklung des Grossmausohrs, Myotis myotis (Borkhausen, 1797). Vest. Ceskoslov. Spol. Zool., 33:202-218.

KRUTZSCH, P. H.

1961. The reproductive cycle in the male vespertilionid bat Myotis velifer. Anat. Rec., 139:309 (abstract).

KUNZ, T. H.

1971. Ecology of the cave bat, *Myotis velifer*, in south-central Kansas and northwestern Oklahoma. Ph.D. dissertation. The University of Kansas, 148 pp.

1973. Feeding ecology of a temperature insectivorous bat *(Myotis velifer)*. M.S. submitted for publication.

LAIRD, A. K.

1966. Postnatal growth of birds and mammals. Growth, 30:349-363.

LAIRD, A. K., S. A. TYLER, and A. D. BARTON

1965. Dynamics of normal growth. Growth, 29:233-248.

MAZÁK, V.

1963. Hair growth in large mouse-eared bat, Myotis myotis myotis Borkhausen, 1797 (Mammalia, Chiroptera), during its praenatal and early postnatal life. Vest. Ceckoslov. Spol. Zool., 27:234-242.

MILLER, G. S., JR., and G. M. ALLEN

1928. The American bats of the genera Myotis and Pizonyx. Bull. U.S. Natl. Mus., 144:viii+218 pp.

MILLER, R .E.
1939. The reproductive cycle in male bats of the species *Myotis lucifugus* and *Myotis grisescens*. J. Morph., 64:267-295.

NYHOLM, E. S.
1965. Zur Okologie von Myotis mystacinus (Leisl.) und M. daubentoni (Leisl.) (Chiroptera). Ann. Zool. Fenn., 2:77-123.

ORR, R. T.
1970. Development: Prenatal and Postnatal. pp. 217-231, *in* Biology of bats (W. A. Wimsatt, ed.), Vol. 2, Academic Press, New York.

PEARSON, O. P., and M. R. KORFORD, and A. K. PEARSON
1952. Reproduction of the lump-nosed bat *(Corynorhinus rafinesquei)* in California. J. Mamm., 33:273-320.

RACEY, P. A.
1969. Diagnosis of pregnancy and experimental extension of gestation in the pipistrelle bat. J. Reprod. Fertil., 19:465-474.

RICE, D. W.
1957. Life history and ecology of *Myotis austroriparius* in Florida. J. Mamm., 38:15-32.

ROER, H.
1968. Nehmen die Weibchen des Mausohrs, *Myotis myotis* (Borkhausen), ihr Neugeborenes auf ihren Nahrungsflugen mit? Zeit. Tierpsychol., 25:701-709 (English summary).

ROER, H., and W. EGSBAEK
1969. Uber die Balz der Wasserfledermaus (Myotis daubentoni) (Chiroptera) in Winterquartier. Lynx, 10:85-91 (English summary).

SHORT, H. L.
1961. Growth and development of Mexican free-tailed bats. Southwestern Nat., 6:156-163.

SLUITER, J. W.
1961. Sexual maturity in males of the bat Myotis myotis. Proc. Kon. Ned. Akad. Wet., Amsterdam, C, 64:243-249.

SMITH, E.
1954. Studies on the life history of non-cave dwelling bats in northeastern Ohio. Ohio J. Sci., 54:1-12.
1956. Pregnancy in the little brown bat. Amer. J. Physiol., 185:61-64.

STONES, R. C., and J. E. WIEBERS
1967. Temperature regulation in the little brown bat. *Myotis lucifugus*. Pp. 97-109, *in* Mammalian hibernation III (K. C. Fisher *et al.*, ed.), American Elsevier, New York.

TINKLE, D. W., and W. W. MILSTEAD
1960. Sex ratios and population density in hibernating *Myotis*. Amer. Midland Nat., 63:327-334.

TINKLE, D. W., and I. G. PATTERSON
1965. A study of hibernating populations of *Myotis velifer* in northwestern Texas. J. Mamm., 46:612-633.

TWENTE, J. W., JR.
1955a. Aspects of a population study of cavern-dwelling bats. J. Mamm., 36:379-390.
1955b. Some aspects of habitat selection and other behavior of cavern dwelling bats. Ecology, 36:706-732.

VAUGHAN, T. A.
1959. Functional morphology of three bats: Eumops, Myotis, Macrotus. Univ. Kansas Publ., Mus. Nat. Hist., 12:1-153.
1970. Flight patterns and aerodynamics. Pp. 195-216, *in* Biology of bats (W. A. Wimsatt, ed), vol. 1, Academic Press, New York.

VON BERTALANFFY, L.
1960. Principles and theory of growth, Pp. 137-259, *in* Fundamental aspects of normal and malignant growth (W. W. Nowinski, ed.), Elsevier Publ. Co., Amsterdam.
WILSON, D. E.
1971. Ecology of *Myotis nigricans* (Mammalia: Chiroptera) on Barro Colorado Island, Panama Canal Zone. J. Zool., 163:1-13.
WIMSATT, W. A.
1944. Growth of the ovarian follicle and ovulation in Myotis lucifugus lucifugus. Amer. J. Anat. 74:129-159.
1945. Notes on breeding behavior, pregnancy, and parturition in some vespertilionid bats of the eastern United States. J. Mamm., 26:23-33.
1960a. An analysis of parturition in Chiroptera, including new observations on *Myotis l. lucifugus.* J. Mamm., 41:183-200.
1960b. Some problems of reproduction in relation to hibernation in bats. Bull. Mus. Comp. Zool., 124:249-267.
1969. Some interrelations of reproduction and hibernation in mammals. Pp. 511-549, *in* Dormancy and survival (H. W. Woolhouse, ed.), Academic Press, New York.

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A REVIEW OF THE CENTROLENID FROGS OF ECUADOR, WITH DESCRIPTIONS OF NEW SPECIES

By

JOHN D. LYNCH[1] AND WILLIAM E. DUELLMAN[2]

Since the description of *Centrolene geckoideum* by Jiménez de la Espada (1872), there have been few contributions to our knowledge of Ecuadorian centrolenid frogs. Boulenger (1882, 1898, 1899) named three Ecuadorian species as *Hyla* or *Hylella.* Noble (1924) recorded another species. Goin (1961) named three new species, and Goodman and Goin (1970) commented on additional Ecuadorian specimens of *Centrolene geckoideum.*

The generic status of these frogs has been reviewed by Noble (1920), Taylor (1951), Goin (1964) and Savage (1967). Taylor (1951) perceived the distinctive features of the assemblage and proposed the recognition of the Centrolenidae, a family occurring from southern México to Perú and Surinam and with an additional proliferation of species in southeastern Brasil.

The Middle American species have been reviewed by Taylor (1949, 1952, 1958), Duellman and Tulecke (1960), Savage (1967), and Savage and Starrett (1967). Taylor and Cochran (1953) summarized the Brasilian species; Cochran and Goin (1970) accounted for the known Colombian species, and Rivero (1968) published on the Venezuelan centrolenids. Additional species have been named from Perú (Boulenger, 1918), Surinam (Goin, 1966), Brasil (Lutz and Kloss, 1952), and Guyana (Goin, 1968).

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[1] Associate in Herpetology, Museum of Natural History, University of Kansas, and Associate Professor, Department of Zoology, University of Nebraska, Lincoln, Nebraska 68508.

[2] Curator, Division of Herpetology, Museum of Natural History, University of Kansas.

Currently the Centrolenidae is composed of two genera—*Centrolene* Jiménez de la Espada, 1872, and *Centrolenella* Noble, 1920; approximately 50 species are recognized in the family. Eight species have been recorded from Ecuador: *Centrolene geckoideum* and *Centrolenella buckleyi, cochranae, fleischmanni, griffithsi, ocellifera, parabambae,* and *petersi.*

Field work in Ecuador from 1967 through 1972 has resulted in the accumulation of nearly 200 specimens, representing all of the previously known Ecuadorian species of *Centrolenella,* two species heretofore unknown from Ecuador, and eleven new species named herein. We have examined the type specimens of all Ecuadorian taxa. Our investigations show the presence of 19 species of centrolenids in Ecuador. We present data on all the *Centrolenella* but include *Centrolene geckoideum* only in the key. Additionally, we treat the Colombian *Centrolenella medemi,* although the species has yet to be found in Ecuador.

Most areas of Ecuador have been explored in the course of our field work. Duellman worked mostly in the Amazonian lowlands and slopes, whereas Lynch spent most of his time at high elevations in the Andes and on the Pacific slopes of the Andes. Both of us spent limited time on the mesic Pacific lowlands. Based on our experience, we have noted a high degree of endemism in the faunas on the Pacific and Amazonian slopes and in some semi-isolated mountain ranges in Ecuador. We suspect that the centrolenid fauna is much larger than the 19 species now known from Ecuador.[3] Accordingly, in this paper we examine the current state of our knowledge of Ecuadorian centrolenids.

Acknowledgments

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[3] Subsequent to the completion of this paper, we received a specimen of an apparently unnamed species of *Centrolenella,* obtained at the Estación Biológica Río Palenque, Provincia Los Ríos. The specimen would be identified in our key as *C. cochranae.*

History Grants, University of Kansas (Duellman and Lynch), Society of Sigma Xi (Lynch), Penrose Fund (Grant no. 5549) of the American Philosophical Society (Lynch), and the Committee on Systematics and Evolutionary Biology, University of Kansas (Lynch). Duellman's study of specimens in European museums was made possible by a grant (no. 5063) from the Penrose Fund of the American Philosophical Society.

Abbreviations for collections used throughout the text are:

AMNH	American Museum of Natural History
BMNH	British Museum (Natural History)
CAS	California Academy of Sciences
KU	University of Kansas Museum of Natural History
LSU	Louisiana State University
RMNH	Rijksmuseum van Natuurlijke Historie
SMF	Senckenbergische Museum Frankfurt
TCWC	Texas Cooperative Wildlife Collection
UMMZ	University of Michigan Museum of Zoology
USNM	United States National Museum (National Museum of Natural History)
ZMB	Zoologisches Museum Berlin

TAXONOMIC CHARACTERS

With the exception of *Centrolene geckoideum,* living centrolenids usually are small, slender-limbed, green frogs. Most preserved examples seem to offer a limited suite of characters useful in their classification. The apparent paucity of characters is in part illusory, for there has been a multiplicity of names applied to comparatively few species in some areas; furthermore, there has been a limited amount of well-preserved material with detailed records of coloration of living frogs. In the following paragraphs we discuss those taxonomic characters found to be useful by us and contemporary investigators (Savage, 1967; Savage and Starrett, 1967).

Prevomerine teeth.—Prevomerine teeth and dentigerous processes are absent in 9 species: *anomala, buckleyi, fleischmanni, griffithsi, megacheira, munozorum, pellucida, peristicta,* and *pipilata.* Judgment on the absence of teeth should be held in abeyance for *anomala* and *pellucida,* inasmuch as we have a single specimen of each. *Centrolenella pellucida* is a member of the *fleischmanni* group, and if it does have prevomerine teeth, it would be the only species of the group to have them. *Centrolenella anomala* seems to be allied most closely to *C. cochranae,* some specimens of which lack prevomerine teeth. Prevomerine teeth usually are absent in *grandisonae.* The teeth usually are present in *cochranae, flavopunctata, ocellifera, prosoblepon,* and *siren,* and are found in all examples examined of *audax* (4), *medemi* (1), *midas* (11), and *resplendens* (2).

Color of bones.—In living and recently preserved specimens of many centrolenids, the bones are green. The color is seen most easily on the ventral surface of the shank. We have seen living examples of all species discussed here except *medemi.* Color of the bones was recorded for most specimens after field work in 1967; our only material of two species was collected in 1967 (*ocellifera* and *resplendens*), and no notations of bone color were made.

Based on color notes of living frogs, the following taxa have green bones: *audax, buckleyi, cochranae, flavopunctata, grandisonae* (pale), *griffithsi* (pale), *megacheira, midas, peristicta* (pale), *pipilata, prosoblepon,* and *siren;* white bones were observed in *anomala, fleischmanni, munozorum,* and *pellucida.* Some specimens of green-boned species collected in 1967 still retain green bones. Dissection of preserved specimens of *medemi, ocellifera,* and *resplendens,* revealed no green pigment in the bones. We are tempted to argue that the bones of these species were white in life; however, we must point out that the pale green bones of *griffithsi* quickly fade to white in preservative.

Humeral spines.—On some centrolenids, a hook-like process extends anteriorly from the deltoid ridge of the humerus. This feature was used initially to distinguish *Centrolenella* and *Cochranella* but is no longer regarded as adequate grounds for generic distinction (Goin, 1964). Humeral spines usually are present only in males, and the spines appear to become more pronounced in larger, and presumably, older individuals. The spine is usually absent in females (Eaton, 1958, reported small spines in female *prosoblepon*). The spines are present in *audax, buckleyi, grandisonae, medemi* (small), *peristicta, pipilata,* and *prosoblepon.* Normally *griffithsi* lacks humeral spines, but one individual (KU 142649) has small humeral spines. The distal end of the humerus of males is provided with expanded lateral flanges in some of our examples of *grandisonae, peristicta,* and *pipilata;* sexual dimorphism of this sort is well-known in some *Eupsophus* and some *Leptodactylus* (Lynch, 1971).

Snout shape.—The shape of the snout in dorsal view (Fig. 1) varies from subacuminate *(fleischmanni)* to round (*audax, buckleyi, flavopunctata, grandisonae, munozorum, ocellifera, pellucida, peristicta, prosoblepon,* and *resplendens)* or truncate *(anomala, cochranae, griffithsi, medemi, megacheira, midas,* and *siren).* Truncate snouts (in dorsal view) result from the protuberant nostrils lending an angular appearance to the top of the snout. Protuberant nostrils

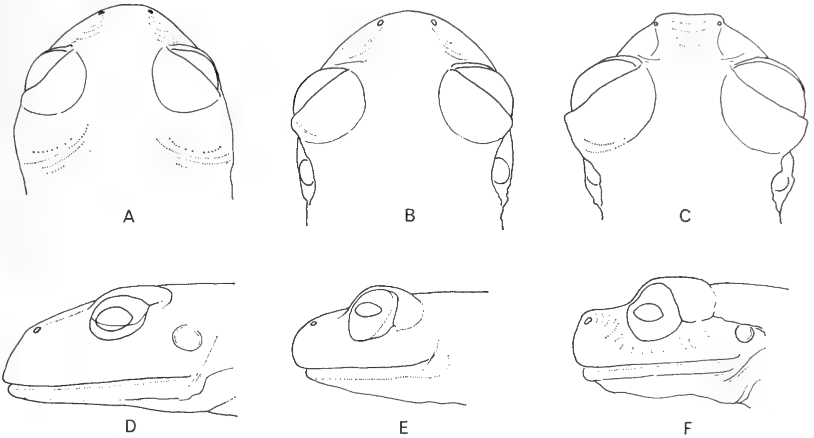

FIG. 1. Heads of *Centrolenella:* Dorsal views. A. *C. fleischmanni,* KU 146606. B. *C. audax,* KU 143290. C. *C. anomala,* KU 143299. Lateral views. D. *C. resplendens,* KU 118053. E. *C. munozorum,* KU 118054. F. *C. griffithsi,* KU 118040.

are also found among some of those species with round snouts (dorsal view) but the nostrils do not extend as far anteriad.

In lateral view (Fig. 1), the snout profile varies from strongly sloping *(resplendens)* to a weakly sloping or rounded *(buckleyi),* to rounded *flavopunctata, grandisonae, munozorum, pellucida, peristicta,* and in some female *prosoblepon),* to truncate *(anomala, audax, cochranae,* weakly in *fleischmanni, griffithsi, medemi, megacheira, midas, ocellifera, pipilata,* most *prosoblepon,* and *siren).* The laterally truncate snouts again reflect the presence of protuberant nostrils (more so than any differences in shape of the underlying skeleton).

An additional feature of the snout is the angularity of the canthus and loreal region. The canthus rostralis is scarcely evident in *fleischmanni, munozorum,* and *pellucida,* whereas it is much more distinct in those frogs having more vertical loreal regions (all other species, except *grandisonae, peristicta,* and *pipilata*).

Tympanum.—Tympana are present in all centrolenids we examined. The tympana are concealed beneath the skin in *medemi, munozorum,* and *pellucida,* but at least partially visible in others (lower one-fourth visible in *buckleyi* to entirely visible in some *fleischmanni, peristicta,* and *pipilata*). The upper edge of the tympanum usually is obscured by a supratympanic fold or may be simply covered by a thickening of the skin in the absence of a distinct supratympanic fold. The extent of the exposed portion of the tympanum is probably not a reliable feature for species recognition.

The tympanic region is directed strongly dorsolaterally (as opposed to being nearly vertical in most frogs) in *fleischmanni, munozorum,* and *pellucida;* this feature, in combination with the weakly marked canthus, seems to give these frogs a flatter head than that seen in the other Ecuadorian species. These species also have a strong dorsolateral orientation to the tympanum. The tympana are strongly oriented laterally (little or no dorsal or posterior inflection) in *grandisonae, ocellifera,* and *peristicta.* The tympana are oriented posterolaterally with little or no dorsal inflection in *anomala, buckleyi, midas, pipilata,* and *siren.* The tympana are oriented dorsolaterally, but much less so than in *fleischmanni* and its allies, in *audax, cochranae, griffithsi, megacheira, prosoblepon,* and *resplendens;* in these frogs there may be little to moderate posterior inflection of the tympana.

Skin texture.—The skin of the venter is coarsely areolate in all species examined. The skin of the dorsal surfaces varies in texture and is useful in species recognition. The dorsal skin of *medemi* is smooth, unlike any other Ecuadorian centrolenid. Most species have finely shagreened skin on the dorsum without warts or spinules *(audax, flavopunctata, fleischmanni, grandisonae, griffithsi, midas, munozorum, ocellifera, peristicta, pellucida, prosoblepon,* and *siren).* Shagreened skin with scattered enameled[4] warts is found in *pipilata* and *resplendens; resplendens* has many more warts (Plate 2C). *Centrolenella cochranae* has scattered warts on a shagreened dorsum; *C. anomala* has a shagreened dorsum with more numerous warts, and *C. megacheira* has pustular skin on the dorsum. The skin on the dorsum of *buckleyi* is shagreened with spinules, which are most numerous laterally.

Dermal ornamentation.—Few species of the family have what Taylor and Cochran (1953) termed "decoration" or tarsal and ulnar folds. We find that many of the folds and tubercles are enameled and thus appear to be distinctive. *Centrolenella grandisonae* has low tubercles along the outer edge of the forearm and tarsus; the tubercles are present distally along the lateral edge of the hand and foot to the digital pads. A similar arrangement of more pronounced tubercles is found in *C. peristicta* (Fig. 3) and *C. pipilata. Centrolenella resplendens* has a scalloped fringe along the outer edge of the hand and arm (Fig. 3), and foot and tarsus (Fig. 4); the fringe continues around the heel. A thin fringe, without warts or scalloping, occurs along the hand and forearm and the foot and tarsus of *C. pellucida.*

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[4] The term "enameled" is used throughout to denote the shiny white elevations found in the skin of some centrolenids.

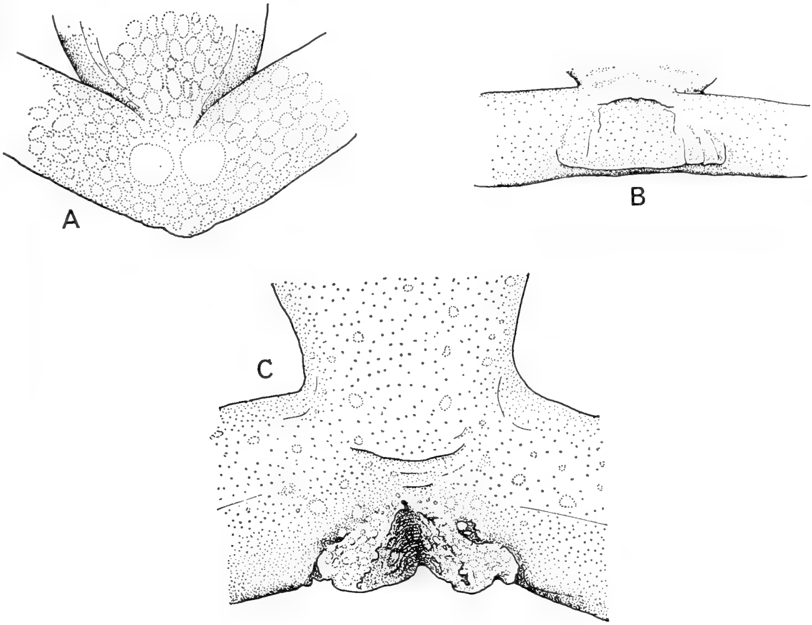


FIG. 2. Anal ornamentation in *Centrolenella.* A. Ventral view of posterior ventrum of *C. siren,* KU 146621. B. Posterior view of anal region of *C. pellucida,* KU 143298. C. Dorsal view of *C. resplendens,* KU 118053.

Most of the Ecuadorian frogs have two to four large, round subanal tubercles (Fig. 2). Five species have more extensive anal ornamentation. Six Ecuadorian species do not have subanal tubercles *(anomala, fleischmanni, medemi, munozorum, ocellifera,* and *pellucida).*

The small tubercles lateral and posteroventral to the vent in *grandisonae, peristicta,* and *pipilata* are enameled and seem to represent a rudimentary character-state for the "anal decoration" character-state reported by Taylor and Cochran (1953); none of these species has enlarged para- or postanal warts or folds. *Centrolenella pellucida* has a transverse fold below the vent (Fig. 2); the fold is enameled. The "anal decoration" is most extensive and unique in *C. resplendens* (Fig. 2). A similar feature appears to be present in Taylor and Cochran's (1953) *surda* of southeastern Brasil. In *resplendens,* a pair of thick folds extends laterally from the vent onto the posterior surface of the thighs; the folds are connected at their lateral extent by a semicircular fold extending medio-ventrally beneath the anus. These folds and the area between them are ornamented with enameled warts and short ridges.

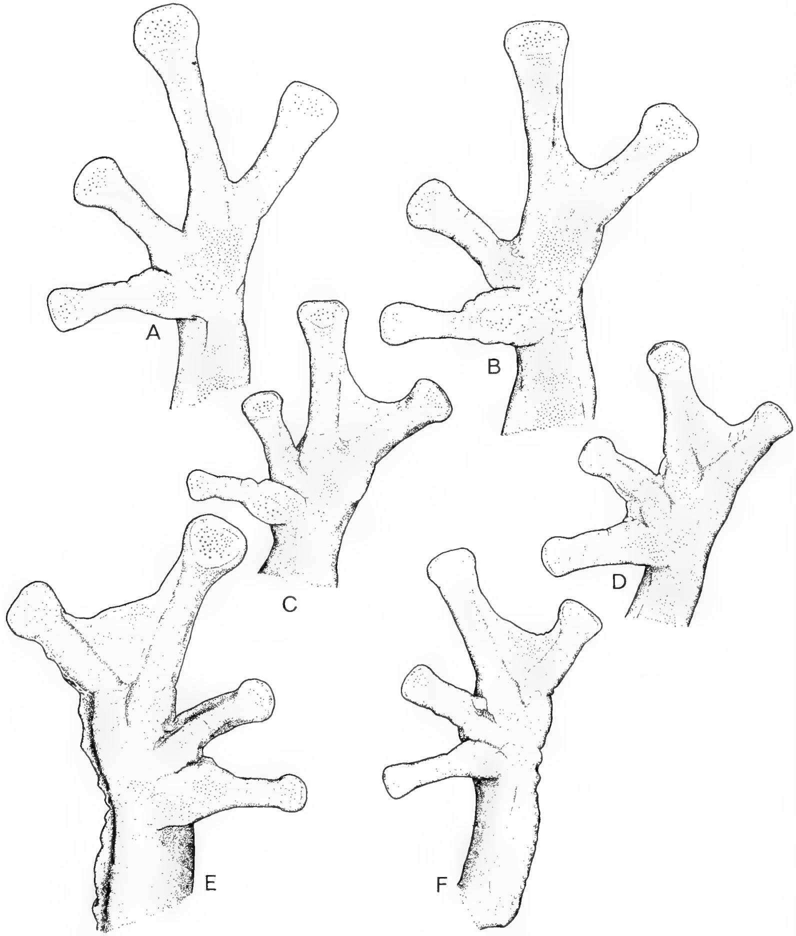


FIG. 3. Palmar views of hands of *Centrolenella*. A. *C. griffithsi*, KU 118040. B. *C. grandisonae*, KU 118047. C. *C. flavopunctata*, KU 121050. D. *C. munozorum*, KU 118054. E. *C. resplendens*, KU 118053. F. *C. peristicta*, KU 118051.

Hands and feet.—The first finger is as long as or longer than the second in all Ecuadorian centrolenids. In two Peruvian species we have examined, the first finger is shorter than the second. The palmar and subarticular tubercles are difficult to see on most preserved examples and are not accorded significance here. The fingers bear discs that are wider than long but vary between being more nearly round or truncate. The species with more rounded finger discs are *buckleyi, fleischmanni, griffithsi, munozorum, pellucida, pipilata, resplendens; megacheira* is intermediate between rounded and truncate discs include *anomala, audax, cochranae, flavopunctata, gran-*

disonae, medemi, midas, ocellifera, peristicta, prosoblepon, and *siren.* The finger discs are larger than those of the toes in all species examined, but in several species *(anomala, audax, fleischmanni, medemi, megacheira, munozorum, pellucida, pipilata, prosoblepon,* and *resplendens)* the discs are more nearly equal in size than in *cochranae, flavopunctata, grandisonae, griffithsi, midas, ocellifera, peristicta,* and *siren.* The fingers bear narrow lateral fringes in *anomala, audax, buckleyi, fleischmanni, grandisonae, megacheira, munozorum, pellucida, peristicta, pipilata, prosoblepon,* and *resplendens* but not in *cochranae, flavopunctata, griffithsi, medemi, midas, ocellifera,* or *siren.*

The extent of webbing of the hands and feet has been used commonly in order to distinguish species of centrolenids. In recording the extent of webbing we have followed Savage and Heyer (1967). The least finger webbing is seen in *anomala, cochranae, griffithsi, megacheira,* and *siren* (Fig. 3); *buckleyi grandisonae,* and *pipilata* have only slightly greater webbing of the fingers (Fig. 3). In these eight taxa the webbing does not enclose the distal subarticular tubercle. The most extensive webbing seen in Ecuadorian *Centrolenella* was found in the holotype of *petersi* and an example referred to *fleischmanni* (KU 121052). In these specimens the web reaches the disc of the fourth finger and nearly to the disc of the third (III1⅓-0IV); the modal webbing for *fleischmanni* is III1½-2IV. The webbing completely encloses the distal subarticular tubercle of fingers III and IV in *flavopunctata, medemi, peristicta,* and *resplendens* (Fig. 3) and is only slightly less extensive in *fleischmanni, midas, ocellifera,* and *prosoblepon* (Fig. 3). The distal subarticular tubercle of IV, but not III, is free of webbing in *audax* and *pellucida.*

Most species studied have a small outer metatarsal tubercle; none was found in *audax, flavomaculata, fleischmanni, medemi, midas, munozorum, ocellifera, pellucida, resplendens,* or *siren.*

The extent of webbing on the feet parallels that of the fingers, but species group less well. The least webbing is seen in *cochranae, griffithsi,* and *siren,* and with only slightly more webbing in *anomala, buckleyi, megacheira,* and *pipilata* (Fig. 4). The webbing formulae for these seven species range from 12-2¼II1½-3^{-}III2^{-}-3IV3-2V of *cochranae* and *siren* to the comparatively well-webbed *pipilata* (I1-2^{+}II1-2^{+}III1-2⅓IV2⅓-1V). Nine species have more webbing than *pipilata* but less than the extensive webbing of *medemi* and *resplendens (audax, flavopunctata, fleischmanni, grandisonae, midas, ocellifera, pellucida, peristicta,* and *prosoblepon).* Toe webbing is most extensive in *medemi* where the web reaches the discs on all but the fourth toe.

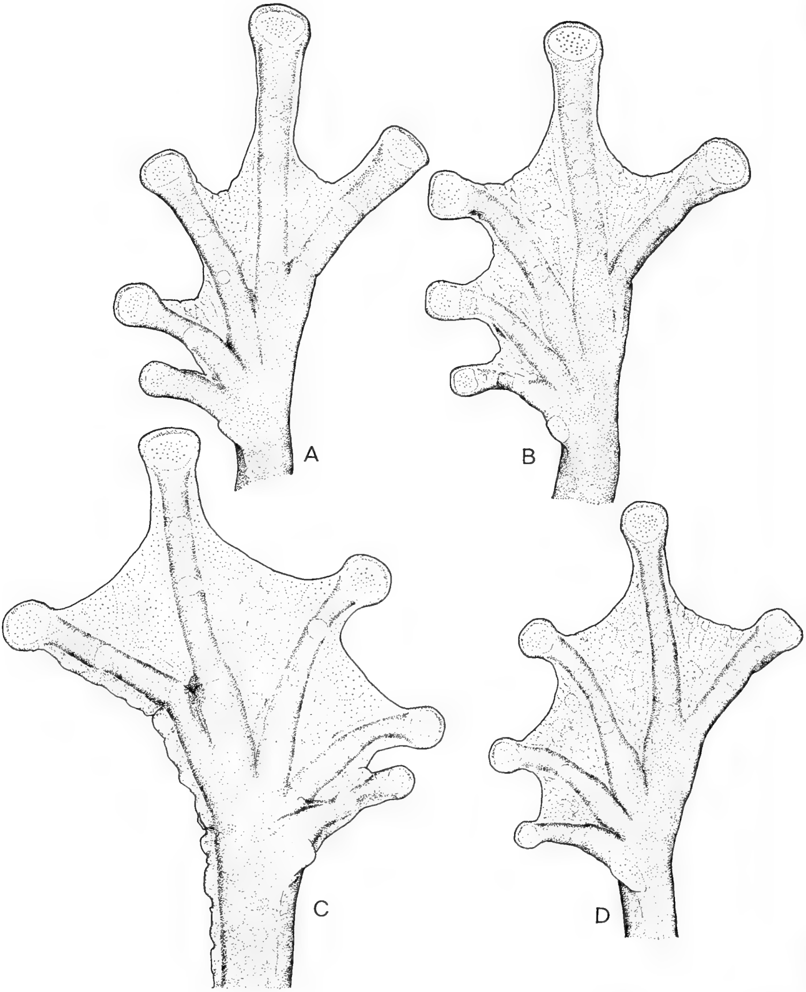


FIG. 4. Plantar views of feet of *Centrolenella*. A. *C. griffithsi*, KU 118040. B. *C. grandisonae*, KU 118047. C. *C. resplendens*, KU 1180653. D. *C. flavopunctata*, KU 121048.

Peritoneal coloration.—The parietal peritoneum is white (heart not visible in life) in all Ecuadorian *Centrolenella* except *fleischmanni, munozorum,* and *pellucida;* in these three species the heart is visible through the skin of the chest. The visceral peritoneum is white in *fleischmanni, munozorum, pellucida,* and *resplendens.* The latter is the only Ecuadorian species with both white parietal and visceral peritonea.

In living frogs, if the heart is visible, the parietal peritoneum is clear; if the heart is not visible, the parietal peritoneum is opaque and white. The character-states of the visceral peritoneum are more difficult to observe in living frogs. If the intestine is dark (as seen through the skin of the venter), the visceral peritoneum is clear; if the intestine is yellow or white, the visceral peritoneum is opaque and white.

In preserved examples, inspection of peritoneal pigmentation is best made by cutting into the abdomen and recording whether the intestine is white or not (visceral peritoneum) and whether the inside of the belly beneath the liver is white or not (parietal peritoneum).

Three peritoneal pigmentation patterns are presently known: 1) clear parietal, white visceral (*fleischmanni* and *pulverata* groups and at least *C. albotunica, eurygnatha,* and *vanzolinii* of southeastern Brasil); 2) white parietal, clear visceral (*prosoblepon* group); and 3) white parietal, white visceral (*antioquiensis* and *resplendens*).

Ground color in preservative.—The ground color of preserved frogs is cream to creamy-white in *fleischmanni* (including the holotype of *petersi*), *munozorum,* and *pellucida.* The ground color of *anomala* is pale brown. The ground color of *flavopunctata, medemi,* and *pipilata* is gray to slate-gray. That of *grandisonae, griffithsi, ocellifera, peristicta,* and *resplendens* is pale to dull lavender and contrasts with the darker lavender ground color of *audax, buckleyi, cochranae, megacheira, midas, prosoblepon,* and *siren.*

Color patterns.—The most simple color patterns are those of *audax, flavopunctata, midas,* and *siren* (white flecks on ground color), *griffithsi* (lavender to black flecks on ground color), *buckleyi* (moderately distinct white labial stripe continuing onto flanks separating lavender or purple dorsum from cream venter), and *fleischmanni* and *munozorum* (faint peppered reticulation of dorsal surfaces). No color pattern is seen in *pellucida.*

The color pattern of *resplendens* consists of many small white spots (enameled warts) on a dull lavender ground color. *Centrolenella medemi* has a simple pattern of large cream spots on the dorsal surfaces, unlike the pattern of any other centrolenid.

The other centrolenids with non-ocellated color patterns include *grandisonae, peristicta,* and *pipilata* with small, diffuse black (or lavender) spots and equally diffuse white spots on the dorsal surfaces and *megacheira* and *prosoblepon* with discrete dark lavender spots on the dorsum and limbs (spotting reduced or absent in *prosoblepon*).

The other three species known from Ecuador *(anomala, cochranae,* and *ocellifera)* and the Peruvian *ocellata* have a dorsal pattern of *ocelli.* The ocelli are large in *ocellata* but small in the three

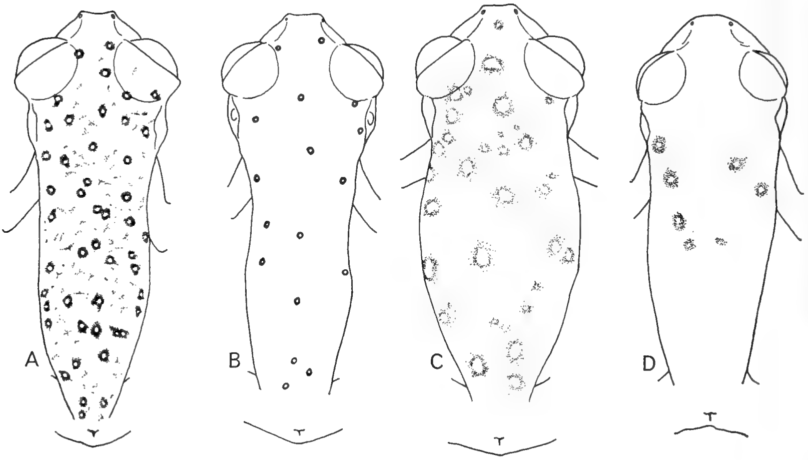


FIG. 5. Dorsal patterns of ocellated *Centrolenella*. A. *C. anomala,* KU 143299. B. *C. cochranae,* KU 121035. C. *C. ocellata,* LSU 25990. D. *C. ocellifera,* KU 118046.

Ecuadorian ocellated *Centrolenella* (Fig. 5). The ocelli of *anomala* are black with white centers; those of *cochranae* are deep lavender with white centers, and those of *ocellifera* faint lavender without white centers. The pattern of *ocellifera* also includes small non-ocellated white spots (Fig. 5).

KEY TO ECUADORIAN CENTROLENID FROGS

1. Discs on fingers as large as eye .... *Centrolene geckoideum*
   Discs on fingers less than half size of eye 2
2. Dorsum tan with black ocelli enclosing cream (orange in life) spots .... *Centrolenella anomala*
   Dorsum white, cream, gray, or lavender (green in life) with or without spots or ocelli 3
3. Heart visible in life; bones white; dorsum cream or white in preservative ocelli absent 4
   Heart not visible in life, bones green (unknown in *medemi, ocellifera,* and *resplendens*); dorsum lavender or slate gray in preservative; ocelli and spots present or absent 6
4. Tympanum visible .... *Centrolenella fleischmanni*
   Tympanum concealed 5
5. Forearm and tarsus each bearing a dermal fold on ventrolateral edge; transverse dermal fold below anus .... *Centrolenella pellucida*

Forearm and tarsus lacking dermal folds; no transverse dermal fold below anus .... *Centrolenella munozorum*

6. Webbing extending no more than midway between basal and distal subarticular tubercles on fourth finger 7

   Webbing extending at least to base of distal subarticular tubercle on fourth finger 10

7. Dorsal skin pustular .... *Centrolenella megacheira*

   Dorsal skin shagreened 8

8. Dorsum with distinct small black ocelli enclosing pale spots .... *Centrolenella cochranae*

   Dorsum without ocelli 9

9. Dorsum with white (yellow in life) flecks .... *Centrolenella siren*

   Dorsum with or without diffuse black flecks .... *Centrolenella griffithsi*

10. Broad, scalloped dermal fringe on ventrolateral edges of forearm and foot; U-shaped anal fold; snout sloping anteroventrally; dorsum with white warts .... *Centrolenella resplendens*

    Not nearly so fancy 11

11. Dorsum of body and limbs slate gray with large cream spots; webbing extending to discs on all but fourth toe .... *Centrolenella medemi*

    Dorsum of body and limbs unicolor, ocellated, or flecked; webbing less extensive on feet 12

12. Dorsum with dark ocelli .... *Centrolenella ocellifera*

    Dorsum without ocelli 13

13. Webbing extending beyond distal subarticular tubercle of fourth finger 14

    Webbing not extending beyond distal subarticular tubercle of fourth finger 16

14. Dorsum unicolor or with distinct dark flecks; no pale flecks .... *Centrolenella prosoblepon*

    Dorsum with pale flecks; diffuse dark flecks present or not 15

15. Dorsum of body slate gray (dark green in life) with white (yellow in life) flecks .... *Centrolenella flavopunctata*

    Dorsum of body pale lavender (pale green in life) with dark lavender spots and few white flecks .... *Centrolenella peristicta*

16. Dorsum with pale flecks, no dark flecks; prevomerine teeth present 17

Dorsum unicolor with dark and pale flecks; prevomerine teeth absent 18

17. Humeral spine present in males; pale flecks numerous on dorsum .... *Centrolenella audax*

Humeral spine absent in males; pale flecks few, principally laterally .... *Centrolenella midas*

18. Dorsum unicolor .... *Centrolenella buckleyi*

Dorsum with dark and pale flecks 19

19. Snout truncate in dorsal and lateral profiles .... *Centrolenella pipilata*

Snout round in dorsal and lateral profiles. .... *Centrolenella grandisonae*

ACCOUNTS OF SPECIES

In the following accounts we attempt to make comparable statements in the diagnoses and descriptions. In order to facilitate comparisons of primary character states among species, we have numbered what we consider to be the primary character in the diagnoses. The webbing formula in the diagnosis of each species is the modal formula; variation is given in the description. Measurements and proportions are for Ecuadorian specimens only, unless otherwise noted.

Specimens designated as paratypes and paratopotypes (in addition to holotypes) are those on which descriptions of new species were based. In some cases measurements of referred specimens have been incorporated into statements of ranges of variation.

Colored photographs of 15 species are reproduced on Plates 1 and 2 (following pages 16 and 26).

Taxonomic changes and their justifications, comments on type specimens and literature, and observations on behavior and ecology are given in the "Remarks" section of each account. All specimens examined are listed in a terminal section of the paper.

Centrolenella anomala new species
Plate 2H

Holotype.—KU 143299, an adult male, 24.1 mm, from the Río Azuela, 1740 m, Quito-Lago Agrio road, Provincia Napo, Ecuador, obtained on 23 October 1971, by William E. Duellman.

Diagnosis.—1) prevomerine teeth absent; 2) bones white; 3) parietal peritoneum white; visceral peritoneum clear; 4) color in life tan with black ocelli with orange-tan centers; in preservative, brown with black ocelli with white spots; 5) webbing between outer fingers III3^{+}-2⅔IV; 6) webbing on foot I2^{-}-2¼II1-2¼III1-2^{+}IV2⅔-1½V; 7) snout truncate in dorsal and lateral profiles; 8) dorsal skin shagreened with minute spicules and elevated warts corresponding to ocelli; 9) arms and legs lacking dermal fringes; 10) humeral spine absent in male; 11) lower two-thirds of tympanum visible, directed posterolaterally with dorsal inclination.

Centrolenella anomala differs from all other centrolenids by being tan instead of green; it further differs from other species having ocellated patterns *(cochranae, ocellata,* and *ocellifera)* by having more ocelli and scattered black flecks between ocelli. Moreover, *anomala* differs from *ocellifera* by having less webbing between the outer fingers, from *cochranae* by lacking prevomerine teeth, and from *ocellata* by having the snout truncate and lower two-thirds of the tympanum visible, whereas in *ocellata* the snout is round and the tympanum is concealed.

Description.—Adult male moderate-sized, 24.1 mm in snout-vent length; females not known. Head slightly wider than body; width of head 33.2 percent of snout-vent length; snout short, truncate in dorsal and lateral profiles (Fig. 1); canthus round; loreal region concave; lips not flared; nostrils nearly terminal on snout, protuberant, directed dorsolaterally; internarial area depressed. Eye large, protuberant, directed anterolaterally. Supratympanic fold very weak, barely covering upper edge of tympanum; tympanum directed posterolaterally with dorsal inclination. Prevomerine dentigerous processes and teeth absent; choanae small, ovoid, near margin of mouth; tongue not notched posteriorly, barely free behind; vocal slits extending from lateral base of tongue to angles of jaws.

Humeral spine absent; ulnar fold and tubercles absent; first finger longer than second; fourth finger nearly as long as third; lateral fringes present on fingers; webbing absent between first and second fingers, vestigial between second and third; webbing formula for outer fingers III3^{+}-2⅔IV; discs broad, truncate; subarticular tubercles large, round, simple; supernumerary tubercles absent; palmar single, ovoid; nuptial excrescences absent. Hind limbs slender; length of tibia 54.4 percent of snout-vent length, tarsal folds and tubercles absent; inner metatarsal tubercle large, elongate; outer metatarsal tubercle small, round; subarticular tubercles large, round; supernumerary tubercles absent; feet about two-thirds webbed; webbing formula I2^{-}2¼II1-2¼III1-2^{+}IV2⅔-1½V; discs on toes slightly smaller and more nearly round than those on fingers.

Skin on dorsal surfaces of head, body, forearms, and shanks with many minute spicules and larger spicules corresponding to ocelli; skin of belly and ventral surfaces of thighs granular; other surfaces smooth; anal opening directed posteroventrally at midlevel of thighs; anal folds and tubercles absent.

Color in preservative: dorsal surfaces of head, body, forearms, fourth fingers, thighs, shanks, feet, and fourth and fifth toes brown with dark brown flecks and head, body, forearms, and shanks with black ocelli enclosing white spots (Fig. 5); other surfaces creamy tan.

Color in life: dorsum tan with small black ocelli enclosing orange-tan spots; chest white; heart not visible; throat, visceral peritoneum, and ventral surfaces of limbs lacking pigment; bones white; iris bronze with black reticulations.

Distribution.—This distinctive species is known only from the type locality, a rivulet flowing into the Río Azuela on the east slope of Volcán Reventador at an elevation of 1740 m (Fig. 6). The small stream is about 50 m north of the bridge over the Río Azuela on the Quito-Lago Agrio road. In this area there is a narrow relatively gentle slope between the steep slopes of Volcán Reventador to the west and the chasm of the Río Coca to the east.

Remarks.—The single specimen was kept alive for two days and two nights, during which time it was observed frequently. At no time did it take on any greenish color; it remained tan with no noticeable change in pigmentation. After 18 months in alcohol the dorsum has a faint lavender tint.

The holotype was on a mossy limb of a bush about 1.5 m above a cascading rivulet at night. *Hyla phyllognatha* and four other species of *Centrolenella (megacheira, pellucida, pipilata,* and *siren)* were found in the same stream and in other small streams nearby in the cloud forest, but no other individuals of *C. anomala* were observed.

Etymology.—The specific name is from the Greek *anomalos* meaning unusual, deviating from the general rule; the name is used in allusion to the distinctive tan color of this species.

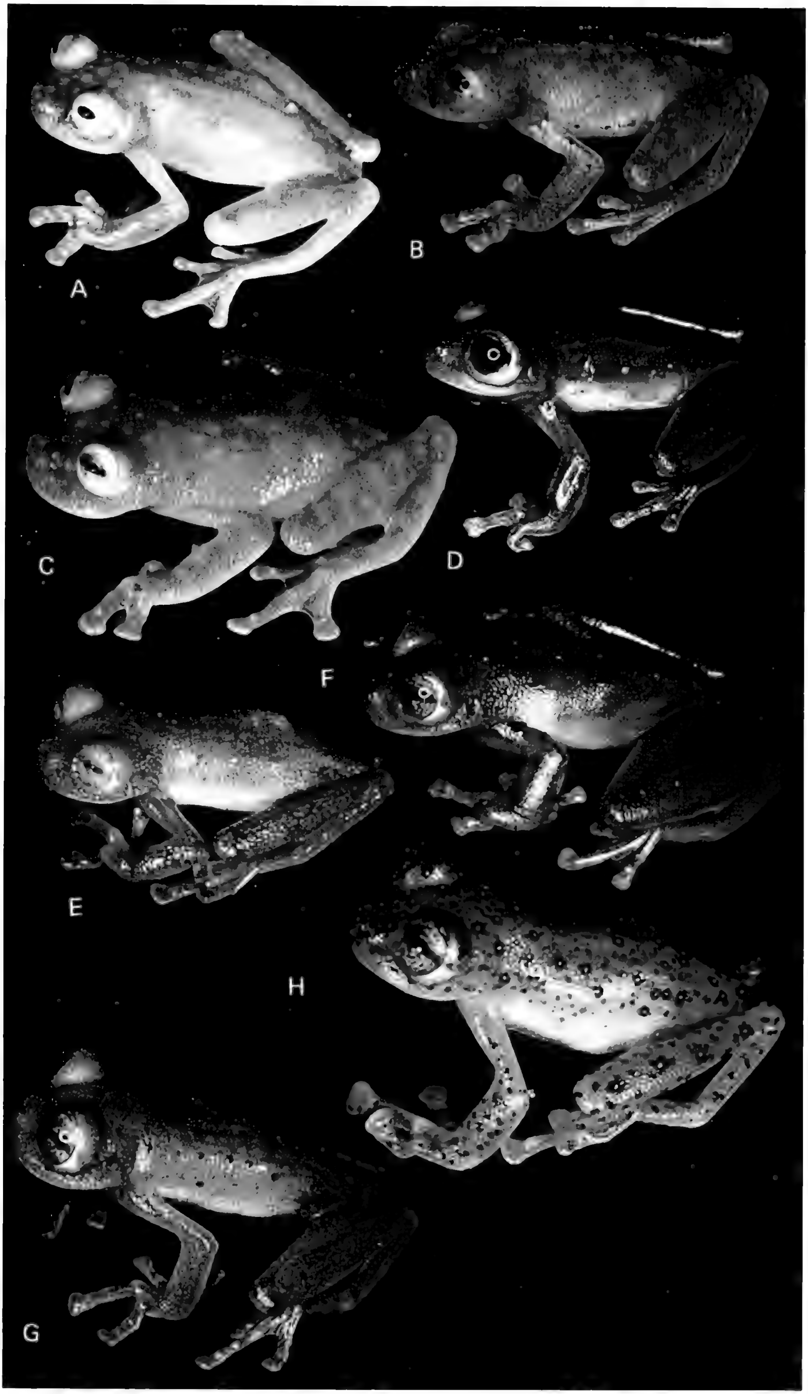
Centrolenella audax new species

Holotype.—KU 146624, an adult male, 23.0 mm, from Salto de

→

PLATE 1. A. *Centrolenella fleischmanni,* KU 146607; B. *C. munozorum,* KU 123225; C. *C. pellucida,* KU 143298 (holotype); D. *C. midas,* KU 123219 (holotype); E. *C. siren,* KU 143293; F. *C. flavopunctata,* KU 123224; G. *C. cochranae,* KU 123216; H. *C. anomala,* KU 143299 (holotype). All × 2.

PLATE 1



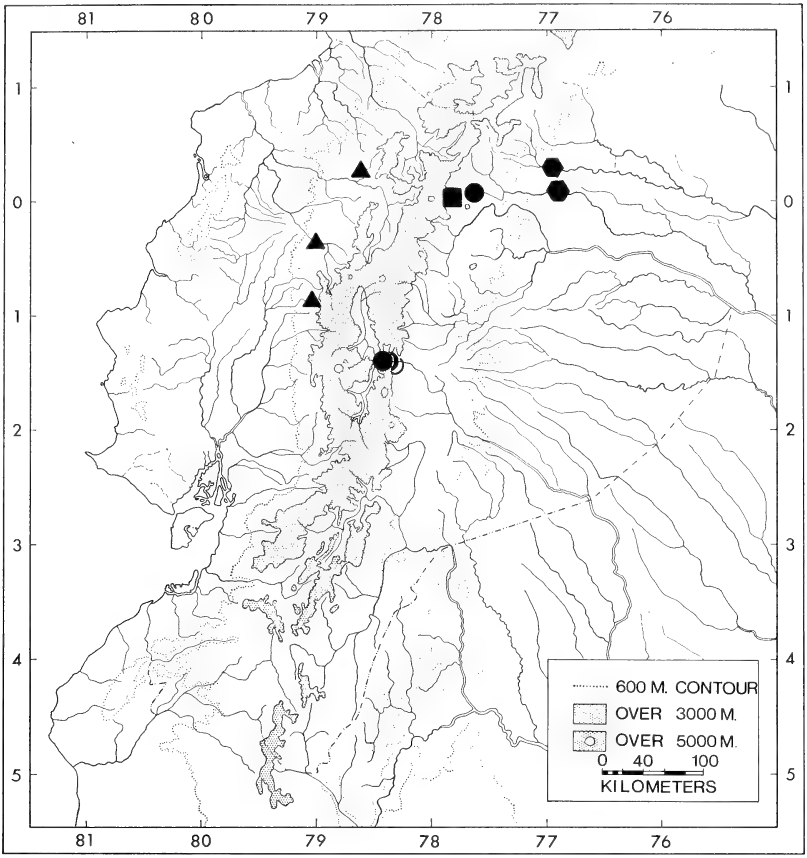


FIG. 6. Distribution of *Centrolenella anomala* (square), *C. cochranae* (circles), *C. ocellifera* (triangles), *C. resplendens* (hexagons).

Agua, 2.5 km NNE of Río Reventador on Quito-Lago Agrio road, 1660 m, Provincia Napo, Ecuador, obtained on 7 April 1972, by William E. Duellman.

Paratypes.—KU 143290 and 143292, adult males, from 16.5 km NNE of Santa Rosa on Quito-Lago Agrio road, 1700 m, Provincia Napo, Ecuador, obtained on 18 October 1971, by Joseph T. Collins and William E. Duellman.

Diagnosis.—1) prevomerine teeth 2-4; 2) bones green; 3) parietal peritoneum white; visceral peritoneum clear; 4) color in life pale green with small yellow flecks; in preservative, lavender with white flecks; 5) webbing between outer fingers III2^+-2IV; 6) webbing on foot I1-2^-II1-2^+III1-2^+IV2^+-1V; 7) snout round in dorsal view, truncate in lateral profile; 8) dorsal skin shagreened; 9) arms and legs lacking dermal folds; 10) humeral spine present in males; 11) lower four-fifths of tympanum visible, directed dorsolaterally with slight posterior inclination.

The coloration of *audax* is like that of *flavopunctata, midas,* and *siren,* but the males of these species lack humeral spines. No other species having humeral spines has a green dorsum with yellow flecks.

Description.—Adult males moderate-sized, 23.0-23-6 mm ($\bar{x}$=23.3, N=3) in snout-vent length; females not known. Head much wider than body, width of head 34.8-43.5 percent ($\bar{x}$=37.8, N=3) of snout-vent length; snout short, round in dorsal view, truncate in lateral profile (Fig. 1); canthus round; loreal region barely concave; lips not flared; nostrils four-fifths distance from eyes to tip of snout, slightly protuberant dorsolaterally; internarial area depressed. Eye moderately large, directed anterolaterally. Supratympanic fold absent; lower four-fifths of tympanum visible, directed dorsolaterally with slight posterior inclination. Prevomerine dentigerous processes posteromedially inclined, narrowly separated medially, between longitudinally elliptical choanae, bearing 2-4 teeth; tongue nearly round, barely free behind; vocal slits extending from midlateral base of tongue to angles of jaws.

Humeral spine large, parallel to humerus; ulnar fold and tubercles absent; first finger longer than second; third finger slightly shorter than fourth; lateral fringes present on fingers; webbing absent between first and second fingers, vestigial between second and third; webbing formula for outer fingers III(2^{+}-2½)-(2^{-}-2^{+})IV; discs broad, truncate; subarticular tubercles small, round, simple; supernumerary tubercles absent; palmar tubercles rectangular, simple; nuptial excrescences absent. Hind limbs moderately slender; length of tibia 51.3-55.6 percent ($\bar{x}$=54.0, N=3) of snout-vent length; tarsal folds and tubercles absent; inner metatarsal tubercle small, elliptical, outer metatarsal tubercle absent; subarticular tubercles small, round; supernumerary tubercles absent; feet about two-thirds webbed; webbing formula I1-(2^{-}-2^{+})II1-(2^{+}-2¼)III1-2^{+}IV2^{+}-1V; discs on toes slightly smaller than those on fingers.

Skin on dorsal surfaces shagreened; skin on belly and proximal ventral surfaces of thighs granular; other surfaces smooth; anal opening directed posteroventrally at upper level of thighs; pair of large tubercles ventral to anus.

Color in preservative: dorsal surfaces of head, body, forearms, thighs, and shanks lavender with small white dots; hands, feet, and ventral surfaces cream.

Color in life: dorsum green with gold flecks; fingers and toes pale yellow; chest white; heart not visible; visceral peritoneum and

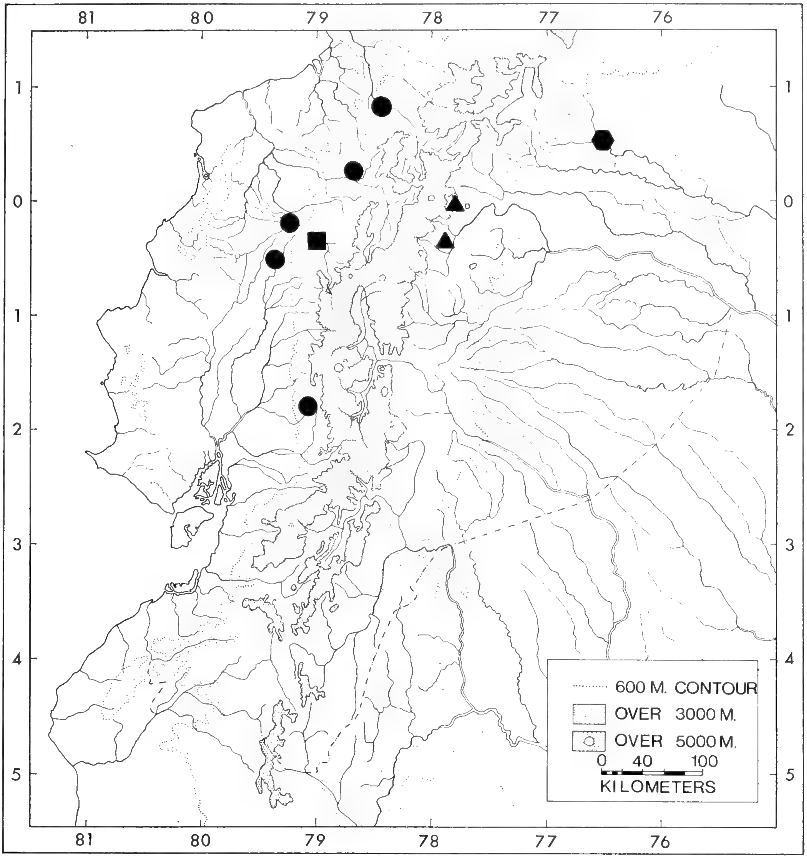


FIG. 7. Distribution of *Centrolenella audax* (triangles), *C. grandisonae* (square), *C. medemi* (hexagon), and *C. prosoblepon* (circles).

ventral surfaces of limbs unpigmented; bones green; iris pale bronze with black reticulations.

Distribution.—This species presently is known from only two localities at elevations of 1660 and 1700 m on the Amazonian slopes of the Cordillera Oriental of the Andes (Fig. 7). The type of locality is a deeply recessed waterfall in a nearly vertical cliff at a point 2.5 km north-northeast of the bridge over the Río Reventador on the Quito-Lago Agrio road.

Remarks.—The holotype was found in a bromeliad on a cliff below and in the spray zone of the waterfall. In another bromeliad a metamorphosing young having a snout-vent length of 13.5 mm and a tail 19.5 mm in length was found. Two individuals were found at night on vegetation over a stream 16.5 km north-northeast of Santa

Rosa; three other species of *Centrolenella* were found there—*megacheira, pipilata,* and *siren.*

Etymology.—The specific name is Latin, meaning daring, and is used in allusion to the precipitous regions inhabited by the species.

Centrolenella buckleyi (Boulenger)
Plate 2E

Hylella buckleyi Boulenger, 1882:420 [Syntypes.—BMNH 78.1.25.16 from Intac, Provincia Imbabura Ecuador; BMNH 80.12.5.201 from "Paitanga" (=Pallatanga), Provincia Chimborazo, Ecuador].

Hyla purpurea Nieden, 1923:267 [Substitute name for *Hyllela buckleyi* Boulenger].

Cochranella buckleyi—Taylor, 1951:35.

Centrolenella buckleyi—Goin, 1964:6.

Diagnosis.—1) prevomerine teeth absent; 2) bones green; 3) parietal peritoneum white; visceral peritoneum clear; 4) color in life dark green; in preservative, purple; 5) webbing between outer fingers III2½-2^+IV; 6) webbing on foot I1½-2II1-2^+III1⅓-2¾IV3^+-1¾V; 7) snout round in dorsal view, in profile round above and slightly sloping anteriorly; 8) dorsal skin shagreened with minute spinules; 9) arms and legs lacking dermal folds; 10) humeral spine present in males; 11) lower one-fourth to one-half of tympanum visible, directed posterolaterally with slight dorsal inclination.

Centrolenella buckleyi is like many specimens of *griffithsi* and some *prosoblepon* in being uniform lavender above in preservative, but it differs from both of these by having an inclined snout in lateral profile, spinules in the dorsal skin, and only the lower one-fourth to one-half of the tympanum visible. It further differs from *griffithsi* by having more webbing on the hand and humeral spines in males, and from *prosoblepon* by having less webbing on the hand and lacking prevomerine teeth.

Description.—Adults large, snout-vent length 28.4-29.5 mm ($\bar{x}$=29.0, N=2) in males, 29.8-34.4 mm ($\bar{x}$=31.7, N=5) in females. Head not as wide as body; width of head 32.5-38.6 percent ($\bar{x}$=34.7, N=7) of snout-vent length; snout short, round in dorsal view, round above and slightly sloping anteriorly in profile; canthus round; loreal region concave; lips flared; nostrils two-thirds distance from eyes to tip of snout, barely protuberant laterally; internarial area flat. Eyes moderately large, directed anterolaterally. Supratympanic fold moderately heavy; lower one-fourth to one-half of tympanum visible, directed posterolaterally with slight dorsal inclination. Prevomerine dentigerous processes and teeth absent; choanae small, ovoid; tongue cordiform, shallowly notched behind; free posteriorly for about one-fourth of its length; vocal slits extending posterolaterally from midlateral base of tongue to angles of jaws.

Humeral spine short, pointed, nearly parallel to humerus; ulnar fold and tubercles absent; first finger equal in length to second; fourth finger slightly shorter than third; lateral fringes present on fingers; webbing absent between first, second, and third fingers; webbing formula for outer fingers III(2^+-2¼)-(2¼-2⅔)IV; discs broadly rounded; subarticular tubercles moderately large, conical, simple; distal tubercle on fourth finger weakly bifid; supernumerary tubercles small, numerous on basal segments; palmar tubercle large, ovoid; nuptial excrescences absent. Hind limbs moderately robust; length of tibia 49.4-56.4 percent ($\bar{x}$=51.2, N=7) of snout-vent length; tarsal folds and tubercles absent; inner metatarsal tubercle large, ovoid; outer metatarsal tubercle small, round; subarticular small, round; supernumerary tubercles small, present basally; toes about three-fourths webbed; webbing formula I(1⅓-1⅔)-(2-2^+)II(1-1^+)-2^+III(1-1⅔)-(2^+-3^+)IV(2¾-3^+)-(1½-2^+)V; discs on toes slightly smaller than those on fingers.

Skin on dorsum shagreened with minute spinules; skin on belly and proximal posteroventral surfaces of thighs granular; other surfaces smooth; anal opening directed posteroventrally at midlevel of thighs; several small and four large tubercles below anus.

Color in preservative: dorsal surfaces, except fingers and toes, purple; other surfaces cream; narrow cream stripe on edge of upper lip in some specimens.

Color in life: dorsal surfaces bright to dark green, sharply demarcated laterally from white lower flanks; chin and most of venter pale green; parietal peritoneum yellow; heart not visible; edge of upper lip, outer edge of tarsus, and anal stripe white; bones green; iris pale copper flecked with black.

Distribution.—*Centrolenella buckleyi* occurs from the Mérida Andes in western Venezuela southward through the Andes and interandean valleys to southern Ecuador (Fig. 8). Although the species has been recorded at elevations as low as 1500 m, authenticated records in Colombia and Ecuador are all above 2000 m; we have found the species at elevations up to 3000 m.

Remarks.—We have found individuals in terrestrial bromeliads and in vegetation in *ciénegas*, the quaking meadows in many high Andean localities. Francisco León of the Universidad Católica in Quito collected two specimens from bromeliads in a *Eucalyptus* grove near Machachi. Thomas H. Fritts obtained one from a bromeliad on an island in Laguna Cuicocha. *Centrolenella buckleyi* may breed in the same situations as other centrolenids—rapid, mountain streams—but *buckleyi* frequents non-stream situations (Laguna Cuicocha, the bog-like *ciénegas*) where trees, if present,

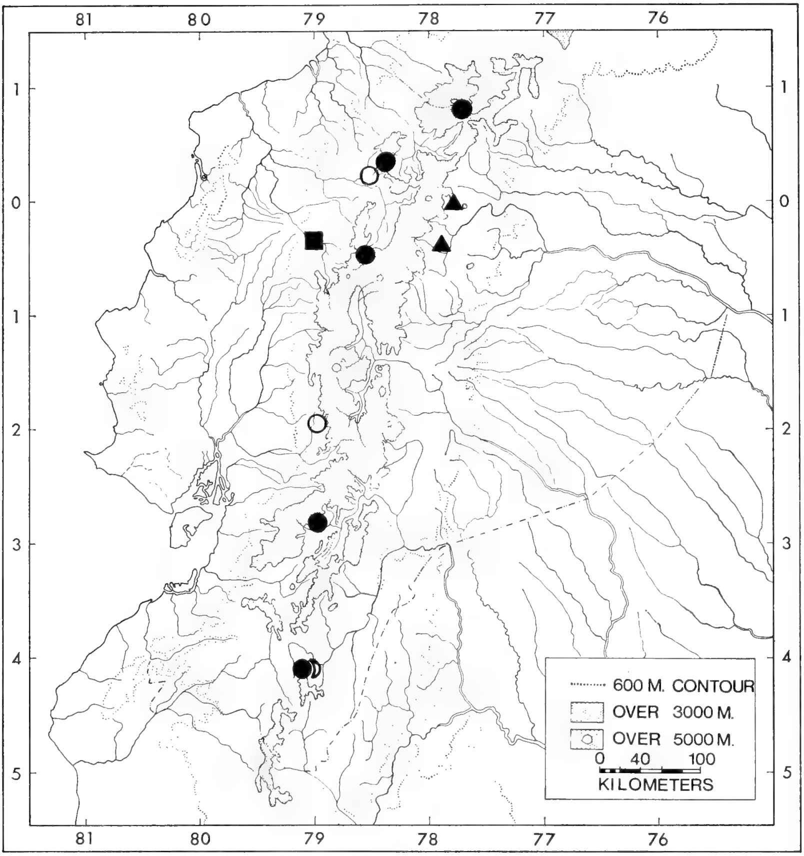


FIG. 8. Distribution of *Centrolenella buckleyi* (circles), *C. peristicta* (square), and *C. pipilata* (triangles); open symbols are literature records.

are small and rarely overhang water. Because of the absence of streams, we suspect that the tadpoles may develop in bromeliads or in *ciénegas,* a radical departture from the adaptive zone of centrolenid frogs.

As noted by Goin (1961:101), one of the syntypes (BMNH 80.12.5.201) is now represented by disarticulated bones and the other (BMNH 78.1.25.16) is missing.

Rivero (1968) named *Centrolenella buckleyi venezuelensis* from the Mérida Andes of western Venezuela. We have not been concerned with northern populations which may or may not be conspecific with *buckleyi;* thus, we use the binomial for the populations in Ecuador.

Centrolenella cochranae (Goin)
Plate 1G

Cochranelle cochranae Goin, 1961:97 [Holotype.—BMNH 1912.11.1.68 from El Topo, Río Pastaza, Provincia Tungurahua, Ecuador].
Centrolenella cochranae Goin, 1964:6.

Diagnosis.—1) prevomerine teeth 0-3; 2) bones green; 3) parietal peritoneum white; visceral peritoneum clear; 4) color in life pale green with minute purple ocelli with red centers; in preservative, lavender with purple ocelli with white centers; 5) webbing between fingers III3-2¾IV; 6) webbing on foot I2-2¼II1½-2½III2^{-}3IV3^{+}-1¾V; 7) snout truncate in dorsal and lateral profiles; 8) dorsal skin shagreened with elevated warts corresponding to ocelli; 9) arms and legs lacking dermal folds; 10) humeral spine absent in males; 11) lower three-fourths of tympanum visible, directed dorsolaterally.

The first impression of the dorsal pattern of *cochranae* is of black flecks on a green ground color; however, upon closer inspection it is evident that the markings actually are small ocelli (Fig. 5). *Centrolenella cochranae* differs from other species having ocellated dorsal patterns *(anomala, ocellata,* and *ocellifera)* by having smaller ocelli and prevomerine teeth (absent in some *cochranae*). Furthermore, the species differs from *anomala* by having a green instead of brown dorsum, from *ocellifera* by having less webbing between the outer fingers, and from *ocellata* by having the snout truncate and the lower three-fourths of the tympanum visible, whereas in *ocellata* the snout is round and the tympanum concealed.

Description.—Adults moderately large; snout-vent length 23.8-26.7 mm ($\bar{x}$=25.0, N=6) in males, 30.0 mm in single female. Head noticeably wider than body; width of head 33.0-35.3 percent ($\bar{x}$=34.0, N=7) of snout-vent length; snout short, truncate in dorsal and lateral profiles; canthus round, loreal region concave; lips moderately flared; nostrils nearly terminal, directed anterolaterally; internarial area depressed. Eye large, protuberant, directed anterolaterally. Supratympanic fold absent; lower three-fourths of tympanum visible, directed dorsolaterally. Prevomerine dentigerous processes absent in one specimen, present in six; processes transverse between choanae, bearing 1-3 teeth; choanae small, ovoid, near edge of mouth; tongue cordiform, free posteriorly; vocal slits extending from midlateral base of tongue to angles of jaws.

Humeral spine absent; ulnar fold and tubercles absent; first finger longer than second; fourth finger slightly shorter than third; lateral fringes absent on fingers; webbing absent between first and second fingers, vestigial between second and third; webbing formula for outer fingers III(3^{-}-3^{+})-(2¾-3)IV; discs broader than deep, rounded; subarticular tubercles small, round, simple; supernumerary tubercles absent; palmar tubercle large, elliptical; nuptial excrescences absent. Hind limbs slender; length of tibia 55.7-61.8 percent ($\bar{x}$=58.7, N=7) of snout-vent length; tarsal folds and tubercles absent; inner metatarsal tubercle large, flat, elongate; outer metatarsal tubercle small, conical; subarticular tubercles small, round; supernumerary tubercles absent; feet about two-thirds webbed; webbing formula I2-(2^{+}-2½)II(1½-1¾)-(2^{-}-2¾)III2^{-}-(3^{-}-3^{+})IV(3^{-}-3^{+})-(2-2^{-})V; discs on toes smaller and more nearly round than those on fingers.

Skin on dorsal surfaces smooth with scattered spicules; skin on belly and ventral surfaces of thighs granular; other surfaces smooth; anal opening directed posteroventrally at midlevel of thighs; pair of large tubercles below anus.

Color in preservative: dorsal surfaces of head and body lavender with small black ocelli enclosing minute white dots or some solid black flecks; other dorsal surfaces creamy tan with black flecks on thighs and shanks of some specimens.

Color in life: pale green with black or purple ocelli enclosing pink or red dots; chest white; heart not visible; visceral peritoneum and ventral and concealed surfaces of limbs unpigmented; bones green; iris pale gray with black flecks.

Distribution.—Most localities from which *Centrolenella cochranae* is known are in the lower valley (1100-1300 m) of the Río Pastaza on the eastern face of the Andes (Fig. 6); additionally the species is known from an elevation of 1150 m in the Cordillera del Dué above the Río Coca (± 180 km NNE of the Río Pastaza valley). On the basis of these few localities it seems that *cochranae,* along with *flavopunctata,* inhabits intermediate elevations between the ranges of the lowland species *(medemi, midas, munozorum,* and *resplendens)* and the numerous species in the higher cloud forests *(anomala, audax, megacheira, pellucida, pipilata,* and *siren).*

Remarks.—Goin (1961:97) described *cochranae* as lacking prevomerine teeth, but he (1964:2) noted the presence of teeth in six other specimens. Six of our seven specimens have prevomerine teeth, and one lacks not only teeth but dentigerous processes.

We compared two of our specimens (KU 121033, 123217) with the holotypes of *cochranae* (BMNH 1912.11.1.68) and *C. ocellata* (Boulenger, 1918) (BMNH 1912.11.1.19) from Huancabamba, Departamento Pasco, Perú. Our specimens compare favorably with the holotype of *cochranae* but are different from *ocellata* in several characters. *Centrolenella ocellata* differs from *C. cochranae* as follows: 1) prevomerine teeth absent; 2) ocelli much larger (Fig. 5); 3) snout truncate; 4) first finger shorter than second.

All of our specimens were obtained at night from vegetation overhanging small mountain streams. The call consists of a single, high-pitched note. Other than the calls, no evidence of reproduction was noted while we were collecting in the range of *cochrane* (April, June, July, August). Individuals seemed to be sparsely distributed in the habitat.

Centrolenella flavopunctata new species

Plate 1F

Holotype.—KU 121048, an adult male, 21.6 mm, from Mera, Provincia Pastaza, Ecuador, obtained on 14 July 1968, by John D. Lynch.

Paratopotypes.—KU 121041, 28 June 1968, John D. Lynch; 121043-46, 2 July 1968, John D. Lynch and Gerald R. Smith; 121049, 14 July 1968, John D. Lynch; 121050-51, 24 July 1968, John D. Lynch.

Diagnosis.—1) prevomerine teeth 0-3 on low processes; 2) bones green; 3) parietal peritoneum white; visceral peritoneum clear; 4) color in life green with pale yellow flecks; in preservative, slate gray with white flecks; 5) webbing between outer fingers III2^--1½IV; 6) webbing on foot I1-1½II0-2^-III1-2^-IV2-1V; 7) snout round in dorsal and lateral profiles; 8) dorsal skin shagreened; 9) arms and legs lacking dermal folds; 10) humeral spine absent in males; 11) lower three-fourths of tympanum visible, directed dorsolaterally with slight posterior inclination.

Centrolenella flavopunctata is like *midas* and *siren* in having a lavender dorsum with white flecks (in life, green with gold flecks) and no black flecks, but it differs from both species by having a rounded, instead of truncate, snout and slightly more webbing on the hands and feet. *Centrolenella siren* further differs from *flavopunctata* by having nearly the entire tympanum visible and strongly inclined posteriorly, whereas only about three-fourths of the tympanum is visible and directed dorsolaterally in *flavopunctata.*

Description.—Adults rather small; snout-vent length 20.6-23.2 mm ($\bar{x}$=21.6, N=7) in males, 24.1-25.7 mm ($\bar{x}$=24.9, N=3) in females. Head slightly wider than body; width of head 34.6-38.3 percent ($\bar{x}$=36.2, N=10) of snout-vent length; snout short, round in dorsal and lateral profiles; canthus round; loreal region barely concave; lips not flared; nostrils nearly terminal on snout, not protuberant, directed antero-dorsolaterally; internarial area barely depressed. Eye moderately large, directed anterolaterally. Supratympanic fold absent; lower three-fourths of tympanum visible, directed dorsolaterally with slight posterior inclination. Prevomerine dentigerous processes small, low, widely separated between longitudinally rectangular choanae, bearing 0-3 teeth; tongue broadly cordiform, barely free posteriorly; vocal slits extending from midlateral base of tongue to angles of jaws.

Humeral spine absent; ulnar fold and tubercles absent; first finger longer than second; fourth finger much shorter than third; fringes absent on fingers; webbing absent between first and second fingers; webbing formula for other fingers II1-(2¾-3^+)III(1½-2)-(1-1⅔)IV; discs truncate, subarticular tubercles small, round, simple; supernumerary tubercles absent; palmar tubercle large, elliptical; nuptial excrescences absent (Fig. 3). Hind limbs moderately robust; length of tibia 55.3-62.0 percent ($\bar{x}$=58.0, N=10) of snout-vent length; tarsal folds and tubercles absent; inner metatarsal tubercle small, flat, elliptical; outer metatarsal tubercle absent; subarticular tubercles small, round; supernumerary tubercles absent; feet about three-fourths webbed; webbing formula I(0-1)-(1-1¾)II(0-1)-(0-2)III(0-1)-(1¾-2^+)IV(2^--2^+)-(0-1)V; discs on toes smaller and more nearly round than those on fingers (Fig. 4).

Skin on dorsal surfaces shagreened; skin on belly and proximal posteroventral surfaces of thighs granular; other surfaces smooth; anal opening directed posteriorly at upper level of thighs; pair of large tubercles below anus.

Color in preservative: dorsal surfaces of head, body, and limbs lavender or slate gray with many minute white flecks; other surfaces dull creamy tan.

Color in life: dorsal surfaces of head, body, and limbs pale green with numerous minute yellow flecks on body and limbs; edge of upper lip pale yellow; fingers and toes yellow; chest white; visceral peritoneum unpigmented; throat pale bluish green; bones green; iris pale grayish white, with or without golden tint, with dark gray or brown flecks or fine reticulations.

Distribution.—Most specimens are from elevations of 1000-1800 m in the Pastaza Valley in the eastern slope of the Andes; the species is also known from an elevation of 720 m in the Serranía de Umbaquí, 200 km NNE of the former locality (Fig. 9). One faded specimen with no visible yellow flecks from San José Abajo, Provincia Napo (AMNH 22187) tentatively is referred to this species. The locality is between 700 and 1000 m on the eastern slope of Volcán Sumaco, about 130 km NE of the Pastaza Valley. *Centrolenella*

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PLATE 2. A. *Centrolenella megacheira,* KU 143245 (holotype); B. *C. griffithsi,* KU 121039; C. *C. resplendens,* KU 118053 (holotype); D. *C. pipilata,* KU 143278 (holotype); E. *C. buckleyi,* KU 144131; F. *C. prosoblepon,* KU 146609; G. *C. peristicta,* KU 121053. All × 2.

PLATE 2

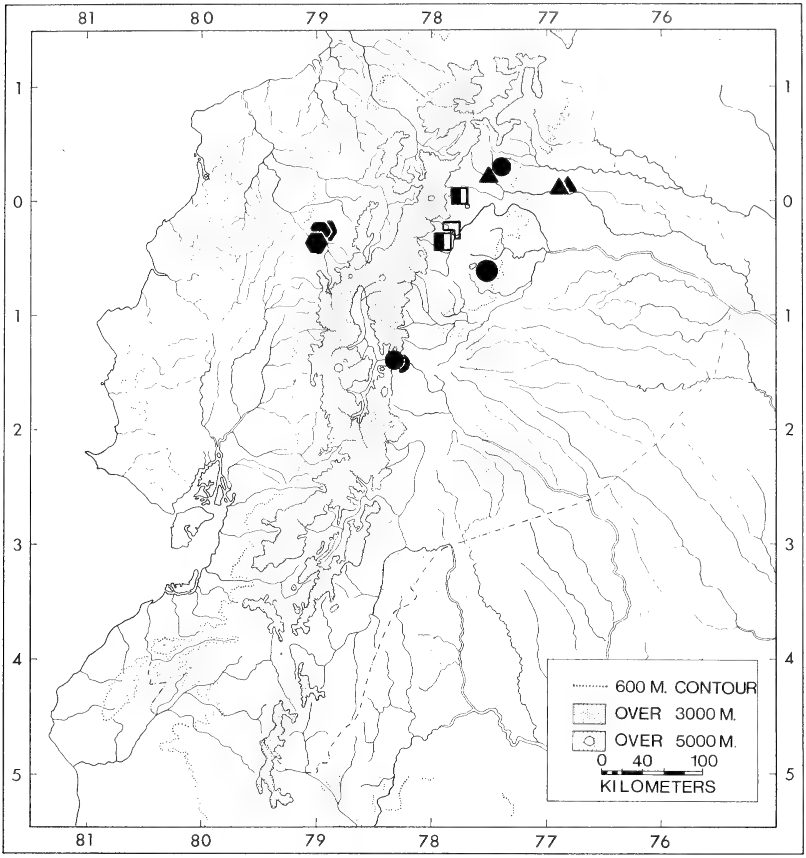

FIG. 9. Distribution of *Centrolenella flavopunctata* (circles), *C. griffithsi* (hexagons), *C. megacheira* (solid squares), *C. midas* (triangles), and *C. siren* (open squares); half closed squares are localities for both *C. megacheira* and *C. siren.*

flavopunctata, together with *C. cochranae,* inhabits intermediate elevations between the ranges of the lowland species *(medemi, midas, munozorum,* and *resplendens)* and the cloud forest inhabitants at higher elevations *(anomala, audax, megacheira, pellucida, pipilata,* and *siren).* Although *cochranae* and *flavopunctata* occur at about the same elevations on the eastern slopes of the Andes, the two species have not been found in sympatry.

Remarks.—One was found on a bush in forest by day; most were collected in a deep ravine. Males were perched on small herbs in the spray-zone of a small waterfall. No eggs were observed although one gravid female was found. At several small streams between Mera and the Río Alpayacu, males were calling on 2, 14, and 24 July

1968. Recently metamorphosed young having snout-vent lengths of 14.5 and 16.0 mm were found on 28 June and 6 July 1968.

Etymology.—The specific name is a combination of the Latin *flavus,* meaning golden yellow, and the Latin *punctatus,* meaning dotted, and is used in reference to the dorsal coloration.

Centrolenella fleischmanni (Boettger)
Plate 1A

Hylella fleischmanni Boettger, 1893:251 [Holotype.—SMF 3760 from San José, Provincia San José, Costa Rica].
Hylella cappellei Lidth de Jeude, 1904:94 [Holotype.—RMNH 4463 from Saramacca, Surinam; synonymy *fide* Goin, 1964:1].
Centrolenella fleischmanni—Noble, 1924:67.
Centrolenella cappellei—Noble, 1926:18.
Cochranella fleischmanni—Taylor, 1951:34.
Cochranella petersi Goin, 1961:96 [Holotype.—BMNH 1902.5.27.24 from Río Durango, Provincia Esmeraldas, Ecuador]. New synonym.
Centrolenella fleischmanni—Goin, 1964:1.
Centrolenella petersi—Goin, 1964.6.

Diagnosis.—1) prevomerine teeth absent, 2) bones white; 3) parietal peritoneum clear; visceral peritoneum white; 4) color in life pale green with pale yellow spots; in preservative, cream with faint dark flecks; 5) webbing between outer fingers III2-1½IV; 6) webbing on foot I1-2^-II0-2III1-2^+IV2^+-1V; 7) snout subacuminate in dorsal view, round in lateral profile; 8) dorsal skin shagreened; 9) arms and legs lacking dermal folds; 10) humeral spine absent in males; 11) tympanum almost entirely visible, directed dorsolaterally with slight posterior inclination.

Centrolenella fleischmanni differs from other Ecuadorian centrolenids that have the heart visible in life and a white dorsum in preservative *(munozorum* and *pellucida)* by having the snout subacuminate in dorsal view and truncate in lateral profile, and the tympanum distinct. The other species have round snouts and the tympanum concealed. Furthermore, *pellucida* differs from *fleischmanni* by having ulnar, tarsal, and anal folds. *Centrolenella orocostalis* from Venezuela differs from *fleischmanni* by having minute enamel (yellow in life) flecks on the dorsum.

Description.—Adult males small; snout-vent length 19.2-21.2 mm ($\bar{x}$=20.4, N=5). Head wider than body; width of head 38.3-40.6 percent ($\bar{x}$=39.2, N=4) of snout-vent length; snout short, shallow, roundly subacuminate in dorsal view, round in lateral profile (Fig. 1); canthus round; loreal region shallowly concave; lips not flared; nostrils three-fourths distance from eye to tip of snout, barely protuberant, directed dorsolaterally; internarial area slightly depressed. Eye large, protuberant, strongly oriented anteriorly. Supratympanic

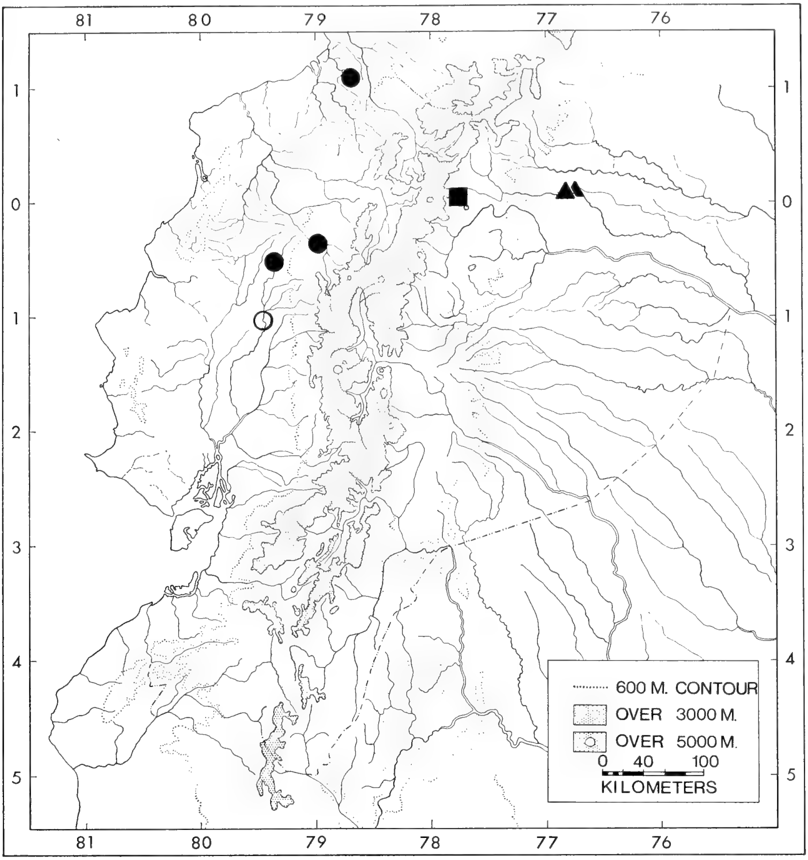

FIG. 10. Distribution of *Centrolenella fleischmanni* (circles), *C. munozorum* (triangles), and *C. pellucida* (square); open symbol is a literature record.

fold absent; tympanum small, about one-fourth diameter of eye, nearly entirely visible, directed dorsolaterally with slight posterior inclination. Prevomerine dentigerous processes and teeth absent; choanae small, round, near margin of mouth; tongue ovoid, free posteriorly for about one-fourth of its length; vocal slits extending from midlateral base of tongue to angles of jaws.

Humeral spine absent; ulnar folds and tubercles absent; first finger longer than second; fourth finger nearly as long as third; lateral fringes present on fingers; webbing vestigial between first and second and second and third fingers; webbing formula for outer fingers III(0-2)-(1⅓-1½)IV; discs moderate, rounded, subarticular tubercles small, round, simple; supernumerary tubercles absent; palmar tubercle small, ovoid; nuptial excrescences absent. Hind limbs slender;

length of tibia 51.9-57.3 percent ($\bar{x}$=55.1, N=4) of snout-vent length; tarsal folds and tubercles absent; inner metatarsal tubercle low, flat, elliptical; outer metatarsal tubercle absent; subarticular tubercles small, round; supranumerary tubercles absent; feet about three-fourths webbed; webbing formula I(0-1)-(1½-2)II(0-1)-(2-2^+)III(1-2^+)-(2-2^+)IV(2-2^+)-1V; discs of toes round, slightly smaller than those on fingers.

Skin on dorsal surfaces of head and body shagreened; skin on belly and ventral surfaces of thighs granular; other surfaces smooth; anal opening directed posteriorly at upper level of thighs; anal folds and tubercles absent.

Color in preservative: dorsum creamy white with scattered black flecks visible under microscope; eyelids and hepatic peritoneum white; skin elsewhere transparent.

Color in life: dorsum pale green with pale yellow or yellowish green spots, so large in some individuals so as to give appearance of a pale frog with darker green reticulations; heart visible; belly white; tips of digits yellow; other surfaces unpigmented; bones white; iris white to pale yellow.

Distribution.—This is the most widespread species of *Centrolenella,* ranging from Veracruz and Guerrero, México to Ecuador and Surinam (Goin, 1964; Savage, 1967). In Ecuador it occurs on the Pacific lowlands and to an elevation of 1460 m at Tandapi on the Pacific slopes of the Cordillera Occidental of the Andes (Fig. 10).

Remarks.—Numerous males were calling over small streams in April at the Estación Biológica Río Palenque north of Quevedo. The single specimen from Tandapi was on a leaf of an herb about 2 m above the ground at night.

Goin (1961:96) diagnosed *petersi* as differing from *fleischmanni* by having more extensive webbing on the hand. One specimen (KU 121052) is like the holotype in having a webbing formula for the outer fingers III0-1⅓IV, whereas other Ecuadorian specimens have III(1½-2)-1½IV. Examination of series of specimens from Costa Rica and Panamá reveals that most fall within the range of variation in the webbing of the hand as displayed by the three Ecuadorian specimens, but three have only one free digit on the third finger and about one and one-half digits free on the fourth finger. Due to the lateral fringes on the fingers, the determination of the point of departure of the web is highly subjective in some specimens. We have observed living *fleischmanni* in México, Guatemala, Costa Rica, and Panamá, as well as in Ecuador. Comparison of colored photographs of living individuals from throughout this range reveals that northern frogs tend to be less distinctively marked than southern ones, but the reticulate pattern is evident in some Panamanian specimens.

Despite the wide geographic range of the species as outlined by Goin (1964:4), he was reluctant to accept the occurrence of *fleischmanni* in Ecuador; he stated: "I have examined the specimen (USNM 60520) that Noble (1924:67) recorded as *fleischmanni* from Guevedo [=Quevedo, 56 km south of a locality where we obtained four specimens], Ecuador, and agree with him that this individual looks like typical *fleischmanni* from along the north coast of South America. It seems improbable to me, however, that this species actually occurs in Ecuador."

We have examined the type specimens of all of the nominal species included in the foregoing synonymy and have compared our findings with data obtained from series of living and preserved frogs. We conclude that the holotype of *Cochranella petersi* and KU 121052 represent the extreme in variation of webbing in *Centrolenella fleischmanni* and that *Cochranella petersi* Goin, 1961, is a junior synonym of *Centrolenella fleischmanni* (Boettger, 1893).

Centrolenella grandisonae Cochran and Goin

Centrolenella grandisonae Cochran and Goin, 1970:513 [Holotype.—BMNH 1910.7.11.68 from Pueblo Rico, Departamento Caldas, Colombia].

Diagnosis.—1) prevomerine teeth usually absent; 2) bones pale green; 3) parietal peritoneum white; visceral peritoneum clear; 4) color in life green with minute yellow, white, and black flecks; in preservative, pale lavender with small gray spots and white flecks; 5) webbing between outer fingers III2½-2$^+$IV; 6) webbing on foot I1-2$^-$II1-2$^-$III1-2IV2$^+$1½V; 7) snout round in dorsal and lateral profiles; 8) dorsal skin shagreened; 9) row of low, indistinct tubercles on ventrolateral edges of forearm and tarsus; 10) humeral spine present in males; 11) tympanum entirely visible, directed laterally with posterodorsal inclination.

Two other Ecuadorian species are lavender (in preservative) with dark spots and white flecks. Of these, *pipilata* differs from *grandisonae* by having ulnar and tarsal folds, truncate snout, and incised webbing. *Centrolenella peristicta* is nearly identical to *grandisonae* in coloration and structural features, except that *peristicta* has more webbing on the hand (1½ phalanges free on fourth finger; 2$^+$ free in *grandisonae*) and is smaller (mean snout-vent length 19.7 mm; 24.8 in *grandisonae*).

Description.—Adults moderately large; snout-vent length in males 23.7-25.8 mm ($\bar{x}$=24.8, N=4); females not known. Head about as wide as body; width of head 24.6-33.3 percent ($\bar{x}$=31.1, N=4) of snout-vent length; snout short, rounded in dorsal view, in lateral view inclined above, truncate below, giving a rounded appearance; canthus rounded; loreal region barely concave; lips not flared; nostrils nearly terminal on snout, slightly protuberant dorsolaterally; internarial area slightly depressed. Eye large, directed anterolaterally. Supratympanic fold weak; entire tympanum visible, directed laterally with posterodorsal inclination. Prevomerine dentigerous processes and teeth absent; choanae small, round; tongue cordiform, notched behind, free posteriorly for about one-fourth of its length; vocal slits extending from midlateral base of tongue to angles of jaws.

Humeral spine blunt, perpendicular to humerus; row of low tubercles on ventrolateral edge of forearm; first finger longer than second; fourth finger much shorter than third; lateral fringes present on fingers; webbing absent between first and second fingers, vestigial between second and third fingers; webbing formula for outer fingers III(2¼-2⅓)-(2^--2^+)IV; discs truncate; subarticular tubercles small, round, simple; supernumerary tubercles absent; palmar tubercle ovoid, simple; nuptial excrescences absent (Fig. 3). Hind limbs slender; length of tibia 54.9-57.3 percent ($\bar{x}$=55.8, N=4) of snout-vent length; row of low, indistinct tubercles on ventrolateral edge of tarsus; inner metatarsal tubercle small, elliptical; outer metatarsal tubercle small, ovoid; subarticular tubercles small, round; supernumerary tubercles absent; toes about two-thirds webbed; webbing formula I(0-1½)-1⅓-2^+)II(0-1)-(1½-2^+)III(1-1¼)-(2-2^+)IV(2-2¼)-(1-1½)V; discs smaller and more nearly round than those on fingers (Fig. 4).

Skin on dorsal surfaces shagreened; skin on belly and proximal posteroventral surfaces of thighs granular, other surfaces smooth; anal opening directed posteriorly at upper level of thighs; pair of large tubercles below anus.

Color in preservative: dorsal surfaces lavender with large dark smudges and small white flecks; other surfaces cream.

Color in life: green with minute yellow and white flecks and dark green and black spots on body and limbs; tips of digits pale yellow; humeral spine bluish green, vocal sac green; chest white; heart not visible; visceral peritoneum transparent; bones green; iris pale golden bronze flecked with black.

Distribution.—Centrolenella grandisonae occurs at moderate elevations on the Pacific slopes of the Cordillera Occidental of the Andes from southwestern Colombia to northwestern Ecuador (Fig. 7). In Colombia it is known from Pueblo Rico, 1540 m and Santa

Leticia, 2000 m, Departamento Caldas, and in Ecuador from Tandapi, 1460 m, Provincia Pichincha.

Remarks.—Three calling males were found along the small stream in cloud forest at Tandapi in July 1967. With the exception of one metamorphosing young found along the Río Tandapi, *grandisonae* was observed only along the one stream, where males were calling from leaves of bushes and trees by a waterfall. None of the other four species of *Centrolenella* known from Tandapi was found along this stream. The metamorphosing young has a snout-vent length of 13.5 mm and a tail stub of 2 mm.

The holotype of *grandisonae* is the largest known specimen of the species (27.4 mm) and is the only one having prevomerine teeth.

Centrolenella griffithsi (Goin)
Plate 2C

Cochranella griffithsi Goin, 1961:99 [Holotype.—BMNH 1940.2.20.4 from Río Saloya, Provincia Pichincha, Ecuador].
Centrolenella griffithsi Goin, 1964:6.

Diagnosis.—1) prevomerine teeth absent; 2) bones pale green; 3) parietal peritoneum clear; visceral peritoneum white; 4) color in life yellowish green with or without dark flecks; in preservative, dull lavender; 5) webbing between outer fingers III3-2⅔IV; 6) webbing on foot I2-2¼II1-2^+III1-2½IV2⅓-1V; 7) snout truncate in dorsal and lateral profiles; 8) dorsal skin shagreened; 9) arms and legs lacking dermal folds; 10) humeral spine absent in males; 11) lower three-fourths of tympanum visible, directed dorsolaterally with posterior inclination.

The diagnostic characters of *griffithsi* resemble those of three other *Centrolenella*—*buckleyi*, *megacheira*, and *prosoblepon.* Of these, *megacheira* is much larger and has pustular dorsal skin. *Centrolenella buckleyi* and *prosoblepon* have more webbing, and the males have humeral spines.

Description.—Adults moderately large; snout-vent length 19.7-26.1 mm ($\bar{x}$=24.1, N=14) in males, 21.6-24.8 ($\bar{x}$=23.4, N=3) in females. Head slightly wider than body; width of head 30.6-34.7 percent ($\bar{x}$=32.3, N=17) of snout-vent length; snout short, truncate in dorsal and lateral profiles (Fig. 1); canthus round; loreal region concave; lips not flared; nostrils nearly terminal on snout, slight protuberant dorsolaterally; internarial area barely depressed. Eye moderately large, directed anterolaterally. Supratympanic fold barely evident; lower three fourths of tympanum visible, directed dorsolaterally with posterior inclination. Prevomerine dentigerous processes and teeth absent; choanae large, quadrangular; tongue cordiform, distinctly notched behind, barely free posteriorly; vocal slits extending from midlateral base of tongue to angles of jaws.

Humeral spine absent; ulnar fold and tubercles absent; first finger longer than second; fourth finger noticeably shorter than third; lateral fringes absent on fingers; webbing absent between first, second, and third fingers; webbing formula for outer fingers III3-2⅔IV; discs broad, rounded; subarticular tubercles small, round, simple; supernumerary tubercles absent; palmar tubercle large, elliptical, simple; nuptial excrescences absent (Fig. 3). Hind limbs slender; length of tibia 52.4-62.3 percent ($\bar{x}$=55.2, N=17) of snout-vent length; tarsal folds and tubercles absent; inner metatarsal tubercle small, ovoid; outer metatarsal tubercle absent; subarticular tubercles small, round; supernumerary tubercles absent; feet about one-half webbed; webbing formula I(2-2^+)-(2^+-2¼)II(1^+-1½)-(2½-3^-)III1½-(2⅓-3^-)IV(2⅓-3^-)-2^-V; discs on toes smaller and more nearly round than those on fingers (Fig. 4).

Skin on dorsal surfaces shagreened; skin on belly and posteroventral surfaces of thighs granular; other surfaces smooth; anal opening directed posteriorly at upper level of thighs; pair of large tubercles below anus.

Color in preservative: dorsal surfaces of head, body, forearms, shanks, and feet dull lavender with or without minute black flecks; other surfaces cream.

Color in life: dorsal surfaces pale yellowish green with or without dark green flecks; tips of digits pale yellow; chest white; heart not visible; visceral peritoneum transparent; bones pale green; iris whitish bronze.

Distribution.—*Centrolenella griffithsi* occurs on the Pacific slopes of the Cordillera Occidental of the Andes from southwestern Columbia to northwestern Ecuador (Fig. 9); the species inhabits cloud forests at elevations of 1200-2170 m.

Remarks.—Most of our specimens were obtained from low vegetation in cloud forest at Tandapi. Males were calling from leaves of herbs and bushes over cascading streams. One was found in the axil of an elephant-ear plant by day. Calling males were observed by Lynch on each of his five trips to Tandapi (March 1968, June 1968, July 1967, 1968, and 1970). Sparsely distributed and sporadically calling males were heard every evening at Tandapi, but the breeding season clearly is in March, when most available sites were occupied by calling males, and vegetation overhanging streams was festooned with egg masses. Eggs were not observed in June or July.

In July 1968, while we were collecting astroblepid catfishes in the gravel at the bottom of a small stream, two centrolenid tadpoles were found. These may be the tadpoles of *griffithsi*, the most abundant of the five species of *Centrolenella* known from Tandapi; only *griffithsi* adults were found along the stream. Structurally identical tadpoles were collected at Pilaló, Provincia Cotopaxi, 2500 m.

Goin (1969:99) gave the type locality as "Río Saloya, Ecuador, 4000 feet." This locality probably is the point on the Río Saloya where it is crossed by the road from Chillogallo to Santo Domingo de los Colorados, the only road west from Quito in 1940, when the specimens were collected. The point where the road crosses the Río Saloyo is about 1200 m. The species is abundant in the next valley south, that of the Río Pilatón.

Centrolenella medemi Cochran and Goin

Centrolenella medemi Cochran and Goin [Holotype.—USNM 152277 from Puerto Asís, Comisaria Putumayo, Colombia].

Diagnonis.—1) prevomerine teeth 2-3; 2) bone color unknown; 3) heart apparently not visible; 4) color in life unknown; in preservative, dark gray with many cream spots; 5) webbing between outer fingers III2^{-}-1½IV; 6) webbing on foot I0-0II0-0III0-1IV1-0V; 7) snout truncate in dorsal and lateral profiles; 8) dorsal skin smooth; 9) arms and legs lacking dermal folds; 10) small humeral spine present in males; 11) tympanum concealed.

Centrolenella medemi is unique among known centrolenids by having a dark gray dorsum with many large, round spots on all dorsal surfaces. The only other Amazonian species having humeral spines, *audax* and *pipilata,* have distinct tympana, less webbing, and a pale green dorsum with small yellow flecks *(audax)* or dark green with black spots and yellow flecks *(pipilata).*

Description.—Adult male moderate in size, 25.3 mm in snout-vent length; head much wider than body; width of head 39.5 percent of snout-vent length; snout moderately short, truncate in dorsal and lateral profiles; canthus round; loreal region barely concave; lips not flared; nostrils nearly terminal, not protuberant, directed dorsolaterally; internarial area flat. Eye moderately large, directed anterolaterally. Supratympanic fold absent; tympanum concealed. Prevomerine dentigerous processes short, transverse between choanae, bearing 2-3 teeth; choanae small, ovoid, near margin of mouth; tongue ovoid, barely free posteriorly; vocal slits extending from midlateral base of tongue towards angles of jaws.

Humeral spine curved, not projecting; ulnar folds and tubercles absent; lateral fringes absent on fingers; webbing formula I2-2½II2^{-}-3^{+}III2^{-}-1½IV; discs large, truncate; subarticular tubercles large, round, simple; supernumerary tubercles absent; palmar tubercle large, simple, ovoid; nuptial excrescences absent. Hind limbs robust; length of tibia 68.8 percent of snout-vent length; tarsal folds and tubercles absent; inner metatarsal tubercle low, elongate; outer metatarsal absent; subarticular tubercles small, round; supernumerary tubercles absent; feet essentially fully webbed; webbing formula I0-0II0-0III0-1IV1-0V; discs on toes slightly smaller and more nearly round than those on fingers.

Skin on belly granular; skin on other surfaces smooth; anal opening directed posteriorly at upper level of thighs; anal folds and tubercles absent.

Color in preservative: all dorsal surfaces slate gray with many round cream spots; ventral surfaces cream. Color in life unknown.

Distribution.—Known only from the type locality at an elevation of about 280 m on the Río Putumayo in Amazonian Colombia (Fig. 7).

Remarks.—This distinctive species is included here in the anticipation that it will be found in Ecuador; the type locality is only 20 km north of the Ecuadorian border.

Centrolenella megacheira new species
Plate 2A

Holotype.—KU 143245, an adult male, 27.1 mm, from a stream 16.5 km NNE of Santa Rosa, 1700 m. on Quito-Lago Agrio road, Provincia Napo, Ecuador, one of a series obtained on 17 October 1971, by Joseph T. Collins and William E. Duellman.

Paratopotypes.—KU 143246-72, BMNH 1971.1854-55, CAS 135498-9, UMMZ 131668 (3) obtained on 17-19 October 1971, by Joseph T. Collins and William E. Duellman.

Diagnosis.—1) prevomerine teeth absent; 2) bones green; 3) parietal peritoneum white; visceral peritoneum clear; 4) color in life green with black spots; in preservative, lavender with black spots; 5) webbing between outer fingers III3^{-}-2⅔IV; 6) webbing on foot I2^{-}-2^{+}II1½-2½III1½-2¾IV3^{-}-1⅔V; 7) snout truncate in dorsal and lateral profiles; 8) dorsal skin pustular; 9) arms and legs lacking dermal folds; 10) humeral spine absent in males; 11) lower three-fourths of tympanum visible, directed dorsolaterally with slight posterior inclination.

Centrolenella megacheira is distinguished from all other Andean species by its large size, pustular dorsal skin, and small amount of webbing on the hands and feet. The presence of black flecks on the dorsum also is characteristic of *prosoblepon,* males of which have humeral spines.

Descriptions.—Adults large; snout-vent length 27.1-32.8 mm ($\bar{x}$=28.2, N=20) in males, 32.1-32.8 mm ($\bar{x}$=32.5, N=3) in females. Head much wider than body; width of head 32.8-37.4 percent ($\bar{x}$=34.3, N=23) of snout-vent length; snout short, truncate in dorsal and lateral profiles; canthus rounded; loreal region slightly concave; lips barely flared; nostrils four-fifths distance from eye to tip of snout, slightly protuberant dorsolaterally; internarial area depressed. Eye large, directed more anteriorly than laterally. Supratympanic fold weak; lower three-fourths of tympanum visible, directed dorsolaterally with slight posterior inclination. Prevomerine dentigerous processes and teeth absent; choanae small, ovoid; tongue cordiform, barely free posteriorly; vocal slits extending from midlateral base of tongue to angles of jaws.

Humeral spine absent; ulnar fold and tubercles absent; hand large; first finger equal in length to second; fourth finger slightly shorter than third; lateral fringes present on fingers; webbing absent between first and second fingers; webbing formula for other fingers II(2^+-2½)-(3½-3¾)III(2½-3^-)-(2½-3)IV; discs broader than deep, rounded; subarticular tubercles large, ovoid, simple; supernumerary tubercles absent; palmar tubercle large, ovoid, simple; nuptial excrescences absent. Hind limbs slender; length of tibia 53.7-62.3 percent ($\bar{x}$=56.9, N=23) of snout-vent length; tarsal folds and tubercles absent; inner metatarsal tubercle large, elliptical; outer metatarsal tubercle small, ovoid; subarticular tubercles small, round; supernumerary tubercles absent; feet about one-half webbed; webbing formula I(2^--2)-(2^+-2½)II(1-1⅔)-(2½-2⅔)III(1⅓-1¾)-(2½-3^-)IV(2⅔-3^-1)-(1½-2^-)V; discs on toes slightly smaller and more nearly round than those on fingers.

Skin on dorsal surfaces pustular; skin on belly and ventral surfaces of thighs granular; other surfaces smooth; anal opening directed posteriorly at upper level of thighs; pair of large tubercles below anus.

Color in preservative: dorsal surfaces of head, body, hind limbs, and forearms lavender with small, round, black dots; hands, feet, upper arms, and ventral surfaces cream.

Color in life: dorsum green with black dots; flanks cream; chest white; heart not visible; visceral peritoneum unpigmented; other ventral surfaces green; iris pale grayish bronze; bones green.

Distribution.—The species currently is known at two localities at elevations of 1700 and 1740 m on the Amazonian slopes of the Cordillera Oriental in Ecuador (Fig. 9). The type locality is a small stream which drains into a tributary of the Río Salado. This stream is crossed by the Quito-Lago Agrio road at a point 16.5 km north-northeast of the village of Santa Rosa.

Remarks.—Individuals were found at night on leaves and stems of bushes and trees overhanging streams in cloud forest. Males were calling in October 1971. At the type locality, *audax, pipilata,* and *siren* were found with *megacheira;* at the Río Azuela, *anomala, pellucida, pipilata,* and *siren* occurred along the same streams with *megacheira.*

Etymology.—The specific name is from the Greek *megas,* meaning large, and the Greek *cheiros,* meaning hand; the name is used in reference to the exceedingly large hands of this species.

Centrolenella midas new species

Plate 1D

Holotype.—KU 123219, an adult male, 19.2 mm, from Santa Cecilia, 340 m, Provincia Napo, Ecuador, obtained on 22 June 1968, by Linda Trueb.

Paratypes.—KU 107026, 23 November 1966, William E. Duellman; KU 146625, 2 April, Martha L. Crump; KU 150622, 25 June 1971, Philip S. Humphrey; KU 150623, 28 August 1971, Martha L. Crump, all from the type locality. KU 125334, 23 May 1969, Thomas H. Fritts, and UMMZ 129314, 6 May 1969; Charles F. Walker from Lago Agrio, 330 m, Provincia Napo, Ecuador.

Diagnosis.—1) prevomerine teeth 1-3; 2) bones green; 3) parietal peritoneum white; visceral peritoneum clear; 4) color in life dark green with yellow flecks; in preservative, lavender with white flecks; 5) webbing between outer fingers III2-2^{-}IV; 6) webbing on foot I1-2II1-2III1-2^{+}IV2^{+}-1V; 7) snout truncate in dorsal and lateral profiles; 8) dorsal skin shagreened; 9) arms and legs lacking dermal folds; 10) humeral spine absent in males; 11) lower two-thirds of tympanum visible, directed dorsolaterally with strong posterior inclination.

Centrolenella midas is like *flavopunctata* and *siren* in having a lavender dorsum with white flecks (in life, green with gold flecks) and no black flecks; it differs from *flavopunctata* by having a truncate, instead of round snout and slightly less webbing on the hands and feet. *Centrolenella siren* differs from *midas* by having less webbing and a more prominent tympanum oriented posterolaterally, instead of dorsolaterally.

Description.—Adults small; snout-vent length 17.4-19.2 mm ($\bar{x}$=18.4, N=3) in males, 20.6-25.6 mm ($\bar{x}$=22.7, N=7) in females. Head wider than body; width of head 33.3-39.1 percent ($\bar{x}$=36.0, N=10) of snout-vent length; snout short, truncate in dorsal and lateral profiles;

canthus round; loreal region concave; lips rounded; nostrils nearly terminal on snout, slightly protuberant dorsolaterally; internarial area depressed. Eye moderately large, directed anterolaterally. Supratympanic fold absent; lower two-thirds of tympanum visible, directed dorsolaterally with strong posterior inclination. Dentigerous processes of prevomers small, low, widely separated between moderately large, round choanae, bearing 1-3 teeth; tongue broadly cordiform, barely free posteriorly; vocal slits extending from midlateral base of tongue to angles of jaws.

Humeral spine absent; ulnar fold and tubercles absent; first finger longer than second; fourth finger noticeably shorter than third; webbing vestigial between first and second fingers; webbing formula for other fingers II(2-2^+)-(3^+-3½)III(2^--2^+)-(1⅔-2^+)IV; discs truncate; subarticular tubercles small, round, simple; supernumerary tubercles absent; palmar tubercle large, elliptical; nuptial excrescences absent. Hind limbs moderately slender; length of tibia 53.1-62.0 percent ($\bar{x}$=57.7, N=10) of snout-vent length; tarsal folds and tubercles absent; inner metatarsal tubercle elongate, rounded in section; outer metatarsal tubercle absent; subarticular tubercles small, round; supernumerary tubercles absent; feet about two-thirds webbed; webbing formula I(0-1⅓)-(2^--2^+)II(½-1)-(2-2^+)III1-(2-2¼)IV(2-2^+)-IV; discs on toes more nearly round than those on fingers.

Skin on dorsal surfaces shagreened; skin on belly and proximal posteroventral surfaces of thighs granular; other surfaces smooth; anal opening directed posteriorly at upper level of thighs; pair of large tubercles below anus.

Color in preservative: dorsal surfaces of head, body, and limbs lavender with few small white flecks on body; other surfaces creamy white.

Color in life: dorsum of head, body, and limbs dark green with a few small yellow flecks dorsolaterally on body; hands and feet dull greenish yellow; chest white; heart not visible; visceral peritoneum unpigmented; iris silvery bronze with black reticulations; bones green.

Distribution.—This species is known from three localities at elevations of 330-570 m along the Río Aguarico in the upper Amazon Basin in Ecuador (Fig. 9). In this area it occurs in sympatry with *munozorum* and *resplendens*.

Remarks.—Individuals have been found throughout the year on leaves of herbs and trees along small rivulets in rainforest. The call consists of three short notes.

Etymology.—The specific name is that of a king in Greek mythology, at whose touch everything turned to gold. The name is associated with this frog known along the Río Aguarico, meaning rich water, in reference to gold found in the river, and in allusion to the gold flecks on the frogs.

Centrolenella munozorum new species

Plate 1B

Holotype.—KU 118054, an adult male, 20.2 mm, from Santa Cecilia, 340 m, Provincia Napo, Ecuador, obtained on 18 June 1967, by John D. Lynch.

Paratypes.—KU 105251, 13 July 1966, Charles M. Fugler; KU 123225, 13 July 1968, William E. Duellman; KU 150620, 13 August 1971, Martha L. Crump; KU 150621, 10 October 1971, Martha L. Crump, all from Santa Cecilia, and UMMZ 129313 from Lago Agrio, 330 m, 14 km E Santa Cecilia, Provincia Napo, Ecuador, 6 May 1969, Charles F. Walker.

Diagnosis.—1) prevomerine teeth absent; 2) bones white; 3) parietal peritoneum clear; visceral peritoneum white; 4) color in life pale green with pale greenish yellow spots; in preservative, creamy white with pale gray reticulations; 5) webbing between outer fingers III1½-1¼IV; 6) webbing on foot I0-1II0-1½III1-2IV2^{-}-1V; 7) snout round in dorsal and lateral profiles; 8) dorsal skin shagreened; 9) arms and legs lacking dermal folds; 10) humeral spine absent in males; 11) tympanum concealed; strongly directed dorsolaterally.

Two other Ecuadorian species have the heart visible in life and a white dorsum in preservative. *Centrolenella pellucida* differs from *munozorum* by having ulnar, tarsal, and anal folds, and *fleischmanni* differs by having the snout subacuminate in dorsal view and truncate in lateral profile and the tympanum is distinct; in *munozorum* and *pellucida* the snout is round, and the tympanum is concealed. The Venezuelan *orocostalis* has enamel white (yellow in life) flecks on the dorsum.

Description.—Adults small; snout-vent length in males 18.8-20.5 mm ($\bar{x}$=19.7, N=5), in one female 20.7 mm. Head wider than body; width of head 37.7-40.7 percent ($\bar{x}$=38.4, N=6) of snout-vent length; snout short, shallow, round in dorsal and lateral profiles (Fig. 1); canthus round; loreal region shallowly concave; lips slightly flared; nostrils about four-fifths distance from eye to tip of snout, barely protuberant, directed dorsolaterally; internarial area slightly depressed. Eye moderately large, protuberant, directed anterolaterally. Supratympanic fold absent; tympanum concealed, strongly directed dorsolaterally. Prevomerine dentigerous processes and teeth absent; choanae small, ovoid, near margin of mouth; tongue ovoid, barely free posteriorly; vocal slits extending from posterolateral base of tongue to angles of jaws.

Humeral spine absent; ulnar fold and tubercles absent; first finger longer than second; fourth finger nearly as long as third; lateral fringes present on fingers; webbing vestigial between first and second and second and third fingers; webbing formula for outer fingers III(1½-2^{-})-(1-1½)IV; discs small, rounded, subarticular tubercles small, round, simple; supernumerary tubercles present on proximal segments of first and second fingers; palmar tubercle small, round; nuptial excrescences absent (Fig. 3). Hind limbs slender; length of tibia 57.5-59.6 percent ($\bar{x}$=58.4, N=5) of snout-vent length in males, 54.1 percent in one female; tarsal folds and tubercles absent; inner metatarsal tubercle small, elongate; outer metatarsal tubercle absent; subarticular tubercles small, round; supernumerary tubercles absent; fringe on inner edge of first toe; toes about three-fourths webbed; webbing formula I0-(1^{-}-⅔)II(0-1)-(1½-2^{-})III(0-1)-(2^{-}-2^{+})IV(2^{-}-2)-(0-1)V; discs on toes round, slightly smaller than those on fingers.

Skin on dorsal surfaces of head and body shagreened; skin on belly and proximal ventral surfaces of thighs weakly granular; other surfaces smooth; anal opening directed posteriorly at upper level of thighs; anal folds and tubercles absent.

Color in preservative: dorsal surfaces of head, body, forearms, thighs, and shanks creamy white with many minute black flecks giving appearance of gray with unpigmented spots; eyelid and hepatic peritoneum white; other surfaces unpigmented.

Color in life: dorsum pale green with pale yellow or yellowish green spots; limbs pale green, with slightly darker crossbars in one; thighs unpigmented; iris pale gold.

Distribution.—Currently this species is known from only two localities along the Río Aguarico in the Amazonian lowlands of Ecuador (Fig. 10).

Remarks.—All individuals were found in lowland rainforest. At Santa Cecilia the frogs were found on leaves of bushes and trees at night: one over a pond, one away from water in primary forest, one on a palm frond 2 m above a stream, and one on an herbaceous leaf more than 2 m above a stream. The specimen from Lago Agrio was obtained from the foliage of a large tree that was felled during the clearing of primary forest.

Etymology.—The specific name is a patronym for Ing. Ildefonso Muñoz B. and Sra. Blanca Muñoz, our congenial hosts at Santa Cecilia.

Centrolenella ocellifera (Boulenger)

Hyla ocellifera Boulenger, 1899:277 [Holotype.—BMNH 98.5.19.3 from Paramba, Provincia Imbabura, Ecuador].
Cochranella ocellifera—Taylor, 1951:35.
Centrolenella ocellifera—Goin, 1964:6.

Diagnosis.—1) prevomerine teeth absent; 2) bones white (?); 3) parietal peritoneum white; visceral peritoneum clear; 4) color in life green with yellow spots; in preservative, pale lavender with faint purple ocelli enclosing white spots; 5) webbing between outer fingers III2-1¾IV; 6) webbing on foot I1-2II1-2^-III1-2IV2^+-1V; 7 snout round in dorsal view, truncate in lateral profile; 8) skin shagreened; 9) arms and legs lacking dermal folds; 10) humeral spine absent in males; 11) lower two-thirds of tympanum visible, directed laterally with slight posterodorsal inclination.

Centrolenella ocellifera has shagreened skin and few large ocelli on the dorsum. Other species having ocellated dorsal patterns *(anomala, cochranae,* and *ocellata)* have minute spicules in the dorsal skin and less webbing between the outer fingers. Furthermore, *ocellifera* differs from *anomala* by having a green instead of brown dorsum, from *ocellata* by having the lower two-thirds of the tympanum visible (concealed in *ocellata*), and from *cochranae* by having larger ocelli, snout round in dorsal view, and prevomerine teeth absent (*cochranae* has small ocelli, snout truncate in dorsal view, and prevomerine teeth usually present).

Description.—Adults moderate-sized; snout-vent length 20.0 mm in male, 26.7 mm in female. Head as wide as body; width of head 32.9-37.0 percent ($\bar{x}$=35.0, N=2) of snout-vent length; snout short, round in dorsal view, truncate in lateral profiles; canthus round; loreal region concave; lips slightly flared; nostrils four-fifths distance from eye to tip of snout, not protuberant, directed laterally; internarial area flat. Eye large, protuberant, directed anterolaterally. Supratympanic fold not evident; lower two-thirds of tympanum visible, directed laterally with slight posterodorsal inclination. Prevomerine teeth absent in one male, 2-3 on transverse processes between choanae in one female; choanae small, rectangular; tongue ovoid, slightly free posteriorly.

Humeral spine absent; ulnar folds and tubercles absent; first finger larger than the second; fourth finger nearly as long as third; fingers extensively webbed; webbing formula I2¾-2II2-3III2-(1½-1¾)IV; fringe on outer edge of fourth finger; discs moderately broad, truncate; subarticular tubercles small, round, simple (distal tubercle on fourth fingers bifid in female); supernumerary tubercles absent; palmar tubercle single, ovoid; nuptial excrescences absent. Hind limbs long, slender; tibia length 52.4-59.5 percent ($\bar{x}$=55.9, N=2) of snout-vent length; tarsal folds and tubercles absent; inner metatarsal tubercle moderately small, elliptical; outer metatarsal tubercle absent; subarticular tubercles small, round; supernumerary tubercles absent; feet about three-fourths webbed; webbing formula I1-2II1-2^{-}III(1^{-}-1)-2IV2^{+}-1V; fringe on inner edge of first toe; discs on toes smaller and more nearly round than those on fingers.

Skin on dorsal surfaces shagreened, that on belly and ventral surfaces of thighs weakly granular; other surfaces smooth; anal opening directed posteriorly at upper level of thighs; anal folds and tubercles absent.

Color in preservative: dorsal surfaces of head, body, and shanks pale lavender, scattered dark brown flecks; three or four thin purple ocelli with cream centers in scapular region (Fig. 5); chest and belly cream; other surfaces transparent.

Color in life: body green with pale yellow spots and dark green flecks on body; limbs paler green; chest white; heart not visible; visceral peritoneum transparent; iris gray-bronze.

Distribution.—*Centrolenella ocellifera* inhabits the Pacific slopes of the Andes (Fig. 6). In addition to the holotype from Paramba (777 m), we have a specimen from Tandapi (1460 m) and have seen a specimen in the Gustavo Orcés-V. collection in the United States National Museum from Pilaló (2320 m).

Remarks.—Our specimen was found at night on a fern in cloud forest. The fern was at the edge of a cliff about 10 m above the Río Pilatón.

Centrolenella pellucida new species
Plate 1C

Holotype.—KU 143298, a gravid female, 22.0 mm from the Río Azuela, 1740 m, Quito-Lago Agrio road, Provincia Napo, Ecuador, obtained on 20 October 1971, by William E. Duellman.

Diagnosis.—1) prevomerine teeth absent; 2) bones white; 3) parietal peritoneum clear; visceral peritoneum white; 4) color in life pale green with diffuse yellow spots; in preservative, uniform cream; 5) webbing between outer fingers III2^{+}-2IV; 6) webbing on foot I1-2^{+}II1-1½III1-2^{+}IV2^{+}-1V; 7) snout round in dorsal and lateral profiles; 8) dorsal skin shagreened; 9) unscalloped dermal fold on outer edge of hand and forearm and on foot and tarsus; transverse dermal fold below anus; 10) humeral spine absent in males; 11) tympanum concealed.

Among the Ecuadorian species *(fleischmanni, pellucida,* and *munozorum)* having the heart visible in life and the dorsum white in preservative, *C. pellucida* is unique in possessing ulnar, tarsal, and anal folds. Moreover, in *C. fleischmanni* the snout is subacuminate in dorsal view and truncate in lateral profile, and the tympanum is distinct; in *C. pellucida* and *C. munozorum* the snout is round, and the tympanum is concealed. The Venezuelan *orocostalis,* a member of the *fleischmanni* group, also lacks dermal folds.

Description.—Males unknown; adult female small, 22.0 mm in snout-vent length; head slightly wider than body; width of head 36.4 percent of snout-vent length; snout short, round in dorsal and lateral profiles; canthus round; loreal region barely concave; lips not flared; nostrils nearly terminal, directed laterally, not protuberant; internarial area flat. Eye large, protuberant, strongly oriented anteriorly. Supratympanic fold absent; tympanum concealed. Prevomerine dentigerous processes and teeth absent; choanae large, oval; tongue ovoid, barely free posteriorly.

Humeral spine absent; narrow, unscalloped dermal fold on ventrolateral edge of forearm and outer edge of hand; fringes absent on fingers; first finger longer than second; fourth finger slightly shorter than third; fingers extensively webbed; webbing formula I2-2$^+$II2$^-$-3III2$^+$-2IV; discs moderately large, rounded; subarticular tubercles small, low; supernumerary tubercles absent; palmar tubercle small, indistinct. Hind limbs slender; tibia length 56.4 percent of snout-vent length; narrow, unscalloped dermal fold along outer edge of tarsus and fifth toe; inner metatarsal tubercle small, ovoid; outer metatarsal tubercle absent; subarticular tubercles small, low; supernumerary tubercles absent; feet about three-fourths webbed; webbing formula I1-2II1-1½III1-2$^+$IV2$^+$-IV; discs on toes round, slightly smaller than those on fingers.

Skin on dorsum of head and body shagreened; skin on other surfaces smooth; anal opening directed posteriorly at upper level of thighs; transverse dermal fold below anus at posteroventral edge of thighs (Fig. 2).

Color in preservative: dorsum creamy white with minute purple flecks visible under magnification; hepatic peritoneum white; skin on ventral surfaces transparent.

Color in life: dorsum pale green with diffuse yellow spots; venter and hidden surfaces of limbs lacking pigment; fingers and toes yellow; parietal peritoneum clear; heart visible; bones white; iris pale silvery bronze.

Distribution.—This small species is known only from the type locality on the east slope of Volcán Reventador on the Amazonian slopes of the Andes (Fig. 10).

Remarks.—The holotype was on the leaf of an herb over a small stream at night. See the account of *anomala* for a detailed description of the type locality and comments on associated species.

Etymology.—The specific name is Latin meaning transparent and is applied to this species having a transparent parietal peritoneum.

Centrolenella peristicta new species

Plate 2G

Holotype.—KU 118051, an adult male, 20.6 mm, from Tandapi, 1460 m, Provincia Pichincha, Ecuador, obtained on 23 July 1967, by John D. Lynch.

Paratopotypes.—KU 118052, 24 July 1967, Marsha Lynch; 121053, 28 July 1968, Gerald R. Smith.

Diagnosis.—1) prevomerine teeth absent; 2) bones pale green; 3) parietal peritoneum white; visceral peritoneum clear; 4) color in life pale green with minute yellow, white, and black flecks; in preservative, pale lavender with dark lavener spots and few white flecks; 5) webbing between outer fingers III2$^-$-1½IV; 6) webbing on foot I1-2$^-$II1-2III1-2$^+$IV2-1V; 7) snout round in dorsal and lateral profiles; 8) dorsal skin shagreened; 9) row of low tubercles on ventrolateral edges of forearm and tarsus; 10) humeral spine present in males; 11) tympanum entirely visible, directed laterally with slight dorsal inclination.

Two other Ecuadorian species are lavender (in preservative) with dark spots and white flecks. Of these *pipilata* differs from *peristicta* by having ulnar and tarsal folds, truncate snout, and incised webbing. *Centrolenella grandisonae* is nearly identical to *peristicta* in coloration and structural features, except that *grandisonae* has less webbing on the hand (2$^+$ phalanges free on fourth finger; 1½ free in *peristicta*) and is larger (mean snout-vent length 24.8 mm; 19.7 mm in *peristicta*).

Description.—Adults small; snout-vent length 18.7-20.6 mm ($\bar{x}$=19.7, N=2) in males, 20.5 mm in one female. Head no wider than body; width of head 32.5-32.7 percent ($\bar{x}$=32.6, N=3); snout short, round in dorsal and lateral profiles; canthus round; loreal region concave; lips rounded; nostrils nearly terminal on snout, slightly protuberant dorsolaterally; internarial area depressed. Eye moderate sized, directed more laterally than anteriorly. Supratympanic fold weak; tympanum entirely visible, directed laterally with slight dorsal inclination. Prevomerine dentigerous processes and teeth absent; choanae small, ovoid; tongue cordiform, shallowly notched behind, barely free posteriorly; vocal slits extending from midlateral base of tongue to angles of jaws.

Humeral spine curved, terminus parallel to humerus; row of low tubercles on ventrolateral edge of forearm; first finger longer than second; fourth finger much shorter than third; lateral fringes present on fingers; webbing vestigial between first and second fingers; webbing formula for other fingers II(2-2½)-3^+III2^--1½IV; discs truncate; subarticular tubercles small, round; distal subarticular tubercle on fourth finger bifid; supernumerary tubercles small, round, present on proximal segments of digits 2-4; palmar tubercle large, ovoid; nuptial excrescences absent (Fig. 3). Hind limbs slender; length of tibia 52.2-58.8 percent ($\bar{x}=54.8$, N=3) of snout-vent length; row of low tubercles on ventrolateral edge of tarsus; inner metatarsal tubercle elliptical; outer metatarsal tubercle small, ovoid; subarticular tubercles small, round; supernumerary tubercles absent; feet about two-thirds webbed; webbing formula I1-(1½-2)II1-(2^--2^+)III1-(2^--2^+)IV(2^--2^+)-1V; discs smaller and more nearly round than those on fingers.

Skin on dorsum shagreened; skin on belly and proximal posteroventral surfaces of thighs granular; other surfaces smooth; anal opening directed posteriorly at upper level of thighs; pair of large tubercles below anal opening.

Color in preservative: dorsal surfaces lavender with dark spots and scattered cream flecks; other surfaces cream.

Color in life: dorsal surfaces pale to medium green with dark green spots and white and yellow flecks; flanks yellow-green; belly yellow; vocal sac green; tips of digits pale yellow; heart not visible; bones green; iris grayish bronze with brown or copper ring around pupil.

Distribution.—This species is known only from Tandapi (formerly Cornejo Astorga), a village at the point where the Quito-Santo Domingo de los Colorados road crosses the Río Pilatón at an elevation of 1460 m on the Pacific slopes of the Cordillera Occidental of the Andes (Fig. 8).

Remarks.—All three individuals were obtained in July on vegetation in cloud forest at night. One was on an elephant-ear leaf; one was on a fern in the spray zone of a waterfall, and one was on a bush over a waterfall. None was calling.

Etymology.—The specific name is derived from the Greek *peristiktos,* meaning dappled, and refers to the spotted color pattern.

Centrolenella pipilata new species

Plate 2D

Holotype.—KU 143278, an adult male, 22.9 mm, from a stream 16.5 km NNE of Santa Rosa, 1700 m, on Quito-Lago Agrio road, Provincia Napo, Ecuador, obtained on 17 October 1971, by William E. Duellman.

Paratopotypes.—KU 143279-83, 17-18 October 1971, William E. Duellman and Joseph T. Collins.

Diagnosis.—1) prevomerine teeth absent; 2) bones green; 3) parietal peritoneum white; visceral peritoneum clear; 4) color in life dark green with diffuse black spots and pale yellow flecks; in preservative, gray with dark and pale flecks; 5) webbing between outer fingers III2¼-2⅔IV; 6) webbing on foot indented I1-2^+II1-2^+III1-2⅓IV2⅓-IV; 7) snout truncate in dorsal and lateral profiles; 8) dorsal skin shagreened with elevated warts corresponding to pale flecks; 9) unscalloped fringe on outer edge of hand, forearm, and foot; fringe with low scallops on tarsus; 10) humeral spine present in males; 11) tympanum entirely visible, directed posterolaterally with no dorsal inclination.

Centrolenella pipilata resembles two other Ecuadorian species in coloration, but both *grandisonae* and *peristicta* differ in having ulnar and tarsal tubercles instead of folds and in having round, instead of truncate, snouts. Two other Ecuadorian species have ulnar and tarsal folds; *pellucida* is white in preservative and in life lacks markings and a white peritoneum, whereas *resplendens* is a much larger, fringe-limbed frog. Males of both of those species lack humeral spines.

Description.—Adults moderately small; snout-vent length 19.5-22.9 mm ($\bar{x}$=21.5, N=10) in males, 21.8-22.1 mm ($\bar{x}$=21.9, N=2) in females. Head noticeably wider than body; width of head 32.9-38.9 percent ($\bar{x}$=35.2, N=12) of snout-vent length; snout extremely short, truncate in dorsal and lateral profiles; canthus round; loreal region barely concave; lips not flared; nostrils three-fourths distance from eye to tip of snout, protuberant anterodorsolaterally; internarial area slightly depressed. Eye large, protuberant, directed more anteriorly than laterally. Supratympanic fold weak; tympanum entirely visible, directed posterolaterally with no dorsal inclination. Prevomerine dentigerous processes and teeth absent; choanae small, ovoid; tongue cordiform, shallowly notched behind, barely free posteriorly; vocal slits extending from midlateral base of tongue to angles of jaws.

Humeral spine blunt, oriented at about 30° from humerus; unscalloped dermal fringe on ventrolateral edge of forearm and outer edge of hand; first finger longer than second; fourth finger noticeably shorter than third; lateral fringes on fingers; webbing absent between first, second, and third fingers; webbing formula for outer fingers III(2^+-2½)-(2-2^+)IV; webbing incised; discs broad, rounded; subarticular tubercles moderately large, subconical, simple; supernumerary tubercles small, present on proximal segments of all digits; palmar tubercle large, ovoid; nuptial excrescences absent. Hind limbs moderately slender; length of tibia 55.7-61.9 percent ($\bar{x}$=59.7, N=12) of snout-vent length; scalloped dermal fold on ventrolateral edge of tarsus; unscalloped dermal fold on outer edge of foot; inner metatarsal tubercle large, ovoid; outer metatarsal tubercle small, round; subarticular tubercles small, round; supernumerary tubercles minute, present on proximal segments of digits; toes about two-thirds webbed; webbing formula I(1-1½)-(2-2^+)II1-(2-2⅓)III(1-1¼)-(2^+-2½)IV(2⅔-2½)-(1-1½)V; discs on toes slightly smaller than those on fingers.

Skin on dorsal surfaces shagreened with elevated warts corresponding to white spots; skin on belly and ventral surfaces of thighs granular; other surfaces smooth; anal opening directed posteroventrally at midlevel of thighs; many small and two large tubercles below anus.

Color in preservative: all dorsal surfaces lavender with dark spots and white dots; ventral surfaces cream.

Color in life: dorsum dark green with diffuse black flecks and pale yellow flecks; flecks on side of head silvery white; chest white; heart not visible; other ventral surfaces pale green; discs pale yellow; bones green; iris pale bronze with black reticulations.

Distribution.—In Ecuador, *C. pipilata* is known from two localities (1700 and 1740 m) on the Amazonian slopes of the Cordillera Oriental of the Andes (Fig. 8).

Remarks.—All individuals were found at night on vegetation along cascading mountain streams in cloud forest. Both females were in amplexus; one deposited a clutch of 18 eggs having clear jelly and pale green yolks. At the Río Azuela, *pipilata* was found in sympatry with *anomala, megacheira, pellucida,* and *siren,* and at 16.5 km north-northeast of Santa Rosa, it was found with *audax, megacheira,* and *siren.*

At first we thought our specimens might be *Centrolenella johnelsi* Cochran and Goin, but the much larger size of *johnelsi* (♂ 29.3 mm) and certain structural differences negated this assignment. Furthermore, *johnelsi* is known only from San Pedro, Departamento Antioquia, in northern Colombia.

See the account of *megacheira* for a description of the type locality.

Etymology.—The specific name is an adjectival derivative of the Latin verb *pipila,* meaning to peep, and refers to the characteristic call of this and many other centrolenid frogs.

Centrolenella prosoblepon (Boettger)
Plate 2F

Hyla prosoblepon Boettger, 1892:45 [Syntypes.—SMF 3756 and ZMB 28019 from "Plantago Cairo" (La Junta), near Limón, Provincia Limón, Costa Rica].
Hyella puncticrus Boulenger, 1896:431 [Syntypes.—BHNH 96.10.8.70-71 from La Palma, Provincia San José, Costa Rica].
Hyla parabambae Boulenger, 1898:125 [Holotype.—BMNH 98.4.28.163 from Paramba, Provincia Imbabura, Ecuador]. New synomym.
Centrolene prosoblepon—Noble, 1924:66.
Centrolene parambae (emendation)—Dunn, 1933:73.
Cochranelle parambae—Taylor, 1951:35.
Cochranella parabambae—Taylor, 1951:35.
Centrolenella prosoblepon—Goin, 1964:5.
Centrolenella parabambae—Goin, 1964:6.

Diagnosis.—1) prevomerine teeth 0-4; 2) bones green; 3) parietal peritoneum white; visceral peritoneum clear; 4) color in life green, usually with black dots; in preservative, lavender, usually with dark lavender dots; 5) webbing between outer fingers III2-1½IV; 6) webbing on foot I1-2II1-2^{+}III1-2IV2^{+}-1V; 7) snout round in dorsal view, truncate in lateral profile; 8) dorsal skin shagreened; 9) arms and legs lacking dermal folds; 10) humeral spine present in males; 11) lower two-thirds of tympanum visible, directed dorsolaterally with posterior inclination.

This species most closely resembles *megacheira* and *griffithsi,* both of which have less webbing and lack humeral spines in males. *Centrolenella megacheira* further differs from *prosoblepon* by having much larger hands and pustular, instead of shagreened, skin on the dorsum. Unspotted *prosoblepon* are colored like *buckleyi,* which also has humeral spines in males, but *buckleyi* has less webbing, an inclined snout, and only the lower one-fourth of the tympanum visible.

Description.—Adults large, snout-vent length 21.7-25.6 mm ($\bar{x}$=24.1, N=5) in males, 25.4-27.2 mm ($\bar{x}$=26.4, N=3) in females. Head slightly wider than body; width of head 33.1-35.6 percent ($\bar{x}$=34.1, N=8) of snout-vent length; snout moderately short, round in dorsal view, truncate in lateral profile; canthus round; loreal region concave; lips slightly flared; nostrils three-fourths distance from eyes to tip of snout, slightly protuberant dorsolaterally; internarial area slightly depressed. Eye moderately large, directed anterolaterally. Supratympanic fold weak; lower two-thirds of tympanum visible, directed dorsolaterally with posterior inclination. Prevomerine dentigerous processes posteromedially inclined, narrowly separated medially between moderately large, ovoid choanae, bearing 0-4 teeth; tongue broadly cordiform, shallowly notched behind, barely free posteriorly; vocal slits extending from posterolateral edges of tongue to angles of jaws.

Humeral spine pointed, oriented about 30° anterior to humerus; ulnar fold and tubercles absent; first finger longer than second; fourth finger slightly shorter than third; lateral fringes present on fingers; webbing absent between first and second fingers, vestigial between second and third; webbing formula for outer fingers III(2^{-}-2^{+})-(1-1⅔)IV; discs broad, truncate; subarticular tubercles small, round, simple; supernumerary tubercles absent; palmar tubercle large, ovoid, simple; nuptial excrescences absent. Hind limbs moderately slender; length of tibia 51.4-57.6 percent ($\bar{x}$=54.6, N=8) of snout-vent length; tarsal folds and tubercles absent; inner metatarsal tubercle small, flat, elliptical; outer metatarsal tubercle small, ovoid; subarticular tubercles small, round; supernumerary tubercles absent; feet about two-thirds webbed; webbing formula I(1-1½)-(2^{+}-2^{+})II1-(2-2^{+})III1-(2^{-}-2^{+})IV(2-2^{+})-1V; discs truncate, slightly smaller than those on fingers.

Skin on dorsal surfaces of head, body, forearms, and shanks shagreened; skin on belly and posteroventral surfaces of thighs granular; other surfaces smooth; anal opening directed posteroventrally at upper level of thighs; pair of large tubercles below anus.

Color in preservative: dorsal surfaces, exclusive of two inner fingers and first three toes lavender, usually with numerous small dark lavender dots; other surfaces cream.

Color in life: dorsal surfaces green with or without black flecks; tips of digits pale yellow; chest white; heart not visible; throat green; bones green; iris grayish white to pale bronze with brown or gray flecks.

Distribution.—This species occurs to elevations of about 1200 m from lower Central America (Caribbean and Pacific slopes in Costa Rica and Panamá) southward on Pacific slopes and lowlands to western Ecuador, where it has been taken at elevations of 220 to 800 m (Fig. 7). We have examined two specimens from the Pacific versant of Colombia. Cochran and Goin (1970:508) listed *C. parabambae* from Medellin, Río Mecaya, and Serranía de Macarena, Colombia. The last two localities are east of the Andes, so it is doubtful if the specimens from there actually are *prosoblepon.*

Remarks.—The identity of *Centrolenella parabambae* has been greatly confused in the literature. As noted by Savage (1967:330): "Apparently the name *[C. parabambae]* has been applied to any population of small, uniformly lavender (in preservative) centrolenids with vomerine teeth from Panama, Colombia, and Ecuador." Savage noted that Panamanian frogs referred to *"parambae"* by

Dunn (1933) are *spinosa*. Two characteristics of *parabambae* (as given in the type description by Boulenger, 1898) are responsible for the confusion: 1) absence of a humeral spine; the holotype is a female; 2) uniformly lavender dorsum, except for dark flecks on hind limbs.

We compared a nearly uniformly lavender female (KU 121055) from Santo Domingo de los Colorados, Ecuador, with the holotype and noted that structurally the two frogs were identical; the holotype has small indefinite dark flecks on the thighs, shanks, and feet, whereas KU 121055 has one fleck on one shank and two and three flecks on the feet. Subsequent comparison of KU 121055 with two females and five males of *prosoblepon* from Ecuador revealed that the only differences were in the numbers and disposition of dark flecks on the dorsum. The numbers of flecks in the nine specimens are (average value for limbs; means in parentheses after ranges): head 0-38 (11.0), body 0-58 (23.1), forearm 0-11 (6.1), thigh 0-10 (5.2), shank 0-23 (9.4), foot 2-11 (5.1). In those specimens having many flecks on the body (49 and 58), the flecks are present over the entire dorsum; in those having fewer flecks (19, 21, 24, 32), the flecks are present only laterally. One individual has only five flecks (all laterally), and two lack flecks on the body. Two individuals have three and five small white flecks dorsally.

One specimen from Colombia has reduced flecking, whereas the other is normal. Cursory examination of series of *prosoblepon* from Costa Rica and Panamá revealed considerable variation in the number of flecks on the dorsum, but no specimens lacked flecks. Taylor (1952:772) mentioned a specimen from Moravia, Costa Rica in which the spotting was ". . . sparse and confined largely to limbs and posterior part of dorsum." The apparent continuum of variation in dorsal pattern and the absence of structural features to distinguish flecked and plain individuals necessitates the placement of *Centrolenella parabambae* (Boulenger, 1898) in the synonymy of *Centrolenella prosoblepon* (Boettger, 1892).

Three of our specimens were found on low vegetation in forest; four others were calling from vegetation over a cascading mountain stream at Balzapamba in July 1970.

Tadpoles agreeing with the description of *prosoblepon* by Starrett (1960:12) were collected late at night as they swam on the bottom of silt-bottomed pools in streams at Balzapamba.

Centrolenella resplendens new species

Plate 2C

Holotype.—KU 118053, an adult male, 27.3 mm, from Santa

Cecilia, 340 m, Provincia Napo, Ecuador, obtained on 14 June 1967, by John D. Lynch.

Diagnosis.—1) prevomerine teeth 2 on low processes; 2) bones white (?); 3) parietal and visceral peritonea white; 4) color in life dark green with white to bluish green flecks; in preservative, dull lavender with white flecks; 5) webbing between outer fingers III2$^-$-1IV; 6) webbing on foot I1-1⅔II0-2$^+$III1-2IV2$^-$-0V; 7) snout round in dorsal view and gradually inclined anteroventrally in lateral view; 8) dorsal skin shagreened with elevated warts corresponding to white flecks; 9) scalloped dermal fold on outer edge of hand, forearm, and elbow, on heel, tarsus, and foot; U-shaped anal fold; 10) humeral spine absent in males; 11) lower four-fifths of tympanum visible, directed dorsolaterally.

Centrolenella resplendens is unlike any other *Centrolenella* known from South America; *euknemos* and *pulverata* from Central America are like *resplendens* in having scalloped dermal folds on the limbs. *Centrolenella pulverata* differs from the other two species by having the heart visible in life, dorsum white in preservative, snout short and slightly inclined anteroventrally, and dorsal skin uniformly granular. In contrast, in *euknemos* and *resplendens* the heart is not visible in life, the dorsum is lavender in preservative, the snout is long and gradually inclined anteroventrally, and the dorsal skin is shagreened with scattered elevations. *Centrolenella resplendens* differs from *euknemos* by having a deeper snout that is round instead of subacuminate in dorsal view, more extensive anal folds, and more extensive webbing. The modal webbing formulae in *euknemos* are: hand—I3-3II3-3¾III2-2IV, foot I1-1½II1-2½III1-2IV2-1V (Savage and Starrett (1967:606).

Description.—Adult male large, 27.3 mm in snout-vent length; females not known. Head slightly wider than body; width of head 34.8 percent of snout-vent length; snout long, round in dorsal view, gradually sloping from nostrils to tip in lateral profile (Fig. 1); canthus round; loreal region barely concave; lips slightly flared; nostrils about two-thirds distance from eyes to tip of snout, not protuberant, directed dorsolaterally; internarial area barely depressed. Eye large, directed more laterally than anteriorly. Supratympanic fold absent; tympanum directed dorsolaterally. Prevomerine dentigerous processes low, short, transverse between choanae, each bearing two teeth; choanae large; longitudinally rectangular; tongue ovoid, barely free posteriorly; vocal slits extending from posterolateral base of tongue to angles of jaws.

Humeral spine absent; scalloped dermal fold around elbow, along ventrolateral edge of forearm and outer edge of fourth finger;

first finger longer than second; fourth finger slightly shorter than third; lateral fringes on fingers; webbing absent between first and second fingers, vestigial between second and third; webbing formula for outer fingers III2^--1IV; discs large, nearly round; subarticular tubercles small, round, simple; supernumerary tubercles absent; palmar tubercle simple, large, ovoid; nuptial excrescences absent (Fig. 3). Hind limbs moderately robust; length of tibia 53.5 percent of snout-vent length; scalloped fold around heel, along ventrolateral edge of foot and outer edge of fifth toe; inner metatarsal tubercle large, triangular; outer metatarsal tubercle absent; subarticular tubercles small, round; supernumerary tubercles absent; feet nearly fully webbed; webbing formula I1-1⅔II0-2^+III1-2IV2^--0V; discs on toes round, slightly smaller than those on fingers (Fig. 4).

Skin on dorsal surfaces of head, body, and limbs, and lateral surface of head and flanks shagreened with small tubercles corresponding to white spots; belly and proximal posteroventral surfaces of thighs granular; other surfaces smooth; anal opening directed posteriorly at upper level of thighs, bordered laterally and ventrally by fleshy tuberculate U-shaped fold; two conical tubercles below fold (Fig. 2).

Color in preservative: head, flanks, and dorsal surfaces of body and limbs (except thumb and toes 1-3) dull lavender with many small, white spots; venter and posterior surfaces of thighs cream.

Color in life: dorsum dark green with white to bluish green spots; fringes on forearm and foot and fold around anus white; venter yellow; iris gray.

Distribution.—Known only from the type locality and Santa María de Sucumbios, Colombia, about 40 km NNW of Santa Cecilia (Fig. 6).

Remarks.—The holotype was perched on a leaf of a bush about 30 cm above the ground during light rain at night in primary rainforest. Subsequent work at Santa Cecilia from 1967 through 1972 has resulted in the collection of thousands of frogs, but no additional specimens of *resplendens* have been found.

The Colombian specimen (AMNH 88083) is a juvenile having a snout-vent length of 16.5 mm. The white dermal folds and flecks are essentially the same as those in the holotype, but the webbing, as typical of juveniles, is less extensive.

Etymology.—The specific name is derived from the Latin verb *resplendo* meaning to glitter, and is used in allusion to the jewel-like appearance of the living frog.

Centrolenella siren new species

Plate 1E

Holotype.—KU 146610, an adult male, 20.7 mm, from a small tributary of the Río Salado, about 1 km upstream from the Río Coca, 1410 m, Provincia Napo, Ecuador, one of a series obtained on 7 April 1972, by William E. Duellman and John E. Simmons.

Paratopotypes.—KU 146611-23, same date and collectors.

Diagnosis.—1) prevomerine teeth 0-2; 2) bones green; 3) parietal peritoneum white; visceral peritoneum clear; 4) color in life green with yellow flecks; in preservative, lavender with white flecks; 5) webbing between outer fingers III2⅔-2½IV; 6) webbing on foot I2-2¼II1⅓-2⅔III1½-3^{-}IV3-2^{-}V; 7) snout truncate in dorsal and lateral profiles; 8) dorsal skin shagreened; 9) arms and legs lacking dermal folds; 10) humeral spine absent in males; 11) lower four-fifths of tympanum visible, directed posterolaterally with slight dorsal inclination.

Centrolenella siren is like *flavopunctata* and *midas* in having a lavender dorsum with white flecks (in life, green with gold flecks) with no black flecks, but it differs from both of those species by having much less webbing on the hands and feet and a more prominent tympanum oriented posterolaterally, instead of dorsolaterally. *Centrolenella flavopunctata* further differs from *siren* by having a rounded, instead of truncate, snout.

Description.—Adults moderately small; snout-vent length 19.8-22.0 mm ($\bar{x}$=20.8, N=14) in males; females unknown. Head much wider than body; width of head 30.0-37.0 percent ($\bar{x}$=34.7, N=14) of snout-vent length; snout extremely short, truncate in dorsal and lateral views; canthus round; loreal region barely concave; lips not flared; nostrils nearly terminal on snout, not protuberant, directed laterally; internarial area flat. Eye moderately large, directed anterolaterally. Supratympanic fold absent; lower four-fifths of tympanum visible, directed posterolaterally with slight dorsal inclination. Prevomerine dentigerous processes small, low, widely separated, between small round choanae, bearing 0-2 teeth; tongue round, barely free posteriorly; vocal slits extending from midlateral base of tongue to angles of jaws.

Humeral spine absent; ulnar fold and tubercles absent; first finger about equal in length to second; fourth finger noticeably shorter than third; fringes absent on fingers; webbing absent between first and second fingers, vestigial between second and third; webbing formula for outer fingers III(2½-2⅔)-(2¼-2½)IV; discs truncate; subarticular tubercles small, round, simple; supernumerary tubercles absent; palmar tubercle large, elliptical; nuptial excrescences absent.

Hind limbs slender; length of tibia 54.8-60.1 percent ($\bar{x}$=57.3, N=14) of snout-vent length; tarsal folds and tubercles absent; inner metatarsal tubercle small, ovoid; outer metatarsal tubercle absent; subarticular tubercles small, round; supernumerary tubercles absent; feet about one-half webbed; webbing formula I2-(2⁺-2¼)II(1¼-1½)-(2½-2¾)III1½-(2¾-3)IV3-(1¾-2)V; discs on toes smaller and more nearly round than those on fingers.

Skin on dorsal surfaces shagreened; skin on belly and ventral surfaces of thighs granular; other surfaces smooth; anal opening directed posteriorly at upper level of thighs; pair of large tubercles below anus (Fig. 2).

Color in preservative: dorsum of head, body, and limbs lavender with many small, white flecks on head and body; other surfaces pale cream.

Color in life: dorsum green with gold flecks; fingers and toes pale yellow; chest white; heart not visible; other ventral surfaces pale dull green; bones green; iris pale bronze with fine black reticulations.

Distribution.—*Centrolenella siren* occurs in cloud forest on the Amazonian slopes of the Andes, where it is known from elevations of 1410-1740 m (Fig. 9). *Centrolenella siren* occurs in sympatry with *anomala, audax, megacheira, pellucida,* and *pipilata.*

Remarks.—All individuals were found at night on low vegetation along small mountain streams in cloud forest. The type locality is a small stream at the south edge of the Papallacta-Lago Agrio road about 300 m west of the bridge across the Río Salado and approximately 1 km up the Río Salado from its confluence with the Río Coca.

Etymology.—The specific name refers to the nymphs of Classical mythology, who by their sweet singing enticed seafarers to destruction; the name is used here in allusion to the fact that the call of these small frogs entices collectors to the nocturnal perils of streams.

DISCUSSION

Savage (1967) recognized three species groups of *Centrolenella* in Central America. He characterized the *fleischmanni* group as having white bones in life, a colorless parietal peritoneum, a white visceral peritoneum, a white ground color in preservative, and in lacking prevomerine teeth and dentigerous processes. The *prosoblepon* group was characterized as having green bones in life, a white (opaque) parietal peritoneum, a colorless visceral peritoneum, lavender ground color in preservative, and prevomerine teeth and dentigerous processes. He recognized a third group for the somewhat annectant *pulverata.*

Three Ecuadorian species *(fleischmanni, munozorum,* and *pellucida)* clearly fit into Savage's *fleischmanni* group. With the exceptions of *anomala, medemi, ocellifera,* and *resplendens,* the remaining Ecuadorian *Centrolenella* agree with Savage's definition of the *prosoblepon* group. The presence of prevomerine teeth and processes is variable in the Ecuadorian representatives of the *prosoblepon* group (*sensu* Savage) but is usually constant within species. However, a single specimen of *cochranae* and one of *prosoblepon* lack teeth and processes, whereas all other specimens of these species examined have them.

Except for the absence of prevomerine teeth and processes, *buckleyi, grandisonae, griffithsi, megacheira, peristicta,* and *pipilata* agree with the definition of the Central American *prosoblepon* group. However, the agreement is weakened by the pale-green (contrasted with green) bones of *grandisonae, griffithsi,* and *peristicta* (a character-state of the *pulverata* group). Savage characterized the *pulverata* group as having pale green bones, a colorless parietal peritoneum (heart visible), opaque visceral peritoneum, yellowish-white ground color in preservative, and prevomerine teeth and processes. On examining the holotype of *pulverata* (ZMB 7842) in 1969, Duellman noted the ground color was lavender. Aside from having pale green bones, *grandisonae, griffithsi,* and *peristicta* do not agree with the definition of the *pulverata* group. We know of no Ecuadorian *Centrolenella* assignable to the *pulverata* group. The Venezuelan *Centrolenella antisthenesi* may be allied with *pulverata; antisthenesi* has a clear parietal peritoneum, opaque visceral peritoneum, prevomerine teeth, lavender dorsum, green bones, and subanal tubercles and lacks a humeral spine.

Three Ecuadorian species (and possibly the Colombian *medemi*) depart from the *fleischmanni-prosoblepon* arrangement. *Centrolenella anomala* is *prosoblepon*-like, except in lacking prevomerine teeth, having white bones, and in lacking a lavender ground color. The opaque parietal peritoneum and brown ground color exclude it from the homogeneous *fleischmanni* group. *Centrolenella ocellifera* and *resplendens* presumably have white bones (green bones were not recorded in their color descriptions in life). Both have prevomerine teeth and low dentigerous processes, an opaque parietal peritoneum, and lavender ground color. *Centrolenella resplendens* differs further in having white visceral peritoneum (a character-state of the *fleischmanni* and *pulverata* groups). The combination of characteristics cited above does not recommend them for any of Savage's (1967) groups.

We noted the absence of large subanal tubercles in *anomala, fleischmanni, medemi, munozorum, ocellifera,* and *pellucida,* and their presence in the remaining Ecuadorian *Centrolenella.* Subanal tubercles are absent in most Central American centrolenids; we found them in *ilex, prosoblepon,* and *pulverata* and in *antioquiensis* (Colombia) and *antisthenesi* (Venezuela). The absence of subanal tubercles in the frogs of the *fleischmanni* group and in *anomala, medemi,* and *ocellifera* (enigmatic in having white bones) thus may not be significant. Tubercles are present in *resplendens* (also enigmatic in presumably having white bones) but these may not be homologous to those in the frogs lacking the elaborate post- and para-anal ornamentation of *resplendens.*

Humeral spines are not known in any frog of the *fleischmanni* group. Goin's (1964) and Savage's (1967) conclusion that presence or absence of the spines cannot be used to support generic separation of *Centrolenella* and *Cochranella* is substantiated here in that an otherwise "normal" *griffithsi* has humeral spines. This specimen may prove to be distinct from *griffithsi* but at present no features other than the humeral spine support that argument. Accordingly, the presence of humeral spines possibly may be intraspecifically variable, at least in *griffithsi.* Small spines occur on the humeri of *medemi* but not in *anomala, ocellifera,* or *resplendens* (species with presumed or known white bones). The presence of humeral spines in *audax, buckleyi, grandisonae, medemi, peristicta, pipilata,* and *prosoblepon* does not suggest to us that these frogs are more closely related to one another than they may be to species lacking humeral spines. This assemblage seems to be heterogeneous: three have prevomerine teeth and processes, two have pale green as compared to green bones, and one lacks subanal tubercles.

Centrolenella antioquiensis and *resplendes* differ from all other known *Centrolenella* by having opaque parietal and visceral peritonea. Otherwise they share few characters; *antioquiensis* has a humeral spine and green bones (absent and white in *resplendens*) and lacks dermal ornamentation and prevomerine teeth (both present in *resplendens*).

The Ecuadorian *Centrolenella* thus far described do not readily fit into the arrangement of Central American forms proposed by Savage (1967). Inspection of Taylor and Cochran's (1953) account of southeastern Brasilian centrolenids reveals comparable lack of fit with Savage's three groups in Central America. Because we anticipate the discovery of many undescribed *Centrolenella* in northwestern South America, at this time we prefer not to alter Savage's groupings or define new species groups based on our study of Ecuadorian species. We offer only the following comments on putative relationships of the 19 species, as described below.

Centrolenella fleischmanni, munozorum, and *pellucida* constitute a well-circumscribed group of species having white bones and a colorless parietal peritoneum (heart visible) in life, a white visceral peritoneum, a white ground color in preservative, and in lacking distinct canthi, subanal tubercles, humeral spines, and prevomerine teeth and processes.

Centrolenella audax, cochranae, flavopunctata, midas, prosoblepon, and *siren* constitute a group having green bones and an opaque parietal peritoneum (heart not visible) in life, a clear visceral peritoneum, a very pale to dark lavender ground color in preservative, and in having distinct canthi, subanal tubercles, and prevomerine teeth and processes. Two of these *(audax* and *prosoblepon)* have humeral spines.

Centrolenella buckleyi, grandisonae, griffithsi, megacheira, peristicta, and *pipilata* fall into a somewhat heterogeneous group agreeing in most respects with that listed above, except in the uniform absence of prevomerine teeth and processes. The bones are pale green in *grandisonae, griffithsi,* and *peristicta; griffithsi* and *megacheira* lack humeral spines.

Centrolenella anomala differs markedly from all other centrolenids in the combination of white bones and an opaque parietal peritoneum in life, clear visceral peritoneum, a brown ground color in life and in preservative, distinct canthi, and in lacking prevomerine teeth and processes, subanal tubercles, and humeral spines. Its ocellated color pattern on a shagreened dorsum with warts and the reduced webbing of the fingers lend it a striking similarity to *cochranae;* the similarity is out-weighed by the numerous differences between the two species.

Centrolenella ocellifera also differs markedly from other centrolenids. The presumably white bones in life, opaque parietal peritoneum, clear visceral peritoneum, and absence of subanal tubercles, coupled with the pale lavender ground color in preservative, distinct canthi, prevomerine teeth and processes, ocellated color pattern, and the absence of humeral spines suggests some relationship with *anomala* or with the group of species listed above, which included *audax* and *cochranae.*

Centrolenella resplendens appears to be trenchantly different from other Ecuadorian *Centrolenella* chiefly because of its dermal ornamentation (scalloped limb fringes, para- and postanal ornamen-

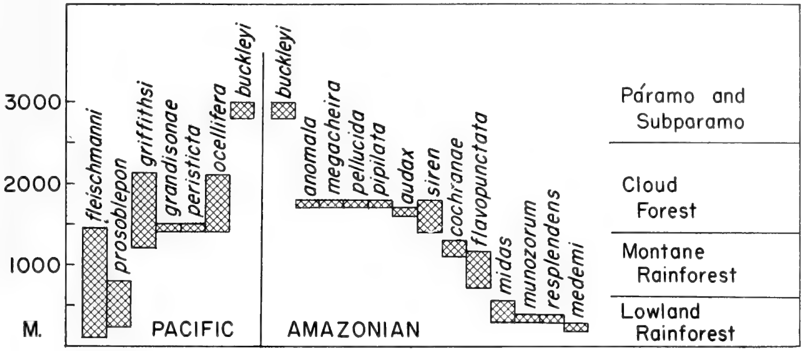

FIG. 11. Altitudinal distributions of *Centrolenella* in Ecuador; vertical line = continental divide.

tation, and enameled warts). Also it differs from other known centrolenids by the following combination of characters: white bones in life, opaque parietal peritoneum, white visceral peritoneum, lavender ground color in preservative, and prevomerine teeth.

Centrolenella medemi differs from all Ecuadorian centrolenids in having smooth skin on the dorsum and the decidedly non-centrolenid color pattern. We do not know the color of the bones in living individuals. Humeral spines are present, although small, and subanal tubercles are lacking. The fully-webbed digits, elongate hindlimbs, and completely concealed tympana, coupled with skin texture and color pattern suggested the possibility that the frog was not a centrolenid but a hylid of the *Cryptobatrachus* and *Stephania* group; however, dissection of the tarsus revealed that the tarsal bones are fused, as in all centrolenids but not in hylids.

Our knowledge of the distribution of *Centrolenella* in Ecuador is limited; even so, some patterns consistent with other groups of frogs (eleutherodactylines, dendobatids, and hylids) are apparent. We can divide the Ecuadorian *Centrolenella* into six ecogeographic assemblages. Each is associated with definite vegetation formations and geographic regions (Fig. 11). These can be summarized as follows:

Lowland Amazonian rainforest.—Four species (*medemi, midas, munozorum,* and *resplendens*) occur only at elevations of less than 600 m in Amazonian rainforest, where they apparently are limited to breeding along small, sometimes intermittent, streams having a low gradient. The apparent restricted ranges of the species probably is a reflection of inadequate collecting; most likely the species will eventually be found in more distant areas in the upper Amazon Basin.

Montane rainforest, Amazonian slopes.—Two species (*cochranae* and *flavopunctata*) inhabit elevations of 700-1300 m on the lower eastern slopes of the Andes. In this area they live along streams with steep gradients. Warm temperatures and high amounts of rainfall prevail throughout the year.

Cloud forest, Amazonian slopes.—This is the richest area in Ecuador for centrolenids; six species (*anomala, audax, megacheira, pellucida, pipilata,* and *siren*) occur at elevations of 1400-1800 m on the Amazonian slopes of the Andes. This area of cool cloud forest daily bathed in mist has luxuriant vegetation and many cascading streams.

Páramo and subparamo.—This cool, windy region has been greatly disturbed by man. Some areas are noticeably drier than others. Throughout the páramo precipitation is lower than in cloud forests, but the low temperatures result in low rates of evaporation. A single species (*buckleyi*) occurs in wet meadows and terrestrial bromeliads in the interandean valleys and on high Amazonian and Pacific slopes between 2500 and 3000 m. Records from lower elevations on the Andean slopes are questionable.

Cloud forest, Pacific slopes.—Five species (*fleischmanni, grandisonae, griffithsi, ocellifera,* and *peristicta*) occur at elevations of 1400-2200 m on the Pacific slopes of the Andes, where the habitat is like that at similar elevations on the Amazonian slopes.

Pacific lowlands.—Two species (*fleischmanni* and *prosoblepon*) are known from mesic forests on the Pacific lowlands, where rainfall is far more seasonal than in the Amazon lowlands. *Centrolenella fleischmanni* occurs up to 1460 m, and *prosoblepon* goes up to at least 800 m.

Excluding the high Andean *buckleyi,* we find 12 species on the Amazonian slopes and lowlands and only six species on the Pacific slopes and lowlands. In addition to the fewer species on the Pacific slopes, there is a difference in altitudinal assemblages. The two species on the Pacific lowlands also inhabit the lower Andean slopes; in the Amazonian region, two distinctive assemblages occur within the same elevational range—one group in the lowlands, and one on the slopes. No species is known from both Pacific and Amazonian slopes or lowlands, except *buckleyi* which is at high elevations.

Greater species richness in cloud forest results in higher numbers of sympatric species there. At Tandapi at an elevation of 1460 m on the Pacific slopes, there are five species (*fleischmanni, grandisonae, griffithsi, ocellifera,* and *peristicta*). At the Río Azuela at an elevation of 1740 m on the Pacific slopes, five species (*anomala, megacheira, pellucida, pipilata,* and *siren*) were found along one small rivulet. Three species *(midas, munozorum,* and *resplendens)* have been found at one locality, Santa Cecilia, at an elevation of 340 m in the Amazon Basin. Two species *(fleischmanni* and *prosoblepon)* occur in sympatry at the Río Palenque at an elevation of 220 m on the Pacific lowlands.

These limited data probably are only suggestive of the true ecological and altitudinal distributions of these small frogs. Hopefully this discussion will serve as a basis for future investigations and not be destined to be the only commentary on them before they and their habitat are eliminated by human activity.

SUMMARY

Our collections from Ecuador contain many centrolenid frogs. Our taxonomic conclusions are based on the examination of holotypes of all of the Ecuadorian centrolenids, study of series of specimens, and observations of the frogs in the field.

We recognize 19 species in Ecuador; one of these, *Centrolene geckoideum,* is not treated in this paper. One Colombian species, *Centrolenella medemi,* is treated, because it probably occurs in eastern Ecuador. Eleven new species are named; seven *(Centrolenella anomala, audax, flavopunctata, megacheira, pellucida, pipilata,* and *siren)* are from the Amazonian slopes of the Andes; three *(Centrolenella midas, munozorum, resplendens)* are from the Amazon Basin, and one *(Centrolenella peristicta)* is from the Pacific slopes of the Andes. *Centrolenella parabambae* (Boulenger, 1898) and *Centrolenella petersi* (Goin, 1961) are placed in the synonymies of *Centrolenella prosoblepon* (Boettger, 1892) and *Centrolenella fleischmanni* (Boettger, 1893), respectively.

Savage (1967) placed the Central American species of *Centrolenella* in three groups: 1) *fleischmanni,* 2) *prosoblepon,* and 3) *pulverata.* The distinction of these three groups in Ecuador is not clear. Three species *(fleischmanni, munozorum, pellucida)* clearly belong to the *fleischmanni* group. *Centrolenella audax, buckleyi, cochranae, flavopunctata, grandisonae, griffithsi, megacheira, midas, peristicta, pipilata,* and *siren* can be placed in the *prosoblepon* group, redefined to include species with or without prevomerine teeth. *Centrolenella anomala, ocellifera,* and *resplendens* cannot be placed in any of the defined groups.

The maximum diversity of *Centrolenella* in Ecuador is in the cloud forests. Six species (five occur sympatrically) inhabit the cloud forests on the Amazonian slopes of the Andes. Five sympatric species occur in the cloud forests on the Pacific slopes of the Andes. In other regions there are fewer species: Amazonian lowlands (4), lower Amazonian slopes of the Andes (2), Pacific lowlands (2). Only *Centrolenella buckleyi* occurs in the high Andes and inter-andean valleys.

We provide the first records of four species from Colombia: *Centrolenella griffithsi, ilex, prosoblepon,* and *resplendens.*

RESUMEN

Nuestros colecciones del Ecuador contienen muchas ranas de la familia Centrolenidae. Nuestros conclusiones taxonomicos son basada en el examinación de los holotípos de todos los centrolenidos ecuatorianos, estudio de serie de ejemplares, y observaciones de las ranas en sus ambientes naturales.

Se reconocen 19 especies de centrolenidos en Ecuador; una, *Centrolene geckoideum,* no está tratado en esta publicación. Un especie colombiano, *Centrolenella medemi,* está tratado, porque probablamente se occuren en el oriente del Ecuador. Once especies nuevas se nombran; siete *(Centrolenella anomala, audax, flavopunctata, megacheira, pellucida, pipilata, siren)* se encuentran en las laderas amazónicas de los Andes, tres *(Centrolenella midas, munozorum, resplendens)* son de la cuenca amazónica, y una *(Centrolenella peristicta)* es de las laderas de Pacífico de los Andes. *Centrolenella parabambae* (Boulenger, 1898) y *Centrolenella petersi* (Goin, 1961) son colocadas en las sinónimias de *Centrolenella prosoblepon* (Boettger, 1892) y *Centrolenella fleischmanni* (Boettger, 1893), respectivamente.

Savage (1967) puse las especies centroamericanas de *Centrolenella* en tres grupos: 1) *fleischmanni,* 2) *prosoblepon,* and 3) *pulverata.* La distinción de estos tres grupos en los centrolenidos ecuatorianos no está lucida. Tres especies *(fleischmanni, munozorum, pellucida)* claramente pertenecen al grupo *fleischmanni. Centrolenella audax, buckleyi, cochranae, flavopunctata, grandisonae, griffithsi, megacheira, midas, peristicta, pipilata prosoblepon,* y *siren* se pueden colocar en un grupo *prosoblepon* redefinido para incluir especies con los dientes prevomerianos presentes o ausentes. *Centrolenella anomala, ocellifera,* y *resplendens* no se pueden colocar en los grupos definidos.

La diversidad maxima en *Centrolenella* en Ecuador está en el bosque neblino. Seis especies (cinco occuren simpatricamente) habitan los bosques neblinos en las laderas amazónicas de los Andes. Cinco especies simpátricos occuren en los bosques neblinos en las laderas de Pacífico de los Andes. En otras regiones hay menos especies: Tierras bajas amazónicas (4), laderas bajas amazónicas

de los Andes (2), la costa (2). Solamente *Centrolenella buckleyi* occure en los Andes altos y en los valles interandinos.

Suplimos las anotaciones primeras de cuatro especies de Colombia: *Centrolenella griffithsi, ilex, prosoblepon,* y *resplendens.*

SPECIMENS EXAMINED

All specimens from Ecuador are listed first, alphabetically by province. Specimens from other countries are listed after Ecuadorian ones.

Centrolenella albotunica.—BRASIL: *São Paulo:* Paranapiacaba, KU 74310-11.

Centrolenella anomala.—*Napo:* Río Azuela, 1700 m, KU 143299.

Centrolenella antioquiensis.—COLOMBIA: *Quindio:* Salento, 1900 m, KU 133466.

Centrolenella antisthenesi.—VENEZUELA: *Aragua:* Rancho Grande, 1075 m, KU 133467-80.

Centrolenella audax.—*Napo:* Salto de Agua, 2.5 km NNE Río Reventador, 1660 m, KU 146624, 146831; 16.5 km NNE Santa Rosa, 1700 m, KU 143290, 143292.

Centrolenella buckleyi.—"Paramo," AMNH 20504. *Azuay:* Sinicay, 2560 m, AMNH 17464. *Carchi:* Tulcán, 3000 m, KU 118005-8. *Chimborazo:* Pallatanga, 1520 m, BMNH 80.12.5.201. *Imbabura:* Laguna Cuicocha, 10 km W Quiroga, 3000 m, KU 138822. *Pichincha:* Llave Pongo, AMNH 20141; Machachi, 2950 m, KU 14829-30. *Zamora-Chinchipe:* 13.5 km E Loja, 2800 m, KU 142648; Sabanilla, AMNH 13530. COLOMBIA: *Cauca:* Coconuco, 3300 m, KU 145087; road to Pacific coast from El Tambo, 2170 m, KU 144131-2; road to Quintana, Quebrada Santa Tereza, 2200 m, KU 144133-4.

Centrolenella cochranae.—*Napo:* south slope Cordillera del Dué, 1150 m, KU 123216-8. *Pastaza:* Abitagua, 8 km NW Mera, 1300 m, KU 121033-35. *Tungurahua:* El Topo, 1220 m, BMNH 1912.11.1.68; 11 km E Río Negro, 1170 m, KU 146605.

Centrolenella euknemos.—PANAMÁ: *Darién:* Laguna, 820 m, KU 77534; Río Jaque, 1.5 km above Río Imamado, 50 m, KU 116439-41. *Panamá:* south slope Cerro La Campana, 820 m, KU 116436. *San Blas:* Camp Summit, 300-400 m, KU 116437-8.

Centrolenella eurygnatha.—BRASIL: *Guanabara:* Tijuca, KU 93220-4.

Centrolenella flavopunctata.—*Napo:* Bermejo No. 4 (well site), 15 km ENE Umbaquí, 720 m, KU 123224; San José Abajo, AMNH 22187. *Pastaza:* Mera, 1140 m, KU 121041-6, 121048-51; Río Alpayacu, 1 km E Mera, KU 121047; 13 km WSW Puyo, 1000 m, TCWC 24032.

Centrolenella fleischmanni.—*Esmeraldas:* Río Durango, 110 m, BMNH 1902.5.27.24. *Los Ríos:* Estación Biológica Rio Palenque, 56 km N Quevedo, 220 m, KU 146606-8, 147580. *Pichincha:* Tandapi, 1460 m, KU 121052. COSTA RICA: *Cartago:* Tapanti, 1200 m, KU 65189-200. *San José:* La Palma, 1520 m, KU 36885-95; San José, 1200 m, SMF 3760. MÉXICO: *Oaxaca:* 4.3-14.8 km N San Gabriel Mixtepec, 580-860 m, KU 137347-51; 9.1-12.7 km S Valle Nacional, 610-790 m, KU 137352-5. PANAMÁ: *Darién:* Río Jaque, 1.5 km above Río Imamado, 50 m, KU 116442-55. SURINAM: Saramacca, RMNH 4463.

Centrolenella grandisonae.—*Pichincha:* Tandapi. 1460 m, KU 118036, 118047-50. COLOMBIA: *Caldas:* Pueblo Rico, BMNH 1910.7.11.68. *Cauca:* Santa Leticia, 2000 m, KU 144129-30.

lower Amazonian slopes of the Andes (2), Pacific lowlands (2). Only *Centrolenella buckleyi* occurs in the high Andes and inter-andean valleys.

We provide the first records of four species from Colombia: *Centrolenella griffithsi, ilex, prosoblepon,* and *resplendens.*

RESUMEN

Nuestros colecciones del Ecuador contienen muchas ranas de la familia Centrolenidae. Nuestros conclusiones taxonomicos son basada en el examinación de los holotípos de todos los centrolenidos ecuatorianos, estudio de serie de ejemplares, y observaciones de las ranas en sus ambientes naturales.

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Centrolenella cochranae.—*Napo:* south slope Cordillera del Dué, 1150 m, KU 123216-8. *Pastaza:* Abitagua, 8 km NW Mera, 1300 m, KU 121033-35. *Tungurahua:* El Topo, 1220 m, BMNH 1912.11.1.68; 11 km E Río Negro, 1170 m, KU 146605.

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Centrolenella grandisonae.—*Pichincha:* Tandapi. 1460 m, KU 118036, 118047-50. COLOMBIA: *Caldas:* Pueblo Rico, BMNH 1910.7.11.68. *Cauca:* Santa Leticia, 2000 m, KU 144129-30.

Centrolenella griffithsi.—Pichincha: 4 km W Chiriboga, 2120 m, KU 142649; Las Maguinas, 2150 m, AMNH 20146; Río Saloya, 1200 m, BMNH 1940.2.20.4; Tandapi, 1460 m, KU 118009-35, 118037-45, 118148, 121036-9, 138823-4. COLOMBIA: *Cauca:* road to Pacific coast from El Tambo, 2170 m, KU 139497-8.

Centrolenella medemi.—COLOMBIA: *Putumayo:* Puerto Asís, USNM 152277.

Centrolenella megacheira.—Napo: Río Azuela, 1740 m, KU 143273-7; 16.5 km NNE Santa Rosa, 1700 m, BMNH 1971.1854-55, CAS 135498-9, KU 143245-72, UMMZ 131668 (3).

Centrolenella midas.—Napo: Lago Agrio, 330 m, KU 125334, UMMZ 129314; Puerto Libre, 570 m, KU 123220-3; Santa Cecilia, 340 m, KU 107026, 123219, 146625, 150662-23.

Centrolenella munozorum.—Napo: Lago Agrio, UMMZ 129313; Santa Cecilia, 340 m, KU 105251, 118054, 123225, 150620-21.

Centrolenella ocellata.—PERÚ: *Ayacucho:* Huanhauchayocc on Tambo-Valle del Apurimac trail, LSU 25989-90. *Pasco:* Huancabamba, BMNH 1912.11.1.19.

Centrolenella ocellifera.—Imbabura: Paramba, 777 m, BMNH 98.5.19.3. *Pichincha:* Tandapi, 1460 m, KU 118046.

Centrolenella orocostalis.—VENEZUELA: *Aragua:* Rancho Grande, KU 133481.

Centrolenella pellucida.—Napo: Río Azuela, 1740 m, KU 143298.

Centrolenella peristicta.—Pichincha: Tandapi, 1460 m, KU 118051-2, 121053.

Centrolenella pipilata.—Napo: Río Azuela, 1740 m, KU 143284-7, UMMZ 131669 (2); 16.5 km NNE Santa Rosa, 1700 m, KU 143278-83.

Centrolenella prosoblepon.—Bolivar: Balsapampa, 800 m, KU 132462-5. *Imbabura:* Lita, 520 m, KU 133482-3; Paramba, 777 m, BMNH 98.4.28.163. *Los Ríos:* Estación Biológica Río Palenque, 56 km N Quevedo, 220 m, KU 146609. *Pichincha:* Santo Domingo de los Colorados, 600 m, KU 121054-5, UMMZ 131671. COLOMBIA: *Cauca:* La Costa, El Tambo, 1200 m, KU 145085; Río Michenque, El Tambo, 900 m, KU 145086. COSTA RICA: *Alajuela:* Cinchona, 1600 m, KU 65172-8. *Heredia:* La Concordia, 1900 m, KU 65159-66. *Limón:* Plantage Cairo, near Limón, SMF 3756, ZMB 28019. *San José:* La Palma, BMNH 96.10.8.70-71, KU 65180-3. PANAMÁ: *Bocas del Toro:* Río Claro near junction with Río Changena, 910 m, KU 116469-78. *Chiriquí:* Finca Ojo de Agua, southeast slope Cerro La Pelota, 1440 m, KU 96346-53; Finca Santa Clara, 1200 m, KU 116458-63.

Centrolenella pulverata.—PANAMÁ, *Chiriquí:* ZMB 7842. *Darién:* Río Jaque, 1.5 km above Río Imamado, 50 m, KU 116493.

Centrolenella resplendens.—Napo: Santa Cecilia, 340 m, KU 118053. COLOMBIA: *Putumayo:* Santa María de Sucumbios, AMNH 88083.

Centrolenella siren.—Napo: Río Azuela, 1740 m, KU 143295-7, 143555, UMMZ 131670 (3); Río Salado, 1 km upstream from Río Coca, KU 146610-23; 16.5 km NNE Santa Rosa, 1700 m, KU 143288-9, 143291, 143293-4.

Centrolenella vanzolinii.—BRASIL: *Guanabara:* Tijuca, KU 93226-30.

LITERATURE CITED

BOETTGER, O.

1892. Katalog der Batrachier—Sammlung im Museum der Senckenbergischen Naturforschenden Gesellschaft im Frankfurt am Main. Frankfurt, 73 pp.

1893. Ein neuer Laubfrosch aus Costa Rica. Ber. Naturf. Gesellsch. Frankfurt, 1892-1893 (1893):251-252.

BOULENGER, G. A.

1882. Catalogue of Batrachia Salientia s. Ecaudata in the collection of the the British Museum, ed. 2. London, xvi + 503 pp.

1896. Descriptions of new batrachians collected by Mr. C. F. Underwood in Costa Rica. Ann. Mag. Nat. Hist. (6)18:340-342.

1898. An account of the reptiles and batrachians collected by Mr. W. F. H. Rosenberg in western Ecuador. Proc. Zool. Soc. London, 1898 (1):107-126.

1899. Descriptions of new batrachians in the collection of the British Museum (Natural History). Ann. Mag. Nat. Hist. (7)3:273-277.

1918. Descriptions of new South American batrachians. *Ibid.,* 9(2):427-433.

COCHRAN, D. M. and C. J. GOIN

1970. Frogs of Colombia. Bull. U.S. Natl. Mus., 288:xii+655 pp.

DUELLMAN, W. E. and J. B. TULECKE

1960. The distribution, variation, and life history of the frog *Cochranella viridissima* in Mexico. Amer. Midl. Nat., 63:392-397.

DUNN, E. R.

1933. Amphibians and reptiles from El Valle de Anton, Panama. Occ. Papers Boston Soc. Nat. Hist., 8:65-79.

EATON, T. H., JR.

1958. An anatomical study of a Neotropical tree frog, *Centrolene prosoblepon* (Salientia: Centrolenidae). Univ. Kansas Sci. Bull., 39: 459-472.

GOIN, C. J.

1961. Three new centrolenid frogs from Ecuador. Zool. Anz., 166:95-104.

1964. Distribution and synonmy of *Centrolenella fleischmanni* in northern South America. Herpetologica, 20:1-8.

1966. A new frog of the genus *Centrolenella* from Suriname. Stud. Fauna Suriname and other Guyanas, 32:77-80.

1968. A new centrolenid frog from Guyana. Quart. Jour. Florida Acad. Sci., 30:115-118.

GOODMAN, D. E., and C. J. GOIN

1970. The habitat of *Centrolene geckoideum* in Ecuador. Herpetologica, 26:276.

JIMÉNEZ DE LA ESPADA, M.

1872. Nuevos batracios americanos. An. Soc. Espana Hist. Nat., 1:85-88.

LIDTH DE JEUDE, T. W. VAN

1904. Reptiles and batrachians from Surinam. Notes Leyden Mus. 25:83-94.

LUTZ, B. and G. R. KLOSS

1952. Anfibios anuros do alto Solimoes e Rio Negro. Mem. Inst. Oswaldo Cruz, 50:625-678.

LYNCH, J. D.

1971. Evolutionary relationships, osteology, and zoogeography of leptodactyloid frogs. Misc. Publ. Mus. Nat. Hist. Univ. Kansas, 53:1-238.

NIEDEN, F.

1923. Das Tierreich. Amphibia. Anura I. Berlin, xxxii+584 pp.

NOBLE, G. K.

1920. Two new batrachians from Colombia. Bull. Amer. Mus. Nat. Hist., 42:441-446.

1924. Some Neotropical batrachians preserved in the United States National Museum with a note on secondary sexual characters of these and other amphibians. Proc. Biol. Soc. Washington, 37:65-72.

1926. An analysis of the remarkable cases of distribution among the Amphibia, with descriptions of new genera. Amer. Mus. Novitates, 212:1-24.

RIVERO, J. A.
1968. Los centrolenidos de Venezuela. Mem. Soc. Cien. Nat. La Salle, 28(81):301-334.

SAVAGE, J. M.
1967. A new tree-frog (Centrolenidae) from Costa Rica. Copeia, 1967(2):325-331.

SAVAGE, J. M. and W. R. HEYER
1967. Variation and distribution of the tree-frog genus *Phyllomedusa* in Costa Rica, Central America. Beitr. Neotrop. Fauna, 5:111-131.

SAVAGE, J. M. and P. H. STARRETT
1967. A new fringe-limbed tree-frog (family Centrolenidae) from lower Central America. Copeia, 1967(3):604-609.

STARRETT, P. H.
1960. Descriptions of tadpoles of Middle American frogs. Misc. Publ. Mus. Zool. Univ. Michigan, 110:1-37.

TAYLOR, E. H.
1949. Costa Rican frogs of the genera *Centrolene* and *Centrolenella*. Univ. Kansas Sci. Bull., 33:67-89.
1951. Two new genera and a new family of tropical American frogs. Proc. Biol. Soc. Washington, 64:33-40.
1952. The frogs and toads of Costa Rica. Univ. Kansas Sci. Bull., 35:577-942.
1958. Notes on Costa Rican Centrolenidae with descriptions of new forms. *Ibid.*, 39:41-68.

TAYLOR, E. H. and D. M. COCHRAN
1953. Frogs of the family Centrolenidae from Brasil. *Ibid.*, 35:1625-1656.

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MORPHOLOGICAL VARIATION IN THE KINKAJOU, *POTOS FLAVUS* (MAMMALIA:PROCYONIDAE), IN MIDDLE AMERICA

By

S. M. KORTLUCKE[1]

The kinkajou, *Potos flavus* (Schreber, 1774), is a medium-sized carnivore of the family Procyonidae. It is a tropical and sub-tropical species, inhabiting both highland and lowland forests from southern Tamaulipas in eastern México, and Guerrero in western México, southward throughout Central America and South America to the Mato Grosso of Brasil. The kinkajou is an arboreal mammal with a long body and tail and short legs. The end of the tail is prehensile. The muzzle is short, the ears short and rounded, and the eyes large and directed forward. The kinkajou is frugivorous, and the jaw is more like that of a primate than that of a carnivore, having a deeply-squared angular process and concave lower margin. The teeth are also modified. The canines are deeply grooved, as in many frugivorous bats, and the shear mechanism common to most carnivores has been shifted to the high, sharp anterior premolars. The fourth upper premolar and all the molars are relatively low in relief, lacking pronounced cusps. The kinkajou is the most specialized of New World species now included in the Procyonidae, and many of its adaptations for arboreal and frugivorous habits are similar to those found in primates.

In the 200 years the kinkajou has been known to science, there has been no comprehensive, systematic review of the species. Two partial reviews exist. Oldfield Thomas (1902) distinguished five races of kinkajous in Middle America and South America, but in-

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[1] Museum of Vertebrate Zoology, University of California, Berkeley, California 94720. This paper is based on research accomplished while the author was a Graduate Assistant at the Museum of Natural History at The University of Kansas.

cluded no report of specimens from Brasil. More recently, Cabrera (1958) reviewed the South American forms. A new review of South American kinkajous by R. M. Wetzel is currently under way (pers. comm.) and should be published shortly.

The present study is limited to kinkajous of México and Middle America. Eight names currently are recognized for populations occurring in this area—*arborensis, boothi, campechensis, chiriquensis, dugesii, guerrerensis, isthmicus,* and *prehensilis* (=*aztecus*). The description of *prehensilis* by Kerr (1792) apparently was based on other written accounts, and the remaining names were erected on the basis of eight or fewer specimens.

Some characters on which these names were based have been shown to be, or at least discussed as, extremely variable. Lönnberg (1921) has shown molar width (used as a taxonomic character for *arborensis, boothi,* and *isthmicus*) to be too variable for use as a taxonomic character. Goodwin (1938, 1946) commented on the variability of the dorsal streak (*arborensis, aztecus, chiriquensis, isthmicus*).

Preliminary examination of specimens for this study showed that certain other characters also appear to be too variable to be useful taxonomically. One such sort of character is that which would require more sophisticated mensural techniques than were available to determine its worth. Included in this category are degree of inflation of the bullae and frontal bones, and degree of palatal depression (all subspecies except *aztecus* and *prehensilis*). Another category includes characters which readily can be shown to be unreliable. Falling into this group is color (*aztecus, campechensis, dugesii, isthmicus;* in addition, *megalotus* Martin, 1836, a name which is germane to this study, as will be seen in the section on taxonomic history). In comparing ranked color codes of individuals, and color code means of populations, and constructing histograms of color code against number of species against number of specimens for locality groups, I found color to be extremely variable. The addition of month of capture to these histograms did not reveal any pattern of seasonal variation. I concluded that color is extremely variable, and appears to have little validity as a taxonomic character. Further study of pelage structure is planned, and may yield additional systematic information.

A third category includes characters which I observed to be age-dependent. This would include width and degree of basioccipital ridge development, and relative width of postorbital area to interorbital area (*arborensis, guerrerensis*). These are untrustworthy especially when correlated with small size (*boothi, dugesii*), because the basioccipital narrows and becomes ridged, and the postorbital breadth decreases as the animal grows older.

These extremely variable characters I excluded from consideration of geographic variation. In addition, statistical tests showed significant differences among age groups and between sexes.

Subsequent to the elimination of these biases, I examined geographic variation, and on the strength of the results of several statistical tests, I have recognized three races of kinkajous—*Potos flavus chiriquensis* (J. A. Allen), *Potos flavus megalotus* (Martin), and *Potos flavus prehensilis* (Kerr).

It is regretted that small samples remain a problem. Even with the large number of specimens available for this study, elimination of young and damaged specimens, and the necessary separation of sexes, resulted in less than optimal numbers for statistical analysis. That the total sample was comprised of specimens of different ages and sexes was, however, an advantage, in that these differences readily could be determined. In addition, results of all tests showed consistent trends in geographic variation, which were statistically significant among populations, even in the presence of great individual variation.

TAXONOMIC HISTORY

The kinkajou first may have been illustrated by Schreber in 1774 in plate 42, fascicle 6, of "Die Säugthiere," under the name *Lemur Simia-Sciurus.* Possibly this name was suggested by Linnaeus' (1758:30) remarks on *Lemur catta;* he stated that *L. catta* was the "Simia-sciurus madagascariensis," or "maucauco" [= macaque]. Schreber's original plate 42 shows an animal with a long body, a long thick tail, and short limbs like a kinkajou; however, the animal also has a bare black face, a long pointed nose, and primate-like hands and feet bearing thumbs and flat nails. Whether this animal was intended to be a kinkajou is impossible to determine. The obvious discrepancies may be the result of artistic conjecture, if the illustration was based on a skin in poor condition. Alternatively, the picture could be the result of the lasting confusion between *Potos* and the potto [*Perodicticus*]. Or, perhaps, Schreber intended that the animal in the original plate 42 represent a potto, for which he subsequently failed to provide a written description.

Schreber's account of the kinkajou was published in fascicle 9, which appeared in 1774, subsequent to the publication of fascicle 6 (Cabrera, 1958:250). Sherborne (1891:588) cited "Gött. g. Anz., . . . 13 July 1776" as stating that all the Th[eil]. i. "ist mitten im Junio 1774 . . . fertig worden," but did not say that it was issued. He added *(loc. cit.)* that Beckmann, in 1774, reviewed the first 8 fascicles [Hefte]. These first eight apparently were available for review prior to the 1774 (Sherborne, *loc. cit.*) publication of fascicle 9. Schreber's description was taken from Pennant (1771), and cited Pennant's page and plate numbers. Instead of using a Latin name, Schreber unfortunately limited himself to the German "Der Maki mit dem Wickelschwantz." He listed his own plate 42 preceding the description. Also in fascicle 9 is a list of plates, including Schreber's plate 42 as *Lemur flavus.* These three factors go together —Schreber's description, Pennant's description and plate number, and Schreber's plate number in the same fascicle referring to the animal as *Lemur flavus.* A later edition of Schreber's work (1840) has at least two plates numbered 42 (A and B), one of which is *Lemur Simia-Sciurus* and the other of which is *Lemur flavus;* the latter clearly is based on Pennant's plate. It is without question an illustration of a kinkajou. Thus, the name *Lemur Simia-Sciurus* which appears only once on a plate bearing the image of an unidentifiable composite animal whose characters do not correspond with the written description, henceforth should be regarded as a *nomen dubium.* Cabrera (1958) has already called attention to this problem, and I am in agreement with him that *flavus* is the correct specific name of the kinkajou.

The matter of the generic name is somewhat clearer. Schreber first used the Linnaean name *Lemur,* because he believed the animal to be a primate. Subsequently, in 1778, after studying the work of Vosmaer, first published in 1771, Schreber assigned the kinkajou to the genus *Viverra.* (Vosmaer did not use Latin names.) Neither of these names is either applicable or available. The first available name is *Potos* E. Geoffroy St.-Hilaire and G. Cuvier (Mag. Encyclopedique, n.s., 2:187, 1795), type, *Viverra caudivolvula* Schreber (1778:453).

Subspecific names currently applied to Mexican and Central American kinkajous (see Hall and Kelson, 1959:894-895) under consideration are as follows:

Potos flavus arborensis Goodwin, 1938 (Type locality.—El Sauce Peralta, Costa Rica), currently applied to specimens from the east coast of Costa Rica.

Potos flavus boothi Goodwin, 1957 (Type locality.—Pueblo Neuvo Solistahuacán, about 60 mi N Tuxtla Gutierrez, Chiapas, México), currently applied to specimens from the mountains of northern Chiapas.

Potos flavus campechensis Nelson and Goldman, 1931 (Type locality.—La Tuxpeña, Champotón, Campeche, México), proposed for specimens from Campeche, Tabasco, northern Guatemala, and probably all of the Yucatan Peninsula, and also applied by Hall and Kelson (1959:894) to specimens from northern Chiapas, southern Guatemala, Honduras, El Salvador, and Nicaragua. Specimens from Nicaragua assigned to *P. f. aztecus* by J. A. Allen, 1910, were included here provisionally by Hall and Kelson (1959:894).

Potos flavus chiriquensis J. A. Allen, 1904 (Type locality.—Boquerón, Chiriquí, Panamá), currently applied to specimens from the west coast of Costa Rica, and from western and central Panamá.

Potos flavus dugesii Villa-R., 1944 (Type locality.—La Esperanza coffee plantation, 45 km NW Huixtla, Chiapas, México), currently applied to specimens from southern Chiapas.

Potos flavus guerrerensis Goldman, 1915 (Type locality.—near Ometepec, Guerrero, México), proposed for specimens from Guerrero and range subsequently extended to include central Oaxaca (Hall and Kelson, 1959:895, map 459).

Potos flavus isthmicus Goldman, 1913 (Type locality.—near head of Río Limón, 5200 ft, Mt. Pirri, eastern Panamá), applied to specimens from Darién.

Potos flavus prehensilis (Kerr, 1792) (Type locality restricted to Atoyac, Veracruz, México, by Hershkovitz, 1959:350), currently applicable to specimens from southern Tamaulipas, San Luis Potosí, Veracruz, and eastern Oaxaca (*aztecus* Thomas, 1902, a synonym).

An additional name that must be considered is *Potos flavus megalotus* (Martin, 1836), originally written as *Cercoleptes megalotus* (type, a Zoological Society of London specimen of unknown locality), used by Thomas (1902) for specimens from Costa Rica and Colombia, and retained by J. A. Allen (1904) for specimens from eastern Colombia. Cabrera (1958:250) used the name *megalotus* for specimens from the entire Andean zone from northern Ecuador through Colombia into eastern Panamá; he placed *P. f. isthmicus* Goldman in synonymy with *megalotus*, together with names applied to various other populations of kinkajous from northeastern South America (*P. f. caucensis* J. A. Allen, 1904; *P. f. tolimensis* J. A. Allen, 1913; *P. f. mansuetus* Thomas, 1914; *P. f. modestus* Lönnberg, 1921).

Cabrera (1958:252) reported that Thomas had designated Santa Marta, Colombia, as the type locality of *megalotus*, but Thomas (1902:267) appears only to have implied this, remarking on the close resemblance between the description of the type and specimens from Santa Marta (and other localities). J. A. Allen (1904:74) restricted use of the name *megalotus* to specimens from eastern Colombia in his description of *chiriquensis* from Panamá, also noting this resemblance. Later, Allen (1913:482), in his description of *tolimensis* from Tolima, Colombia, remarked that Thomas did not designate a type locality for *megalotus*. Allen retained the name "for the Santa Marta form to which it was definitely assigned in 1904" [by Allen]. So it does not appear that a type locality has been formally designated for *megalotus*. Therefore, I have done so under the synonymy for *Potos flavus megalotus* which appears beyond.

MATERIALS AND METHODS

Specimens examined are housed in three major museum collections: The University of Kansas Museum of Natural History, Lawrence, Kansas (KU), the National Museum of Natural History, Washington, D.C. (USNM), and the American Museum of Natural History, New York (AMNH). In all, 295 specimens were available for study, of which 169 were skins accompanied by skulls, 81 were skins only, and 33 were skulls only. The remainder were alcoholic specimens, skin and skeleton, or baculum only (1). Specimens were grouped according to geographic origin, sex, and age. Data recorded on skin labels were noted. These included (inconsistently) external measurements, reproductive condition, stomach contents, and ecological notes. Color of pelage was examined, and compared with a coded series of representative skins from the collection of The University of Kansas Museum of Natural History.

Skulls were separated into four age classes (see variation with age), and a total of eight standard measurements, accurate to 0.1 mm, were taken on each: condylobasal length, zygomatic breadth, least interorbital breadth, postorbital breadth, breadth of braincase, mastoid breadth, length of maxillary tooth-row measured on left side of cranium where possible, and breadth of rostrum (greatest width in plane of canines).

Many skulls were damaged by shot, and therefore unusable for analysis. For example, among specimens in the collection of The University of Kansas Museum of Natural History, 38 of 65 skulls (58%) have some degree of damage from shot. Cranial anomalies were noted (Kortlucke, 1972:16-17).

Tooth wear was divided into four stages—minimal, moderate, heavy, and extreme. Dental anomalies and diseases were noted, but no tooth was removed from the bone for these observations (Kortlucke, 1972:18-22, Tables 5 and 6). Available bacula were measured, but insufficient numbers were available for statistical analysis.

In order to create workable sample sizes, localities were grouped, but in no instance did any grouped locality include more than one physiographic region or more than one named race of kinkajou. The resultant samples (Fig. 1) are:

MÉXICO (samples 1-11): 1—*Veracruz* (males only): 75 mi S Rivera; 12.5 mi N Tihuatlán; 2—*Veracruz:* Coyamé, 7 mi E Catemaco; Lake Catemaco; 13 mi E San Andrés Tuxtla; 3 km E San Andrés Tuxtla; 3—*Veracruz:* Arroyo Saoso, 7 km S, 37 km E Jesús Carranza; 20 km E, 55 km ESE, 25 km SE, 30 km SE, 35 km SE, and 38 km SE Jesús Carranza; 4—*Guerrero:* Acapulco; near Ometepec; 1 mi SW Omilteme; Papayo; 5—*Oaxaca* (females only): Vista Hermosa; 6—*Oaxaca:* 2 mi S Tollocito; Veracruz border, 3 mi S Río Jaltepec; 7—*Oaxaca:* 3 mi NE El Jicaro; La Concepción; 20 mi NE La Ventosa; Limón; Santiago Guevéa; Santiago Lachiguiri; Santo Domingo; Tapanatepec; Tres Cruces; 8—*Tabasco:* Las Minas; 5 mi SW Teapa; 9—*Chiapas:* Pueblo Neuvo Solistahuacan; 10—*Yucatán* (males only): 8 km N, 10 km W Tizimín; 11—*Campeche* (females only): Dzibalchén; 7 km N, 51 km E Escarcega; La Tuxpeña; 12—GUATEMALA: *Petén:* Laguna de Petenxil; road to Río San Roman, NW Chinajá; *No province:* Finca Salache; 13—HONDURAS (females only): *Santa Barbara:* Santa Barbara; *Tegucigalpa:* El Caliche Cedros; 14—NICARAGUA: *Esteli:* 8 mi S Condega; *Jinotega:* 5.5 km N, 16 km E Jinotega; Peña Blanca; *Matagalpa:* 1 km NE Esquipulas; Matagalpa; Río Tuma; Tepeyac; Uluce; *Nueva Segovia:* Ocotal; 15—NICARAGUA (females only): *Boaco:* Santa Rosa, 17 km N, 15 km E Boaco; 16—NICARAGUA: *Zelaya:* Cara de Mono; El Recreo; 17—NICARAGUA: *Carazo:* 3 km N, 4 km W Diriamba; *Granada:* Finca Santa Cecilia, 6.5 km SE Guanacaste; *Managua:* 10 mi SW Managua; *Rivas:* 11 km S, 3 km E Rivas; 18—COSTA RICA (males only): *Cartago:* El Sauce

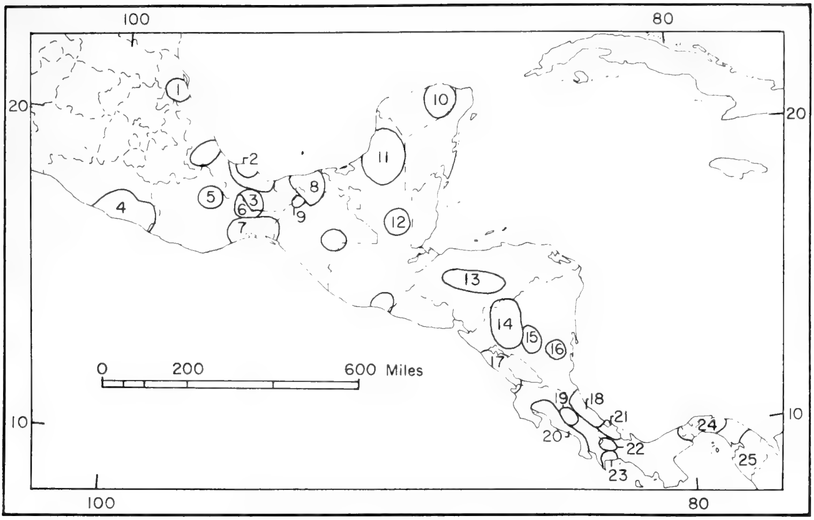

FIG. 1. Geographic location of grouped samples. Those numbered were used in analyses; those unnumbered were represented by specimens of which only the skin was available.

Peralta; *Limón:* Olivia; Pandora; Talamanca; 19—COSTA RICA: *San José:* Monte Redondo; San Antonio; San José; 20—COSTA RICA (females only): *Puntarenas:* Palmar; *San José:* Jabillo Pirrís; San Geronimo Pirrís; PANAMÁ (samples 21-25): *Bocas del Toro:* Almirante; Boca del Drago; Bocas del Toro; 7 km SSW Changuinola; Río Changuinola; Río Teribe; Sibube; 22—(females only): *Chiriquí:* Casa Lewis, Cerro Punta; Casa Tilley, Cerro Punta; Volcán; 23—*Chiriquí:* Boquerón; Progreso; Río Corutu, between Puerto Armuelles and Costa Rican border; 24—*Canal Zone:* Barro Colorado Island; Chagres Valley; Gatun; Río Indio, near Gatun; *Panamá:* near Agua Clara; Cerro Azul; La Zumbadora; junction of Río Bayano and Río Cañito; *San Blas:* Mandinga; 25—*Darién:* Cana; Cerro Malí; Cerro Tacarcuna; El Real; Jaque; La Laguna; Mt. Pirri; Río Chicao; Río Chucunaque; near junction of Río Jaque and Río Imamado; Río Jaque; mouth of Río Paya; Río Platanal region; Tacarcuna region; Tapalisa.

All statistical analyses were carried out on the GE-Honeywell 635 Computer at The University of Kansas Computer Center. Variation with age, secondary sexual variation, and geographic variation were examined by the UNIVAR program written by Power; this program yields standard statistics (mean, range, standard deviation, standard error of the mean, variance, and coefficient of variation). Single-classification Analysis of Variance (*F*-test, significance level, 0.05) is used in this program to test between means of groups. Where means are found to be significantly different, the Sums of Squares Simultaneous Test Procedure (SS-STP) based on ranked means is used to determine maximally non-significant subsets. This same program was used to test for presence or absence of geographic variation, by testing among means of geographically-grouped samples.

In addition, another program available in the Numerical Taxonomy System at The University of Kansas, the NT-SYS Version 2, was utilized to display trends in geographic variation. This program has subroutines that compute matrices of Pearson's product-moment correlations and of taxonomic distance coefficients from basic data matrices. Cluster analyses are made using the unweighted pair group method based on arithmetic averages (UPGMA) on the correlation and distance matrices, yielding phenograms for each. The phenograms are then compared with the matrices and a coefficient of cophenetic correlation is computed for each phenogram-matrix comparison. Other subroutines generate character correlation matrices, and matrices of the first three principal components based on correlations among characters are computed, and then displayed in two-dimensional plots. Subprogram CORDST was utilized with the Variance-Covariance option (V-CV) since the data were all of the same type (cranial measurements). A more complete description of the computer techniques utilized may be found in Smith (1972:8-10).

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NONGEOGRAPHIC VARIATION

Variation with Age

Three classes of pelage—neonate, juvenal, and adult—were observed. A specimen (USNM 270806) born at the National Zoological Park in Washington, D.C., appears to have died soon after birth (cranial bones completely unfused) on 17 June 1942; it has neonate pelage. The hair is coarse. It is also sparse, especially on the throat, chest, venter, inguinal region, and ventral surface of tail. The head is dark grayish brown. Stripes of dark grayish brown and grayish beige are longitudinal on the back and transverse on the sides; the rump is grizzled. The tail is uniformly dark gray above and beige below, and the belly is beige.

Juvenal pelage is similar in color to that of the adult, but not as bright, and the texture is softer than that of the adult. Juvenal pelage is relatively long and somewhat wavy or fuzzy in appearance. There appears to be more underfur than in adult pelage. Adult pelage generally is short and dense, more or less comparable to that of the woolly monkey. Certain specimens have somewhat longer, silkier pelage than others; the occurrence of such pelage could not be correlated with sex, season, or geographic origin.

Skulls were separated into four age classes: 1) *young*—still having all or part of the deciduous dentition; 2) *juvenile*—permanent dentition usually in unworn state, cranial sutures clearly visible, basisphenoid generally unfused anteriorly and posteriorly, and basioccipital wide and flat; 3) *subadult*—sutures on dorsal side of cranium fused (only anterior portion of nasal sutures evident), generally little wear on teeth, basisphenoid generally fused posteriorly and unfused anteriorly, and temporal ridges still widely separated; and 4) *adult*—sutures obliterated, basisphenoid completely fused, some development of basioccipital median ridge, some degree of wear on teeth, and sagittal crest developed for at least three-fourths of its length in males, and one-half its length in females. Although four stages of tooth wear were recognized, this character proved to be too variable to be useful in subsequent analyses.

In order to perform univariate analysis, a grouped sample of adequate size had to be created. After examination of the numbers of usable specimens available from all localities, it was decided that the area north of the Isthmus of Tehuantepec would be the most reasonable one for such a grouping. Analysis was run on all usable specimens from the Mexican states of Guerrero, Oaxaca, and Veracruz (samples 1-7, Fig. 1), totals (age class in parentheses), as follows: males, 22(4), 5(3), and 7(2); females, 12(4), 7(3), and 5(2). Sample size varied if a measurement was missing because of breakage or anomaly, but no specimen was used if more than two measurements were missing.

Results of the Analysis of Variance among age groups (Table 1) show five of eight measurements for each sex to be significantly different at the 0.05 level or above.

There were no significant differences among groups for either sex, with respect to breadth of braincase and length of maxillary tooth-row; this suggests that these two cranial features, highly important for feeding and other phases of survival, tend to develop more quickly than others. Individual variation, as revealed by coefficients of variation, is well within normal range ($CV \leq 5.0$) for these two measurements (Kortlucke, 1972, Table 2).

TABLE 1.—Results of Analysis of Variance among three age classes of *Potos flavus* from Guerrero, Oaxaca, and Veracruz.

Measurement	Mean Square Values		F-Values (3.34/3.44)	
	♂♂	♀♀	♂♂	♀♀
Condylobasal length	73.1	57.15	9.857***	4.88*
Zygomatic breadth	121.5	174.68	28.83 ***	25.26***
Least interorbital breadth	10.58	5.21	6.82 **	3.29 n.s.
Postorbital breadth	28.28	17.50	10.87 ***	5.40*
Breadth of braincase	0.77	0.89	0.841 n.s.	1.07 n.s.
Mastoid breadth	19.14	59.71	4.43 *	18.41***
Length of maxillary tooth-row	2.77	1.72	3.10 n.s.	1.77 n.s.
Breadth of rostrum	2.50	3.76	2.76 n.s.	3.78*

***=$P \leqq 0.001$; **=$P \leqq 0.01$;
*=$P \leqq 0.05$.

The SS-STP shows two maximally non-significant subsets of age classes 4-3 and 3-2 for condylobasal length (males and females), least interorbital breadth (males), postorbital breadth (females), mastoid breadth (males), and breadth of rostrum (females).

In males, age class 4 is overlapped conspicuously at the small end of the range by age class 3, but it is consistently higher at the large end of the range. For example, in condylobasal length, age class 3 has a range of 85.1-88.8; in contrast, age class 4 has a range of 85.5-95.1.

This is not true of the adult females, which are smaller than adult males. Other features of differential growth patterns among females are discussed beyond.

Zygomatic breadth and postorbital breadth for males group age classes 3-2 and separate age class 4, whereas zygomatic breadth and mastoid breadth of females link age classes 4-3 and separate age class 2.

These results might be interpreted as permitting the use of both age classes 4 and 3 in analyses, but because of extensive linkage of age classes 3 and 2, I judged it advisable to use only those specimens from the adult age class (4) for the statistical examinations.

Secondary Sexual Variation

Adult specimens from the sample used in the analysis of variation with age were used to determine secondary sexual variation. Results of the Analysis of Variance (Kortlucke, 1972, Table 3) show a significant difference between groups at the 0.01 level for zygomatic breadth and postorbital breadth, and at the 0.05 level for condylobasal length, least interorbital breadth, breadth of braincase, and length of maxillary tooth-row. Males are found to be larger in each case. There is no significant difference between groups for mastoid breadth or rostral breadth. These results dictated separation of the sexes for further analyses.

Individual Variation

Variation in size.—This was found to be generally within normal limits (CV≦5.0). Six samples of five or more specimens for both males and females were examined by univariate statistical analysis. Adult specimens from samples 3 and 6(1), 7(2), 16(3), 21(4), 24(5), and 25(6) (Fig. 1) were used for this analysis.

Highest coefficients of variation are seen for least interorbital breadth and postorbital breadth, especially for females. The states of these particular characters are age-dependent, so that even within age class 4, there is still more variation for them than for other measurements. Females appear to mature more slowly in these cranial features, possibly owing to the demands of maternity. Coefficients of variation for these two measurements range from 5.17 to 10.88 among 4 of 6 samples for males (sample 2, least interorbital breadth, sample 3, postorbital breadth, samples 5 and 6, both measurements), and 6 of 6 samples for females (sample 3, postorbital breadth, sample 4, least interorbital breadth, samples 1, 2, 5, 6, both measurements).

Four additional coefficients of variation of greater than 5.00 are condylobasal length, males, sample 2, 6.66; mastoid breadth, males, sample 6, 8.76; mastoid breadth, females, sample 4, 6.16; and zygomatic breadth, females, sample 4, 5.62.

Sixteen of the other 72 values are less than 5.00 but greater than 4.00, and the remaining 56 are less than 4.00.

Variation in color.—Preliminary separation of skins in the collection of The University of Kansas Museum of Natural History on the basis of geographic origin revealed no definitive trends, nor did separation on the basis of season within geographic regions. Skins were then sorted by color alone. This resulted in six color groups; one skin was chosen to be representative from each group. These six skins were assigned code numbers from pale to dark, and skins at other institutions were compared with them and rated accordingly. Color groups recognized were: 1) yellow-beige; 2) pale brown; 3) pale gray; 4) golden brown; 5) reddish brown; and 6) dark brown. Skins appearing intermediate between two color groups were scored as a half unit between them. The resulting data first were arranged in a series of histograms to determine if seasonal variation was a factor. The total range of color was observed in skins taken in eight months of the year. In two months (September, $N=6$, December, $N=9$), the observed range was 2-6, and in October ($N=12$) the observed range was 4-6; no November-taken specimens were available. One specimen (USNM 338353) was described on the skin label as "molting—foreparts new gray, rear old orange." This specimen was taken on Cerro Tacarcuna, Panamá, in the month of February.

A series of histograms was constructed for grouped geographic samples plotting numbers of specimens against color codes, to which months of capture were added. Wide color range is apparent within samples as well as within months. There is a trend from paler color in the north to darker color in the south, but where sufficient numbers of specimens were available, the range of color for any geographic sample was great. Means were computed for each of the grouped localities, but these, when used together with means of cranial measurements in a preliminary multivariate analysis, display most of the variation as being individual rather than geographic. Therefore I decided that color has limited validity as a taxonomic character.

Bacular Morphology

The baculum is straight or slightly curved, subcylindrical, and terminates in a tetrad of short rounded processes, two of which are directed laterally and upward, and two of which are directed anteriorly. These four terminal bacular processes distinguish *Potos* from all other members of the subfamily Procyoninae (Pocock, 1921). Most of the bacula examined are relatively long and slender, but one, from a specimen from near Diriamba, Nicaragua, is short (57.6 as compared with a range of 69.2 to 77.2) and thick (4.7 as compared with a range of 3.6 to 4.4). Insufficient numbers of bacula were available for statistical analysis.

Bacula examined.—GUATEMALA: *Santa Rosa:* Astillero (1). MÉXICO: *Oaxaca:* 2 mi S Tollocito (1); *Veracruz:* vicinity of Jesús Carranza (5). NICARAGUA: *Carazo:* 3 km N, 4 km W Diriamba (1); *Zelaya:* Cara de Mono (1). PANAMÁ: *Bocas del Toro:* Almirante (4); *Darién:* Río Paya (2).

GEOGRAPHIC VARIATION

The first step in the assessment of geographic variation is to determine whether there are statistically significant differences among groups (localities). Small sample sizes severely limited the number of groups available for testing, but there were six localities from which five or more specimens were available. These were, from north to south, as follows: 1—southern Veracruz in the vicinity of Jesús Carranza and the adjoining area of Oaxaca-Veracruz border in the region of Río Jaltepec (10 males, 5 females, shown in samples 3 and 6 on Figure 1); 2—southeastern Oaxaca (5, 5, sample 7); 3—southeastern Nicaragua in the vicinity of El Recreo (5, 5, sample 16); 4—western Panamá in the vicinity of Almirante (5, 6, sample 21); 5—central Panamá (9, 8, sample 24); and 6—eastern Panamá (7, 5, sample 25). The six groups were analyzed by means of a single-classification Analysis of Variance. The Sums of Squares Simultaneous Test Procedure is then executed if significant differences are found among groups. Results of this

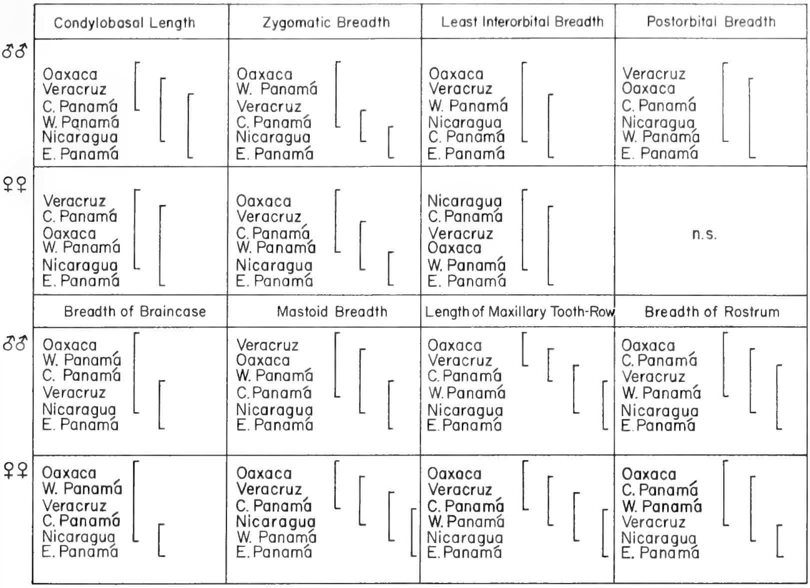

FIG. 2. Results of the Sums of Squares Simultaneous Test Procedure on six samples of male and female specimens of *Potos flavus*.

test (Fig. 2, Table 2) show significant differences for all but one measurement, that of postorbital breadth in females. As mentioned above, I believe that this is due to the fact that the postorbital breadth decreases with age. The bone in the postorbital region becomes thicker and heavier as it is constricted; therefore, it is possible this feature does not mature as quickly in females owing to differential demands on the calcium supply by developing embryos. Results of the SS-STP on these measurements show a non-continuous cline in size from larger in the north to smaller in the south. Specimens from Oaxaca are listed first (largest) in

TABLE 2.—Analysis of Variance in six samples of *Potos flavus*. Interlocality Variance—Intergroup Mean Square Values.

Measurement	♂♂	♀♀
Condylobasal length	55.48***	25.74**
Zygomatic breadth	64.88***	44.09***
Least interorbital breadth	6.75**	2.90*
Postorbital breadth	11.59**	2.50 n.s.
Breadth of braincase	5.74**	6.11**
Mastoid breadth	25.12***	20.70***
Length of maxillary tooth-row	11.82***	4.86***
Rostral breadth	4.88***	6.69***

***=P≦0.001; **=P≦0.01;
*=P≦0.05.

six of eight measurements for males (second in the remaining two), and first in five of eight measurements for females (third and fourth for the remaining measurements tested). In eight measurements (five for males, three for females), southern Veracruz is listed either first or second. It is listed third four times, and fourth twice. Specimens from central Panamá appear to be somewhat larger than specimens from Nicaragua, appearing above Nicaragua seven times for both males and females. Specimens from western Panamá also appear above those in the Nicaraguan sample seven times for males and five times for females. Eastern Panamá always appears sixth on the list. The maximally non-significant subsets do not yield much useful information as to natural groups, because they are highly variable, probably owing to small sample sizes and non-contiguous localities.

Given, however, the significant differences among groups, I decided to examine the specimens in these groups by multivariate analysis to see whether any meaningful groups appeared.

At first glance, the phenograms generated did not appear to be particularly informative, so I attempted to determine which localities were more consistently linked. In the correlation phenogram for males, there were two major groups, separated at – 0.2250. The first is comprised of subgroup 1 (Veracruz, 2 specimens; Oaxaca, 3; Nicaragua, 1); subgroup 2 (Veracruz, 1; Oaxaca, 1; Nicaragua, 1; Central Panamá, 1; Eastern Panamá, 4); subgroup 3 (Veracruz, 1; Nicaragua, 2; western Panamá, 1; central Panamá, 1); subgroup 4 (Veracruz, 4; Oaxaca, 2). The second was comprised of two subgroups—subgroup 5 (Oaxaca, 1; central Panamá, 4; western Panamá, 3); subgroup 6 (Nicaragua, 1; western Panamá, 1; central Panamá, 3, and eastern Panamá, 3). Simple totals seem to yield two groups, one northern and one central, with eastern Panamá falling equally in both. Totals for the first group included fourteen specimens from Oaxaca and Veracruz as opposed to only seven from the central region and four from eastern Panamá. The second major subgroup contained but one specimen from the northern part of the range, the remainder being nine from the central region and three from eastern Panamá. Coefficient of cophenetic correlation for this phenogram was very low, being only 0.561 (Fig. 3).

The distance phenogram for males, with a (low) coefficient of cophenetic correlation of 0.690, was similarly examined. This phenogram also has two major subgroups; one is composed of seven specimens from the northern part of the range and five from western and central Panamá. The second contains eight from the north, twelve from central localities, and all seven specimens from eastern Panamá; six of the last fall out together in secondary subgroup 5, which also includes one from Oaxaca, 2 from Nicaragua, and one each from western Panamá and central Panamá (Fig. 4).

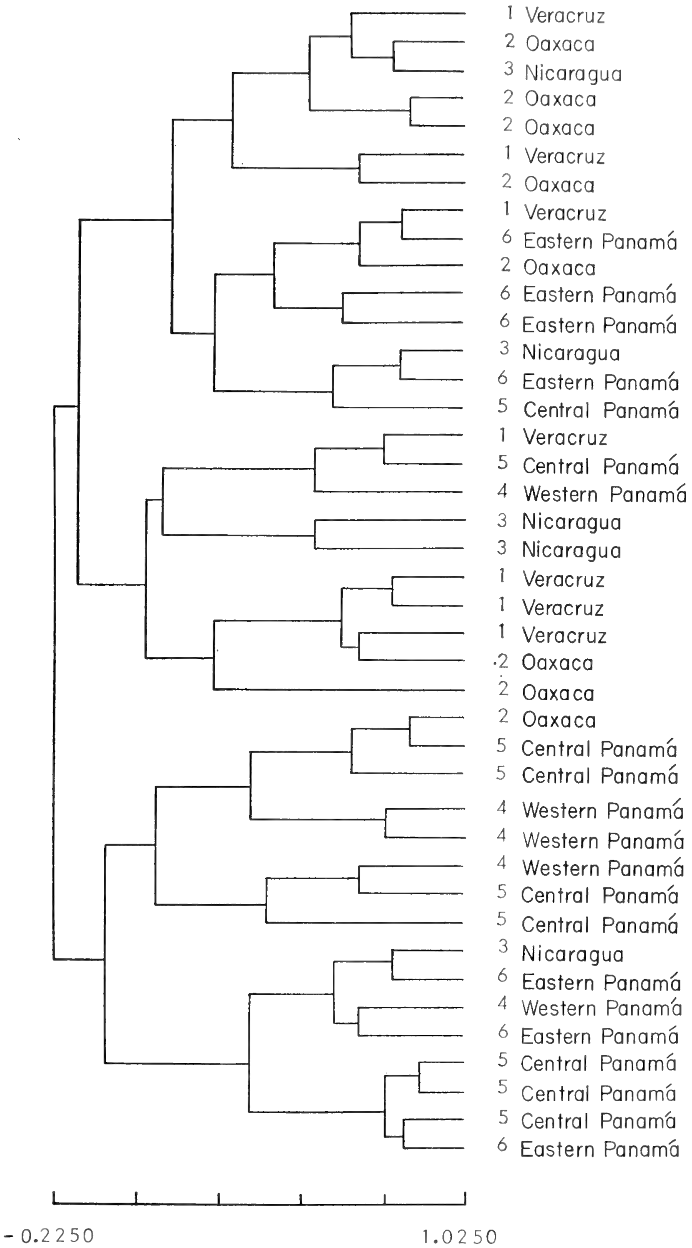

FIG. 3. Correlation phenogram for male specimens of *Potos flavus;* coefficient of cophenetic correlation=0.561.

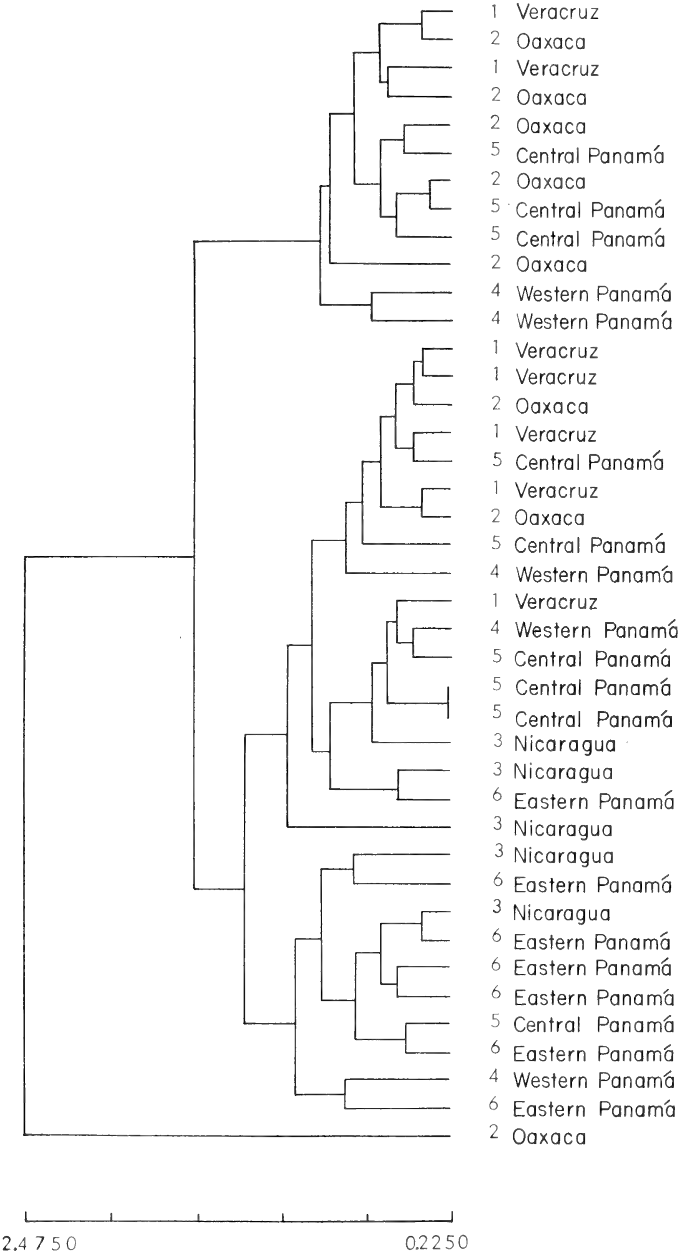

FIG. 4. Distance phenogram for male specimens of *Potos flavus;* coefficient of cophenetic correlation=0.690.

For females, the correlation phenogram contains two major subgroups, the second of which was further divided at a low level of correlation. The first major subgroup includes sixteen specimens from the central part of the range, and one each from the north and from eastern Panamá. The second contains nine from the north (seven of which fall into the first of two secondary subgroups), three from the central part of the range, and four from eastern Panamá; these last are all contained within one of the two secondary subgroups. This phenogram has a coefficient of cophenetic correlation of 0.666 (Fig. 5).

The distance phenogram for females is composed of two major subgroups, the first of which is small, and contains eight specimens from the northern part of the range, and two from the central part. The second major group contains a large secondary subgroup composed of seventeen specimens from the central part of the range, and only two from the north, and one from eastern Panamá. The other secondary subgroup is composed of four specimens from eastern Panamá. The coefficient of cophenetic correlation for this phenogram, while still low, is higher than that of any of the others, being 0.699 (Fig. 6).

I hesitated to place emphasis on the levels at which any of the groups are separated, because the samples are small, not all areas are contiguous, and the coefficients of cophenetic correlation are low. However, the results, together with those of the foregoing univariate analysis and subjective evaluations based on examination of the specimens, appear to indicate a trend for the specimens examined to fall generally into three recognizable groups—those from the north, individuals from the central part of the range, and specimens from extreme eastern Panamá.

As expected, two-dimensional projections of the Principal Components (Figs. 7-10) reveal no truly isolated clusters, because clinal variation within an extremely variable species would not be so displayed. Thus, in each instance, the central and most heavily populated part of the entire cluster is composed basically of a group of specimens from the northern and central parts of the range. More of the northern specimens fall out to the left side (large-size), and specimens from eastern Panamá fall mainly in a small and somewhat more isolated cloud to the right (small-size) side.

Along Principal Component I (Table 3) for males, heavily loaded factors are condylobasal length, zygomatic breadth, and mastoid breadth, and to a less degree, least interorbital breadth, postorbital breadth, breadth of braincase, and length of maxillary tooth-row. Principal Component I accounts for 75 percent of the variation. Principal Component II is most heavily loaded for condylobasal length and postorbital breadth, with zygomatic breadth next highest, and accounts for 11 percent of the variation. Principal

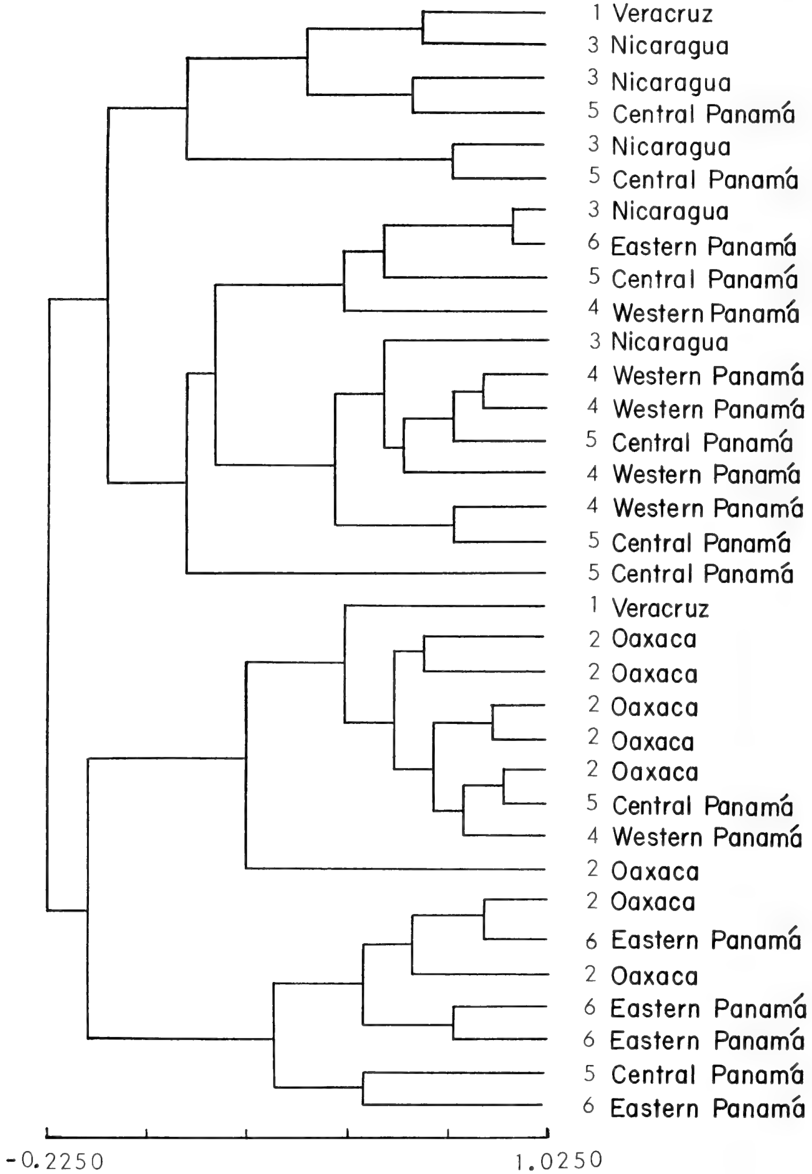

FIG. 5. Correlation phenogram for female specimens of *Potos flavus;* coefficient of cophenetic correlation=0.666.

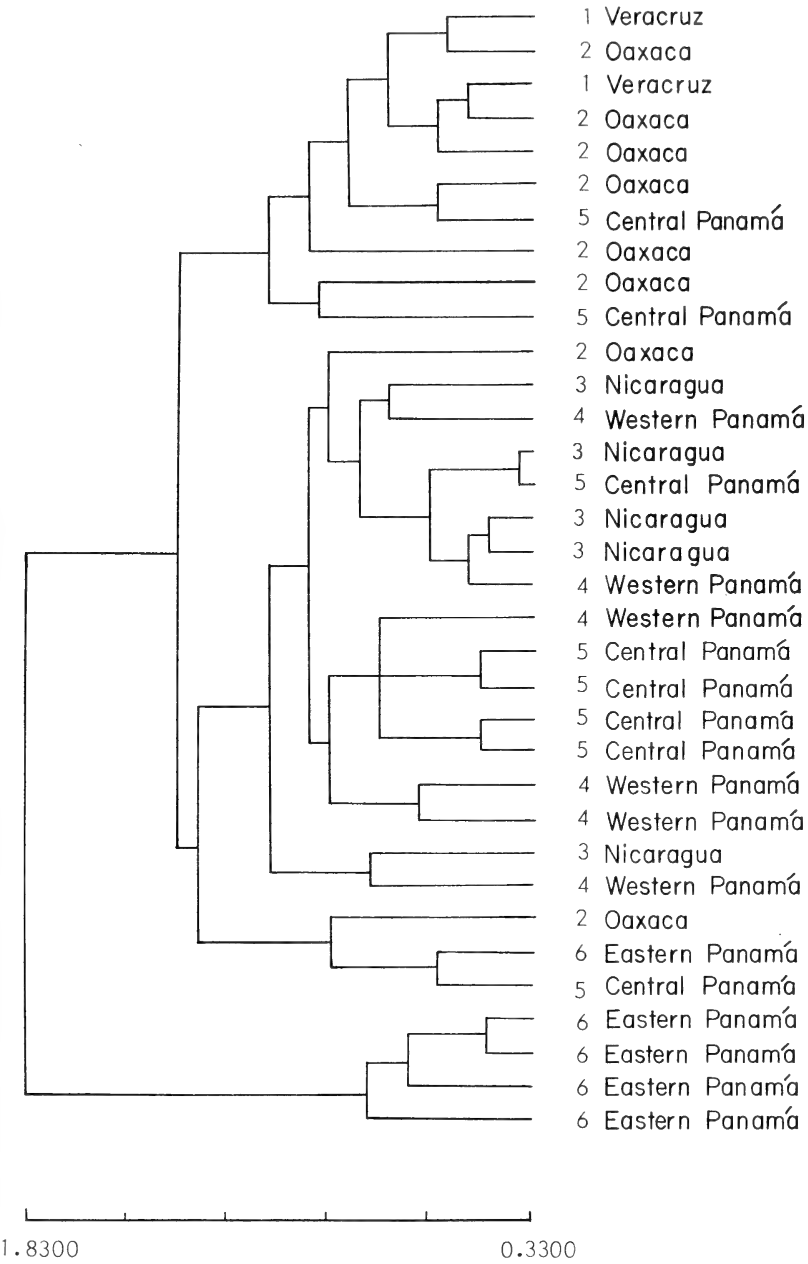

FIG. 6. Distance phenogram for female specimens of *Potos flavus;* coefficient of cophenetic correlation=0.699.

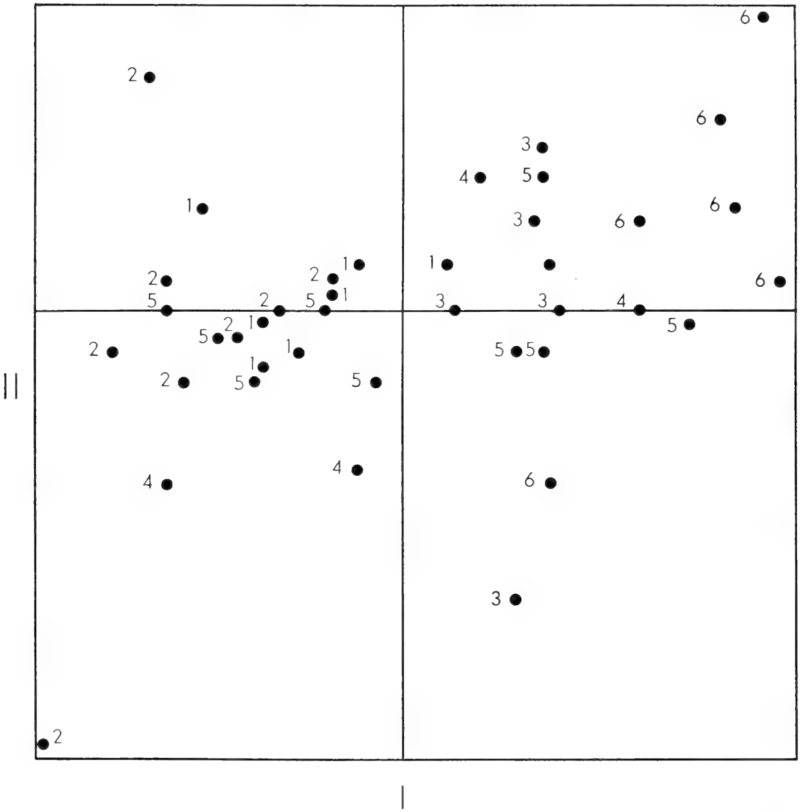

FIG. 7. Two-dimensional projection of Principal Components I and II illustrating the phenetic position of male specimens of six samples of *Potos flavus*.

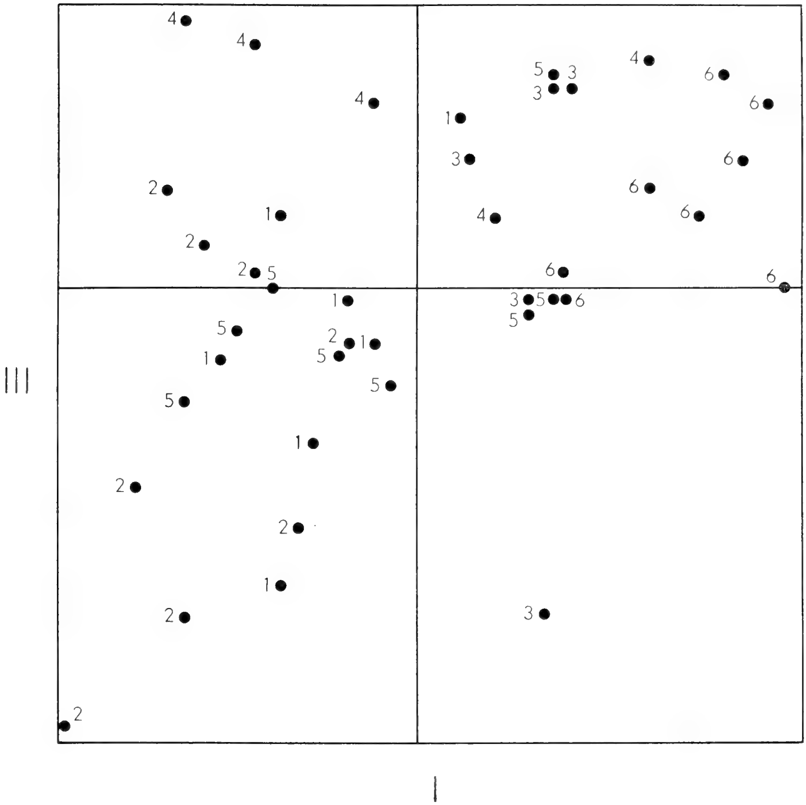

FIG. 8. Two-dimensional projection of Principal Components I and III illustrating the phenetic position of male specimens of six samples of *Potos flavus*.

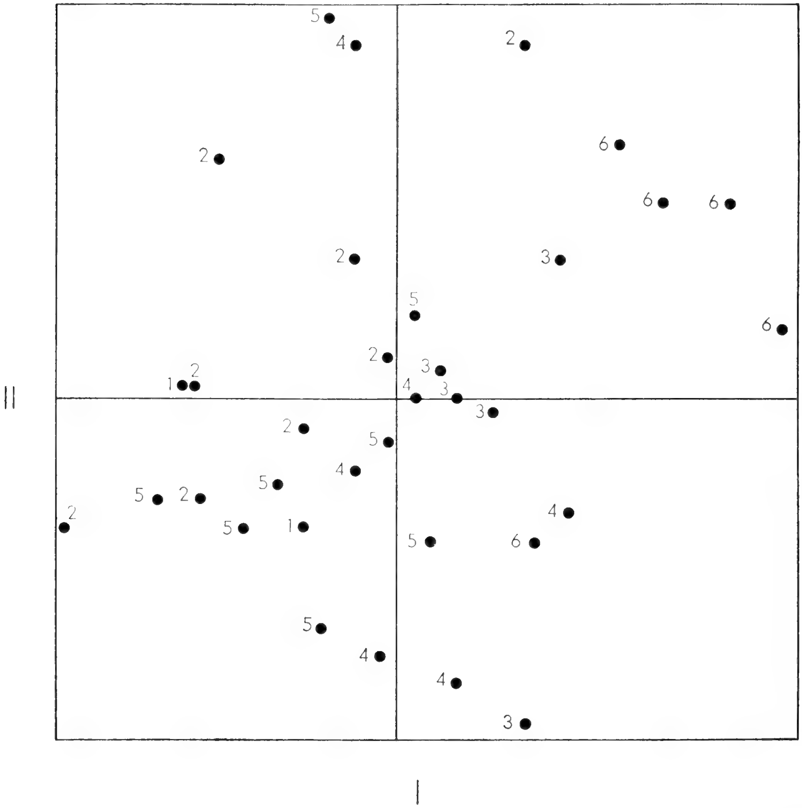

FIG. 9. Two-dimensional projection of Principal Components I and II illustrating the phenetic position of female specimens of six samples of *Potos flavus*.

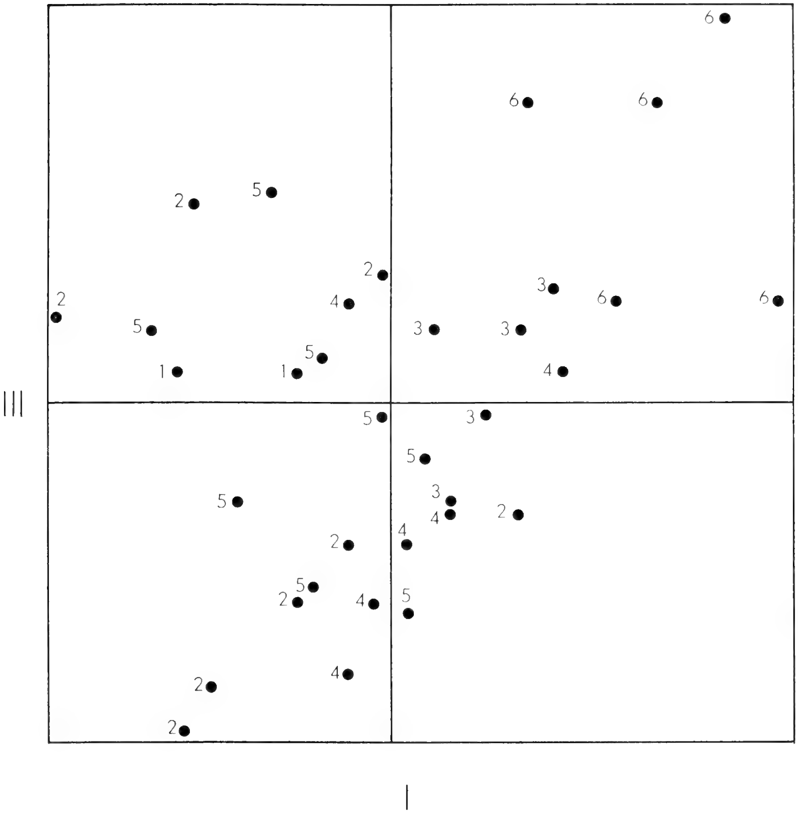

FIG. 10. Two-dimensional projection of Principal Components I and III illustrating the phenetic position of female specimens from six samples of *Potos flavus*.

TABLE 3.—Factor Matrix from variance-covariance analysis of male and female *Potos flavus.*

Measurement	Factor I	Factor II	Factor III
Condylobasal length	–3.198/–2.897	1.659/ 0.060	–0.271/ 1.257
Zygomatic breadth	–3.403/–2.869	–0.724/ 0.021	0.746/–0.970
Least interorbital breadth	–1.214/–0.608	–0.313/–0.590	–0.330/ 0.006
Postorbital breadth	–1.391/–0.184	–1.006/–1.621	–1.165/ 0.258
Breadth of braincase	–1.102/–0.933	–0.541/–0.458	0.157/–0.664
Mastoid breadth	–2.302/–2.010	–0.303/ 0.462	0.373/–0.044
Length of maxillary tooth-row	–1.198/–0.966	0.150/ 0.110	–0.612/ 0.153
Breadth of rostrum	–0.843/–0.970	0.064/–0.188	0.058/–0.358

Component III, which accounts for 6 percent, is heavily loaded for postorbital breadth, and secondarily for length of maxillary tooth-row and zygomatic breadth. Total trace of variance accounted for by the three Principal Components is 92 percent. For females, Principal Component I is heavily loaded for condylobasal length, zygomatic breadth, and mastoid breadth, as for males; secondarily, but to a lesser degree than for males, the component is loaded for breadth of braincase and length of maxillary tooth-row. Additionally, breadth of rostrum is loaded to the secondary degree, which is not true for males. Principal Component I accounts for 70 percent of the variation. Principal Component II (10%) is heavily loaded only for postorbital breadth, which appears for males along with three other measurements, but the spread for females appears to be somewhat greater than for males. Principal Component III (9%) for females is loaded for condylobasal length and zygomatic breadth, and, to a lesser degree, breadth of braincase. Total variation accounted for is 89 percent.

Separation appears greatest for the specimens from eastern Panamá. Specimens from Oaxaca and, to a lesser extent, those from Veracruz, appear mainly interspersed with the rather large specimens from central Panamá. In contrast, specimens from Nicaragua and western Panamá, along with remaining specimens from central Panamá and Veracruz, fall out mainly in the central part of the plots.

In summary, the Principal Components analysis corroborates the evidence emerging from the foregoing analyses—i.e., this species shows non-continuous clinal variation from larger size in the north to smaller size in the south, with a population of fairly large-sized animals in central Panamá.

On the basis of these analyses, I formed the hypothesis that there are three basic groups of highly variable kinkajous in México and Central America—one from north of the Isthmus of Tehuantepec, one from the central part of the range, and one from eastern Panamá. In order to test this hypothesis, I took all available specimens from all parts of the range (as listed below), which increased somewhat the sample size, and examined them by means of the UNIVAR program. This *a priori* test was employed to show whether there were significant differences among groups, and if so, then maximally non-significant subsets should display the three groups in order of decreasing size.

Specimens examined were 62 males and 53 females, as follows:

MÉXICO (samples 1-11): 1 (Fig. 1)—*Veracruz:* 75 mi S Rivera, 2 males; 2—*Veracruz:* vicinity of San Andrés Tuxtla, 2 males, 1 female; 3—vicinity of Jesús Carranza, 7 males, 2 females; 4—*Guerrero:* vicinities of Omilteme and Ometepec, 3 males; 6—*Oaxaca:* vicinity of Río Jaltepec, Tollocito, 3 males, 3 females; 7—*Oaxaca:* vicinity of El Jicaro, La Concepción, 20 mi NE La Ventosa, Santo Domingo, Tapanatepec, Tres Cruces, 5 males, 5 females; 8—*Tabasco:* Las Minas, 1 female; 9—*Chiapas:* Pueblo Nuevo Solistahuacan, 1 female; 11—*Campeche:* Dzibalchén, 7 km S, 51 km E Escarcega. La Tuxpeñá, 3 females; 12—GUATEMALA: *Petén:* Laguna de Petenxil, road to Río San Roman, 2 males, 1 female; 13—HONDURAS: *Santa Barbara:* Santa Barbara, 1 female; 14—NICARAGUA: *Jinotega:* vicinity of Jinotega, and *Matagalpa:* vicinity of Esquipulas, 2 females; 15—NICARAGUA: *Boaco:* Santa Rosa, and *Matagalpa:* Río Tuma, Uluce, 4 males, 1 female; 16—NICARAGUA: *Zelaya:* Cara de Mono, El Recreo, 5 males, 5 females; 17—NICARAGUA: *Carazo:* vicinity of Diriamba, and *Granada:* vicinity of Guanacaste, 2 males, 1 female; 18—COSTA RICA: *Limón:* El Sauce Peralta, Pandora, 1 male, 1 female; 19—COSTA RICA: *San Jose:* Monte Redondo, 1 male; 20—COSTA RICA: *Puntarenas:* Palmar, 1 female; 21—PANAMÁ: *Bocas del Toro:* vicinity of Almirante, 5 males, 6 females; 22—PANAMÁ: *Chiriquí:* Cerro Punta and Volcán, 1 male, 2 females; 23—PANAMÁ: *Chiriquí:* Boquerón, Río Corutu, 3 males, 1 female; 24—PANAMÁ: *Canal Zone,* and *Panamá:* Agua Clara, Cerro Azul, Chagres Valley, junction of Río Bayano and Río Cañito, La Zumbadora, 9 males, 10 females; 25—PANAMÁ: *Darién:* Río Chicao, Río Paya, Río Platanal, Mt. Pirri, Tacarcuna, Tapalisa, 7 males, 5 females. Samples 1-7 represented group 1, samples 8-24 represented group 2, and sample 25 represented group 3.

The test supported the hypothesis. As can be seen in Table 4 for males and Table 5 for females, statistically significant differences among the three groups were found for all but one measurement, again, interestingly, that of postorbital breadth in females, which has been mentioned above as an age-dependent character maturing more slowly in that sex.

For males, the results of the test were very clear. In all but two measurements (breadth of braincase and breadth of rostrum), the three groups were separated into three maximally non-significant subsets in order of decreasing size, and from north to south in geographic origin, as predicted. The females, as expected, did not display such a clear pattern. As in males, groups one and two were linked for breadth of braincase and breadth of rostrum, and additionally, for least interorbital breadth. Maxillary tooth-row showed groups two and three to be linked. In no case were the subsets listed in any other order than from north to south. Had the results of the test shown overlap among the three subsets for most measurements for both sexes, or had the three groups been listed in any other order, different conclusions would have been reached. How-

TABLE 4.—Results of Analysis of Variance run on eight cranial measurements from three samples of male specimens of *Potos flavus*.

Meas.	Loc.	*N*	Mean	Range	CV	LSS	MS	F
CB	1	19	89.5	85.5-95.1	2.88	I		
	2	32	85.3	80.0-91.7	3.33	I	178.33	25.31^{***}
	3	6	81.5	79.1-82.8	1.76	I		
ZB	1	21	64.9	61.8-68.7	3.02	I		
	2	32	62.1	57.1-69.3	4.42	I	169.68	29.43^{***}
	3	6	56.5	54.4-58.6	2.88	I		
LB	1	21	21.6	19.4-24.8	6.36	I		
	2	33	20.8	18.5-22.9	5.27	I	21.47	15.22^{***}
	3	7	18.8	17.7-20.4	5.17	I		
PB	1	21	22.1	18.8-27.0	7.83	I		
	2	32	20.6	17.5-24.6	7.80	I	33.38	11.58^{***}
	3	7	18.7	15.8-21.5	10.87	I		
BB	1	22	41.1	39.5-43.1	2.43	I		
	2	31	40.6	37.8-43.1	3.25	I	12.80	8.27^{**}
	3	7	38.7	36.5-41.4	4.08	I		
MB	1	22	47.9	44.2-52.1	4.39	I		
	2	31	45.8	42.3-49.9	4.30	I	32.75	16.71^{***}
	3	7	43.2	41.0-45.7	3.77	I		
MX	1	22	27.0	24.9-28.7	3.36	I		
	2	33	25.2	22.4-26.9	3.94	I	66.14	38.06^{***}
	3	7	24.0	23.2-24.8	2.28	I		
BR	1	21	23.9	22.7-25.7	4.01	I		
	2	32	23.3	21.1-25.2	4.46	I	9.90	9.96^{***}
	3	7	22.0	20.2-22.9	4.08	I		

$^{***}=P\leqq0.001$; $^{**}=P\leqq0.01$; $^{*}=P\leqq0.05$.

ever, I believe that sufficient significant differences are shown to justify recognition of these three groups taxonomically. The problem of the subspecies is, of course, still being discussed by many systematists, but I believe the concept is useful when used judiciously. It is a valid concept according to the International Code of Zoological Nomenclature, and as Mayr (1969:43) states, "sensible use of the category subspecies is still a convenient device for classifying population samples in geographically variable species." The subspecies category provides a practical method of place assignment in large collections, and is a generally useful shorthand for reference to certain specimens. It provides also, when carefully used, information for ecologists in their search for the reasons for variation, as well as possible clues for geneticists with regard to problems concerning genetic drift and other mechanisms.

Allocation of particular specimens to the three groups are found in the following taxonomic accounts, together with appropriate synonymies, descriptions, and measurements. Localities from which specimens were examined are plotted on the distribution map (Fig. 11).

TABLE 5.—Results of Analysis of Variance run on eight cranial measurements from three samples of female specimens of *Potos flavus*.

Meas.	Loc.	*N*	Mean	Range	CV	LSS	MS	F
CB	1	8	86.8	81.0-91.6	4.44	I		
	2	32	83.9	80.2-88.5	3.01	I	60.64	7.81*
	3	5	80.6	76.8-83.4	3.08	I		
ZB	1	10	65.6	58.7-65.9	3.50	I		
	2	36	60.6	56.8-66.2	3.60	I	97.02	20.85***
	3	5	55.0	52.9-57.3	3.37	I		
LB	1	10	20.4	18.1-21.7	5.54	I		
	2	37	20.3	17.8-22.8	5.18	I	5.91	5.17**
	3	5	18.7	17.7-20.3	5.71	I		
PB	1	10	20.2	17.1-22.2	8.78			
	2	37	20.6	16.7-24.9	9.30		0.57	0.17 n.s.
	3	5	20.3	19.1-22.5	6.43			
BB	1	10	40.2	38.7-41.6	2.30	I		
	2	37	39.6	37.1-43.1	3.40	I	14.48	9.53***
	3	5	37.3	36.7-38.2	1.64	I		
MB	1	10	48.0	44.8-49.7	3.48	I		
	2	38	45.3	41.2-48.8	3.99	I	46.48	15.57***
	3	4	42.7	42.3-43.2	0.88	I		
MX	1	10	26.3	24.6-28.5	4.23	I		
	2	38	24.8	23.0-27.8	4.00	I	11.84	11.22***
	3	5	23.9	22.9-25.0	3.26	I		
BR	1	10	23.3	22.1-24.7	3.87	I		
	2	37	22.6	20.1-24.0	4.23	I	12.16	14.15***
	3	5	20.6	19.8-21.4	3.26	I		

***=P≦0.001; **=P≦0.01; *=P≦0.05.

SYNOPSIS OF SUBSPECIES

Potos flavus prehensilis (Kerr)

Viverra prehensilis Kerr, 1792, Anim. Kingd., Class I, Mammalia, p. 169.

Potos flavus prehensilis, Hershkovitz, 1959, Jour. Mamm., 40:341, August 20, type locality restricted to Atoyac, Veracruz.

Potos flavus aztecus Thomas, 1902, Ann. Mag. Nat. Hist., (7) 9:266, April, holotype from Atoyac, Veracruz.

Potos flavus guerrerensis Goldman, 1915, Proc. Biol. Soc. Washington, 28:133, June 29, type from near Ometepec, Guerrero.

Holotype.—Unknown.

Distribution.—From southern Tamaulipas and San Luis Potosí in eastern México, southward through Veracruz and Oaxaca, thence westward through Guerrero, and possibly to Michoacán (Thomas, 1902:268).

Diagnosis.—A large kinkajou, generally pale in color (average near Ridgway's (1912) Clay); larger and paler than any other Middle American subspecies.

External measurements.—Males, followed by females (mean (range)±1 SE (N)): total length, 1019.4 (885-1330)±24.1 (17), 973.6 (939-1046)±9.48 (11); length of tail, 506.8 (434-570)±9.86

(16), 481.9 (392-533)±12.78 (11); hind foot, 109.4 (98-127)±1.83 (17), 103.9 (95-114)±1.56 (11); ear, 42.7 (36-55)±1.48 (12), 41.9 (36-48)±1.35 (9). Selected cranial measurements, males, females (mean (range)±2 SE (N)): condylobasal length, 89.5 (85.5-95.1)±1.18 (19), 86.8 (81.0-91.6)±2.72 (8); zygomatic breadth, 64.9 (61.8-68.7)±0.85 (21), 62.6 (58.7-65.9)±1.39 (10); length of maxillary tooth-row, 27.0 (24.9-28.7)±0.39 (22), 26.3 (24.6-28.5)±0.70 (10) (Kortlucke, 1972, Table 10).

Remarks.—The northernmost record of occurrence of the kinkajou is Leopold's (1959:437) report of an animal sighted near Acuña, Tamaulipas. The northernmost known specimens are from near Xilitla, San Luis Potosí (Dalquest, 1950:12; 1953:181). On the west coast, specimens are available from Guerrero, and Thomas (1902:268) mentioned specimens from "Michoacan (Mexican Museum)." Goldman distinguished *guerrerensis* from *aztecus* on the basis of several cranial characters, although he stated that the two were similar in size and color. Certain of the characters he used—for example, the degree of inflation of the auditory bullae—were not measured for this study because adequate craniometric techniques were not available. Also there appeared to be considerable variation in such characters within populations. Another character used by Goldman, the degree of narrowness and ridging of the basioccipital, is age-dependent. Among measurements collected for this study, there is complete overlap between those for specimens from Guerrero and those for specimens from Oaxaca and Veracruz.

Potos flavus chiriquensis J. A. Allen

Potos flavus chiriquensis J. A. Allen, 1904, Bull. Amer. Mus. Nat. Hist., 20:72, February 29, holotype from Boquerón, Chiriquí, Panamá.

Potos flavus campechensis Nelson and Goldman, 1931, Jour. Washington Acad. Sci., 21:482, November 19, holotype from La Tuxpeña, Champotón, Campeche.

Potos flavus arborensis Goodwin, 1938, Amer. Mus. Novit., 987:1, May 13, holotype from El Sauce Peralta (about 1000 ft), a farm on the Atlantic railroad less than half way from San José to Limón, Costa Rica.

Potos flavus dugesii Villa-R., 1944, Anal. Inst. Biol. Univ. Nac. México, 15:323, holotype from La Esperanza coffee plantation, 45 km NW Huixtla, 760 m, Chiapas.

Potos flavus boothi Goodwin, 1957, Amer. Mus. Novit., 1830:1, May 3, holotype from Pueblo Neuvo Solistahuacán, about 60 mi N Tuxtla Gutierrez, *ca.* 7000 ft, Chiapas.

Holotype.—AMNH 18926, adult male, collected by J. H. Batty on October 22, 1901. External measurements (from skin label): head and body, 485; tail, 505; hind foot, 80; ear, 42.5. Cranial measurements: condylobasal length, 84.8; zygomatic breadth, 59.0; least interorbital breadth, 21.3; postorbital breadth, 24.6; breadth of braincase, 41.4; mastoid breadth, 43.4; length of maxillary tooth-row, 25.5; breadth of rostrum, 23.6.

Distribution.—From the Yucatan Peninsula southward, including Tabasco, Campeche, and Chiapas, through Middle America to central Panamá, east to, but not including, Darién.

Diagnosis.—A medium-sized kinkajou smaller in size and generally darker in color than *prehensilis,* but larger than and, at least north of Costa Rica, generally paler than specimens from Darién.

External measurements.—Males, followed by females (mean (range)±1 SE (N)): total length, 960.9 (890-1100)±18.29 (12), 932.2 (845-1051)±11.92 (20); tail, 473.8 (420-505)±8.30 (12), 463.2 (408-513)±7.08 (17); hind foot, 93.8 (80-106)±2.99 (12), 98.7 (85-140)±2.85 (19); ear, 39.1 (37-42)±0.86 (seven), 39.8 (35-45)±0.58 (18). Selected cranial measurements, males, females (mean (range)±2 SE (N)): condylobasal length, 85.3 (80.0-91.7) ±1.00 (32), 83.9 (80.2-88.5)±0.89 (32); zygomatic breadth, 62.1 (57.1-69.3)±0.97 (32), 60.6 (56.8-66.2)±0.73 (36); length of maxillary tooth-row, 25.2 (22.4-26.9)±0.35 (33), 24.8 (23.0-27.8)± 0.32 (38) (Kortlucke, 1972, Table 10).

Remarks.—Three of the names placed in synonymy here (*arborensis, boothi, dugesii*) are based at least in part on a characteristic that is age-dependent—that is, postorbital breadth greater than interorbital breadth. Without a series of specimens of different ages this is not apparent. Descriptions of *chiriquensis* and *arborensis* were based in part on molar breadth, a character shown by Lönnberg (1921:26-27) to be taxonomically untrustworthy. Presence or absence of a dorsal streak was used in describing *chiriquensis, campechensis,* and *dugesii,* although Goodwin consistently (for example, 1938 and 1946) stated that this streak is a highly variable character. Such characters as degree of depression of palate, degree of inflation of bullae and frontals, and length and shape of postorbital processes require more exact craniometric techniques to determine their worth than are presently available. Nelson and Goldman described *campechensis* as medium-sized, but the skull of the type specimen, a female, has large measurements in comparison even with *prehensilis* (condylobasal length, 88.2; zygomatic breadth, 60.8; interorbital breadth, 20.0; postorbital breadth, 18.2; breadth of braincase, 37.8; mastoid breadth, 47.2; length of maxillary tooth-row, 25.8). This specimen is certainly fully adult, as can be seen from the relationship between interorbital and postorbital breadths.

Potos flavus megalotus (Martin)

Cercoleptes megalotus Martin, 1836, Proc. Zool. Soc. London, p. 82, September 13, holotype from unknown locality; type locality here designated as Santa Marta, Colombia.

Potos flavus megalotus, Thomas, 1902, Ann. Mag. Nat. Hist., (7) 9:266, April.

Viverra caudivolvula Cuvier, 1839, Règn. Animal, 3rd ed., 1, plate 2, fig. 1 (not Schreber, 1777) [citation *in* Cabrera, 1958:251].

Potos flavus caucensis J. A. Allen, 1904, Bull. Amer. Mus. Nat. Hist., 20:75, February 29, holotype from Castilla Mts., upper Cauca region, 6000 ft, Colombia.

Potos flavus brachyotus Trouessart, 1910, Arc. Mérid. Equat., 9, part 1, A6, plate 1 (not Martin, 1836) [citation *in* Cabrera, 1958: 251].

Potos flavus isthmicus Goldman, 1913, Smiths. Misc. Coll., 60(22):14, February 28, holotype from near head of Río Limón, Mt. Pirri, 5200 ft, eastern Panamá.

Potos flavus tolimensis J. A. Allen, 1913, Bull. Amer. Mus. Nat. Hist., 32:481, September 25, holotype from Giradot, about 1500 ft, Magdalena Valley, Tolima, Colombia.

Potos flavus mansuetus Thomas, 1914, Ann. Mag. Nat. Hist., (8) 13:362, March, holotype from S. Domingo, W of Quito, 1760 ft, Ecuador.

Potos flavus modestus Lönnberg, 1921, Ark. Zool., 14(4):24, August 16 (not Thomas, 1902, which is restricted by Cabrera, 1958:251, to mountains of western Ecuador).

Holotype.—Specimen belonging to the Zoological Society of London, presented by George Vaughan, Esq., from unknown locality, here designated as Santa Marta, Colombia.

Distribution.—From Darién, Panamá, southeastward into South America where the distribution includes northern Colombia and the whole Andean zone to northern Ecuador (after Cabrera, 1958: 251).

Diagnosis.—Smaller in size and darker in color than any other North American kinkajou.

Measurements.—Males, followed by females (mean (range) ± 1 SE (N)): total length, 911.5 (903-920) ± 8.50 (two), 881.2 (820-931) ± 24.82 (five); tail, 476.0 (470-482) ± 6.0 (two), 446.0 (405-480) ± 14.78 (five); hind foot, 100.5 (98-103) ± 2.50 (two), 90.5 (86-95) ± 1.84 (four). Selected cranial measurements, males, females (mean (range) ± 2 SE (N)): condylobasal length, 81.5 (79.1-82.8) ± 1.17 (six), 80.6 (76.8-83.4) ± 2.22 (five); zygomatic breadth, 56.5 (54.4-58.6) ± 1.33 (six), 55.0 (52.9-57.3) ± 1.66 (five); length of maxillary tooth-row, 24.0 (23.2-24.8) ± 0.41 (seven), 24.0 (22.9-25.0) ± 0.70 (five) (Kortlucke, 1972, Table 10).

Remarks.—Because I have not examined specimens of the species from South America, I have followed the arrangement of Cabrera (1958:251) with regard to distribution and synonymy.

Thomas (1902:267-268), in rehabilitating Martin's name, alleged that *C. megalotus* agreed closely in color with Colombian animals (from Medellin, Colombia) and that specimens from Costa Rica, and from Valdivia and Santa Marta, Colombia, could not be distinguished from it. J. A. Allen (1904:74) restricted the name *megalotus* to specimens from eastern Colombia, stating that his specimens from Santa Marta agreed far better with the type or description of *C. megalotus* than did specimens from Chiriquí. He also stated that he would have preferred to discard the name *megalotus* as unidentifiable, but that Thomas had rehabilitated it, and, under the first-reviser principle, the name may be retained for a portion of the alleged range.

Had I followed the taxonomic arrangement of Handley (1966: 789), it would have been necessary to remove the name *isthmicus* from the synonymy of *megalotus* and reinstate it as a valid name. I believe, however, that since Cabrera was dealing with a larger area than was Handley, and probably examined specimens from eastern Panamá before placing the name *isthmicus* in synonymy with *megalotus,* that the more judicious course of action is to retain Cabrera's taxonomic arrangement, at least for the present.

SUMMARY

Examination of 295 specimens shows the kinkajou, *Potos flavus,* to be highly variable individually. Investigation of generic and specific names validates *Potos flavus* as correct in accordance with the International Code of Zoological Nomenclature. A review of the names applied to North American populations shows the eight in current use to give a distorted picture of geographic variation, because these names were based on extremely small samples and highly variable characters, including some that are age-dependent. Nongeographic variation was first examined in order to eliminate it from the further analysis of geographic variation. Age-related size variation is sufficient that specimens must be sorted into age categories for any adequate analysis to follow. Analysis of secondary sexual variation yielded similar results, so males and females were separated for further analysis. Histograms of color were made for each sample locality, with color code plotted against number of specimens and month of capture; these demonstrated wide variation in color at any given locality for any time of year, and no seasonal trends were evident. There was a trend from paler color in the north to darker color in the south. Bacular morphology was described and measurements given.

Geographic variation was examined by both the UNIVAR program, which performs a single-classification Analysis of Variance, in which, if statistically significant differences are found among groups, the Sums of Squares Simultaneous Test Procedure is implemented, and by the NT-SYS Version 2.

The results of these tests show consistent trends in geographic variation, even under the handicaps of small sample sizes and great individual variation. After determining that the basic trend in size from larger in the north to smaller in the south did in fact exist, an *a priori* experimental test run on three groups of specimens, from the northern, central, and southern parts of the range, confirmed the hypothesis that highly significant differences were present among these groups. These results are interpreted as justifying the recognition of three subspecies, which are *Potos flavus chiriquensis* J. A. Allen, *Potos flavus megalotus* (Martin), and *Potos flavus prehensilis* (Kerr).

RESUMEN

Al examinar 295 espécimenes de kinkajous, *Potos flavus,* se encontró que eran individualmente muy variables. La investigación del nombre genérico y específico dió como válido y correcto el nombre de *Potos flavus,* que esta de acuerdo con el código internacional de nomenclatura zoológica. Se hizo una revisión de los nombres dados a las poblaciones de Norte América, monstrando una idea distorsionada de le variación geográfica con los nombres que se usan actualmente, debido a que se han basado en muestras extremadamente pequeñas y con características muy variables, incluyendo algunas que son dependientes de la edad. En primer lugar se examinó la variación no-geográfica con el fin de eliminarla en posteriores análisis de variación geográfica. Para llevar a cabo cualquier análisis adecuado de clasificación por edades, basta relacionar la variación del tamaño de los espécimenes con la edad. El análisis de variación sexual secundaria dió resultados similares, de tal manera que para análisis posteriores se separaron en machos y hembras. Con las muestras de cada localidad se hicieron histogramas del color, poniendo códigos para cada color analizándose contra el numero de espécimenes y el mes de captura; esto demostró una amplia variación del color en una dada localidad, en cualquier época del año, sin ninguna tendencia estacional evidente. Hubo una tendencia a encontrar colores pálidos en el norte y oscuros en el sur. Se dieron medidas y se describió la morfología bacular.

La variación geográfica se examinó por dos métodos: usando el programa UNIVAR, el cual ejecuta un análisis de varianza sencillo, si se encuentra diferencia estadística entre los grupos se emplea el procedimiento de la suma de quadrados simultaneos (SS-STP); y el programa de NT-SYS Versión 2. Hay una separación general de las poblaciones en cada una de los grandes intervalos fisiográficos el Istmo de Tehuantepec y el Istmo de Panamá. Las tres poblaciones asi delimitadas fueron ensayadas *a priori* aún mas por análisis de varianza, el resultado confirmó la hipótesis de que había diferencias altamente significativas entre los groupos. Estos resultados son interpretados como reconocimiento justificado de tres subespecies, las cuales son: *Potos flavus chiriquensis* J. A. Allen, *Potos flavus megalotus* (Martin), y *Potos flavus prehensilis* (Kerr).

SPECIMENS EXAMINED

Potos flavus prehensilis

MÉXICO: *Guerrero:* Acapulco, 2 (USNM); near Ometepec, 3 (USNM, one the type of *guerrerensis*); 1 mi SW Omilteme, 1 (USNM); Papayo, 1 (USNM). *Oaxaca:* 3 mi N El Jicaro, 1 (AMNH); La Concepción, 1 (AMNH); 20 mi NE La Ventosa, 7 (AMNH); Limón, 1 (AMNH); 3 mi S Río Jaltepec, Oaxaca-Veracruz border, 4 (AMNH); Santiago Guevéa, 1 (AMNH); Santiago Lachiguiri, 1 (AMNH); Santo Domingo, 2 (USNM); Tapanatepec, 2 (AMNH); 2 mi S Tollocito [=Tollosa], 3 (KU); Tres Cruces, 1 (AMNH); Vista Hermosa, 1 (KU). *Veracruz:* Arroyo Saoso, 7 km S, 37 km E Jesús Carranza, 3 (KU); Coatzocoalcos region, 4 (KU); Coyame, 7 mi E Catemaco, 1 (AMNH); 20 km E Jesús Carranza, 300 ft, 7 (KU); 55 km ESE Jesús Carranza, 450 ft, 1 (KU); 25 km SE Jesús Carranza, 250 ft, 7 (KU); 35 km SE Jesús Carranza, 1 (KU); 38 km SE Jesús Carranza, 500 ft, 1 (KU); 30 km SSE Jesús Carranza, 300 ft, 1 (KU); Lake Catemaco, 2 (AMNH); 3 km N Presidio, 1 (KU); Río Blanco, 20 km WNW Piedras Negras, 1 (KU); 75 mi S Rivera, 2 (USNM); 13 mi N San Andrés, 1 (AMNH); 3 km E San Andrés Tuxtla, 1 (KU); 7 km SE San Juan de la Punta, 400 ft, 1 (KU); 12.5 mi N Tihuatlán, 300 ft, 2 (KU).

Additional records.—Guerrero (Davis and Lukens, 1958:355): Acahuizotla, 2800 ft; 3 km E Acahuizotla, 2500 ft; Acapulco, Agua del Obispo, 3200 ft; Ometepec, 1000 ft; Papayo, 200 ft. *México:* Cuidad de México (Gaumer, 1917:219). *San Luis Potosí* (Dalquest, 1953:181): 9 km NNE Xilitla; above Xilitla at Cerro San Antonio. *Tamaulipas* (Leopold, 1959:437, Alvarez, 1963:458): near Acuña.

Potos flavus chiriquensis

COSTA RICA: *Cartago:* El Sauce Peralta, *ca.* 1000 ft, 1 (USNM, holotype of *arborensis*). *Limón:* Olivia, 1 (USNM); Pandora, 2 (USNM); Talamanca, 1 (USNM). *Puntarenas:* Palmar, 3 (AMNH). *San José:* Jabillo Pirrís, 1 (USNM); Monte Redondo, 1 (USNM); San Antonio, 1 (USNM); San Geronimo Pirrís, 1 (USNM); San José, 2 (USNM). *No locality:* 5, (USNM).

GUATEMALA: *Petén:* Laguna de Petenxil, 5 mi E Flores, 2 (AMNH); road to Río San Roman, NW Chinajá, 1 (KU); no specific locality, 1 (USNM). *Santa Rosa:* Astillero, 25 ft, 1 (KU). *No province:* Finca Salache, 1 (AMNH). *No locality:* 2 (USNM).

HONDURAS: *Santa Barbara:* La Mica, 1 (AMNH); Santa Barbara, 3 (AMNH). *Tegucigalpa:* El Caliche Cedros, 1 (AMNH).

MÉXICO: *Campeche:* Dzibalchén, 1 (KU); 7 km N, 51 km E Escárcega, 3 (KU); La Tuxpeña, 1 (USNM, holotype of *campechensis*). *Chiapas:* Gineta Mts., 2 (USNM); Pueblo Nuevo Solistahuacán, about 60 mi N Tuxtla Gutierrez, 7000 ft, 1 (AMNH, type of *boothi*); Zapaluta, 2 (KU). *Tabasco:* Las Minas, 1 (USNM); Macuspana region, 1 (KU); 5 mi SW Teapa, 1 (KU). *Yucatán:* 8 km N, 10 km W Tizimín, 2 (KU).

NICARAGUA: *Boaco:* Santa Rosa, 17 km N, 15 km E Boaco, 300 m, 2 (KU). *Carazo:* 3 km N, 4 km W Diriamba, 600 m, 1 (KU). *Estelí:* 8 mi S Condega, 1 (KU). *Granada:* Finca Santa Cecilia, 6.5 km SE Guanacaste, 660 m, 1 (KU); La Calera, 1 (USNM). *Jinotega:* Hda. La Trampa, 5.5 km N, 16 km E Jinotega, 1 (USNM); Peña Blanca, 2 (AMNH). *Managua:* 10 mi SW Managua, 1 (KU). *Matagalpa:* 1 km NE Esquipulas, 420 m, 2 (KU); Hacienda Tepeyac, 1 (KU); Matagalpa, 4 (AMNH); vicinity of Matagalpa, 1 (KU); Río Tuma, 1 (AMNH); Tepeyac, 2 (USNM); Tuma, 2 (AMNH); Uluce, 2 (AMNH). *Nueva Segovia:* Ocotal, 2 (AMNH). *Rivas:* 11 km S, 3 km E Rivas, 50 m, 1 (KU). *Zelaya:* Bonanza, 850 ft, 2 (KU); Cara de Mono, 50 m, 2 (KU); El Recreo, 25 m, 13 (KU); Kukallaya [=Cuculaya] River, 1 (USNM). *No locality:* 1 (AMNH).

PANAMÁ: *Bocas del Toro:* Almirante, 14 (USNM); Boca del Drago, 2 (USNM); 7 km SSW Changuinola, 3 (USNM); Río Changuinola, 3 (USNM); Río Teribe, 1 (USNM); Sibube, 2 (USNM); no specific locality, 1 (USNM). *Canal Zone:* Barro Colorado Island, 4 (USNM); Chagres Valley, 2 (USNM); Gatun, 11 (USNM); Paraiso, 1 (USNM); Río Indio, near Gatun, 4 (USNM). *Chiriquí:* Boquerón, 5 (AMNH); Casa Lewis, Cerro Punta, 1 (USNM); Casa Tilley, Cerro Punta, 1 (USNM); Cerro Punta, 1 (USNM); El Volcán, 2 (AMNH, USNM); Progreso, 4 (USNM); Río Corutu, 2 (USNM);

Río Corutu, between Puerto Armuelles and Costa Rican boundary, 3 (USNM). *Herrera:* "Herrera Province, Canal Zone," 1 (USNM). *Los Santos:* Guanico Arriba, 1 (USNM). *Panamá:* near Agua Clara, 2 (USNM); Cerro Azul, 6 (USNM); Cerro La Campaña, S slope, 800 m, 1 (KU); La Zumbadora, 2 (USNM); junction of Río Bayano and Río Cañito, 3 (USNM). *San Blas:* Mandinga, 1 (USNM); no specific locality, 4 (USNM).

Additional records.—BRITISH HONDURAS (Hershkovitz, 1951:561): *Belice:* Kate's Lagoon. *Stann Creek:* Bokowina; Dog Creek; Double Falls; Silkgrass. COSTA RICA (Goodwin, 1957:429): *Cartago:* El Copey de Dota; El Muñeco. *San José:* Alto Jabillo Pirrís. EL SALVADOR (Burt and Stirton, 1961:44): *Ahuachapan:* Barro de Santiago. *La Libertad:* Zapotitan. *Morazan:* Mt. Cacaguatique. *San Miguel:* Río San Miguel; Volcán de San Miguel. *Santa Ana:* Volcán de Santa Ana. *Usulutan:* Puerto del Triunfo. *No province:* Cerro de los Naranjos; Colinas de Jucuaran; Hda. Los Planes; Hda. San Antonio; Km 80 between San Salvador and San Miguel. MÉXICO: *Campeche:* Xcanja (Gaumer, 1917:219). *Chiapas* (Villa-R., 1949:503): 1 mi S Finca Prusia, 1160 m; Paval, 480 m. *Panamá:* Bogava (Goldman, 1920:160).

Potos flavus megalotus

PANAMÁ: *Darién:* Cana, 1800 ft, 4 (USNM); Cerro Malí, 3 (USNM); Cerro Malí, 4700 ft, 2 (USNM); Cerro Tacarcuna, 4100 ft, 4 (USNM); El Real, 1 (USNM); Jaque, 3 (USNM); La Laguna, 3 (USNM); Mt. Pirre, near head Río Limón, 5200 ft, 2 (USNM, one the type of *isthmicus*); middle Río Chicao, Río Jaque, 1 (USNM); Río Chucunaque, 1 (USNM); headwaters Río del Medio and Río Patos, 1 (USNM); Río Jaque, 1 (USNM); mouth of Río Paya, 4 (USNM); Río Platanal, 3 (USNM); Tacarcuna, 4 (AMNH); Tacarcuna, Casita Camp, 2700 ft, 2 (USNM); Tacarcuna, Laguna Camp, 4000 ft, 1 (USNM); Tacarcuna Village Camp, 3200 ft, 1 (USNM); Tapalisa, 400 ft, 3 (AMNH).

LITERATURE CITED

Allen, J. A.

1904. Mammals from southern México and Central and South America. Bull. Amer. Mus. Nat. Hist., 20:29-80.

1910. Additional mammals from Nicaragua. *Ibid.,* 28:87-115.

1913. New mammals from Colombia and Ecuador. Bull. Amer. Mus. Nat. Hist., 32:469-484.

Alvarez, T.

1963. The Recent mammals of Tamaulipas, México. Univ. Kansas Publ., Mus. Nat. Hist., 14:363-473.

Burt, W. H., and Stirton, R. A.

1961. The mammals of El Salvador. Misc. Publ. Mus. Zool., Univ. Michigan, 117:1-69.

Cabrera, A.

1958. Catalogo de los mamíferos de America del Sur. Rev. Mus. Argentino Cienc. Nat., 4:iv+307 pp.

Dalquest, W. W.

1950. Records of mammals from the Mexican state of San Luis Potosí. Occas. Papers Mus. Zool., Louisiana State Univ., 23:1-15.

1953. Mammals of the Mexican state of San Luis Potosí. Louisiana State Univ. Studies, Biol. Ser., 1:1-229.

Davis, W. B., and Lukens, P. W., Jr.

1958. Mammals of the Mexican State of Guerrero, exclusive of Chiroptera and Rodentia. Jour. Mamm., 39:347-367.

GAUMER, G. F.
1917. Monografia de los mamíferos de Yucatán. Dept. de Talleres Graficos de la Secretaria de Fomento, México, xii+332 pp.
GOLDMAN, E. A.
1913. Descriptions of new mammals from Panama and Mexico. Smiths. Misc. Coll., 60:1-20.
1915. Five new mammals from Mexico and Arizona. Proc. Biol. Soc. Washington, 28:133-138.
1920. Mammals of Panama. Smiths. Misc. Coll., 69:1-309.
GOODWIN, G. G.
1938. Four new mammals from Costa Rica. Amer. Mus. Novit., 987:1-5.
1942. Mammals of Honduras. Bull. Amer. Mus. Nat. Hist., 79:107-195.
1946. Mammals of Costa Rica, *Ibid.,* 87:271-473.
1957. A new kinkajou from México and a new hooded skunk from Central America. Amer. Mus. Novit., 1830:1-4.
HALL, E. R., and KELSON, K. R.
1959. The mammals of North America. The Ronald Press, New York, 2, viii+547-1083+79 pp.
HANDLEY, C. O., JR.
1966. Checklist of the mammals of Panama, pp. 753-795 *in* Wenzel, R. L., and Tipton, V. J., eds. Ectoparasites of Panama, Field Mus. Nat. Hist., Chicago, xii+861 pp.
HERSHKOVITZ, P.
1951. Mammals from British Honduras, Mexico, Jamaica and Haiti. Fieldiana Zool., Chicago Nat. Hist. Mus., 31:547-569.
1959. Nomenclature and taxonomy of the netropical mammals described by Olfers, 1818. Jour. Mamm., 40:337-353.

KERR, R.
1792. The Animal Kingdom. . . , Edinburgh, xii+644 pp.

KORTLUCKE, S. M.
1972. Morphological variation in the kinkajou, *Potos flavus* (Mammalia: Procyonidae), in México and Middle America. Unpubl. thesis, The University of Kansas, Lawrence, pp. 1-42.

LEOPOLD, A. S.
1959. Wildlife of Mexico. The game birds and mammals. Univ. California Press, xiii+568 pp.

LINNAEUS, C.
1758. Systema Naturae. . . , Upsala, 1-823.

LÖNNBERG, E.
1921. A second contribution to the mammalogy of Ecuador with some remarks on Caenolestes. Ark. Zool., 14(4):24-28.

MARTIN, R.
1836. [Remarks at meeting of Zoological Society of London]. Proc. Zool. Soc. London, 81-83.

MAYR, E.
1969. Principles of Systematic Zoology. McGraw-Hill, New York, xi+428 pp.

NELSON, E. W., and GOLDMAN, E. A.
1931. A new kinkajou from Mexico. Jour. Washington Acad. Sci., 21: 482-483.

PENNANT, T.
1771. Synopsis of Quadrupeds. Chester, xxvi+382 pp.

POCOCK, R. I.
1921. The external characters and classification of the Procyonidae. Proc. Zool. Soc. London, 389-446.

RIDGWAY, R.
1912. Color standards and color nomenclature. Washington, D.C., privately printed, iv+44 pp.
SCHREBER, J. C. D.
1774. Die Säugthiere in Abbildungen nach der Natur, mit Beschreibungen. Erster Theil, Erlangen, 1-190.
1778. Die Säugthiere. . . , Dritter Theil, Erlangen, 283-590.
1840. Die Säugthiere. . . , Supplementband. Erlangen, plates.
SHERBORNE, C. D.
1891. On the dates of the parts, plates, and text of Schreber's 'Säugthiere.' Proc. Zool. Soc. London, pp. 587-592.
SMITH, J. D.
1972. Systematics of the chiropteran family Mormoopidae. Univ. Kansas Mus. Nat. Hist., Misc. Publ., 56:1-132.
THOMAS, O.
1902. On the geographical races of the kinkajou. Ann. Mag. Nat. Hist., (7) 9:266-270.
1914. On various South-American mammals. *Ibid.,* (8) 13:345-363.
VILLA-R., B.
1944. Dos nuevos mamíferos de Chiapas. Anal. Inst. Biol. Univ. Nac. México, 15:319-329.
1949. Mamíferos de Soconusco, Chiapas. *Ibid.,* 19:485-528.
VOSMAER, A.
1804. Article 9 and plate IX *in* Naturkundige beschryving eener uitmundende versameling van geldsame gedierten bestaande in Oost- en Westindische. . . , J. B. Elwe, Te Amsterdam.

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POPULATION STRUCTURE AND SURVIVORSHIP IN SOME COSTA RICAN LIZARDS

By

HENRY S. FITCH[1]

Interest in tropical communities and insight into their functioning have developed at an accelerating pace in recent years. Lizards often are present in great variety and in high population numbers; thus they can be sampled readily, and provide excellent material for demographic studies potentially significant to a knowledge of community ecology. However, there have been few studies of tropical lizard populations, especially in the Neotropical Region. The present study of tropical lizard populations was undertaken in 1965. By obtaining information on the life histories and demography of a substantial number of diverse species of tropical lizards within a limited geographic area, I was able to compare these data with similar data available for the Temperate Zone. Because several of the species included have close relatives in temperate climates, it was anticipated that comparative study of life history and demography would elucidate evolutionary trends in tropical and temperate environments.

A number of studies has been made of the reproduction and population biology of Old World tropical lizards (mainly agamids, geckos and skinks). Among these are studies in central and west Africa (Marshall and Hook, 1960; Harris, 1964), India (Asana, 1931; Pandha and Thapliyal, 1967; Sanyal and Prasad, 1967), Borneo (Inger and Greenberg, 1966), the Philippines (Alcala and Brown, 1967), the New Hebrides (Baker, 1947) and Australia (Wilhoft, 1963; Wilhoft and Reiter, 1965; Bustard, 1968, 1969; Pianka, 1971). There have been few comparable studies of Neotropical lizards. Those of Hirth (1963) on *Ameiva quadrilineata*

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[1] University of Kansas Natural History Reservation, Lawrence, Kansas 66045.

and *Basiliscus vittatus* and Sexton *et al.* (1963, 1971) on *Anolis limifrons* are notable.

Some outstanding population studies of lizards in the United States are those of Blair (1960) on *Sceloporus olivaceus,* Tinkle (1967) on *Uta stansburiana* and Kennedy (in press) on *Sceloporus undulatus.* Many other studies, though less intensive or prolonged, have revealed some population parameters of the species investigated. For example, it has been shown that most lizards in the southern half of the United States mature in their first year after one season of hibernation, and most produce two or more broods in each breeding season. Included in the latter group are: *Sceloporus undulatus; S. olivaceus; S. jarrovi* (Carpenter, 1960); *Uma inornata, U. notata, U. scoparia* (Mayhew, 1964a, 1964b, 1966a, 1966b); *Uta stansburiana; Crotaphytus collaris* (Fitch, 1956); *Crotaphytus wislizenii* (Turner, *et al.,* 1969); *Leiolopisma laterale* (Fitch and Greene, 1965) and *Cnemidophorus sexlineatus* (Fitch, 1958). Among species that range farther north, such as *Sceloporus occidentalis, S. graciosus,* and *Eumeces fasciatus,* maturity is delayed until the second year and one brood per season is the rule (Fitch, 1954, 1970). In a few, such as *Eumeces obsoletus* (Hall, 1971), *Ophisaurus attenuatus* (Fitch, 1970), and *Xantusia vigilis* (Miller, 1951), maturity is postponed until the third or even the fourth year and only one brood is produced per season. Consequently, one can conclude that the foregoing species and temperate zone species in general, are characterized by populations consisting of discrete annual age groups. Most lizards in temperate regions hibernate, and some spend as much as two-thirds of the year in continuous dormancy. In general, the longer the hibernation the more pronounced is the seasonal restriction of the breeding cycle; thus such events as ovulation, spermatogenesis, and copulation occur only at certain times of year, and breeding occurs in the early part of the season of activity. In the warmer parts of the temperate region, lizards such as *Uta stansburiana* and various kinds of *Sceloporus* are active intermittently even in winter; they either do not hibernate at all, or have only brief periods of incomplete dormancy. In these species, as well as those that have more complete hibernation, reproduction is controlled by the seasonality of the annual cycle. Reproduction occurs in spring and early summer, and rarely extends into late summer or autumn. The following study of Costa Rican lizards was undertaken in order to describe population parameters of tropical species and thereby facilitate comparison of these with their near relatives in the Temperate Zone. Also, I have attempted to assess the effects of relatively uniform year-round climates as contrasted with climates that are strongly seasonal.

In recent literature pertaining to tropical ecology, various predictions, rules, and models have been proposed; some are based on actual data and others on purely theoretical considerations. Both types require supporting evidence from further field studies. An attempt is made below to examine critically such proposals, including those pertaining to lizards (Tinkle, Wilbur and Tilley, 1970) and those of a more general sort—*r*-selection and *K*-selection (MacArthur and Wilson, 1967; Pianka, 1970), and "coarse-grained" vs. "fine-grained" environments—in the light of my own findings.

Methods and Materials

In February and March 1965 I collected samples of lizards at several localities in Costa Rica. In October and November 1967 I selected 14 localities for study areas in Costa Rica; several of these had been sampled in 1965, and form transects across the country from east to west and from north to south representing the main climatic types. On these areas, populations of lizards were sampled at intervals averaging approximately six weeks, from October 1967 to September 1968, with further sampling in January-March 1969, August-September 1969 and January-March 1970.

From west to east (localities 1-11) and north to south (localities 6 and 12-14) locations of the study areas, and their most important species of lizards are as follows: 1) Playas del Coco, Guanacaste Province, sea beach and thorny scrub, with open groves and a few large trees: *Sceloporus variabilis* Wiegmann, *Cnemidophorus deppii* Wiegmann, *Ctenosaura similis* (Gray). 2) Sardinal, Guanacaste Province, 90 m, gallery forest along ravine: *Anolis cupreus* Hallowell. 3) Río Higuerón at Finca Taboga, Guanacaste Province, lowland xeric riparian forest and grassland: *Basiliscus basiliscus* (Linnaeus) and *Ctenosaura similis.* 4) Río Congo at La Irma, Guanacaste Province, 100 m, riparian groves and dry pastures: *Anolis cupreus* and *Basiliscus basiliscus.* 5) Boca de Barranca, Puntarenas Province, sea beach and Marbella Hotel grounds, with many native and exotic trees: *Sceloporus variabilis, Cnemidophorus deppii, Gonatodes albogularis* (Duméril and Bibron), *Anolis cupreus* and *Ctenosaura similis.* 6) San José, San José Province, 1197 m, suburban lots with scattered trees and tall grass; fences along railway and coffee groves: *Anolis cupreus, Anolis intermedius* Peters, and *Sceloporus malachiticus* Cope. 7) Cartago, Cartago Province, 1450 to 1750 m, roadside rock outcrops; rocky and brushy pasture: *Sceloporus malachiticus.* 8) Turrialba, Instituto Interamericano de Ciéncias Agrícolas, Cartago Province, 602 m, groves and plantations: *Anolis limifrons* Cope and *Leiolopisma cherriei* (Cope). 9) Portéte, Limón Province, sea beach with coral rock and coconut grove: *Basiliscus vittatus* Wiegmann. 10) Limón, Limón Province, seaside city park with giant fig trees: *Gonatodes albogularis.* 11) Beverly, Limón Province, 15 m, banana and cacao groves: *Anolis limifrons* and *Anolis humilis* Peters. 12) San Miguel de Sarapiquí, about 500 m, Alajuela Province, subtropical rain forest along mountain stream: *Anolis humilis* and *Anolis lionotus* Cope. 13) Hacienda El Prado, 1910 m, Alajuela Province, pasture with relict trees of original cloud forest: *Anolis tropidolepis* Boulenger. 14) Quepos, Puntarenas Province, sea beach at mouth of Río Cañas, with open sand, beach wrack deposited by the river, coconut grove, and mangrove swamp: *Ameiva quadrilineata* (Hallowell) and *Ctenosaura similis.*

Most lizards captured were measured and marked with paint, and toe-clipped to facilitate individual recognition. Relatively few of the individuals recorded in a sample are represented in the next sample from the same area because population turnover due to mortality, natality, emigration and immigration is relatively rapid on all areas. Even under optimum conditions it was never possible to record all individuals present on any specific area. Findings regarding growth, temperature relationships, spatial relationships and reproductive cycles have been discussed elsewhere (Fitch, 1973).

Various methods, including trapping, noosing, and catching by hand, were utilized in obtaining lizards. However, some abundant species are too wary and elusive to be captured by any of the usual methods. In these species snout-vent length was estimated to the nearest mm in individuals seen at close range in the field. On many occasions the same lizard was first estimated and then captured and measured; these sets of records provided a basis for judging the accuracy of the estimates. Estimates were usually within 2 percent.

Some samples (*Anolis tropidolepis, A. humilis, A. limifrons, Sceloporus variabilis, Leiolopisma cherriei, Gonatodes albogularis* at Boca de Barranca) are based entirely upon actual measurements of individuals captured and handled. Other samples (*Gonatodes albogularis* at Limón, *Ameiva quadrilineata*) are based mainly on estimates, and some (*Cnemidophorus deppii, Basiliscus basiliscus, B. vittatus, Ctenosaura similis*) are based upon both sorts of data.

Histograms (Figs. 1-17) show composition by size groups of the populations sampled. Seasonal trends are strong in some and weak in others. In some instances (*Sceloporus variabilis, Anolis tropidolepis, A. intermedius*), sex could be determined readily even in hatchlings; thus sex ratio is shown for each size category in the population. In most kinds, sex is less readily discerned in the young and is shown only for the sexually mature size classes. In *Ctenosaura similis, Cnemidophorus deppii* and *Ameiva quadrilineata* sex often was not determined in the observed adults. In both species of *Basiliscus,* adult males are readily distinguished from females, but adolescent males and adult females are much alike in size and appearance; therefore sexes are not shown separately on the graph.

In the histograms, samples from February and March are composites from 1968, 1969 and 1970. Likewise, samples from August and September of 1968 and 1969 were combined. Samples from April, May, June, and July are exclusively from 1968 and samples from October and November are from 1967. In the upper left of each figure, three horizontal bars show the size range considered typical for young in their first, second and third months, respectively. These are based on the average growth rates of recaptured marked young of different sizes, but with some subjective judgments to allow for the slight stunting that occurs at first after toe-clipping, and the difficulty of distinguishing newly hatched indiviuals from those that have already made some growth. Dotted extensions of each bar represent estimates of the size range for the majority of individuals including those that exceed the most typical growth rate or fall short of it.

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RESULTS

In the present study, populations are partially analyzed by segregation into sex- and size-groups. On the basis of growth of numerous young marked and recaptured, size can be equated with age to some extent, especially in the immature lizards. Judged on the basis of its size and appearance, each individual has a fairly wide range of possible ages, but has one "most probable" age that can be calculated from the average growth rate at each stage of development.

Population structure rarely has been mentioned in published reports upon field studies of lizards. Often there are differences in behavior (that may cause differences in susceptibility to capture) between the sexes and between young and adults, so that any sample obtained is somewhat biased. Growth rates may vary widely from time to time and place to place, or between individuals, and the status of any individual in the population can be known with certainty only if it was marked as a hatchling. In the tropics there is more complexity and diversity than in the Temperate Zone where most populations of lizards have two or more size classes, sometimes discrete and sometimes widely overlapping. Size classes result from discontinuous reproduction and the fact that each population consists of a series of cohorts, ranging in age from the young (normally the most numerous and most distinct) to the old; the latter are few in number not readily distinguishable from the next younger cohort. The population structure can remain stable only in an unchanging environment where reproduction goes on continuously at a constant level.

In every population sample that I obtained, there is possibility of bias. For example, gravid females of *Cnemidophorus deppii* are noticeably slower and less elusive than adult males, and therefore are better represented in my samples. Similarly, in *Basiliscus basiliscus* old adults are much more wary than juveniles and tend to stay nearer shelter. However, successive samples from the same areas were presumably all subject to the same bias, and therefore should reflect fairly accurately the changes in population structure that occur throughout the year.

Information concerning longevity in free-living lizards is also scarce and difficult to obtain. Mark-and-recapture studies usually have not been pursued with sufficient intensity or continued for a sufficient length of time to demonstrate longevity. The 29-month span of operations on some of my study areas perhaps was inadequate to demonstrate longevity in any of the species studied, but it does permit comparison of the rates of population turnover. The rate of turnover is closely linked with survivorship; species having the longest life expectancy have relatively slow turnover. However, vagility, the degree of unnatural disturbance to which a study area is subjected, and the size of the study area all affect population turnover, and in some instances these effects are independent of mortality. A population consisting partly of transient individuals or one in which frequent changes in home range occur, would show turnover even without any mortality. In all of the species included in my study, recapture records have shown that home ranges are remarkably small, but in each kind there are occasional long movements. On small study areas such movements can affect appreciably the amount of population turnover. The "survivorship" of various species shown in figures 18 and 19 is probably somewhat reduced in each instance by movement away from the study areas, but in most instances disappearance from the study areas is believed to result from actual mortality.

The 21 local populations sampled show a remarkable diversity in their structure and stability; no two of them are alike. In some instances the same species sampled in different areas show notably altered patterns. In other instances a species sampled in areas having somewhat different climates has similar or parallel trends; in some of these (*Anolis humilis, Sceloporus malachiticus*) samples from different areas were combined to increase sample size. Different species of lizards sampled at the same times and places often differed strikingly in the structure and stability of their populations. Therefore, generalizations are difficult to make, but there are trends which are correlated with climate, with habits and habitat of the species, and with phylogenetic relationships. The populations sampled could be arranged in various ways to emphasize their similarities or differences. They form a gradient. At one extreme are species that have constant reproduction with females producing offspring frequently and acyclically. At the other extreme are species in which individuals reproduce only once in the annual cycle, and all produce at about the same time, resulting in a population of well defined and separate annual cohorts. For convenience and clarity I prefer to recognize four distinct types of populations, although these grade into each other to some extent. A type 1 population, with stable age structure is relatively uncommon and results from year-round reproduction at a constant level. A type 2 population also has year-round reproduction but with changing level in response to the seasonal weather cycle, resulting in a fluctuating age structure. A type 3 population is characteristic of areas having a severe dry season which inhibits reproduction, resulting in a seasonally changing structure, with mostly adults at some times of year and mostly immatures at other times. A type 4 population results from a short annual breeding season and delayed maturity.

The Type 1 Population.—In the type 1 population there is no temporal change in the level of reproduction and stability has been attained. Individuals of all sizes and ages are constantly present in the population in unvarying ratios. Four of the 21 populations sampled fit best with type 1, but none fits perfectly. The best fit is an anole of montane cloud forest on the continental divide, and the remaining three are species of a warm, wet climate in the Caribbean lowlands. In some instances differences between successive samples may have been due to chance and inadequate sample size, but in most instances the differences probably reflect small changes in the level of reproduction or reproductive success, that are responses to weather and climate.

At Hacienda El Prado the cloud forest habitat of *Anolis tropidolepis* is always cool and moist. Temperature change from winter to summer is only about 3°C (Fitch, 1972). Although precipitation is greatly reduced in February and March, moisture shortage does not become critical. Mist and drizzle are frequent even in the driest part of the year. There is never a scarcity of drinking water nor of moist sites for egg-laying. Cloud cover is variable and often persistent, but because these lizards carry on their activities at relatively low temperatures without basking, they are not handicapped by lack of sunshine.

Analysis of eight samples from different times of year shows that

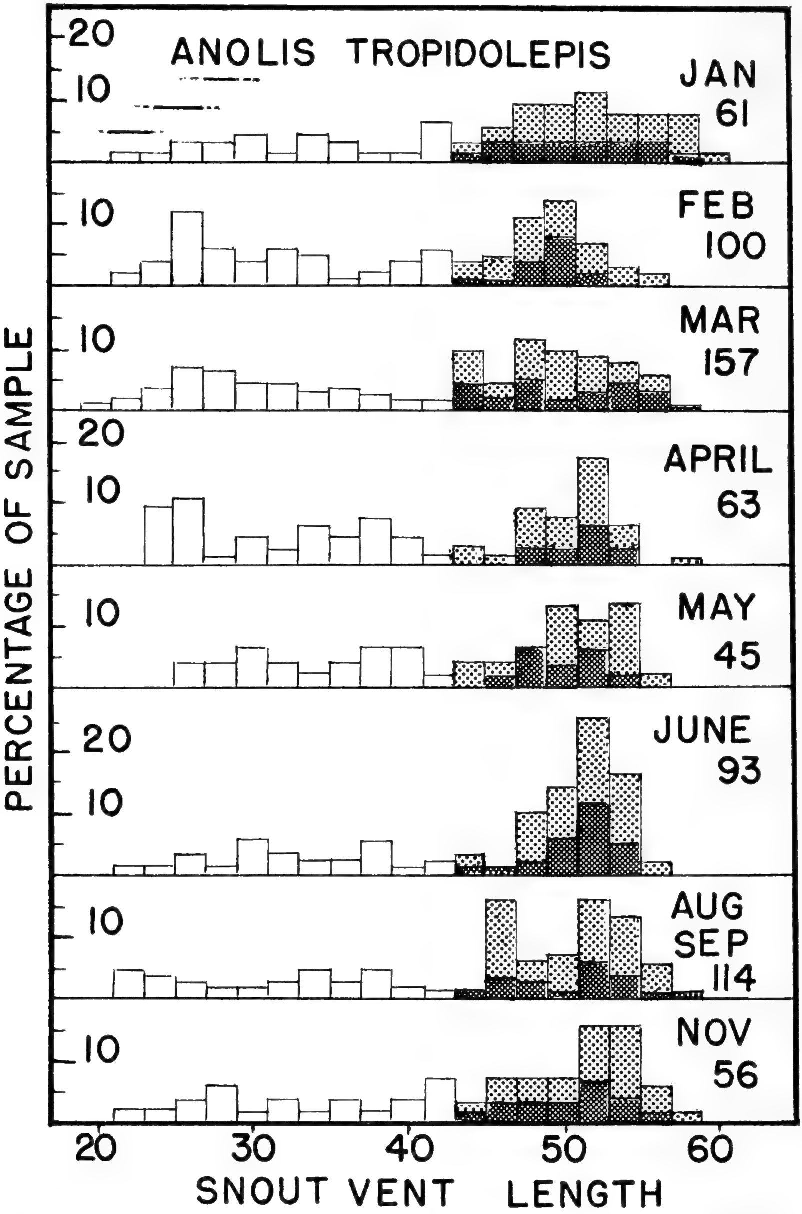

FIG. 1.—Population structure (Type 1) in *Anolis tropidolepis* at Hacienda El Prado. Individuals are grouped into eight seasonal categories and into 2-millimeter size classes for each period. Open columns show immatures, lightly shaded columns are adult males, and heavily shaded columns are adult females. Lines at left show usual size range of first-, second-, and third-month young, and numbers at right show sample sizes.

in each sample the greatest concentration of individuals is in the size range of 49 to 55 mm, small to medium adults. Young (23-29 mm) in their first few weeks of life also are well represented, and throughout the year individuals of every size (and age) from hatchlings (23 mm) up to large adults (57 mm) are present (Fig. 1). Every adult female examined was gravid. There is continuous production of eggs throughout the year, with an average interval of about 30 days between ovipositions for a given female.

Anolis humilis also represents a type 1 pattern (Fig. 2). Its habitat is in leaf litter and on buttressed roots in rain forest. Seasonal change in its habitat is slight. October, November, and December are missing from the samples. The data are from pooled samples from Beverly and San Miguel de Sarapiquí, because there are no obvious differences in the trends between these localities, which are 132 km apart and represented by comparable numbers of records. On the average, the females of *Anolis humilis* are larger than the males. All adult females in each of the eight months of sampling appeared to be gravid; presence of eggs (one uterine egg

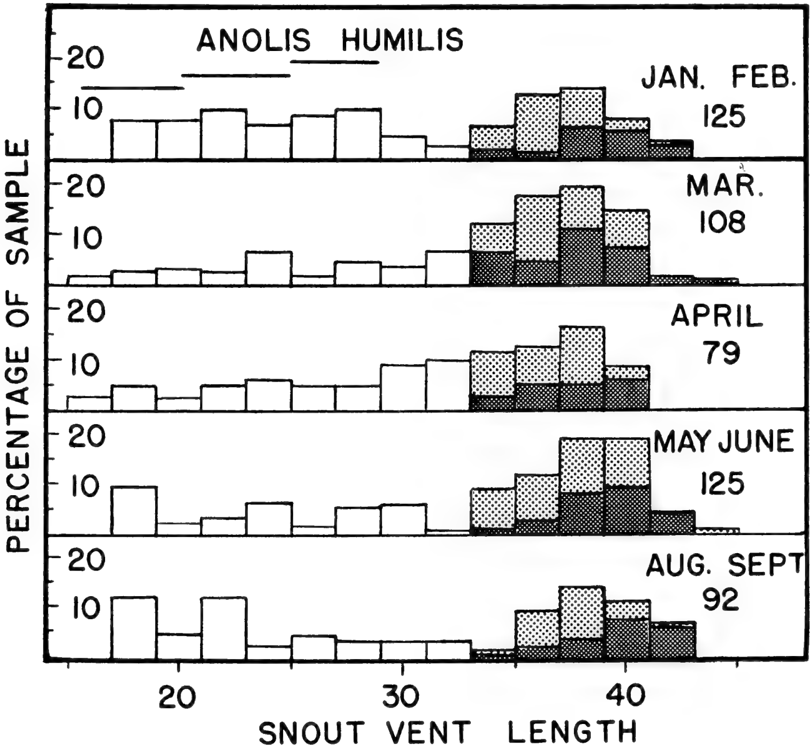

FIG. 2.—Population structure (Type 1) of *Anolis humilis* as shown by combined samples from Beverly and San Miguel de Sarapiquí. Explanation as in Fig. 1.

on each side, or on one side with an enlarged ovarian follicle on the other) was confirmed in the 78 that were actually dissected. Small young are least well represented in March, April, May, and June; this suggests some reduction of the rate of reproduction in the drier part of the year, but there is no true dry season within the range of *A. humilis.*

Also present on the study area at San Miguel de Sarapiquí is *Anolis lionotus,* a semi-aquatic species usually found on bare rocks or cobble at the edge of swift mountain streams. *Anolis lionotus* seems to conform with the type 1 pattern but only 42 are recorded on my study area, and some parts of the year are not represented. The best sample consists of 20 anoles obtained on 16 and 17 April; there are graduated sizes from hatchlings to large adults. All adult females examined appeared to be gravid, and 17 in the University of Kansas Museum of Natural History, from various localities in Costa Rica in January, June, July, and August contain eggs.

Gonatodes albogularis from the city park in Limón in the Caribbean lowlands also seems to conform to a type 1 pattern (Fig. 3). Each sample contains young of various age groups and adults, with no well defined seasonal change discernible among the samples. The high population density, low ratio of hatchlings and other young to adults, and relatively small average and maximum size in adults of this urban population are thought to be symptoms of overcrowding and cannibalism in the absence of the usual predators. Samples from the Pacific Coast at Boca de Barranca, in a seasonably dry climate (Fig. 16) are much different, showing a type 3 pattern, with a high ratio of young for most of the year.

The Type 2 Population.—In type 2 populations, reproduction is continuous throughout the year, but its level changes in response to climatic factors in areas where there is some seasonality. As a result, individuals of all ages are always present but in constantly changing ratios. Presumably the sequence of change is repeated regularly in each annual cycle. The amount of change differs greatly among populations of different species and covers a wide range between type 1 and type 3. Type 2 is the prevalent pattern for most species in the Caribbean lowlands. In this region, which originally was mostly rain forest, the climate is warm and generally wet, but with relatively dry weather in February, March, and April. Possibly in dry periods reproduction is inhibited by limited supplies of drinking water and of sites for egg-laying. Probably more important are the reduced supplies of insect food during dry periods.

Ameiva quadrilineata sampled at Quepos (Fig. 4) is typical of type 2. Reproduction continues throughout most or all of the year, but there is seasonal change in the level of reproduction resulting in changed composition of the population. Depressed or halted production in the dry season, January to April, results in a scarcity of small young in late spring and early summer, and a

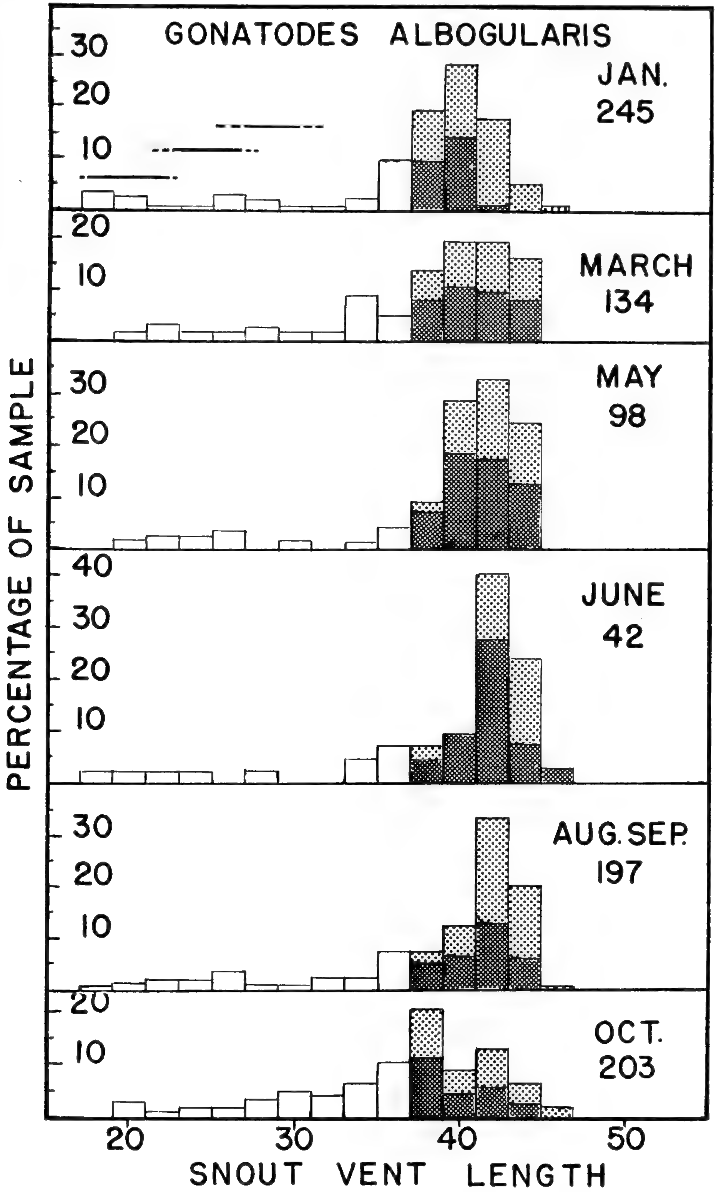

FIG. 3.—Population structure (Type 1) in *Gonatodes albogularis* at Limón. Explanation as in Fig. 1.

scarcity of middle-sized lizards in late summer when a new crop of hatchlings has appeared. Successive increments of young accumulate through the wetter part of the year; growth is remarkably rapid, so that by the dry season the population is rather evenly

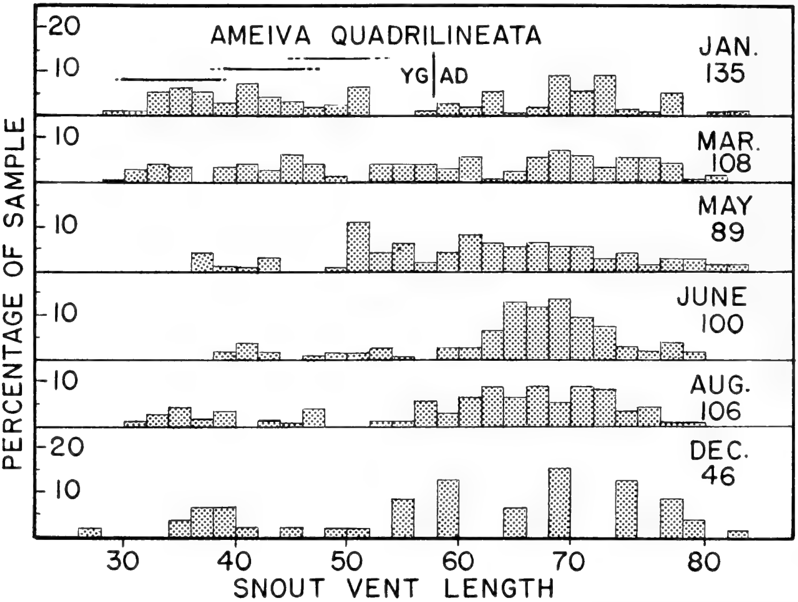

FIG. 4.—Population structure (Type 2) in *Ameiva quadrilineata* at Quepos. Explanation as in Fig. 1, but sex is not shown, and an arbitrary dividing line between (most) young and (most) adults is indicated.

distributed among all size groups. In the Caribbean versant, where the annual precipitation is more evenly distributed, egg production changes less. At Tortuguero, Limón Province, Costa Rica, Hirth (1963) found evidence that the peak of egg-laying is in May and June; thus young are most abundant in August and September, although some hatching continues throughout the year. In the even wetter climate of Pandora in southern Limón Province, Smith (1968) found that all mature females were gravid and concluded that there is uninterrupted reproductive activity throughout the year.

Anolis limifrons was found to be one of the most abundant species, and large, year-round samples were obtained at both Beverly and Turrialba (Figs. 5 and 6). At both localities anoles of all sizes are present throughout the year, but young constitute only a small percentage of the total in April and May (after several months of below-average precipitation) and increase to a majority of the total in October and November late in the rainy reason.

The population structure of *Basiliscus vittatus* at Portéte parallels that of *Anolis limfirons* in its seasonal trends; thus a few small young are present during the driest part of the year (February to April) or immediately after it, but the proportion of young increases in the wetter part of the year (Fig. 7). At Tortuguero, 79 km

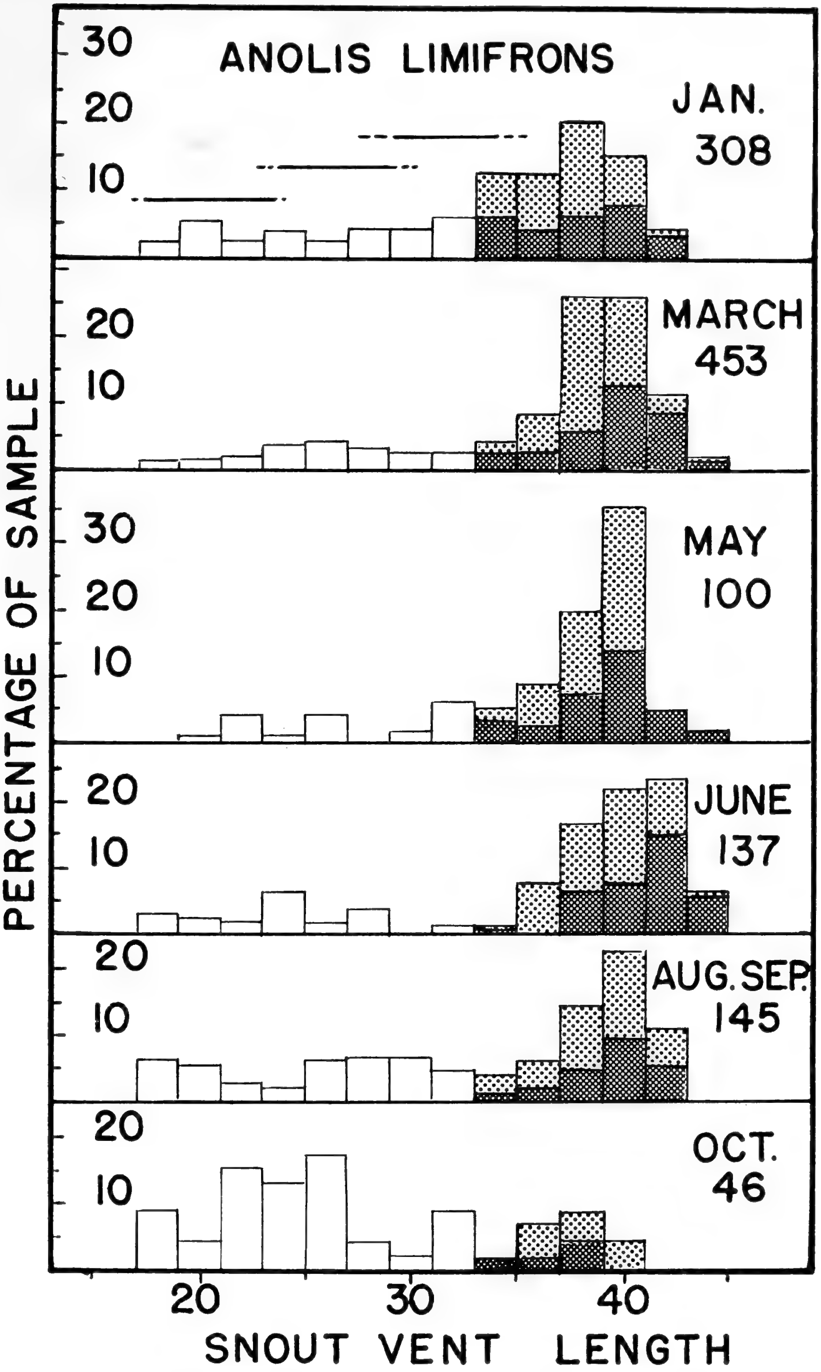

Fig. 5.—Population structure (Type 2) of *Anolis limifrons* at Beverly. Explanation as in Fig. 1.

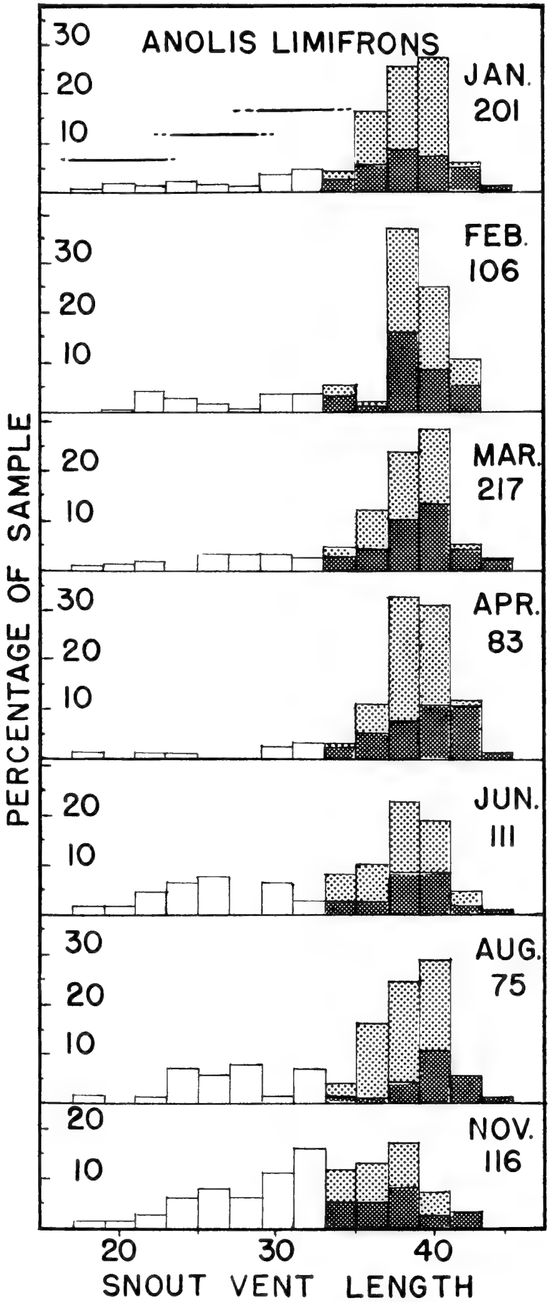

FIG. 6.—Population structure (Type 2) of *Anolis limifrons* at Turrialba. Explanation as in Fig. 1.

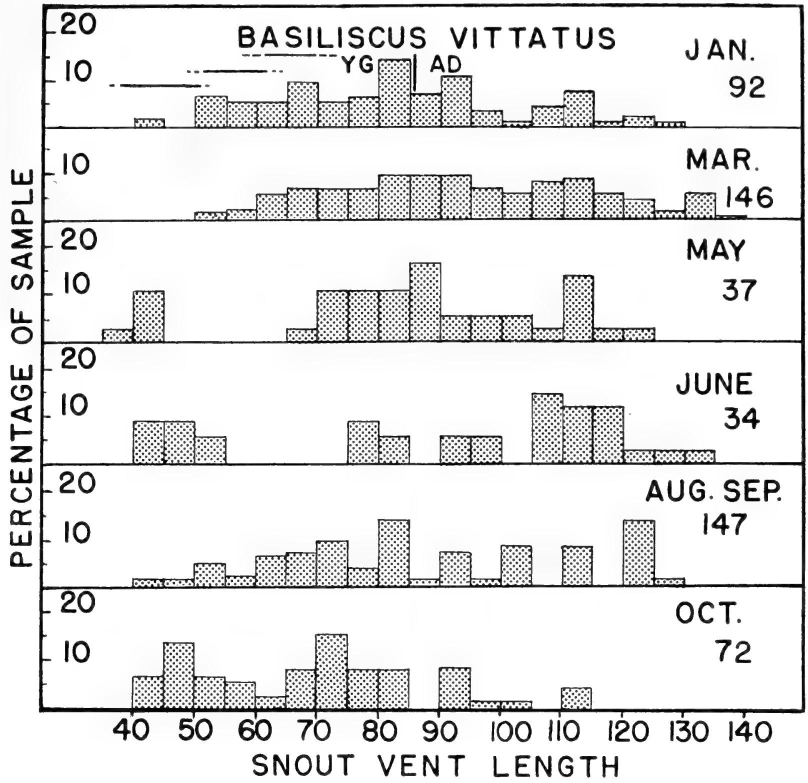

FIG. 7.—Population structure (Type 2) of *Basiliscus vittatus* at Portéte. Explanation as in Fig. 4, but with individuals grouped in 5-millimeter size classes.

northwest along the Caribbean Coast, Hirth (1963) found juveniles at all seasons but they were more abundant in August and September than they were earlier in the year. Hirth did not obtain samples in the late rainy reason when presumably juveniles would have been even more abundant.

Leiolopisma cherriei at Turrialba was found to undergo more pronounced seasonal changes than any of the species discussed above. Pooled samples from the drier part of the year, January through April, consist mostly of large adults; the few young present were well grown. From May through November the ratio of young increases (Fig. 8). At the end of the rainy season (November) and through the dry season (January to April) most adult females are nonreproductive or have only small ovarian follicles, whereas most have uterine eggs or large follicles from May through August. In general, the Caribbean lowlands have a warmer and wetter climate than Turrialba and egg-bearing females have been found in March

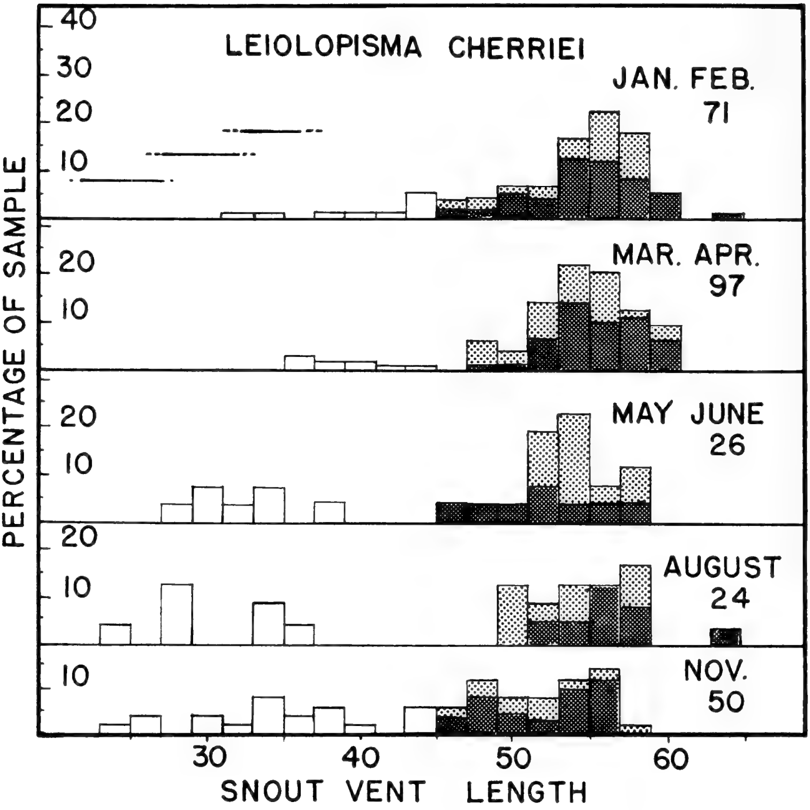

FIG. 8.—Population structure (Type 2) of *Leiolopisma cherriei* at Turrialba. Explanation as in Fig. 4.

(Greene, 1969; Fitch, 1973). No samples are available from the western part of Costa Rica, where seasonal constraints are probably greater than they are on the Caribbean versant. Perhaps this skink conforms to both type 2 and type 3 patterns in response to different climates in different parts of its range.

The Type 3 Population.—The type 3 population is characteristic of species that divide their annual cycle into an extended breeding season and a nonbreeding season of comparable length. The annual population cycle passes from a stage of relative homogeneity with only adults present at the beginning of the breeding season, to a heterogeneous stage at the end of the breeding season characterized by a mixture covering the full range from hatchlings to adults. Differences in lengths of breeding and nonbreeding periods, and the rapidity with which the young develop, result in notable differences between the kinds that have been assigned to type 3.

A type 3 pattern prevails in the parts of Costa Rica that have a severe dry season, the northwest (Guanacaste and northern Puntarenas provinces) and the Meseta Central including high and relatively dry parts of the Caribbean versant. In type 3, reproductive cycles correspond in general with the wetter half of the year. Individual females may produce eggs at regular intervals throughout the rainy season, but as the dry season sets in, production stops abruptly. Typically, all age groups from hatchlings to old adults are then present in the population but subsequently there are no increments of young for approximately half the year; hence, the youngest are arriving at adolescence as a new breeding season begins. Early in the breeding season the population consists largely of adults or adolescents, but young soon appear and become increasingly prominent; some may mature with sufficient rapidity to breed before the onset of the dry season. Some adults may survive through two breeding seasons or even more, but in most species there is a high percentage of population turnover from one year to the next. Population structure is continually changing in a predictable annual pattern.

Anolis cupreus conforms with type 3. It was studied at three lowland localities and one on the Meseta Central; the four populations show only minor differences in their seasonal trends. In December the population consisted of a mixture of all size groups but by March only adults were present. In summer a new crop of young appeared. At first their small size distinguished them from the adults; however by late autumn the size classes had merged. *Anolis intermedius* has a similar pattern (Fig. 9). It occurs at medium to high elevations on the Meseta Central and was sampled at San José. In a pooled sample (January-February from three years) there are individuals of nearly all sizes but few small juveniles. In samples from February-March and April-May, young are progressively fewer and larger, and in June there are only adults. In August-September there are adults and many hatchlings and juveniles but no young in later stages of growth. In November-December all sizes are represented, with a large majority consisting of immatures.

Cnemidophorus deppii conforms to the type 3 pattern, especially at Playas del Coco (Fig. 10). The samples from March, May, and July have progressively fewer young; only two of 89 are immature in July. In August hatchlings and juveniles are in evidence; November and December samples consist mostly of immature lizards. Samples from Boca de Barranca (Fig. 11) are notably different in having numerous juveniles in April, May and June-July as well as in August. This suggests that egg production continues through the dry season, although there is a reduction in the rate of production at that time of year. The dry season is somewhat less severe than at Playas del Coco. The Boca de Barranca samples are from the

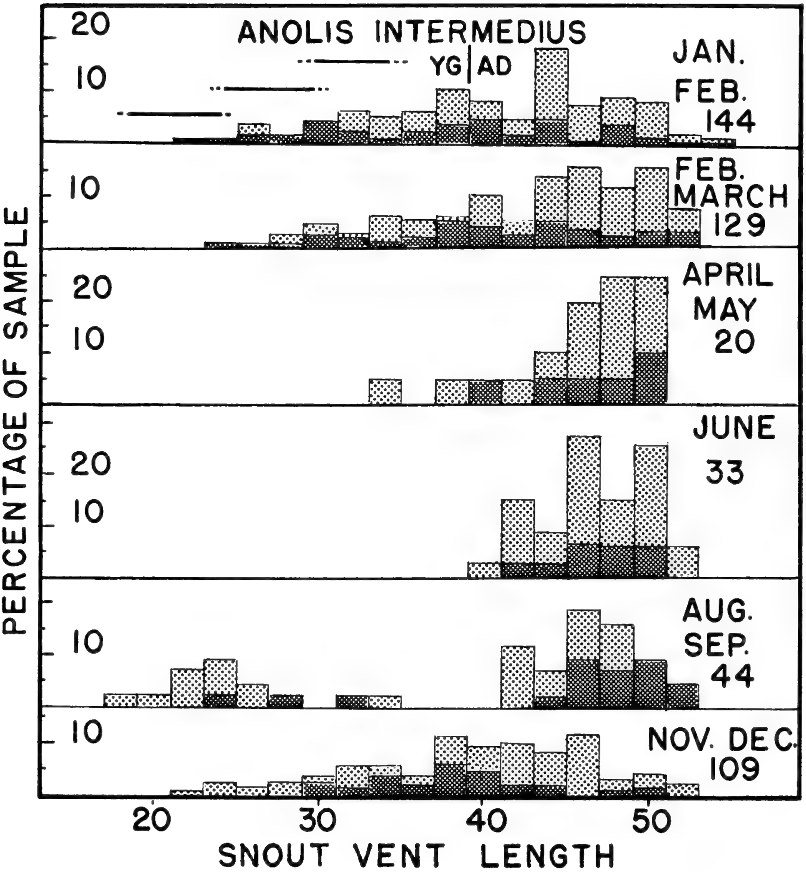

Fig. 9.—Population structure (Type 3) of *Anolis intermedius* at San José. Explanation as in Fig. 1.

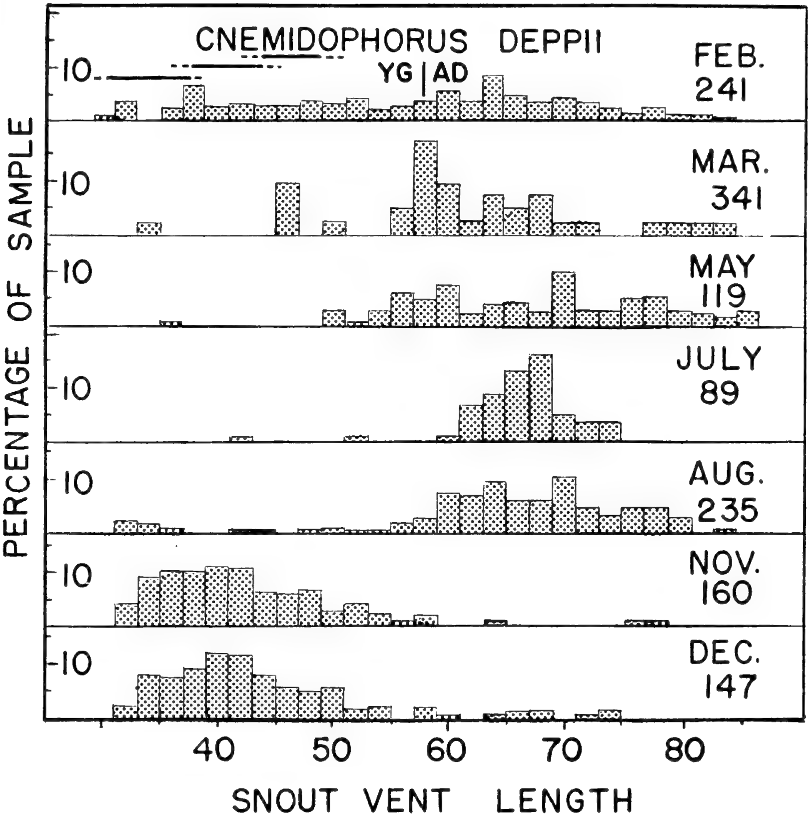

FIG. 10.—Population structure (Type 3) of *Cnemidophorus deppii* at Playas del Coco. Explanation as in Fig. 4.

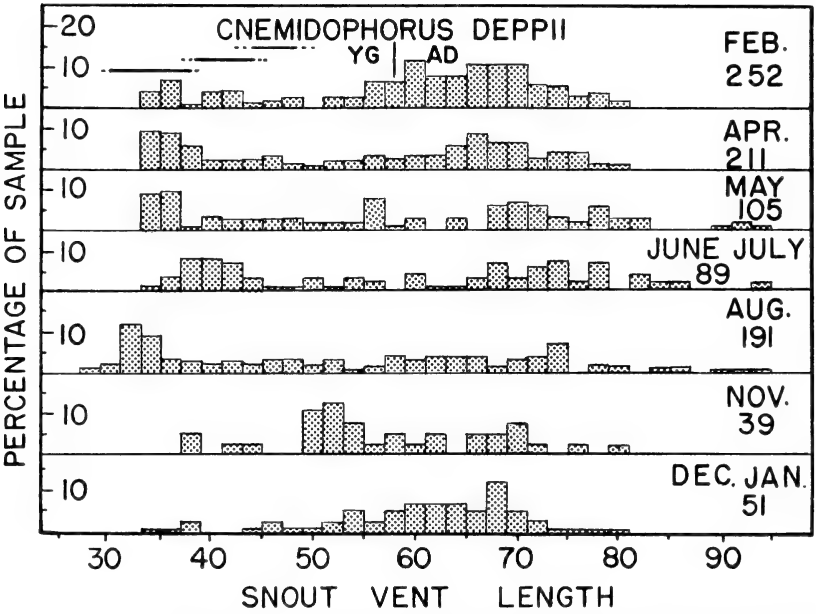

FIG. 11.—Population structure (Type 3) of *Cnemidophorus deppii* at Boca de Barranca. Explanation as in Fig. 4.

grounds of the Marbella Hotel where flower beds and yards are regularly sprinkled in the dry season. Perhaps in this small area the sprinkling partially nullified the effects of the dry season by providing drinking water, damp sand for oviposition, and a concentration of insect food.

Sceloporus variabilis at Playas del Coco and Boca de Barranca is fairly typical of a type 3 pattern. At Boca de Barranca (Fig. 12) samples from February, April, May and June-July consist mostly of adults. There are young of various sizes in February but they become fewer and larger as the dry season progresses, with no further increments of hatchlings. Average size of sexually mature individuals also increases during the dry season. In August a new crop of hatchlings appears. By November and December, the population consists mainly of young, the largest already overlapping in size

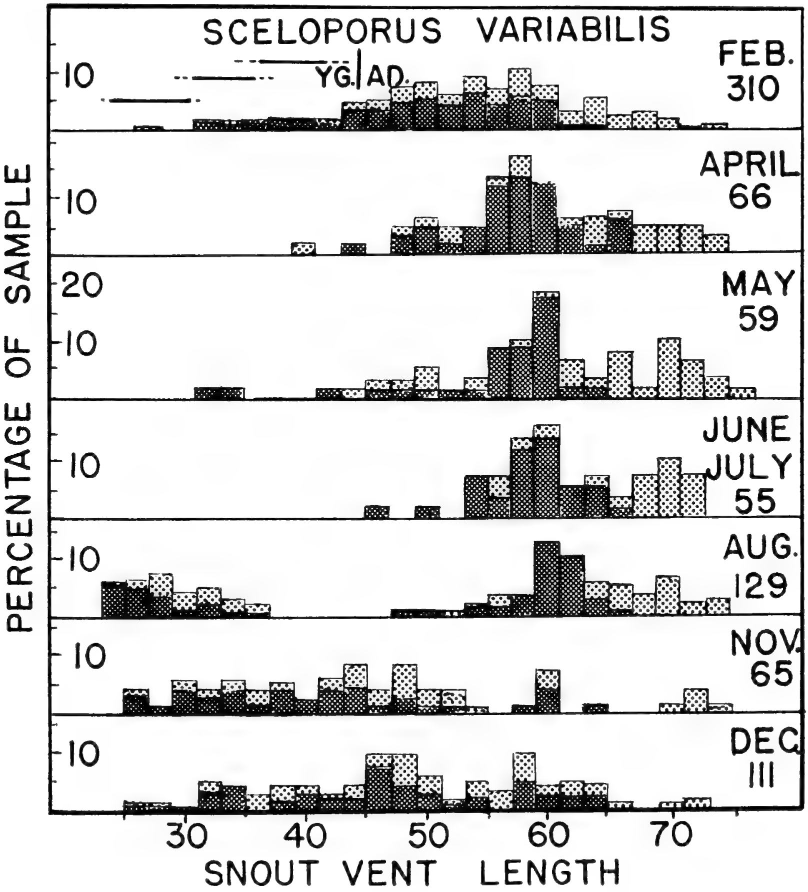

Fig. 12.—Population structure (Type 3) of *Sceloporus variabilis* at Boca de Barranca. Explanation as in Fig. 1, but sex is indicated in all sizes.

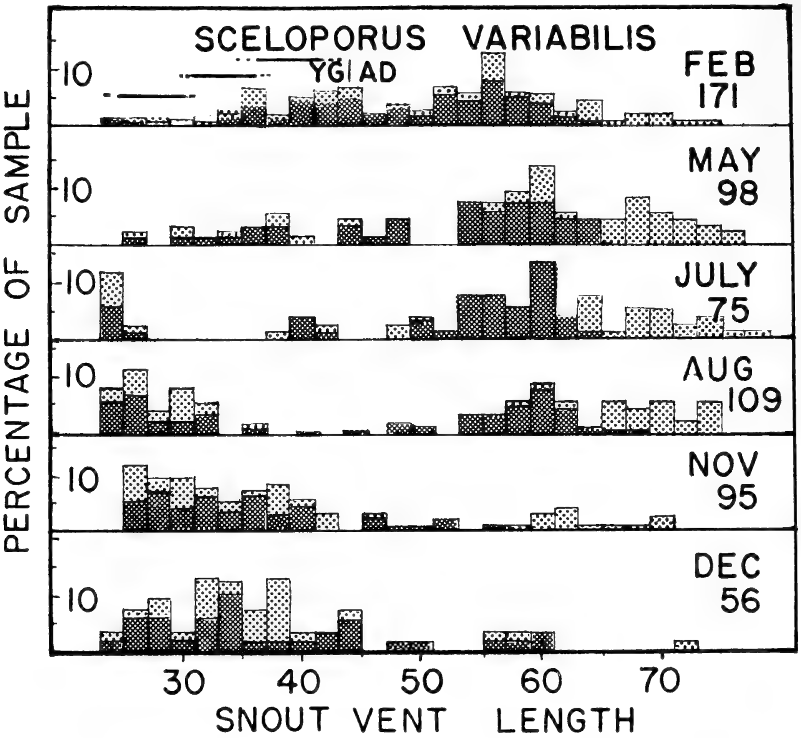

FIG. 13.—Population structure (Type 3) of *Sceloporus variabilis* at Playas del Coco. Explanation as in Fig. 1, but sex is indicated in all sizes.

the preceding generation. At Playas del Coco (Fig. 13) the trend is similar but not so well defined. In May there are more young, some still near hatchling size. This would seem to indicate production of eggs even in the dry season. The summer hatchlings appear in early July, before they are present at Boca de Barranca.

Basiliscus basiliscus fits the type 3 pattern poorly. In this large, semi-aquatic lizard, population parameters are much affected by local conditions in different streams. Regardless of the time of year every population sample obtained had a high proportion of immature individuals (Fig. 14). In each sample these immatures tend to be concentrated in one or two dominant size classes representing relatively brief periods of concentrated and successful reproductive activity; these periods do not correspond closely between different localities, or between different years at the same locality. Amount and distribution of precipitation is critical.

Although *Sceloporus malachiticus* most nearly conforms with a type 3 pattern, it is unique in some respects (Fig. 15). Samples from Cartago and San José were pooled; these localities are 19 km apart

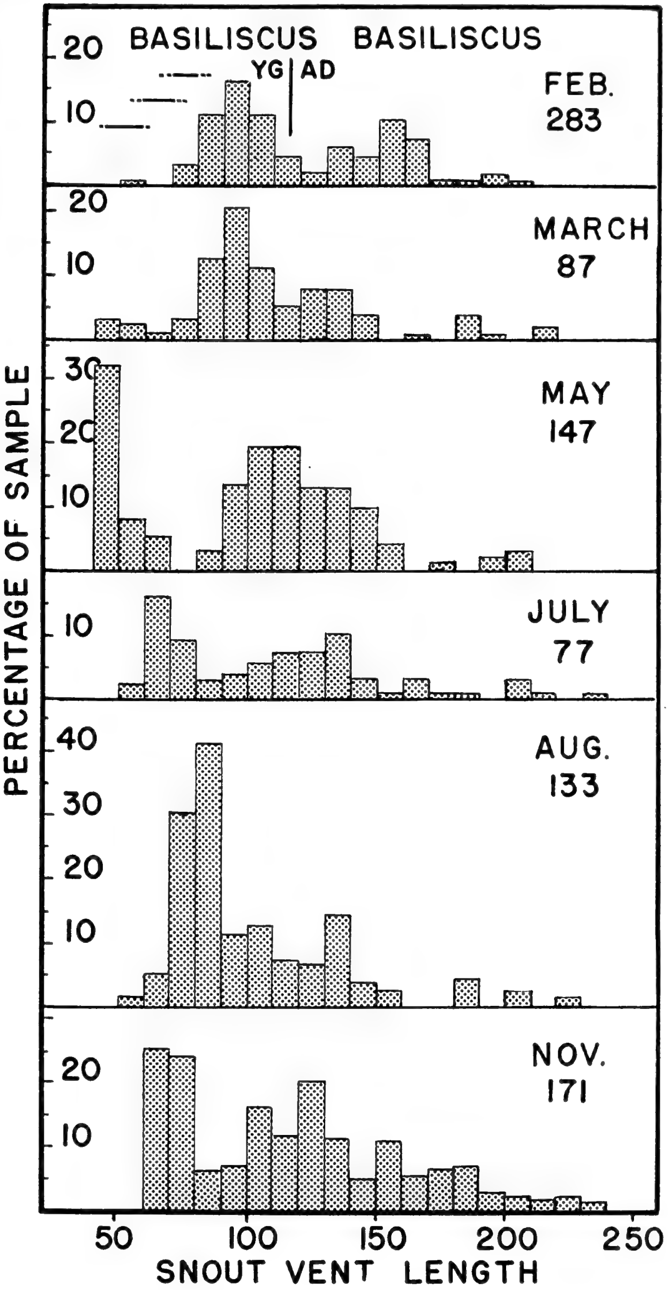

FIG. 14.—Population structure (Type 3) of *Basiliscus basiliscus* at Finca Taboga, Río Higuerón. Explanation as in Fig. 4, but with individuals grouped in 10-millimeter size classes.

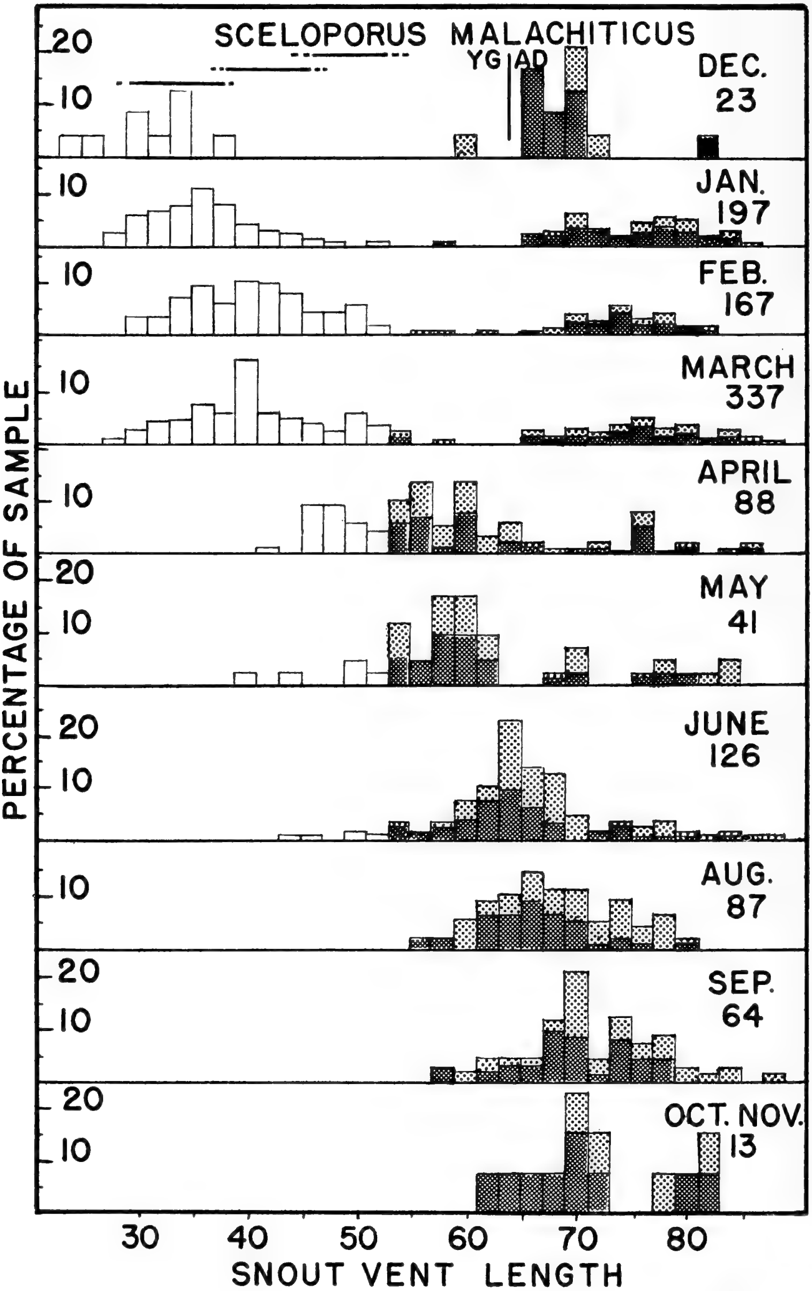

Fig. 15.—Population structure (Type 3) of *Sceloporus malachiticus* as shown by combined samples from Cartago and San José. Explanation as in Fig. 1.

and separated by the continental divide. Cartago has a slightly cooler and drier climate, but seasonal trends in *S. malachiticus* populations seem to correspond closely enough at the two localities to justify combination of the samples. In the dry season there is no reproductive activity. When the rainy season starts in April and May, ovarian follicles begin to enlarge and ovulation occurs in summer (Marion and Sexton, 1971). This lizard is viviparous, and gestation is prolonged, with births occurring in December and January. Females produce only one litter annually. In winter the recently born juveniles constitute a large part of the population. By late spring their cohort has grown sufficiently to overlap adults in size. Through the summer and autumn months, juveniles are scarce. Nearly all females are gravid in summer but a few retarded young fail to gain maturity until late in the summer.

At higher altitudes, with relatively low temperature, less insolation, and a less severe dry season, the seasonal pattern indicated by figure 15 is not developed. Growth is delayed, so that females are usually somewhat more than a year old when they produce their first litters and births are scattered throughout the year.

Although *Gonatodes albogularis* has a type 1 pattern in the Caribbean lowlands, it conforms to a type 3 pattern at Boca de Barranca, where there is a seasonally dry climate (Fig. 16).

The Type 4 Population.—The type 4 population is most familiar to investigators because it occurs in those kinds of lizards that penetrate farthest into the temperate zone, and live in areas having a long, severe winter and a short growing season. There is a short annual breeding season resulting in production of a cohort of young which usually require more than one year to mature. Consequently the population is structured with several discrete annual age groups, one or more of which consist of immatures that do not participate in the breeding season. Surprisingly, type 4 populations occur in the tropics and even in the relatively uniform climate of rain forests, as well as in northern areas.

I found type 4 populations only in the large iguanines, *Ctenosaura similis* and *Iguana iguana,* and I did not obtain adequate population samples of the iguana. However, both of these lizards have a short annual breeding season, and the young mature late in the second year at the earliest. Data from pooled samples of *Ctenosaura similis* from various localities in western Costa Rica show that after the annual crop of eggs hatches in spring there are two distinct size groups of young, hatchlings and yearlings (Fig. 17). The former grow more rapidly and by late autumn they overlap the yearlings in size. The samples available for the iguana are smaller and less well distributed, but indicate that the iguana follows a similar pattern. The occurrence of hatchlings and the distribution of dates of egg-laying indicates that the breeding sea-

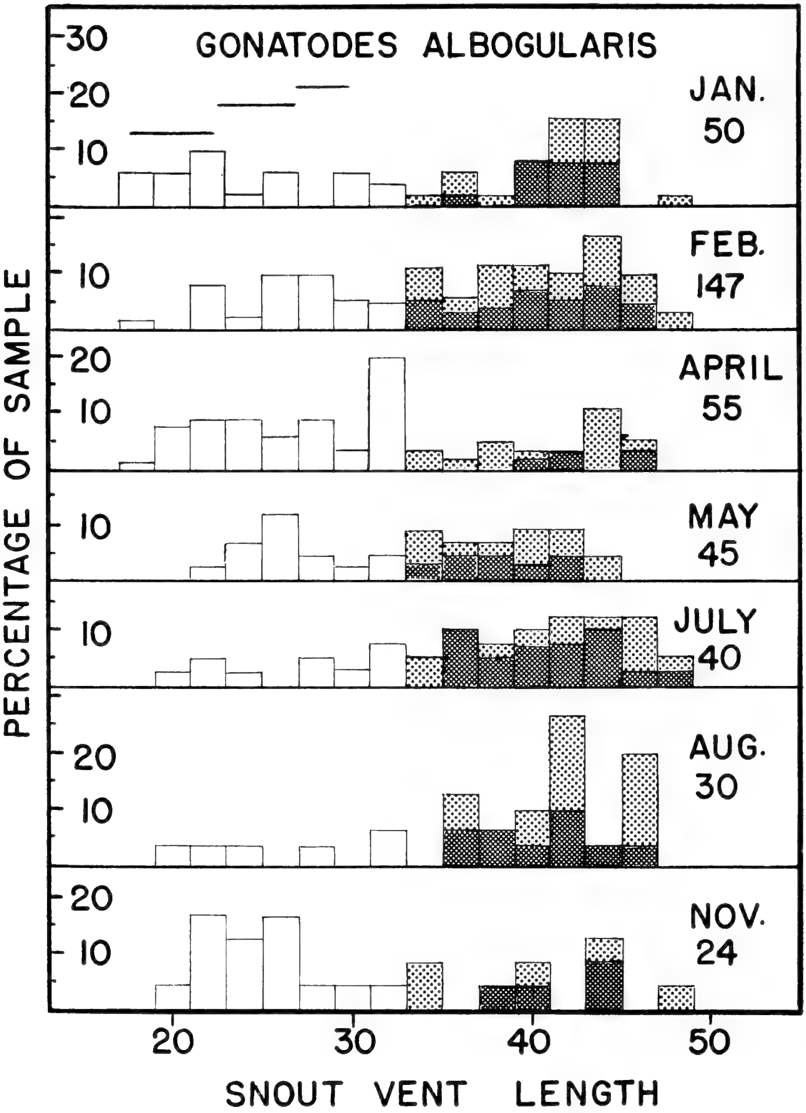

FIG. 16.—Population structure (Type 3?) of *Gonatodes albogularis* at Boca de Barranca. Explanation as in Fig. 1.

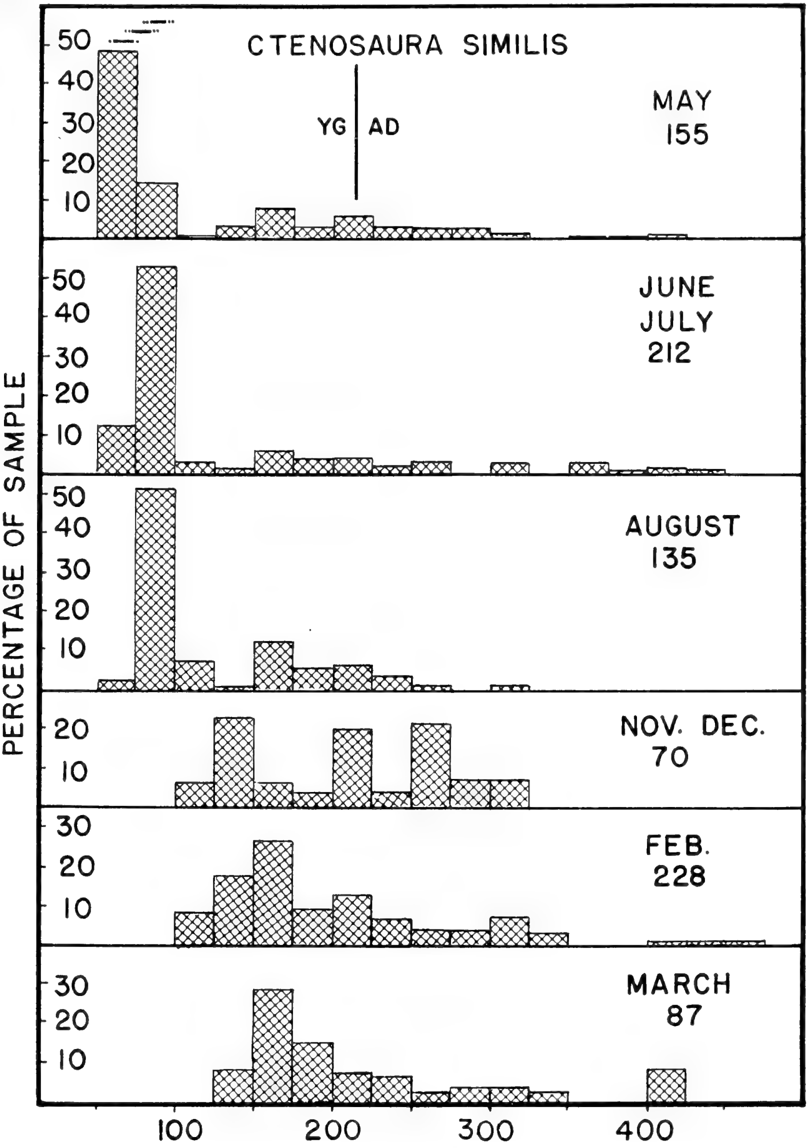

FIG. 17.—Population structure (Type 4) of *Ctenosaura similis* in Guanacaste and Puntarenas provinces. Explanation as in Fig. 4, but with individuals grouped in 25-millimeter size classes.

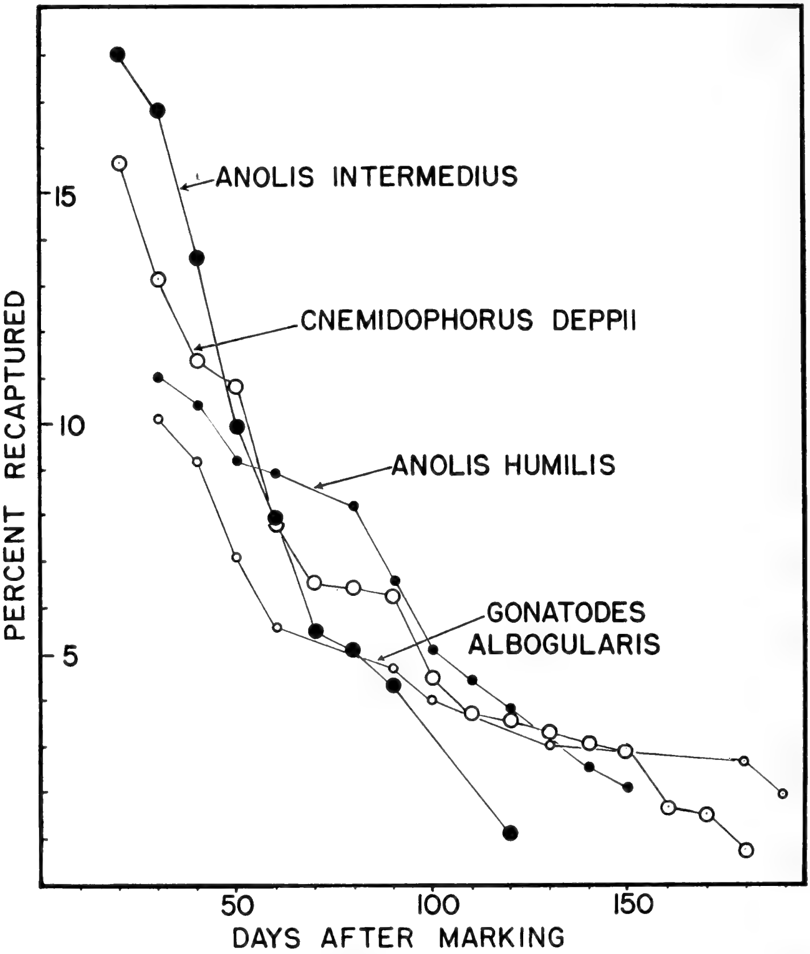

FIG. 18.—Cumulative percentages of marked lizards of four species recaptured indicating trends of survivorship.

son is somewhat less restricted than in the ctenosaur, with the possibility that individual females lay more than one clutch in the course of a season. Iguanas are restricted to warm lowlands, but occur both in seasonally dry areas and those that are humid. In the latter they are exceptional in having a breeding season limited to a short part of the year.

Survivorship.—Under natural conditions longevity differs greatly among the many kinds of lizards studied, and is not closely correlated with the types of seasonal schedule and population structure described above. Although the 29-month span of my field work was long enough to yield significant information about longevity, drastic disturbance of nearly all the study areas (e.g., tree-cutting,

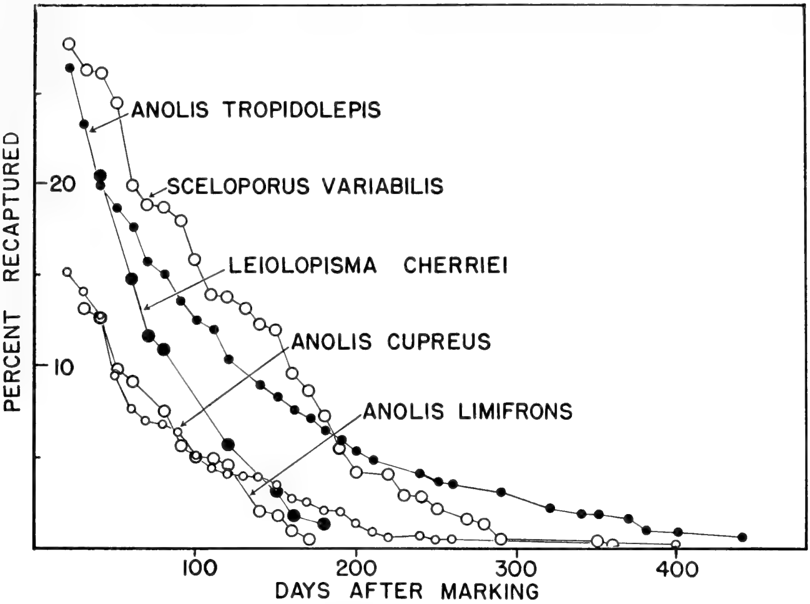

FIG. 19.—Cumulative percentages of marked lizards of five species recaptured after varying intervals, indicating trends of survivorship.

bull-dozing, flood, or unusually high tide) prevented the lizards from surviving as long as they would have in undisturbed habitats; some populations were more drastically affected than others. Figures 18 and 19 show rates of disappearance of the marked individuals of several species from the study areas and perhaps provide the basis for a rough comparison of their mortality rates.

In the smaller anoles (*Anolis limifrons, A. humilis, A. intermedius*) and in *Ameiva quadrilineata, Cnemidophorus deppii* and *Sceloporus variabilis,* sexual maturity is attained at an age of four to six months. Population turnover is extremely rapid, and the records suggest that individuals rarely if ever survive through two full breeding seasons. In *Gonatodes albogularis, Sceloporus malachiticus,* and especially in the montane *Anolis tropidolepis,* maturity is delayed until late in the first year, population turnover is somewhat slowed, and longevity is greater. In the basilisks, large size and delayed maturity are correlated with even slower population turnover. Seemingly the mortality rate is high in young, but adults are relatively safe. Adults are exceedingly elusive, especially those of *Basiliscus basiliscus,* but some individuals of both species were captured and marked. In the late stages of the field work individuals of both species (mostly *B. vittatus*) that could not be caught alive were shot. These were found to include individuals marked soon after the beginning of field work, and they revealed that in *B. vittatus* at least, normal life expectancy is much greater than in any of the smaller kinds of lizards studied (Table 1). *Ctenosaura similis* might be expected to have even greater longevity than *Basiliscus* because of its large size and delayed maturity. However, adults are too wary to be caught and marked except on a few occasions and nothing was learned of longevity.

DISCUSSION

In a pioneer study, Baker (1947) demonstrated that in tropical rain forest of Espirítu Santo in the New Hebrides there is well defined seasonality in the skink *Emoia cyanura.* Espirítu Santo lies at 15° 15′ south latitude; day length, precipitation and temperature change little throughout the year. Although breeding occurs throughout the year, its level changes markedly from a peak in the warmest part to a trough at the opposite extreme when temperature averages only 2°C lower. Thus these lizards are highly sensitive to changes in the physical environment and respond in the level of their reproductive activity. Many later studies of local lizard populations in a variety of tropical environments have extended these findings. In general, such investigations have shown that tropical lizards often have long breeding seasons, but that year-round reproduction occurs only in rain forest and even there the level of reproduction tends to be positively correlated with the amount of precipitation. Elsewhere, in regions of seasonal drought, the breeding season tends to correspond with the wet season; reproduction ceases or declines to a relatively low level in the dry season. Seasonal interruption of reproduction, or reduction in its level results in changing population structure, with certain age groups either missing or less well-represented than both older and younger groups.

In their investigation of evolutionary strategies in the reproduction of lizards, Tinkle, Wilbur, and Tilley (1970) compiled data from the literature on 27 tropical species along with a larger number of kinds from temperate regions. They stated, "Lizards are clearly divided into two strategies: early-maturing, multiple-brooded vs. late maturing, single-brooded. . . ." Contrasting the tropical species with the temperate, they found in the former: larger average

TABLE 1.—Survivorship in Marked Lizards of Various Species

Species	Marked in 1967-68	Recaptured > 6 mos.	Recaptured > 12 mos.	Recaptured > 18 mos.	Recaptured > 24 mos.
Sceloporus variabilis	604	70(11.6%)	0	0	0
Anolis humilis	305	6(1.9%)	1(.33%)	0	0
Anolis cupreus	1482	48(3.24%)	3(.20%)	0	0
Anolis tropidolepis	316	27(8.45%)	7(2.22%)	0	0
Basiliscus vittatus	90	6(6.66%)	4(4.45%)	2(2.22%)	2(2.22%)

size at sexual maturity, larger adult female size, slightly smaller number of eggs per clutch, and a higher ratio of oviparous to viviparous species. Of the 15 tropical species discussed here, only one, *Ctenosaura similis,* is late-maturing and single-brooded, whereas nine are early maturing and multiple-brooded. The other four are somewhat intermediate; the viviparous *Sceloporus malachiticus* is single-brooded, and *Basiliscus basiliscus, B. vittatus* and *Anolis tropidolepis* have somewhat delayed maturity. As to size, most of the 15 species are small, but the average is raised by the relatively gigantic *Ctenosaura similis* and also by the two species of *Basiliscus.* With few exceptions, the number of eggs is small. The clutch consists of only one egg in the six species of anoles and the gecko, *Gonatodes albogularis.* In the two teiids and the skink, the average clutch size is between 2 and 3. The average clutch size is 3.0 in *Sceloporus variabilis,* 3.9 in *Basiliscus vittatus,* 4.6 in *Sceloporus malachiticus,* 6.0 in *Basiliscus basiliscus.* Only *Ctenosaura similis* has large clutches of more than 20 eggs. Of the 15 species, only *Sceloporus malachiticus* is viviparous; of the 58 species of lizards recorded from Costa Rica, there are only three that are known to be viviparous.

Tinkle, *et al.* (1970) noted the absence of a significant correlation between clutch size and body size at maturity in tropical lizards. However, such correlation definitely does exist in the 15 species that I investigated. Doubtless the lack of correlation found by Tinkle *et al.* resulted, at least in part, from the fact that insular species (having few natural enemies and reduced clutch size) were included along with mainland kinds. Also, their list included species of *Draco,* which parallels *Anolis* in specialization for an active, arboreal existence, including reduction in clutch size. If the insular species and the species of *Draco* are excluded, the remaining 12 examples of Tinkle *et al.* do show high correlation of body size and number of eggs per clutch.

A much different combination of ecological traits from those hypothesized for tropical lizards by Tinkle *et al.* (1970) would be expected from concepts of selection proposed or developed by Dobzhansky (1951), MacArthur and Wilson (1967), Pianka (1970) and also MacArthur (1972). They recognized two basic types of selection to which populations are subject, depending on the type of environment. "*K*-selection" is most characteristic of environmental type best exemplified by a tropical rain forest. In this type, physical factors are relatively benign and stable. Weather is predictable. The populations of a given organism tend to be stable, and often in equilibrium near the carrying capacity. Interspecific and intraspecific competition is usually keen, and mortality is density-dependent. Animals are highly adapted to their communities and are "fit" so that they have notable longevity, with slow development, delayed maturity, large body size, few young per clutch, repeated reproduction and parental care (occasionally expressed in viviparity). Conversely, "*r*-selection" is most characteristic of an environment typified (in extreme form) by an Arctic tundra. There, environmental conditions are unstable and often harsh. Weather is subject to extremes, which may bring about catastrophic decimation of animal populations in a density-independent fashion. As a result populations are unstable, are often below the carrying capacity, and competition may be lax. Selection favors a short life span, rapid development, early maturity, small size, energy channeled into a single, early reproductive effort, with a large number of offspring, and lack of parental care.

Most terrestrial environments fall somewhere between these two extremes. Presumably the assemblage of tropical lizard species dealt with in the present study represents environments that are most likely to show *K*-selection. Table 2 is designed to test conformity of each species with the two types of selection on the basis of eight separate criteria. A species that conformed with *r*-selection in all respects would have a rating of 8, one that conformed with *K*-selection would have a rating of 24 and one that was intermediate would have a rating of 16. Assuming that the criteria used are appropriate and that the ratings have been made correctly, it appears that none of the species conforms entirely with either type, but that 12 of the 15 fit *r*-selection better than *K*-selection.

"Coarse-grained" and "fine-grained" environments have been recognized by several recent authors as producing different types of selection, the latter permitting more specialization and closer adaptation. According to Levins (1968) a species "loses fitness in a heterogeneous environment. It would be better off specialized, but the uncertainty of the environment forces niche expansion." Compared on this basis, the 15 species of this study seem to have members in each type of environment and some that are intermediate. *Basiliscus basiliscus* is perhaps the best example of a species living in a coarse-grained environment. Within the area where it occurs it is not generally distributed but is limited to watercourses and their vicinity, and along them it is irregularly distributed with concentrations where there are log jams, uprooted large trees, or undermined banks with dense thickets. These alternating features are accentuated by seasonal change; a stream that is a rushing torrent during the rainy season may be reduced to a series of puddles in the dry season, and the log jams and thickets that are used as shelter may be drastically altered or swept away completely in time of flood. *Basiliscus vittatus* and *Anolis lionotus* are also streamside species subject to some of the same coarse-grained features. *Ctenosaura similis* and *Sceloporus malachiticus* are usually associated with irregularly distributed environmental features such as rock outcrops, buildings, or hollow trees, and their

TABLE 2.—*r*-selection and *K*-selection in Some Costa Rican Lizards

	Size (S-V in mm) 1=35-60 2=70-150 3=300 or more	Time to maturity in mos. 1=3-5 2=6-10 3=more than 12	Sexual dimorphism 1=size and color 2=color and/or display organ 3=little or none	Number of eggs or young 1=7 or more 2=3-6 3=1 or 2	Number of broods 1=5 or more 2=2-4 3=1	Population turnover 1=1 year 2=1-2 years 3=more than 2 yrs.	Habitat stability 1=seral 2=intermediate 3=stable	Habitat uniformity 1=coarse 2=intermediate 3=fine	Selection rating *r*=8 *K*=24
Ameiva quadrilineata	2	2	1	3	2	1	1	1	13
Anolis cupreus	1	1	1	3	1	1	2	2	12
Anolis humilis	1	1	2	3	1	1	3	2	14
Anolis intermedius	1	1	2	3	1	1	2	2	13
Anolis limifrons	1	1	2	3	1	1	2	2	13
Anolis lionotus	1	1	2	3	1	2	2	1	13
Anolis tropidolepis	1	2	2	3	1	2	3	3	17
Basiliscus basiliscus	2	2	1	2	2	3	1	1	14
Basiliscus vittatus	2	2	1	2	2	3	1	1	14
Cnemidophorus deppii	1	1	1	2	2	1	1	1	10
Ctenosaura similis	3	3	1	1	3	3	2	1	17
Gonatodes albogularis	1	1	1	3	1	2	3	3	15
Leiolopisma cherriei	1	2	3	3	2	2	3	2	18
Sceloporus malachiticus	2	2	1	2	3	2	2	1	15
Sceloporus variabilis	1	1	1	2	2	1	1	1	10

environments are likewise coarse-grained. In contrast the species of leaf litter in rain forest (*Anolis humilis, Leiolopisma cherriei*) or those of tree-trunks (*Gonatodes albogularis, Anolis tropidolepis*) have fine-grained environments. Again, there is no definite correlation between these environmental types and population structure or survivorship.

CONCLUSIONS

Four types of population structure were found to result from the varying climates and reproductive strategies in the 15 species of tropical lizards studied in Costa Rica. Type 1 is a stable population with all ages constantly represented, from the most numerous and youngest to the relatively scarce oldest lizards; type 2 also has all age groups constantly present, but their ratios are constantly changing, with an older group sometimes better represented than a younger one reflecting fluctuation in the level of reproduction. Type 3 results from seasonality of breeding, and changes throughout the annual cycle, from relative homogeneity (with all adults) to heterogeneity with immatures of all sizes as well as adults. Type 4 consists of a structured population of many successive annual cohorts, and results from a short annual breeding season and delayed maturity, paralleling trends in the kinds of lizards that occur farthest from the equator.

Small body size, rapid population turnover, frequent reproduction, oviparity, small clutch-size, type 2 or 3 population structure, and sexual dimorphism (in color or display organs or body size or all three) are characteristic of the populations studied with few exceptions. Although occurring in communities that would be expected to have mainly *K*-selection, the species do not conform consistently to the criteria expected in products of *K*-selection. The majority of the species fit better with the criteria of *r*-selection, but each species shows some mixture of the two sets of traits, and no two species are alike in this respect.

In contrast with lizard populations of the temperate zones, those of the tropics are less restricted to seasonal schedules. Living in more constant environments, they are able to distribute their activities, such as those concerned with reproduction, over a greater part of the annual cycle. The iguanid anoles and the sphaerodactyline geckos, two groups that are highly successful in the Neotropical region, have progressed farthest in this regard; in rain forests and cloud forests their reproductive effort is uniformly distributed over the entire year. The female lays one egg at a time, the left and right ovaries alternating, so that, usually carrying two eggs in different stages of growth, she is not much handicapped and continues her normal activities. Aside from its various other implications, the one-egg clutch may be regarded as an extreme specialization for an active way of life. Each egg may be left in a different place (though both groups are known to use communal nests at times). Eggs are deposited in damp sheltered places, but are not buried in special nest burrows.

Therefore production of eggs and oviposition involve a minimum of stress. Dispersal of eggs in time and space provides security from: a) catastrophic events such as flood or drought which might catch the eggs or young at a vulnerable stage, b) concentrated predation, c) intense intraspecific competition for food and space, such as might occur when many young emerge simultaneously from the same nest.

Climates in the tropics that have strong seasonality impose annual cycles on their lizard populations. In areas that have a severe dry season, the lizards' annual cycles are comparable with those that occur in species of the temperate zones except that there is no hibernation period. There is a breeding season of varying length but confined to one part of the year and presumably adjusted to avoid the worst rigors of the year-round climate and exploit the benefits, such as adequate moisture for the incubating egg, and an abundant supply of suitable food (usually insects) for the breeding adults and/or the hatchlings. Even in the wet climate of the Caribbean lowlands some lizards, especially those of seral situations, such as *Anolis limifrons, Basiliscus vittatus* and *Leiolopisma cherriei* alter the level of their reproductive activity in response to wetter or drier weather at certain times of year. In general, heavy precipitation is correlated with heightened reproduction, whereas drought is correlated with slowing or cessation of reproductive activity.

The long and severe dry season of western Costa Rica (Guanacaste and northern Puntarenas provinces, where monthly precipitation in December, February, March, and early April is usually less than 25 mm) limits reproduction mainly to the wetter half of the year in most species. An extreme case is *Ctenosaura similis* which is limited to a short and concentrated breeding season, with large clutches of eggs, relatively small hatchlings, and delayed maturity as facets of its reproductive strategy. In ctenosaurs, the young differ from adults in their behavior, microhabitats (Henderson, 1973), size and type of food items (Montanucci, 1968) hence intraspecific competition is minimized. In *Basiliscus basiliscus, Iguana iguana* and *Anolis cupreus* there is a less well-defined segregation of young and adults.

SUMMARY

Free-living populations of 15 species of lizards were studied at 14 localities in Costa Rica; the study sites include a wide range of altitudes, habitats and climates. Mark and recapture studies were

carried out over a three-year period for most of the species. At most of the localities two or more species were studied simultaneously; thus the results provide a basis for both intraspecific and interspecific comparisons.

Unlike lizards of the Temperate Zone, the tropical species included in this study all are active throughout the year; however most of them show some seasonality in their annual cycles. Their different population structures result largely from the timing of reproduction and rate of development and survivorship of the cohorts of young produced. In some kinds, population structure changed markedly in response to seasonal changes in the weather. Recognizable components of individual populations were adult males and females, and immatures at various stages of development. Snout-vent length is highly correlated with age in immatures; there is less correlation in adults because growth continues after attainment of maturity.

On the basis of their population structures, reproduction and survivorship, the species studied can be arranged in a graduated series from those of small size, early maturity, high production, and rapid turnover, to those that are large and have delayed maturity, low production and slow turnover. Four fairly distinct but overlapping types of population structure can be recognized within this range. Type 1 is confined to climates lacking seasonal contrast and results from year-round reproduction at a uniform level. The population structure is stable and includes individuals of all ages in unchanging ratios. This type is best exemplified by *Anolis tropidolepis* of montane cloud forest, and less perfectly by *A. humilis,* probably *A. lionotus,* and by *Gonatodes albogularis,* all of the Caribbean rain forest. Type 2 also has year-round reproduction with all ages represented in the population at all times, but the level of reproduction and the ratios of different age groups undergo constant seasonal change. This type occurs in wet climates that have moderate seasonal change and was found developed to various degrees in *Ameiva quadrilineata, Anolis limifrons, Basiliscus vittatus,* and *Leiolopisma cherriei.* Type 3 is characteristic of areas having a long dry season, where lizards generally confine their reproduction to the wetter part of the year. At the beginning of the breeding season the population consists essentially of reproductive adults, but subsequently successive increments of young are added until all classes from hatchlings to adolescents are found along with the adults (by then reduced to relatively low numbers) at the end of the breeding season. Type 3 prevails in northwestern Costa Rica and was found in *Anolis cupreus, A. intermedius, Basiliscus basiliscus, Cnemidophorus deppii, Gonatodes albogularis, Sceloporus variabilis* and *S. malachiticus.* The latter species is transitional to type 4 which otherwise was found only in the large iguanid

Ctenosaura similis. In type 4 there is a relatively short annual breeding season and delayed maturity resulting in a sharply structured population that consists of several or many discrete annual age groups at least two of which are immatures.

Survivorship was judged from the rate at which marked individuals disappeared from the populations on the small study areas, but some of the turnover was caused by shifts of individuals and this spatial displacement could not be evaluated accurately. In most species, population turnover was rapid, with most individuals replaced in the course of a year. It was especially rapid in the smaller species of anoles, in *Cnemidophorus deppii, Ameiva quadrilineata* and *Sceloporus variabilis.* In contrast to these species the montane *Anolis tropidolepis* and the two species of basilisks are notably longer lived and individuals often survive for more than a year. *Ctenosaura similis* clearly is in a class by itself surviving longer than any of the smaller kinds of lizards studied.

Previous findings and predictions about populations of tropical lizards are partially borne out by the present findings. Conforming with trends indicated by Tinkle *et al.* (1970), most of the tropical lizards included in this study have relatively small clutches, and have a low ratio of viviparous to oviparous kinds compared with some from the temperate zone. However, the lack of correlation between size of female and number of eggs per clutch reported by Tinkle *et al.* is not borne out. Most of the species were found to conform to the strategy of early maturity and multiple broods. Only one of the 15, *Ctenosaura similis,* definitely conforms to the opposite strategy of late maturity and single broods. Appraised by some of the main criteria of *r*-selection and *K*-selection, no species of the 15 is fully committed to either type; instead all are intermediate in some degree, with a majority favoring *r*-selection.

RESUMEN

Poblaciones salvajes de 15 especies de lagartos fueron estudiadas en 14 localidades en Costa Rica; los lugares de estudio incluyen un amplio rango de altitudes, habitats y climas. Estudios de marca y recaptura fueron llevados a cabo por un período de tres años para la mayoría de las especies. En la mayoría de las localidades dos o más especies fueron estudiadas simultáneamente; por lo tanto los resultados proporcionan una base para comparaciones intraespecíficas e interespecíficas.

A diferencia de los lagartos de las zonas templadas, las especies tropicales incluidas en este estudio son activas durante todo el año; sin embargo, casi todas muestran periodicidad en sus ciclos anuales. Las diferentes estructuras de las poblaciones resultan mayormente de la regulación del tiempo de reproducción y la tasa de desarrollo y sobrevivencia de las cohortes de jóvenes producidas. En algunos tipos la estructura de las poblaciones cambiaba marcadamente en respuesta a cambios periódics en el clima. Componentes reconocibles de poblaciones individuales fueron machos y hembras adultos, e inmaduros a varios niveles de desarrolo. La distancia (cabeza-tronco) está altamente correlacionada con la edad en los inmaduros; hay menor correlación en los adultos porque el crecimiento continua despues de la madurez.

En base a las estructuras de sus poblaciones, reproducción y supervivencia, las especies estudiadas pueden ser agrupadas en una serie gradual de aquellos de tamaño pequeño, temprana madurez, alta producción, y rápido reemplazo, a aquellos que son grandes, y que tienen madurez tardía, baja producción y reemplazo lento. Cuatro tipos de estructuras de poblaciones bastante diferenciables pero sobreponibles pueden ser reconocidas en este rango. El tipo 1 está confinado a climas sin contrastes de estaciones y resulta de reproducción durante todo el año a un nivel uniforme. La estructura de la población es estable e incluye individuos de todas las edades en proporciones invariables. Este tipo está bien representado por *Anolis tropidolepis* de selvas nubladas de montaña, y menos perfectamente por *A. humilis,* probablemente *A. lionotus,* y por *Gonatodes albogularis,* todos de las selvas lluviosas del Caribe. El tipo 2 tambien tiene reproducción durante todo el año con todas las edades representadas en la población durante todo el tiempo, pero el nivel de reproducción y las proporciones de diferentes grupos de edades cambian constantemente con los cambios de estaciones. Este tipo ocurre en climas húmedos que tienen un cambio de estaciones moderado y fué encontrado desarrollado en varios grados en *Ameiva quadrilineata, Anolis limifrons, Basiliscus vittatus,* y *Leiolopisma cherriei.* El tipo 3 es característico de áreas que tienen una larga estación seca, donde los lagartos confinan su reproducción a las partes más húmedas del año. Al comienzo del período de cría la población consiste esencialmente de adultos en capacidad de reproducirse, pero incrementos subsecuentes de los jóvenes son añadidos hasta que todas las clases desde reciente nacido hasta adolescentes son hallados junto con adultos (entonces disminuidos a pequeños números) al comienzo de cada período de cría. El tipo 3 prevalece en el noreste de Costa Rica y se encuentra en *Anolis cupreus, A. intermedius, Basiliscus basiliscus, Cnemidophorus deppii, Gonatodes albogularis, Sceloporus variabilis,* y *S. malachiticus.* Esta última especie es una transición con el tipo 4 que de otra forma fué hallado solamente en la iguanida grande, *Ctenosaura similis.* En el tipo 4 hay un período relativamente corto de cría y madurez tardía resultando en una marcada estructura de población que consiste de varios o muchos grupos discretos de edades al menos dos de los cuales son inmaduros. La supervivencia fué estimada de la razón a la cual los individuos marcados desaparecían de las poblaciones en las pequeñas áreas estudiadas, pero parte del reemplazo fué causado por desplazamientos de individuos, y este desplazamiento de espacio no pudo ser evaluado con precisión. En la mayoría de las especies el reemplazo de la población fué rápido, con casi todos los individuos reemplazados en el curso de un año. Fué esencialmente rápido en las especies mas pequeñas de *Anolis,* en *Cnemidophorus deppii, Ameiva quadrilineata,* y *Sceloporus variabilis.* En contraste con estas especies la montañosa *Anolis tropidolepis* y las dos especies de basiliscos son notablemente de vida más larga e individuos frecuentemente sobreviven por más de un año. *Ctenosaura similis* está claramente en una clase por sí misma sobreviviendo por mayor tiempo que cualquiera de las especies mas pequeñas de lagartos estudiadas.

Anteriores resultados y predicciones sobre poblaciones de lagartos tropicales son parcialmente anulados por estos resultados. De acuerdo a tendencias indicadas por Tinkle *et al.* (1970) los lagartos tropicales incluidos en este estudio tienen mayormente nidadas pequeñas, y una proporción pequeña de tipos vivíparos a ovíparos comparados con algunos de las zonas templadas. Sin embargo, la falta de correlación entre el tamaño de la hembra y el número de huevos por nidada reportados por Tinkle *et al.* no fué anulado. Se halló que la mayoría de las especies se adhieren a la estrategia de temprana madurez y multiples camadas. Solo una de las 15, *Ctenosaura similis,* se adhiere definitivamente a la estrategia opuesta de tardía madurez y una única camada. Ectimadas por algunos de los criterios fundamentales de selección-*r* y selección-*K* ninguna de las 15 especies puede ser catalogada como una u otra, pero todas fueron intermedias en algún grado, con una mayoría favoreciendo selección-*r*.

LITERATURE CITED

Alcala, A. C., and W. C. Brown
1967. Population ecology of the tropical scincoid lizard, *Emoia atrocostata,* in the Philippines. Copeia, 1967 (3):596-604.

Asana, J. J.
1931. The natural life history of *Calotes versicoor* (Boulenger) the common blood-sucker. Jour. Bombay Nat. Hist. Soc., 34:1041-1047.

Baker, J. R.
1947. The seasons in a tropical rain-forest. Part 6. Lizards (*Emoia*). Jour. Linn. Soc. London, 41(279):243-247.

Blair, W. F.
1960. The rusty lizard, a population study. University of Texas Press, Austin, xvi+185 pp.

Bustard, H. R.
1968. The ecology of the Australian gecko *Heteronotia binoei* in northern New South Wales. Jour. Zool., 156(4):483-497.
1969. The population ecology of the gekkonid lizard *Gehyra variegata* (Duméril and Bibron) in exploited forests in northern New South Wales. Jour. Animal Ecol., 38:35-51.

CARPENTER, C. C.

1960. Parturition and behavior at birth of Yarrow's spiny lizard (*Sceloporus jarrovi*). Herpetologica, 16(2):137-138.

DOBZHANSKY, T.

1951. Genetics and the Origin of Species. Columbia Univ. Press, New York.

FITCH, H. S.

1954. Life history and ecology of the five-lined skink, *Eumeces fasciatus.* Univ. Kansas Publ. Mus. Nat. Hist., 8:1-156.

1956. An ecological study of the collared lizard (*Crotaphytus collaris*). *Ibid.,* 8:213-274.

1958. Natural history of the six-lined racerunner (*Cnemidophorus sexlineatus*). *Ibid.,* 11:11-62.

1970. Reproductive cycles of lizards and snakes. Misc. Pub. Mus. Nat. Hist. Univ. Kansas, 52:1-247.

1972. Ecology of *Anolis tropidolepis* in Costa Rican cloud forest. Herpetologica, 28:10-21.

1973. A field study of Costa Rican lizards. Univ. Kansas Sci. Bull., 50:39-126.

FITCH, H. S., and H. W. GREENE

1965. Breeding cycle in the ground skink. *Lygosoma laterale.* Univ. Kansas Publ. Mus. Nat. Hist., 15:565-575.

GREENE, H. W.

1969. Reproduction in the Middle American skink, *Leiolopisma cherriei* (Cope). Herpetologica, 25:55-56.

HALL, R. J.

1971. Ecology of a population of the Great Plains skink (*Eumeces obsoletus*). Univ. Kansas Sci. Bull., 59:357-388.

HARRIS, V. A.

1964. The life of the rainbow lizard. Hutchison Tropical Monographs, Hutchison and Co., Ltd., London, 174 pp.

HENDERSON, R. W.

1973. Ethoecological observations of *Ctenosaura similis* (Sauria: Iguanidae) in British Honduras. Jour. Herpetology, 7(1):27-33.

HIRTH, H. F.

1963. The ecology of two lizards on a tropical beach. Ecol. Monogr., 33:83-112.

INGER, R. F., and B. GREENBERG

1966. Annual reproductive patterns of lizards from a Bornean rain forest. Ecology, 47(6):1007-1021.

LEVINS, R.

1968. Evolution in changing environments. Monographs in population biology, No. 2. Princeton Univ. Press, New Jersey, ix+120 pp.

MACARTHUR, R. H.

1972. Geographical ecology: Patterns in the distribution of species. Harper & Row, Inc., New York, xviii+269 pp.

MACARTHUR, R. H., and E. O. WILSON

1967. The theory of island biogeography. Princeton Univ. Press, Princeton, New Jersey.

MARION, K. R. and O. J. SEXTON

1971. The reproductive cycle of the lizard *Sceloporus malachiticus* in Costa Rica. Copeia, 1971(3):517-526.

MARSHALL, A. J., and R. HOOK

1960. The breeding biology of equatorial vertebrates: reproduction of the lizard *Agama agama lionotus* Boulenger at Lat. 0° 01′ N. Proc. Zool. Soc. London, 134:197-205.

MAYHEW, W. W.
1964a. Photoperiodic responses in three species of the lizard genus *Uma.* Herpetologica, 20:95-113.
1964b. Reproduction in the sand-dwelling lizard *Uma inornata. Ibid.,* 21:39-55.
1966a. Reproduction in the psammophilous lizard *Uma scoparia.* Copeia, 1966(1):114-122.
1966b. Reproduction in the arenicolous lizard *Una notata.* Ecology, 47(1): 9-18.
MILLER, M. R.
1951. Some aspects of the life history of the yucca night lizard, *Xantusia vigilis.* Copeia, 1951(2):114-120.
MONTANUCCI, RICHARD R.
1968. Comparative dentition in four iguanid lizards. Herpetologica, 24:305-315.
PANDHA, S. K., and J. P. THAPLIYAL
1967. Egg laying and development in the garden lizard, *Calotes versicolor.* Copeia, 1967(1):121-125.
PIANKA, E. R.
1970. On *r* and *K* selection. American Naturalist, 100:592-597.
1971. Ecology of the agamid lizard *Amphibolurus isolepis* in western Australia. Copeia, 1971(3):527-536.
SANYAL, M. K., and M. R. N. PRASAD
1967. Reproductive cycle of the Indian house lizard, *Hemidactylus flaviviridis* Rüppell. Copeia, 1967(3):627-633.
SEXTON, O. W., H. F. HEATWOLE, and E. H. MESETH
1963. Seasonal population changes in the lizard, *Anolis limifrons,* in Panama. Amer. Midl. Nat., 69:482-491.
SEXTON, O. W., E. P. ORTLEB, L. M. HATHAWAY,
R. E. BALLINGER, and P. LICHT
1971. Reproductive cycles of three species of anoline lizards from the Isthmus of Panama. Ecology, 52:201-215.
SMITH, R. E.
1968. Studies on reproduction in Costa Rican *Ameiva festiva* and *Ameiva quadrilineata* (Sauria: Teiidae). Copeia, 1968:236-239.
TINKLE, D. W.
1967. The life and demography of the side-blotched lizard, *Uta stansburiana.* Misc. Publ. Mus. Zool. Univ. Michigan, 132:1-182.
TINKLE, D. W., H. M., WILBUR, and S. G. TILLEY
1970. Evolutionary strategies in lizard reproduction. Evolution, 24(1): 55:74.
TURNER, F. B., J. R. LANNOM, JR., P. A. MEDICA, and G. A. HODDENBACH
1969. Density and composition of fenced populations of leopard lizards (*Crotaphytus wislizenii*) in southern Nevada. Herpetologica, 25 (4):247-256.
WILHOFT, D. C.
1963. Reproduction in the tropical Australian skink, *Leiolopisma rhomboidialis.* Amer. Midl. Nat., 70(2):442-461.
WILHOFT, D. C., and E. O. REITER
1965. Sexual cycle of the lizard, *Leiolopisma fuscum,* a tropical Australian skink. Jour. Morph., 116(3):379-387.

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SYSTEMATICS OF THE GENUS *RHOGEESSA* (CHIROPTERA: VESPERTILIONIDAE)

By

RICHARD K. LAVAL[1]

The several species of Neotropical bats of the vespertilionid genera *Rhogeessa* and *Baeodon* include some of the smallest of living mammals, although one species approaches in size the common big brown bat, *Eptesicus fuscus,* of North America. Most of the species occur at low elevations, in habitats ranging from desert scrub to rain forest, and appear to be insectivorous. They range from the lowlands of northern México to southern Brasil, but are poorly represented in collections from South America south of Venezuela and Colombia.

Allen (1866) described the genus *Rhogeessa* including two species, *R. parvula* and *R. tumida.* He implied close relationships of *Rhogeessa* with *Nycticejus* [=*Nycticeius*], *Nyctinomus* [=*Tadarida*], and with the Noctilionidae. Dobson (1878) referred *Rhogeessa* to a subgenus of the genus *Vesperugo* [=*Vespertilio*]. However, Thomas (1892) retained *Rhogeessa* as a full genus, and stated that it was most closely related to *Nycticejus* [=*Nycticeius*]. Subsequently, Miller (1897) and others have followed Thomas. Miller (1906) erected a new genus, *Baeodon,* for *Rhogeessa alleni* Thomas. Although Simpson (1945) included *Baeodon* in *Rhogeessa,* other recent authors, including Tate (1942), Hall and Kelson (1959), and Koopman and Cockrum (1967) have retained them as separate genera.

The eight nominal species of *Rhogeessa* were described in the following sequence: *R. parvula* (Tres Marías Islands, Nayarit) and

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[1] Adjunct Professor, Department of Systematics and Ecology, and Research Associate, Museum of Natural History, University of Kansas. (Present address: Organization for Tropical Studies, Universidad de Costa Rica, Ciudad Universitaria, Costa Rica, C.A.)

R. tumida (Veracruz) by H. Allen in 1866; *R. alleni* (Jalisco) by Thomas in 1892; *R. minutilla* (Margarita Island) and *R. gracilis* (Puebla) by Miller in 1897; *R. io* (Venezuela) and *R. velilla* (Ecuador) by Thomas in 1903, and *R. bombyx* (Colombia) by Thomas in 1913. Hall (1952) reduced *R. tumida* to a subspecies of *R. parvula*, an arrangement followed by Hall and Kelson (1959) and several authors prior to 1959. No new taxa were described in the genus *Rhogeessa* until Goodwin's (1958) revision, in which he named three subspecies, *R. tumida major* (Oaxaca), *R. tumida riparia* (Venezuela), and *R. parvula aeneus* (Yucatán). At the same time he included *R. bombyx* as a subspecies of *R. tumida*, and reduced *R. minutilla*, *R. io*, and *R. velilla* to subspecies of *R. parvula*.

The distributional ranges Goodwin gave for the seven subspecies he recognized suggest a montage of isolated subspecies, some separated by gaps of over 1500 miles. On the basis of my preliminary examination of specimens in the Museum of Natural History at the University of Kansas, I concluded that his taxonomic arrangement failed to elucidate the actual intra- and interspecific relationships within the genus. Comments made by Alvarez and Aviña (1965) and by Jones, *et al.* (1971) also suggest the need for a revision of the genus *Rhogeessa*. Therefore, with the 650 specimens now available, I have undertaken a new revision, employing multivariate statistical analyses.

MATERIALS AND METHODS

A total of 653 specimens of *Rhogeessa* was examined. Included were 8 *alleni* (2 bacula), 350 *R. tumida* (43 bacula), 160 *R. parvula* (28 bacula), 112 *R. minutilla* (11 bacula), 9 *R. gracilis* (4 bacula) and 14 (1 baculum) of an unnamed species. Although a substantial number of juvenal specimens was encountered, no more than one per locality was included in the total number of specimens examined. Because many important specimens are preserved in alcohol, skulls from these specimens were removed and cleaned.

I examined the following holotypes: *R. gracilis; R. tumida; R. tumida major; R. tumida riparia; R. parvula; R. parvula aeneus; R. minutilla.* Holotypes of *R. alleni, R. bombyx, R. io,* and *R. velilla* were examined for me by J. E. Hill of the British Museum of Natural History. C. O. Handley of the National Museum of Natural History generously made available to me his notes on the holotypes of *R. io*, as compared with various specimens in the NMNH. Topotypes of *R. velilla* and *R. parvula* were examined by me.

I recorded all available label and field note information, plus three external measurements, length of fur, nine cranial measurements, three bacular measurements, color of dorsum and of venter, presence or absence of sagittal crest, age (adults: phalangeal epiphyses ossified; juveniles: epiphyses not ossified) and toothwear (1—none; 2—present but scarcely noticeable; 3—easily noticeable on canines and molars, but little cusp detail obscured; 4—heavy, much cusp detail obscured). Measurements were taken following in general the methods outlined by Handley (1959), with exceptions or additions as noted below: forearm (FA); third metacarpal (3MC); tibia (from center of knee joint to point of attachment of calcar to ankle); fur (greatest length in center of dorsum); greatest length of skull (GLS—including incisors); depth of braincase (DB); postorbital width (POW); mastoid width (MW); width across second upper molars (M2-M2); width of second upper molar (M2—as measured with ocular micrometer); maxillary toothrow (MAX); mandibular toothrow (MAND); measurements of bacular length, depth, and width follow LaVal (1973, Fig. 1).

A set of nine specimens (Table 1) was chosen as color standards and matched to named colors from Ridgway (1912). Unfortunately certain specimens, notably those from northwestern Venezuela, fell outside the limits of variation delimited by the color standards; these were compared directly with Ridgway (1912).

TABLE 1. Colors from Ridgway (1912) applied to specimens used as color standards (tip color only).

Specimen no.	Color no.	Dorsum	Venter
TCWC 19756	1	Fuscous-Black	Buffy Brown
KU 102619	2	Hair Brown	Cartridge Buff
KU 29886	3	Tawny-Olive	Light Ochraceous-Buff
KU 107494	4	Buffy Brown	Cartridge Buff
KU 105565	5	Buckthorn Brown	Light Ochraceous-Buff
KU 90754	6	Pinkish Cinnamon	Cinnamon Buff
UNM 27545	7	Warm Buff	Light Ochraceous-Buff
KU 97050	8	*ca.* Light Ochraceous-Buff	Pinkish Buff
KU 61171	9	Dresden Brown	Light Ochraceous-Buff

Karyotypes were not examined by me, but I have seen partial results of a study of karyotypic variation in the genus now being conducted by R. J. Baker (pers. com.) and his students. Baker and Patton (1967) documented the differences in karyotypes between *R. tumida* from Chiapas and *R. parvula* from Sonora and Nayarit. Specimens identified by Baker and Patton as *R. gracilis* are not of that species (Baker, pers. com.) and are almost certainly *R. parvula*, collected at the opposite end of the long cline beginning in Sonora.

Scanning electron micrographs were made of hairs from the mid-dorsal region of specimens of each species. Because the appearance of *Rhogeessa* hairs varies substantially depending on the angle of view and the portion of the hair photographed, all photographs were made of the mid-section of each hair; the hair was oriented so that the side of the scales bearing the V-shaped depression in the rim would face the film. Polaroid negatives (4 × 5 in) were exposed for 70 seconds on a ETEC Autoscan scanning electron microscope, made available to me by the Department of Entomology, Kansas State University, Manhattan.

Penes were removed from 89 of the males examined, and cleared and stained to reveal the bacula, using Anderson's (1960) method. Bacula were measured with an ocular micrometer.

All data recorded were punched on IBM cards, and statistical analyses performed on the GE 635 computer at the University of Kansas Computation Center. Although *t*-tests performed between the sexes indicated a significant level of sexual dimorphism for some measurements at some localities, the small sample sizes prevalent in this genus made separation of the sexes impractical. Samples usually contained a fairly well-balanced proportion of the two sexes, which would tend to offset any possible bias due to sexual dimorphism.

Gabriel's Sum of Squares Simultaneous Testing Procedure (SS-STP) was performed, first with all species in the same analysis, and then each species was analyzed separately. An SS-STP program available at the University of Kansas Museum of Natural History (as modified by Gary Powers) gives 13 standard statistics, calculates and lists non-significant subsets, and prints these in graphic form, with means in descending sequence (Figs. 10, 11, 13). The SS-STP procedure, as related to systematics, is discussed by Smith (1972), who lists some of the more important literature references.

The University of Kansas Numerical Taxonomy Program (NT-SYS) developed by E. J. Rohlf, J. Kishpaugh, and R. Bartcher was utilized to give the following statistical information: 1) standardized data correlations between localities and a two-dimensional phenogram based on these; 2) cophenetic correlation, in which cophenetic values are plotted on scatter diagrams against the correlation coefficients used in the phenogram; 3) standardized data distances between localities, and a two-dimensional phenogram based on these; 4) a second cophenetic correlation, plotting cophenetic values against distance coefficients; 5) a principal component analysis in which the first five principal components are calculated; 6) a Varimax Factor Rotation by the Kaiser Method; and 7) the variance-covariance matrices projected onto the principal components (both rotated and non-rotated), and two-dimensional scattergrams plotting each of the principal components against each of the others.

A stepwise discriminant analysis was also carried out, using the University of California BMD07M program; this program identifies each individual specimen based on the criteria derived from the analysis. It computes canonical correlations and coefficients for canonical variables, and plots the first two canonical variables on a two-dimensional scattergram.

All of the multivariate analyses were computed using the same nine characters, all of which are skin and skull measurements made by myself. These were chosen for several reasons, one of which dealt with problems resulting from missing data. Discriminant function analysis indicated that all contributed significantly to variation observed among the samples analyzed. Other characters examined either did not contribute to variation among samples, or contributed so strongly to singling out one or more species or samples that I felt they would tend to obscure the close relationships which are typical of species within this genus. Further, I wanted to see if a multivariate analysis based on a few measurements made of morphological characters, which I would expect to be highly correlated, would support suspected relationships based on other kinds of characters (such as distribution of hair on uropatagium, size of i3, presence of cingual cusps, bacula, hair, etc.). Blackith and Reyment (1971) stated that "Where the organisms are fairly closely related, and all the measurements are quantitative, ... Satisfactory analyses have been made with as few as three to six characters, although ten might be regarded as more optimal. . . ."

In the analyses performed by the NT-SYS program, only sample means were utilized. To help assure that means used would be representative of the geographic area which they represented, several small samples often were pooled (for example, several samples of one or two specimens each from various localities on the Caribbean slope of Honduras were combined). In other cases, large samples from a single locality were utilized. The areas from which each of the samples was taken, along with the abbreviations used in this paper, are as follow: Tamaulipas, coast (Tamp 1); Tamaulipas, interior (Tamp 2); San Louis Potosí (SLP); Veracruz, northern (VC-N); Veracruz, central (VC-C); Veracruz, southern (VC-S); Campeche (Camp); Yucatán and northern Quintana Roo (Yuc); Chiapas, Pacific Coast (Chiapas); Oaxaca, Pacific slope (Oax); Guerrero (Guer); Michoacán (Mich); Colima (Colima); Jalisco (Jal); Nayarit (Nay); Sinaloa, southern (Sin-S); Sinaloa, central (Sin-C); Sonora (Son); Guatemala, Pacific Coast (Guat); El Salvador (El Salv); Honduras, Caribbean slope (Hond); Nicaragua, Caribbean slope (Nic); Costa Rica, Interior (CR); Panamá, Pacific slope (Pan); Colombia, north (Colomb); Venezuela, northwest (Venez-NW, 1-5); Venezuela, coast (Venez-C, 1-2); Venezuela, interior (Venez-int); Venezuela, northeast (Venez-NE); Trinidad (Trin); Guyana (Guyana). All specimens of *R. gracilis*, *R. alleni*, and the unnamed species are pooled into single samples.

Fewer samples, each representing more individual samples combined into larger pooled samples, were used in the stepwise discriminant analysis, because the kind of output generated by that program would be unintelligible if a very large number of individual samples were chosen. These samples, along with their abbreviations, are as follows: Southwestern México—Oaxaca and Guerrero (SWMEX); Michoacán (MICH); West-central México—Jalisco, Colima, Nayarit, southern Sinaloa (WCMEX); Northwestern México—northern Sinaloa and Sonora (NWMEX); Eastern México—Tamaulipas, San Luis Potosí, and Veracruz (EMEX); Northern Yucatan Peninsula (YUC); Central America—Tabasco through Panamá, excluding Caribbean slope from Nicaragua to Panamá (CENTAM); Caribbean slope from Nicaragua to Panamá (NICPAN); Northern Colombia (COLOMB); Northern Venezuela (VENEZ); Arid northwestern Venezuela and extreme northeastern Colombia (DRYVEN); Guyana (GUYANA); Trinidad (TRIN); all *R. gracilis* (GRACIL); all *R. alleni* (ALLENI); all specimens of the unnamed species (MIRA).

Although sexual dimorphism in size was detected within some samples, *t*-tests did not show it to be consistently significant. On the average, females are as much as 4% larger than males. However, in *R. minutilla* from Venezuela, males are slightly larger on the average.

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ANALYSIS OF CHARACTERS

Goodwin (1958), in his revision of the genus *Rhogeessa,* stated that the genus (exclusive of *Baeodon*) could be separated into three species: "a big eared species with thin flying membranes [*gracilis*], a large species with short ears and thick membranes [*tumida*], and a small species [*parvula*]." He further stated that "The proportionate length of the forearm and color of the pelage cannot be relied on as determining factors except in a very general way. Cranial measurements can also be confusing unless accompanied by comparative material." As might be anticipated from these introductory remarks, Goodwin did not state clearly how to distinguish among *parvula, tumida,* and the various subspecies into which he divided them.

As suggested by Goodwin, skin and skull measurements are inadequate for distinguishing among species, except in the case of *R. alleni,* which is larger in most cranial variates than any other species examined, and the new species, *R. mira,* which is smaller than any specimens of *R. parvula* from Michoacán or adjoining states. However, in the multivariate analyses, notably the principal component analysis, the canonical variate analysis, and the discriminant function analysis, the measurements taken were adequate to discriminate many of the samples from each other (see table 4, and Figs. 4, 7, 8, 12). The discriminant function analysis indicated that greatest length of skull and forearm were the best and second best discriminators, respectively. Thus, I chose these two variables to demonstrate geographic variation by means of univariate analyses.

Color of fur.—Variation in relative positions of light and dark bands seems to separate *alleni* and *gracilis* from all other species. Individual variation in contrast between bases and tips renders pelage coloration of limited usefulness in identification of individual specimens of the other four species, but differences are evident when series are compared. Molting individuals take on a grayish cast because dark gray hairs grow up throughout the old pelage before it is shed. Thus, newly molted individuals are much darker in color than individuals in old pelage. In the species which have pale bases and darker tips, individual color variation is accounted for primarily by differences in tip color, whereas color differences among samples and species typically result from variation in basal color.

Length of fur.—Although some individual variation in fur length occurs, this character is sufficiently constant within a population to separate certain species, and to illustrate geographic variation among populations in a single species.

Distribution of fur on uropatagium.—This character evidences so little individual variation that it is a fairly reliable means of separating one of the species from the other five species.

Degree of toothwear.—Toothwear was negligible in about 90 percent of specimens examined, except in the case of *R. minutilla,* in which more than 35 percent of the specimens had moderate to heavy toothwear.

Lingual cingulum of C1.—In all species except *gracilis* and *mira* two (rarely one) cusps are present on the lingual cingulum of the C1. These cusps are variable in development, from higher and sharper than the example shown in figure 1A, to lower and more rounded. They tend to be obscured in individuals with heavy toothwear. In the species lacking cusps, the cingulum is perfectly smooth and straight, lacking even the slightest swelling (Fig. 1B).

Bacula.—With the exception of *R. alleni,* bacula of the various species are not sharply differentiated from each other. Although

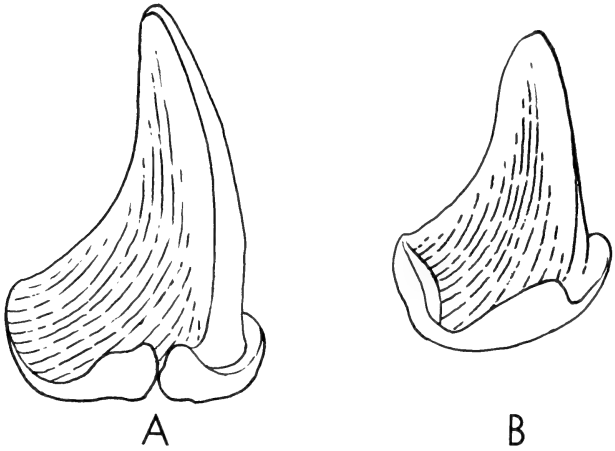


Fig. 1. Upper right canine of two species of *Rhogeessa,* lingual view. A. *R. parvula,* UA 10319, Jalisco; B. *R. mira,* UNAM 8594, Michoacán. ×25.

bacular shape shows substantial geographic and individual variation within species, it also seems to differ among species in areas of sympatry and near sympatry (Fig. 2). Single bacula of *parvula, tumida, gracilis,* and *alleni* were illustrated and described by Brown, *et al.* (1971), but these authors did not examine bacular variation.

Microstructure of hair.—Benedict (1957) examined hairs from

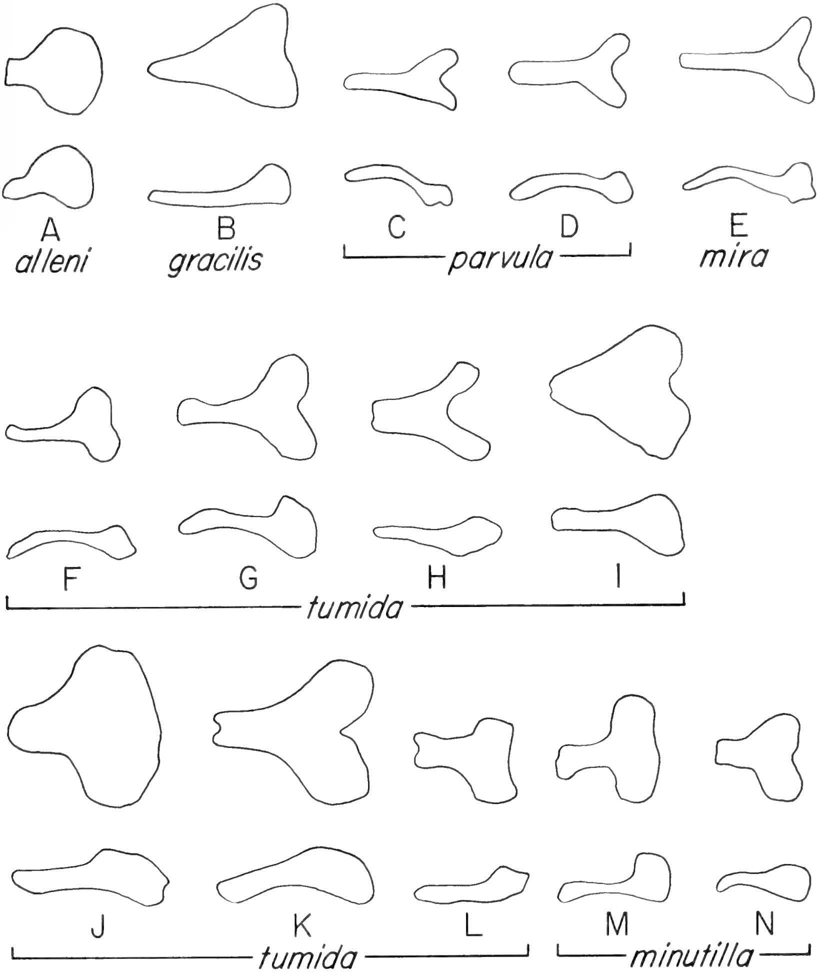


FIG. 2. Top and lateral outline views of bacula of 14 specimens of *Rhogeessa.* A. *R. alleni,* KU 97307, Michoacán; B. *R. gracilis,* KU 92951, Jalisco; C. *R. parvula,* KU 97080, Sinaloa; D. *R. parvula,* UNAM 8865, Guerrero; E. *R. mira,* UNAM 8953. Michoacán; F-L, all *R. tumida:* F. KU 55172, Tamaulipas; G. KU 82923, Veracruz; H. LACM 18683, Chiapas; I. TCWC 24127, Nicaragua; J. MVZ 113936, Colombia; K. KU 119073, Venezuela; L. AMNH 66824, Ecuador; M. *R. minutilla,* NMNH 441783, Venezuela; N. *R. minutilla,* NMNH 441805, Venezuela. ×25.

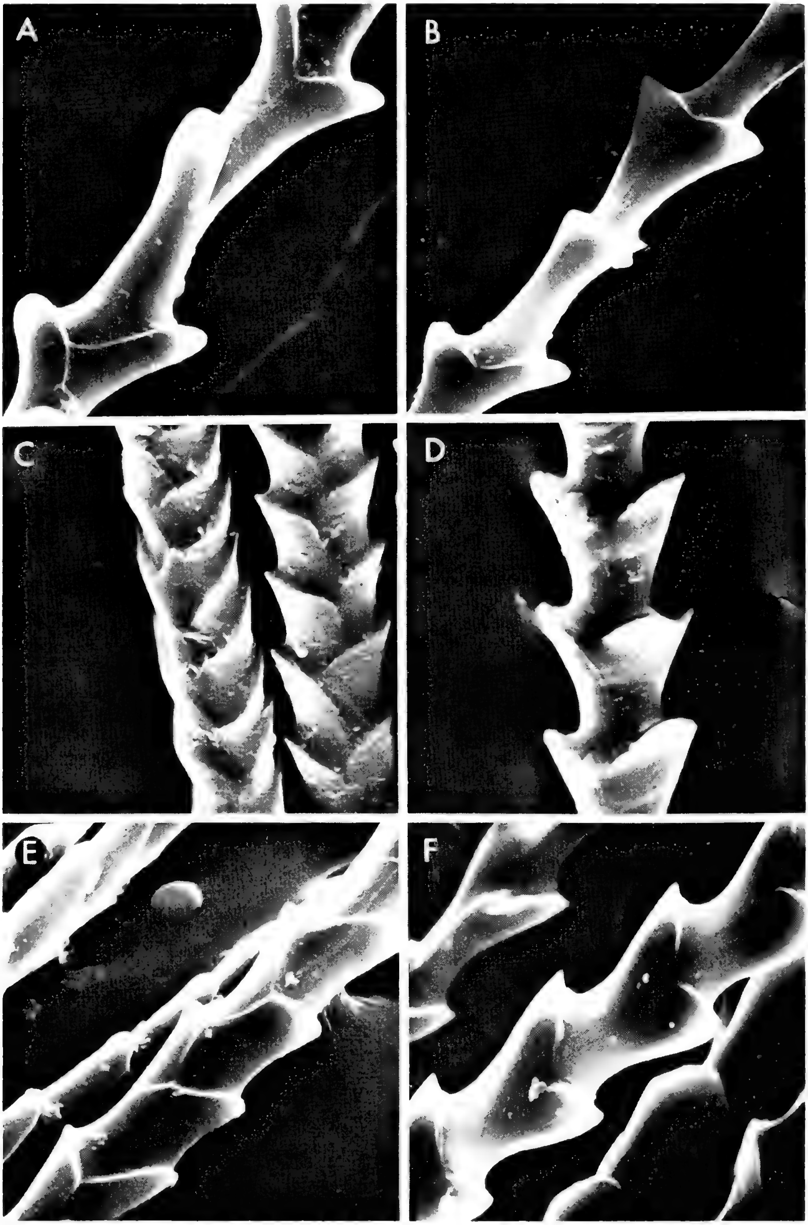


FIG. 3. Scanning electron micrographs of hairs of six species of *Rhogeessa*. A. *R. mira,* UNAM 8593, Michoacán; B. *R. parvula,* KU 107494, Jalisco; C. *R. minutilla,* AMNH 130673, Venezuela; D. *R. alleni,* KU 61171, Oaxaca; E. *R. tumida,* KU 119073, Venezuela; F. *R. gracilis,* KU 97050, Jalisco. ×1400.

most of the known genera of bats, including hairs from a specimen of *R. parvula.* Unfortunately, she neither illustrated a hair from *Rhogeessa* nor stated where the specimen was captured, and she had only a light microscope at her disposal. Benedict (1957) and Quay (1970) implied that hair structure was most useful as a taxonomic tool at the generic and suprageneric levels. Although the relationship (if any) of geographic, sexual, age, and individual variation to hair structure cannot be evaluated here because of small sample sizes, it is evident (Fig. 3) that there are differences in hair structure among species of *Rhogeessa.*

The two similar lowland species of western México, *R. mira* and *R. parvula,* differ from all other species in that each scale is rotated 90° along its linear axis, in relation to adjoining scales; in the other species scales are in alignment with each other. Based on hair structure, two other groupings seem to be evident. In *R. alleni* and *R. gracilis* the scales appear to be cone-shaped rings which are bilaterally symmetrical, subtending a full 360° (the coronal scales of Benedict). In *R. tumida* and *R. minutilla* the scales are alternate and overlapping (imbricate scales of Benedict) with the visible portion subtending an angle of 180° or perhaps slightly greater.

SYSTEMATIC ACCOUNTS

Rhogeessa H. Allen, 1866

Rhogeessa H. Allen, 1866:285 [Type species.—*Rhogeessa parvula* H. Allen, 1866, designated by G. S. Miller, 1897 in accordance with page priority].

Baeodon G. S. Miller, 1906:85 [Type species.—*Rhogeessa alleni* Thomas, 1892, by original designation]. Valid as a subgenus.

Description.—As given by H. Allen (1866) and G. S. Miller (1897) except as noted below. Skull drawings appear in Hall and Kelson (1959; *R. parvula*) and G. S. Miller (1897; *R. tumida*); skull photographs are included by Goodwin and Greenhall (1961; *R. tumida* and *R. minutilla*). The i3 varies in size from minute (visable only under magnification) to only slightly smaller than i2; i1 and i2 tricuspid, with outer cusp much lower than other two cusps; i3 bicuspid or unicuspid; lingual cingulum of C1 well developed, usually with accessory cusps; parastyle, paracone, protocone, and first and second commissures are only structures present on M3; width of posterior half of m3 substantially less than width of anterior half; maxillary cheek teeth converging anteriorly; basisphenoid pits absent; rostrum narrower than braincase; membranes relatively thin; baculum saddle-shaped at proximal end, with well-developed proximal lateral knobs, poorly-developed proximal median knob, and long, usually narrow shaft, circular or elliptical in cross section near distal end; length 0.50 to 0.80 mm; penis short, 3-4; baculum extends to within 0.5 of distal end of penis.

Table 2. Measurements of individual and pooled samples from selected localities, arranged to demonstrate geographic variation. Mean±2 standard errors of the mean.

	FA	3MC	GLS	DB	POW	MW	M2M2	C1C1	MAX
				R. alleni					
W. Mexico	33.0±.78	31.9±.82	15.0±.16	5.4±.11	3.2±.05	7.8±.12	6.0±.14	4.3±.13	5.4±.08
				R. gracilis					
W. Mexico	32.1±.88	30.4±.78	13.5±.29	4.8±.17	3.1±.13	6.7±.22	4.9±.15	3.4±.14	4.6±.09
				R. parvula					
Oaxaca	31.2±.78	30.0±.66	13.5±.20	4.8±.16	3.2±.07	7.1±.14	5.4±.07	3.7±.17	4.8±.08
Guerrero	30.5±.43	29.4±.48	13.3±.14	4.8±.12	3.1±.07	6.9±.12	5.3±.10	3.6±.09	4.7±.06
Michoacán	29.9±.84	28.6±.64	13.0±.09	4.7±.08	2.9±.15	7.1±.10	5.3±.07	3.8±.07	4.7±.04
Colima	28.9±.43	28.0±.39	12.6±.15	4.6±.10	3.1±.06	6.8±.11	5.2±.07	3.6±.05	4.4±.07
Jalisco	28.6±.67	27.3±.53	12.7±.17	4.6±.10	3.1±.07	6.8±.12	5.0±.09	3.6±.06	4.4±.07
Nayarit	27.5±.34	26.6±.35	12.2±.11	4.5±.08	3.1±.07	6.6±.08	4.9±.06	3.4±.04	4.2±.06
Sinaloa-S	28.1±1.01	26.7±.82	12.2±.12	4.4±.06	2.9±.04	6.6±.11	4.9±.16	3.4±.17	4.3±.17
Sinaloa-C	27.9±.33	26.8±.33	12.3±.18	4.4±.10	3.0±.05	6.5±.08	4.9±.06	3.4±.05	4.2±.07
Sonora	28.3±.53	26.8±.58	11.9±.21	4.3±.12	2.9±.04	6.3±.08	4.8±.11	3.3±.07	4.2±.06
				R. mira					
Michoacán	26.0±.40	25.4±.42	11.4±.11	4.4±.10	2.8±.08	6.2±.10	4.6±.08	3.2±.06	3.9±.05
				R. tumida					
Tamp. 1	31.5±.47	30.9±.36	13.4±.11	5.0±.06	3.3±.07	7.0±.06	5.5±.06	3.8±.05	4.6±.06
Tamp. 2	31.6±.22	31.1±.28	13.4±.08	4.9±.05	3.3±.04	7.0±.06	5.4±.05	3.8±.04	4.7±.03
SL Potosí	30.2±.36	29.5±.37	13.1±.11	4.9±.07	3.3±.05	6.9±.07	5.4±.07	3.8±.06	4.6±.06
Veracruz-N	31.2±.76	30.5±.63	13.5±.18	5.0±.14	3.3±.06	7.0±.13	5.6±.12	3.9±.06	4.8±.06
Veracruz-C	30.1±.59	29.0±.63	13.2±.15	4.8±.11	3.4±.08	6.8±.10	5.5±.14	3.9±.08	4.7±.07
Veracruz-S	29.9±.51	29.1±.40	13.1±.13	4.8±.08	3.3±.06	7.0±.09	5.5±.07	3.9±.08	4.7±.05
Campeche	29.0±.65	28.2±.53	12.8±.19	4.7±.14	3.1±.11	6.7±.18	5.1±.12	3.6±.12	4.4±.06

TABLE 2. *Concluded.*

	FA	3MC	GLS	DB	POW	MW	M2M2	C1C1	MAX
Yucatán	27.1±.81	26.1±.67	12.4±.24	4.5±.10	3.0±.09	6.4±.08	5.0±.14	3.6±.16	4.3±.12
Chiapas	29.4±.72	28.5±.66	13.5±.21	5.0±.09	3.4±.08	7.0±.13	5.7±.10	3.8±.08	4.8±.04
Guatemala	29.2±.95	28.1±.66	12.8±.23	4.7±.12	3.3±.09	6.9±.17	5.4±.17	3.7±.13	4.5±.09
El Salvador	29.0±.52	28.0±.43	12.6±.19	4.6±.09	3.2±.08	6.8±.09	5.2±.09	3.6±.08	4.4±.08
Honduras	29.7±.69	28.8±.55	13.0±.15	4.7±.09	3.3±.09	6.8±.13	5.3±.06	3.7±.07	4.5±.05
Nic. (Carib.)	30.0±1.62	28.8±1.14	13.3±.45	4.9±.21	3.3±.11	7.1±.23	5.4±.20	3.8±.10	4.6±.13
Costa Rica	30.2±1.33	29.3±1.06	13.1±.12	4.9±.07	3.3±.06	7.0±.08	5.3±.05	3.7±.06	4.5±.06
Panamá	29.6±.50	28.3±.44	12.7±.18	4.6±.09	3.2±.05	6.8±.12	5.2±.07	3.6±.10	4.3±.06
Colombia	28.7±1.30	27.8±1.11	12.4±.22	4.5±.16	3.2±.06	6.7±.18	5.1±.12	3.5±.06	4.3±.18
Venez.NW	27.7±.47	26.9±.23	12.5±.07	4.5±.14	3.2±.07	6.6±.11	5.2±.10	3.6±.06	4.2±.10
Venez.-C	28.7±.85	27.8±.72	12.5±.23	4.5±.08	3.2±.10	6.9±.10	5.1±.16	3.6±.10	4.3±.04
Venez.-NE	28.0±.38	27.0±.50	12.7±.14	4.5±.10	3.2±.10	6.9±.19	5.2±.14	3.7±.12	4.4±.11
Venez.-Int.	28.2±.72	27.3±.69	12.6±.33	4.6±.13	3.1±.05	6.7±.10	5.1±.10	3.6±.08	4.3±.08
Trinidad	29.5±.63	27.7±.37	12.7±.42	4.6±.21	3.2±.11	6.7±.35	5.1±.17	3.6±.14	4.4±.10
Guyana	28.5±.50	27.4±.54	12.6±.13	4.6±.14	3.3±.07	6.7±.10	5.3±.05	3.6±.07	4.4±.07
R. minutilla									
Venezuela 1	26.8±.58	26.4±.66	12.5±.13	4.4±.08	3.0±.04	6.6±.10	5.0±.08	3.6±.05	4.4±.07
Venezuela 2	27.8±.49	27.0±.55	12.8±.17	4.6±.11	3.0±.06	6.8±.09	5.1±.10	3.8±.06	4.6±.09
Venezuela 3	27.0±.41	26.5±.35	12.5±.10	4.5±.06	2.9±.05	6.5±.06	5.0±.07	3.6±.05	4.4±.05
Venezuela 4	26.9±.42	26.3±.44	12.4±.12	4.4±.07	2.9±.05	6.5±.10	5.1±.09	3.6±.07	4.3±.08
Venezuela 5	27.3±.25	27.1±.20	12.9±.11	4.6±.08	3.0±.04	6.8±.06	5.1±.05	3.7±.06	4.6±.05

Comparisons.—Although *Rhogeessa* shares its dental formula with several other genera of bats, only *Nycticeius* has been suggested to be a close relative. The only diagnostic differences noted by any authors relate to the lower incisors, which are well spaced, of uniform size, and have three cusps of equal size in *Nycticeius.* In my comparison of *N. humeralis,* type species of its genus, with *Rhogeessa,* the following additional differences were observed in *Nycticeius:* mesostyle of M3 present, but low; third commissure of M3 present; width of posterior half of m3 only slightly less than width of anterior half; maxillary toothrows parallel; basisphenoid pits present; rostrum nearly as wide as braincase; membranes relatively thick; baculum with enlarged distal knob, relatively small proximal lateral knobs, and poorly developed proximal median knob (see Plate I in Hamilton, 1949); length about 2.25 to 2.6 in four specimens; penis long, about 7-8; baculum extends from midpoint of penis to a point about 1.5 short of distal end of penis. The karyotype of *N. humeralis* differs in numerous ways from those of *R. tumida* and *R. parvula* (Baker and Patton, 1967). Karl Koopman (pers. com.) checked the list of characters listed above in seven additional species of *Nycticeius* (*schlieffeni, pallidus, greyi, balstoni, rueppelli, hirundo,* and *albofuscus*). Information on bacula and karyotypes was not available. Most of the other characters seemed to be consistent among the specimens of the species examined by Dr. Koopman, except penes were seen only for *greyi, balstoni,* and *hirundo;* the mesostyle and third commissure of M3 and the relative widths of anterior and posterior halves of m3 in *rueppelli* were more like *Rhogeessa* than in other species of *Nycticeius;* basisphenoid pits were rather weakly developed in some species.

Subgenus **Baeodon** G. S. Miller, 1906

Baeodon G. S. Miller, 1906:85 [Type species.—*Rhogeessa alleni* Thomas, 1892, by original designation].

Description.—As in account of genus, except as follows: i3 unicuspid, peglike, one sixth to one eighth cross-sectional area of i2; postorbital width narrow relative to overall skull size; skull large relative to body; first phalanx of third digit long relative to third metacarpal.

Rhogeessa (Baeodon) alleni Thomas

Rhogeessa alleni Thomas, 1892:477 [Holotype.—BMNH 93.2.5.25 from Santa Rosalia, near Autlán, Jalisco, México; A. C. Buller, collector].

Baeodon alleni—G. S. Miller, 1906:85.

Holotype.—British Museum of Natural History 93.2.5.25, adult female, preserved in alcohol, faded, skull removed. Measurements in table 3.

TABLE 3. Measurements of holotypes.

	FA	3MC	TIB	FUR	GLS	DOB	POW	MW	M2M2	C1C1	MAX	MAND	M2
tumida	30.5	29.5	11.0	--	13.0	5.0	3.2	6.5	5.1	3.6	4.6	--	--
io[a]	27.9	27.2	10.9	3–4	12.0	--	3.1	--	4.9	3.3	4.3	5.3	1.3
velilla[b]	27.9	27.3	10.8	3–4	11.8	4.3	3.2	6.5	5.1	3.3	4.2	5.2	1.2
bombyx[b]	31.5	30.4	12.4	3–4	14.3	5.4	3.6	7.4	6.0	4.2	5.0	6.3	1.5
aeneus	27.9	26.7	--	4	12.4	4.6	3.0	6.6	5.0	3.4	4.2	5.3	--
riparia	28.4	28.0	10.0	4	12.7	4.4	3.3	7.2	5.4	3.8	4.4	5.4	--
parvula	28.0	26.9	--	--	--	--	2.8	--	4.6	3.3	4.0	--	--
major	31.7	29.5	12.5	6	13.4	4.9	3.0	7.1	5.5	3.9	4.8	6.0	--
mira	26.2	26.1	10.4	4	11.1	4.3	2.6	6.0	4.5	3.1	3.8	--	1.0
minutilla	25.8	25.0	10.1	5	12.2	--	3.0	--	5.1	3.6	4.5	5.3	--
alleni[b]	34.8	33.6	14.9	4–5	15.6	5.5	3.3	8.0	6.3	4.5	5.5	6.8	2.0
gracilis	33.4	30.0	13.0	6	13.6	--	3.1	--	5.0	3.3	4.7	--	--

[a] Measurements taken by J. E. Hill and C. O. Handley.

[b] Measurements taken by J. E. Hill.

Description.—A very large species of *Rhogeessa*, with tribanded dorsal fur and minute i3. Distal one fourth of dorsal hairs close to Dresden Brown, center one half buffy, and basal one fourth gray; ventrally, tips close to Light Ochraceous-Buff, bases gray; fur 4-6; dorsum of uropatagium almost bare; average ratio of third metacarpal to first phalanx of third digit 2.20:1; sagittal crest present in 8 of 9 skulls; sagittal and occipital crests form "helmet" above occiput; i3 average diameter 0.1, with little variation; cusps on lingual cingulum of C1 small, one or two in number; skull large in all dimensions except postorbital width.

Bacula.—The two *R. alleni* bacula examined are 0.44, 0.50 in length, 0.20, 0.22 in depth, and 0.44, 0.28 in width. In addition to their short lengths, these two bacula are notable for their short shaft and widely flaring proximal lateral knobs, with convex proximal margins (Fig. 2A). Although these bacula are quite distinct

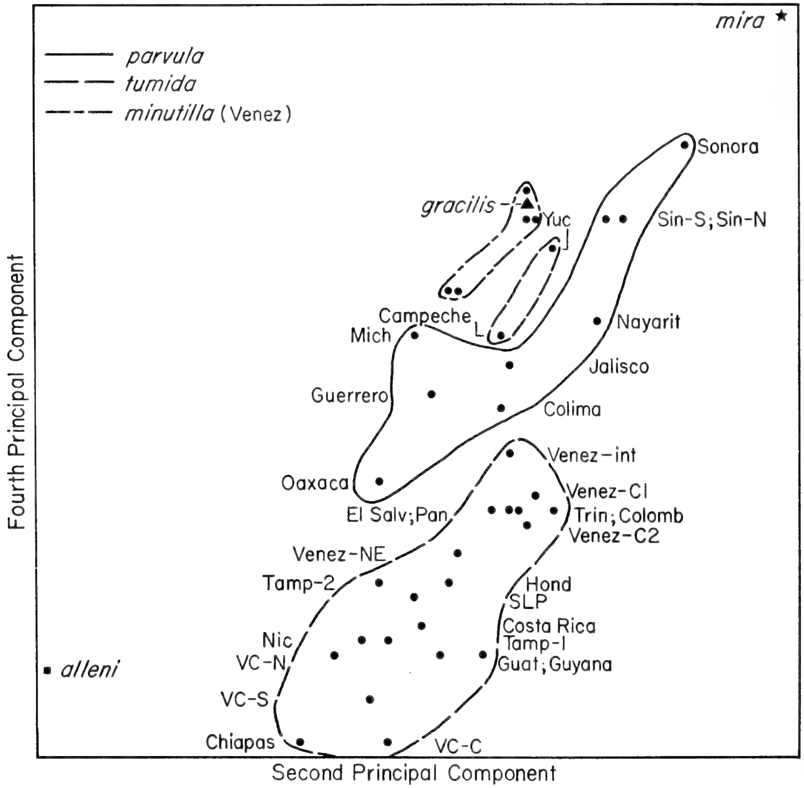


FIG. 4. Scatter diagram of second and fourth principal components of six species of *Rhogeessa*. Each symbol represents a sample mean. The symbols for *gracilis* (triangle), *alleni* (square), and *mira* (star) represent single pooled samples of all available specimens of those species.

from those of any other North American species of *Rhogeessa,* a few South American specimens of *R. tumida* possess bacula with similar development of the lateral knobs; however, the bacula have a longer shaft and greater length than those of *alleni.*

Comparison.—*Rhogeessa* (*Baeodon*) *alleni* is larger in cranial measurements (except postorbital width) than any specimens of the three species with which it occurs sympatrically in southwestern México (Table 2). Among the samples of specimens from southwestern México compared in table 2, *t*-tests showed that mean ratios of third metacarpal to first phalanx were significant between *parvula* and *alleni,* and between *gracilis* and *alleni,* at $P = < .001$, with no overlap. *Rhogeessa alleni* is separated from both by the characters given in the subgeneric description of *Baeodon.* It is easily separated from *gracilis* by the shorter ears and relatively narrow basal band of the dorsal fur; it can be easily distinguished from *parvula* by the three-banded dorsal fur (two-banded in *parvula*). In the multivariate analyses presented graphically here, Figs. 4, 6, 7, 8, 12, 14), *alleni* is distinctly separated from the other species of *Rhogeessa,* supporting assignment of that species to a monotypic subgenus. No specimens were misidentified by the discriminant function analysis (Table 4).

Distribution.—Mountains of western México, from central Oaxaca north to central Jalisco (Fig. 5). Altitudinal range from 125 m to 2000 m. Vegetation at the seven known localities seems to be either desert scrub or thorn forest. Although *R. alleni* may be more widespread than these few records indicate, it is probably restricted to western México northwest of the Isthmus of Tehuantepec.

Reproduction.—An individual caught on 6 August was not pregnant, and another female taken on 29 November was not lactating. An adult male captured on 28 March had testes 3 mm long. No juveniles were found.

Remarks.—In removing *alleni* from the genus *Rhogeessa* and erecting the genus *Baeodon* for it, Miller (1906) only mentioned a single diagnostic character, the minute i3. Relative size of teeth and even number of teeth vary within other vespertilionid genera. In *R. parvula* size of i3 is variable, and in some specimens approaches the condition observed in *R. alleni.* In most other characters, *alleni* is clearly similar to other species of *Rhogeessa,* although it has by far the largest skull of any species in the genus. For these reasons there seems to be no justification for assignment of *R. alleni* to a genus separate from *Rhogeessa.*

It should also be mentioned that the nominal species *Baeodon meyeri* Pine is not a *Rhogeessa* (see Pine, *et al.* 1971) and will not be treated in this revision.

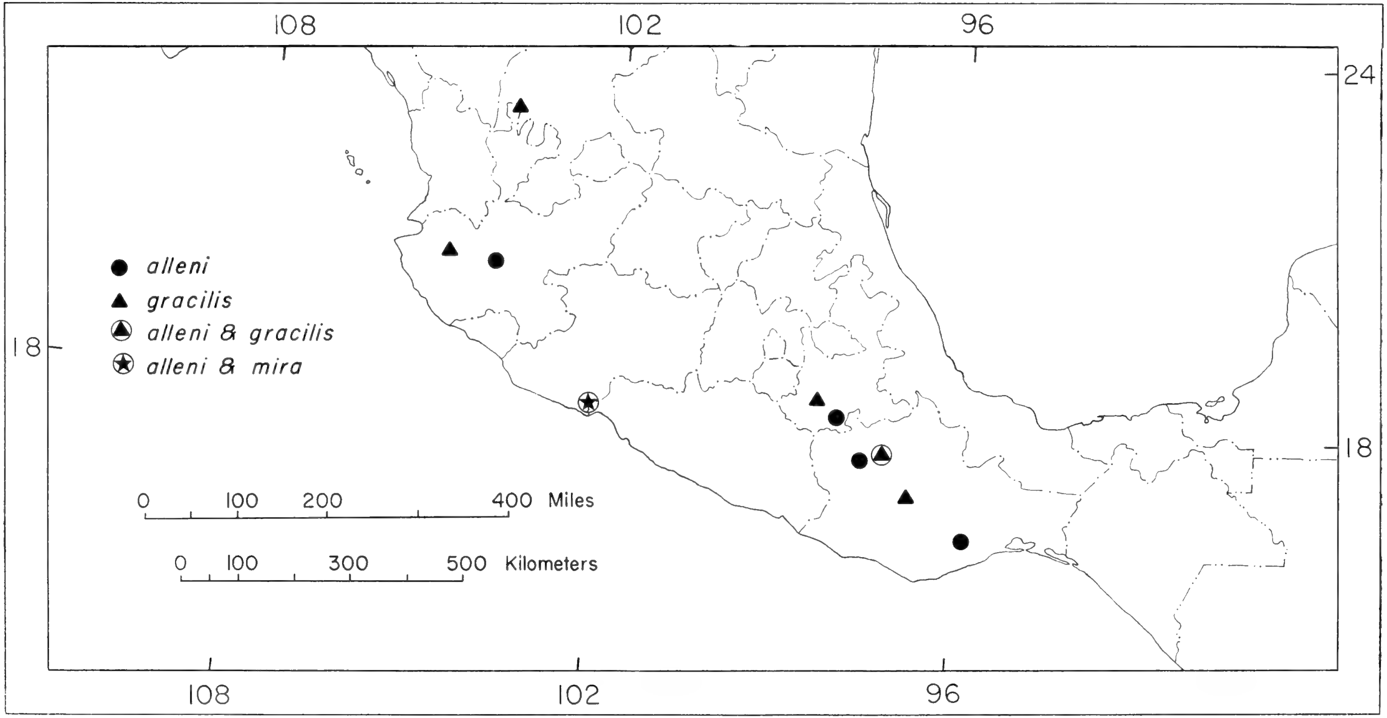


FIG. 5. Map showing localities from which were examined specimens of one or more of three species of *Rhogeessa*.

Subgenus **Rhogeessa** H. Allen, 1866

(see citation under account of genus)

Description.—As in account of genus, except that cross-sectional area of i3 always greater than one sixth cross-sectional area of i2; postorbital width wide relative to overall skull size; skull small relative to body; first phalanx of third digit usually short relative to third metacarpal.

Rhogeessa (Rhogeessa) gracilis G. S. Miller

Rhogeessa gracilis G. S. Miller, 1897:126 [Holotype.—NMNH 70694 from Piaxtla, Puebla, México, elevation 1100 m; E. W. Nelson and E. A. Goldman, collectors].

Holotype.—National Museum of Natural History 70694, adult male, preserved in alcohol with skin peeled back from skull; penis and baculum removed, cleared, and stained; baculum 0.72 in length, 0.20 in depth, 0.44 in width. Compared with KU 97050. Other measurements in table 3.

Description.—A large species of *Rhogeessa* with very long ears (average length 18, based on collectors' measurements), long, three-banded dorsal fur, and relatively narrow skull. Distal one fourth of dorsal hairs close to Light Ochraceous-Buff; center one fourth a paler buff, and basal one half dark grayish brown; ventrally, tips close to Pinkish Buff, bases dark grayish brown; fur 6-7; dorsum of uropatagium with sparse fur extending almost to knees; mean of ratios of third metacarpal to first phalanx of third digit 2.56 to 1; sagittal crest present in 7 of 8 skulls, but poorly developed, as are occipital crests; i3, 0.2 or greater in width, nearly as large as i2; lingual cingulum of C1 low, smooth, lacking cusps; skull moderate in size, but relatively narrow; slope of forehead steep; braincase inflated.

Bacula.—Measurements of four *R. gracilis* bacula: 0.72-0.80 in length, 0.16-0.28 in depth, and 0.40-0.54 in width. As viewed from above (Fig. 2B) the triangular outline of the baculum of *gracilis* differentiates it from the other three species with which it occurs sympatrically. In lateral profile the relatively straight shaft contrasts with the normally curved shaft of the other species.

Comparisons.—The large ears and unique color banding pattern allow *gracilis* to be separated easily from all other species. Likewise, the skull differs from those of other *Rhogeessa* in the relatively steeply sloping forehead, inflated braincase, and narrow lateral dimensions. In superficial appearance, the skull could be mistaken for that of a *Myotis*. In other species of the genus, the skulls are similar to those of *Eptesicus*, with respect to their widths and the slightly sloping foreheads, and their tendency to form a supraoccipital "helmet."

The distance phenogram (Fig. 6) separates *gracilis* rather well from the other samples of similarly-sized individuals of other species. The discriminant function analysis correctly identified all specimens (Table 4), and the plot of the first and second principal components (not figured) placed *gracilis* well outside the main cluster of sam-

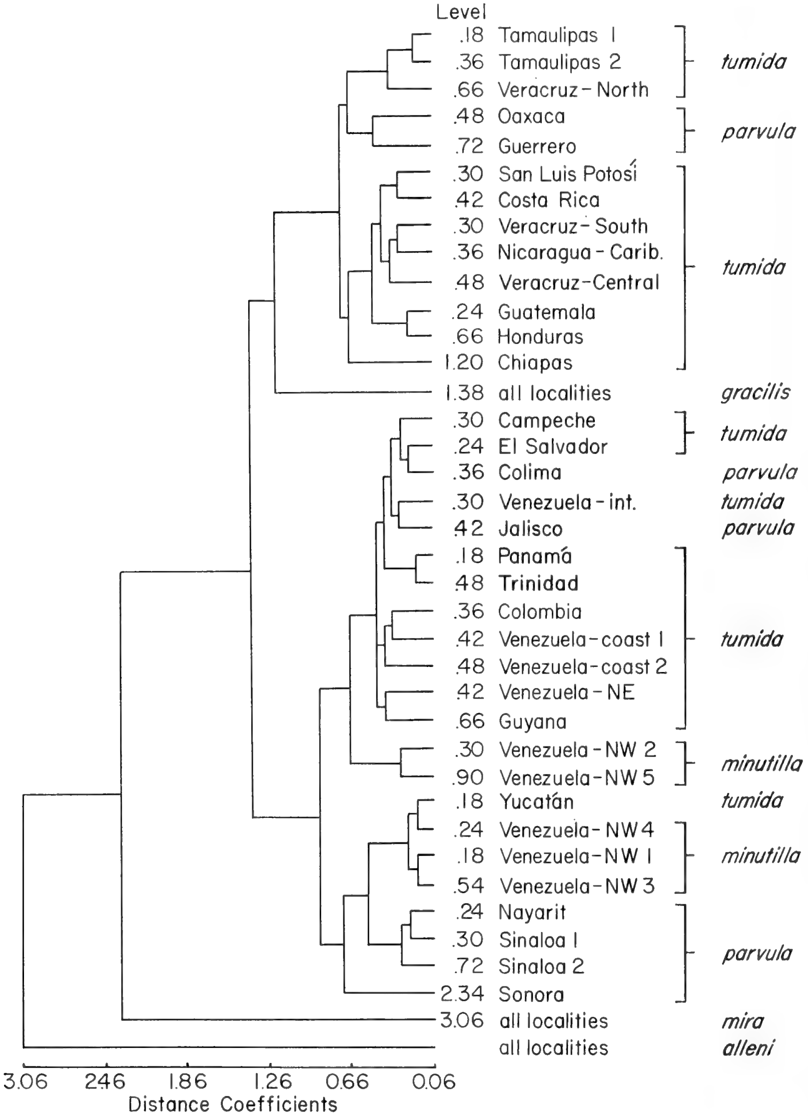


FIG. 6. Distance phenogram of species and pooled samples of *Rhogeessa*, based on multivariate analysis of 9 mensural characters. Computed from the distance matrix. The cophenetic correlation is 0.860.

ples. Although other multivariate methods were of little value, they suggested that *gracilis* is more closely related to the other species of the subgenus *Rhogeessa* than it is to *Baeodon.*

Distribution.—Mountains of western México, from Jalisco, Oaxaca, and Puebla (Fig. 5). Altitudinal range from 600 m to 2000 m. The three specimens in the University of Kansas collection were taken at three localities described as follows by the collector: "pine-oak forest"; "oak forest"; "deciduous forest along stream, pine-oak forest on hills." However, it is not safe to assume that *gracilis* is restricted to this kind of vegetation, because one of the other specimens was taken at 600 m, where the predominating vegetational association in western México is thorn forest and desert scrub.

Reproduction.—A female captured on 15 May contained two 17 mm embryos. Two subadults taken on 27 July were nearly adult in size. No other information concerning reproduction in the species is available.

Rhogeessa (Rhogeessa) parvula H. Allen

Rhogeessa parvula H. Allen, 1866:285 [Holotype.—ANSP 1832 from Tres Marías Islands, Nayarit, México; Col. Grayson, collector].

Rhogeessa tumida major Goodwin, 1958:4 [Holotype.—AMNH 175263 from San Bartolo Yautepec, Oaxaca, México, 800 m; Thomas MacDougall, collector].

Holotype.—Academy of Natural Sciences of Philadelphia 1832, adult, sex indeterminant (male, according to Allen, 1866); skin disintegrated; skull intact but damaged, i3 notably smaller than i1 or i2; compared with KU 105565 and KU 107494 from Jalisco, and KU 90754 from Sinaloa. Measurements in table 3.

Description.—A small to moderate-sized *Rhogeessa* with short ears and relatively hairy uropatagium. Distal one third of dorsal hairs, Hair Brown to Warm Buff; basal two thirds, which may or may not contrast with tips, pale grayish to buff to pale yellow; ventrally, tips from Cartridge Buff to Light Ochraceous-Buff, bases concolor to slightly contrasting with tips; fur 3-7; sparse to moderately thick fur on dorsum of uropatagium usually extends halfway from knees to feet; ratio of third metacarpal to first phalanx of third digit averaging 2.66 to 1 in area of sympatry with *alleni* and *gracilis;* sagittal crest absent in 115 of 131 skulls; i3 varies in size from nearly equal to i2, to minute, but never as small as in *alleni;* lingual cingulum of C1 well-developed, bearing two cusps of variable size; in some, cusps much higher than in example of figure 1A; skull small to moderate in size; forehead slope slight; postorbital width narrow in relation to length of skull.

Bacula.—The average dimensions of 28 bacula are: length, 0.63 (0.48-0.76); depth, 0.13 (0.08-0.20); and width, 0.34 (0.22-0.42). Bacula of *parvula* are characterized by a long, slender, curved

TABLE 4. Identification of individual specimens within each sample by discriminant function analysis. Table is read from left to right.

		SWMEX	WCMEX	NWMEX	MIRA	ALLENI	EMEX	CENTAM	NICPAN	YUCATAN	GRACILIS	COLOMB	VENEZ	MINUTILLA	GUYANA	TRINIDAD
R. parvula	SWMEX	19	1	0	0	0	3	1	2	0	0	0	0	1	0	1
	WCMEX	7	26	11	3	0	0	1	1	6	0	1	7	4	2	6
	NWMEX	0	2	10	0	0	0	0	0	0	0	0	0	0	0	0
	MIRA	0	0	0	13	0	0	0	0	0	0	0	0	0	0	0
	ALLENI	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0
R. tumida	EMEX	2	0	0	0	0	67	6	4	0	1	2	0	0	1	1
	CENTAM	3	2	2	0	0	8	17	9	1	0	11	7	0	5	10
	NICPAN	0	0	0	0	0	1	0	5	0	0	0	1	1	0	0
	YUCATAN	0	1	0	0	0	0	0	0	4	0	0	0	0	0	0
	GRACILIS	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0
R. tumida	COLOMBIA	1	0	0	1	0	1	1	0	0	0	2	0	0	2	1
	VENEZ	0	2	2	0	0	0	0	0	1	0	4	11	1	1	3
	MINUTILLA	1	6	1	0	0	0	0	0	10	0	0	1	42	1	0
R. tumida	GUYANA	0	0	0	0	0	1	0	0	1	0	1	1	0	6	0
	TRINIDAD	0	0	1	0	0	0	1	0	0	0	0	0	0	0	3

shaft, roughly elliptical in cross-section, and by short proximal knobs, extending at a 45° angle to the sagittal plane of the baculum, separated proximally by an indentation, and curving ventrally around urethra (Figs. 2C and 2D); width approximately one half length of baculum. They differ from most *tumida* bacula in being more slender, from both the dorsal and lateral aspects. Juveniles and some adults (sexually immature individuals?) with shorter shaft and knobs.

Comparisons.—Rhogeessa (*Rhogeessa*) *parvula* are easily distinguished from *alleni and gracilis,* as outlined under the accounts of those species. This species differs from *R. mira* in its greater size and the presence of cusps on cingulum of C1. In the Isthmus of Tehuantepec *parvula* and *tumida* are known from localities only 50 miles distant, and are probably sympatric. Here the two species cannot be distinguished on the basis of size. (Table 2). Chiapan specimens of *tumida,* as compared to Oaxacan specimens of *parvula,* are differentiated by darker tips of dorsal fur, which contrast more sharply with bases. The uropatagium is virtually bare, and the i3 is nearly as large as the i2.

The two most consistent characters for separating *parvula* and *tumida,* fur coverage on uropatagium and relative size of i3 and i2, seem to be exaggerated in the Isthmus of Tehuantepec, where sympatry may occur. No specimens from that area exhibit intermediacy in these characters. For these reasons it seems advisable to regard *parvula* and *tumida* as species.

The discriminant function analysis (Table 4) correctly identified 76 of 115 specimens; of the 39 incorrectly identified, all but 8 were identified as being *R. tumida.* The plot of the second and fourth principal components (Fig. 4) reveals a close relationship between *parvula* and the two samples of *tumida* from the Yucatan Peninsula, but shows good separation between *parvula* and the other species, including most samples of *tumida.* The canonical scattergrams (Figs. 7 and 8) indicate a wide overlap with *tumida.*

Distribution and geographic variation.—Western México, from central Sonora south and east to the Isthmus of Tehuantepec (Fig. 9). Altitudinal range from sea level to 1600 m; however, the highest elevation recorded from Nayarit and states to the north is 600 m. Vegetational associations from which *R. parvula* is known include scrub desert, thorn forest, tropical deciduous forest, and pine-oak forest. Broad-leafed and evergreen forests (mostly cloud forest) of various compositions occur locally in portions of the range of *parvula,* but I am unable to establish definitely that any specimens were taken in those kinds of vegetation.

Variation in *R. parvula* is essentially clinal. Size measurements indicate increasing size from north to south (Table 2), with topotypes from the Tres Marías Islands close to specimens from Sonora.

The north-south cline and widely overlapping non-significant subsets are well illustrated by the measurements of forearm (Fig. 10) and greatest length of skull (Fig. 11). Distance coefficients suggest that the cline is steeper south of Jalisco (Fig. 15), but there is no logical point at which a line separating two subspecies might be drawn. There is a tendency for specimens from more southerly localities to have fur extending farther out the uropatagium, to be brighter in color, to have longer fur, to have relatively smaller i3, and to have a more well developed sagittal crest; all of these trends appear to be clinal, with perhaps the most rapid changes occurring in Michoacán (one known locality) and the western half of Guerrero (no known localities). Were it not for the intermediacy of the series from Michoacán, it could easily be maintained that the northern and southern populations represented two subspecies (or two species, *fide* Goodwin, 1958).

Reproduction and molt.—Pregnant females were recorded from the months of February (27th), March, April, May, and early June.

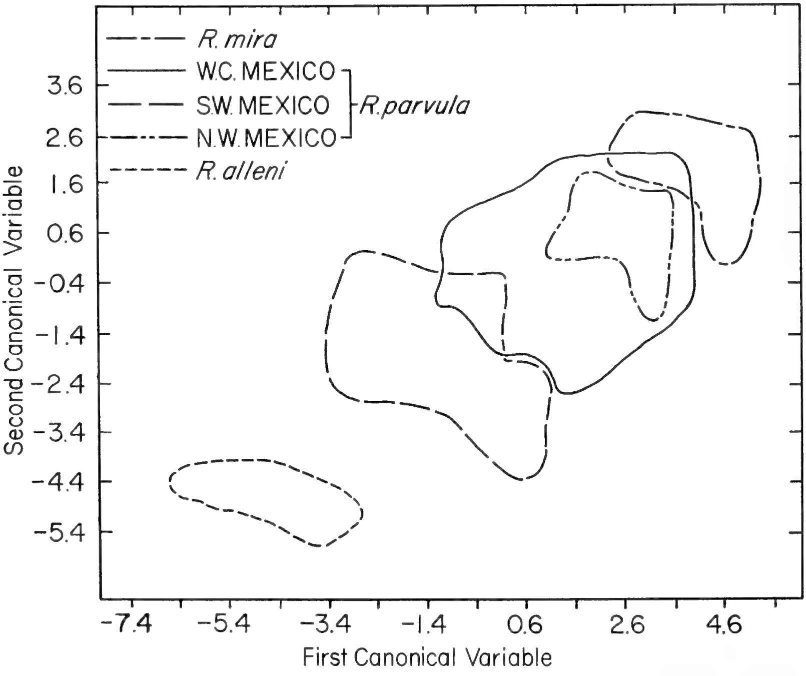


FIG. 7. Scatter diagram from first two canonical variables for three species of *Rhogeessa* from western México. The lines were formed by connecting the outlying dots within each of the 5 pooled samples. The spaces enclosed by the lines originally contained the following number of dots, each representing an individual specimen: *R. mira*, 13; WCMEX, 75; SWMEX, 28; NWMEX, 12; *R. alleni*, 7. Specimens of unknown identity may be plotted on canonical scattergrams for purposes of identification. See Appendix 1.

Lactating females were taken during April (27th), May, June, and July (3rd). Because few embryo measurements are available, there is no indication of any definite growth trends or patterns. The only juveniles (flying young) recorded were taken on 14 June, 18 July, 9 September, and 18 September. The presence of flying young and embryos in Guerrero in June and February-March, respectively, suggests that parturition occurs earlier in the southern portion of the range of *R. parvula.* At least eight females from Sinaloa and Sonora contained two embryos, but two bats from Guerrero and one from Sonora contained only one embryo each. One female was molting on 4 July, which would be anticipated, if she had just weaned her young. The new pelage was dark gray, contrasting sharply with the pale, old pelage. Two males from July and several females from August and September exhibited very dark-colored tips, suggestive of recent molt. Negative data showed that some females collected on various dates during March, April, May, June, July, and September were not pregnant. Weights for 30 non-pregnant individuals varied from 3 to 8. No seasonal trends in weight could be detected.

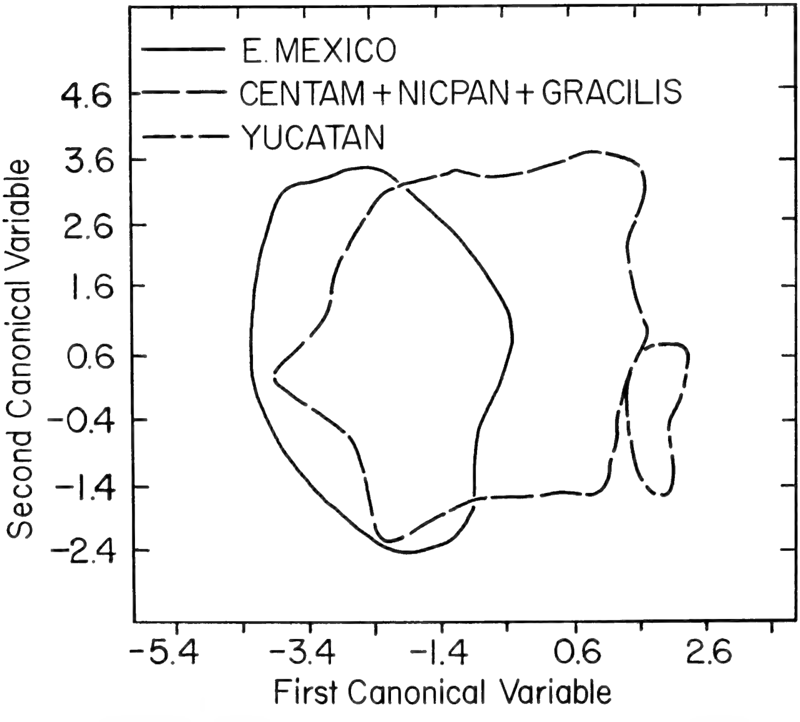


FIG. 8. Scatter diagram from first two canonical variables for three pooled samples of *Rhogeessa tumida.* The following numbers of dots are enclosed by the lines: EMEX, 85; CENTAM + NICPAN + GRACIL, 90; Yucatán, 5.

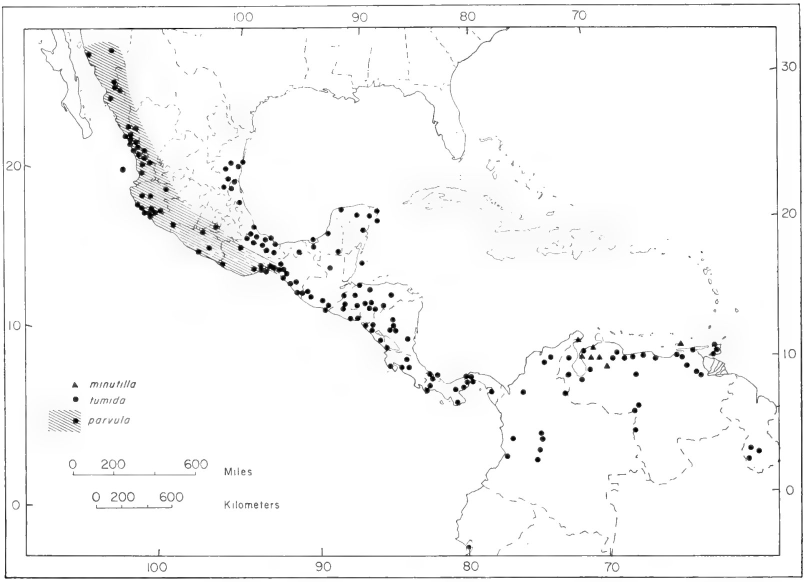


FIG. 9. Map showing localities from which were examined specimens of one of three species of *Rhogeessa*. The shaded area represents the distribution of *R. parvula*, the unshaded area, *R. tumida*. The triangles representing *minutilla* are all in northwestern Venezuela and adjacent Colombia, plus the island of Margarita.

Remarks.—Goodwin (1958) used size as the major criterion for separating *parvula* and *tumida*. He lacked specimens from Jalisco, Nayarit, and Sinaloa where a clinal change occurs; therefore, it is not surprising that he identified the larger specimens from southwestern México as *tumida*. Specimens of *tumida* from adjoining Chiapas and Veracruz are much like Oaxacan *parvula* in size. Goodwin also assigned populations of small individuals from the Yucatan Peninsula and parts of South America to *parvula*. In addition to the nominate subspecies, he assigned four other subspecies to *parvula*. One of these, *minutilla*, is here regarded as a species; the other three are relegated to the synonymy of *tumida*.

Rhogeessa (Rhogeessa) mira, new species

Holotype.—Universidad Nacional Autónoma de México 8594, adult male, skin, skull, and baculum, from 20 km N El Infiernillo, Michoacán, México, elevation 125 m; collected by Ticul Alvarez, 29 November 1964. Collector's measurements, overall length, 70; tail, 33; foot, 6; ear, 12; length of testis, 9; external and cranial measurements in Table 3.

Etymology.—The specific epithet *mira* is feminine for the Latin *mirus*, meaning wonderful, astonishing, or extraordinary. These

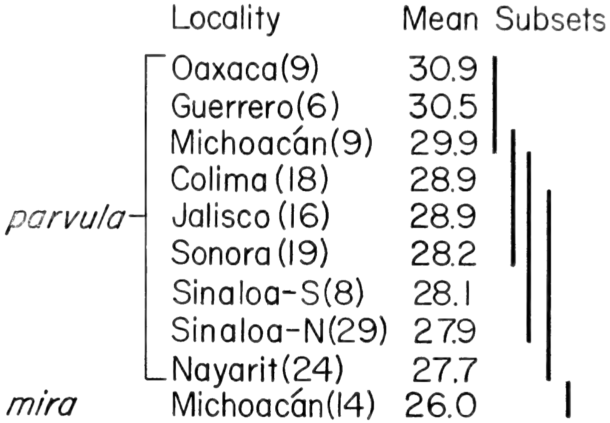


FIG. 10. SS-STP analysis showing geographic variation in forearm length in *Rhogeessa parvula.* The vertical bars connect samples within each non-significant subset (at the 0.05 level). For example, the mean of Sinaloa-S is not significantly different from the mean of Sonora, but is significantly different from the mean of *mira.*

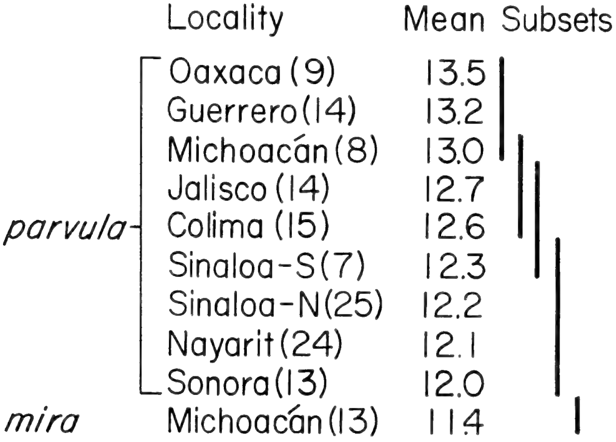


FIG. 11. SS-STP analysis showing geographic variation in greatest length of skull of *Rhogeessa parvula.*

were my initial reactions upon examining a specimen of *R. mira* and comparing it with the much larger species taken at the same locality, *R. alleni* and *R. parvula.*

Description.—An extremely small *Rhogeessa* with smooth-edged lingual cingulum of C1 and external characteristics much as in *R. parvula.* Distal one third of dorsal hairs Buckthorn Brown to Buffy Brown; basal two thirds more buffy than tips, not contrasting strongly with tips; ventrally, overall color like that of bases of dorsal hairs, tips not contrasting; fur 4; sparse fur on dorsum of uropatagium extends to or past knees; sagittal crest absent; i3 only slightly smaller than i2; lingual cingulum of C1 smooth, lacking the slightest suggestion of cusps; skull very small; forehead slope moderate.

Baculum.—Measurements of the single baculum examined (Fig. 2E) are: length 0.66, depth 0.12, and width 0.34. It could not be distinguished from bacula of some *R. parvula.*

Comparisons.—R. mira is easily distinguished from the other three species in western México on the basis of size. It resembles *gracilis* in its smooth lingual cingulum of C1. Otherwise it could not possibly be confused with *gracilis* or *alleni.* The lack of cingual cusps, small overall size, and relatively large size of i3 separate it from sympatric *parvula.* Nine specimens of *parvula* from the type locality of *mira* are all redder and yellower than any specimens of *mira* caught at the same time, or at any other time. Furthermore, there is no size overlap among specimens of the two species caught at the type locality. Certain specimens of *parvula* from Sonora and the Tres Marías Islands are almost as small as *mira,* but tend to have a less steeply sloping forehead, wider and longer rostrum, cingual cusps on C1, smaller, more crowded i3, and less fur on uropatagium. Small individuals of *tumida* and *minutilla* from Yucatán, Venezuela, and Ecuador differ in color, skull outline, cingual cusps, nearly bare uropatagium, and shape of baculum.

Generally, the multivariate analyses placed *mira* well away from most samples of all other species. Based on these analyses alone, *mira* would seem almost as distinct from other *Rhogeessa* as in *R. alleni.* However, in external and cranial characters not included in the multivariate analyses, *mira* is more similar to the others, especially to *parvula.* In the univariate analysis *mira,* which had the lowest means among all samples for most of the variates measured, usually formed a nonsignificant subset with Sinaloa and Sonora, with Sonora, or alone (as in Figs. 10 and 11).

Remarks.—All the specimens from 7 km N El Infiernillo were caught in nets over a small cement water trough, in an area of cactus-mesquite vegetation (Alvarez and Aviña, 1965). Collected at the same time were *R. alleni, R. parvula, Balantiopteryx plicata, Macrotus waterhouseii,* and *Micronycteris megalotis.* The *Rhogeessa* were taken on five nights, 25 and 27 March, and 26, 28, and 29 November, all in 1964. The capture of three species of *Rhogeessa* during one night, in one net, is of interest, because each of the three is in a non-overlapping size range. This suggests successful partition of the feeding niche, possibly based on prey size. The failure to achieve this kind of diversity within the genus *Rhogeessa* outside of western México could be accounted for by the presence of additional Neotropical species of the genus *Myotis* in those areas, although this suggestion is highly speculative at this time. It is also noteworthy that *R. mira* is among the smallest of all species of bats, although it exceeds in size specimens of the species *Tylonycteris pachypus* of Southeast Asia, and possibly specimens of certain species of *Pipistrellus*, notably *P. mimus.*

Rhogeessa (Rhogeessa) tumida H. Allen

Rhogeessa tumida H. Allen, 1866:286 [Holotype.—ANSP 1831 (skin), NMNH 37329 (cranium), and NMNH 84021 (lower jaw) from Mirador, Veracruz, México, *ca.* sea level; Dr. Sartorius, collector].

Rhogeessa io Thomas, 1903:382 [Holotype.—BMNH 94.9.25.1 from Valencia, Carabobo, Venezuela; A. Mocquerys, collector].

Rhogeessa velilla Thomas, 1903:383 [Holotype.—BMNH 99.8.1.5 from Puná, Isla Puná, Gulf of Guyaquil, Ecuador, elev. 10 m; P. O. Simons, collector].

Rhogeessa bombyx Thomas, 1913:569 [Holotype.—BMNH 13.10.29.1 from Condoto, Chocó, Colombia, elev. 300 ft; Dr. H. G. F. Spurrell, collector].

Rhogeessa tumida riparia Goodwin, 1958:5 [Holotype.—AMNH 69968 from Cumanacoa, Sucre, Venezuela, elev. 700 ft; G. H. H. Tate, collector].

Rhogeessa parvula aeneus Goodwin, 1958:6 [Holotype.—AMNH 91234 from Chichén-Itzá, Yucatán, México, elev. *ca.* 10 m; R. T. Hatt, collector].

Holotype.—"Museum of Smithsonian Institution" 8195, male, is the number listed by H. Allen (1866) as the holotype of *tumida.* Part of the confusion regarding the location, status, and numbers of the various parts of the holotype was discussed by Hall (1952). The skin, in alcohol and appearing to be a female, is in the Academy of Natural Sciences of Philadelphia, no. 1831. Two labels are with the specimen; one reads "1831 Harr. Allen Rhogeëssa tumida Mirador, Mex. TYPE H. Allen." The other bears only the number 8195. The cranium, NMNH 37329, is now in a vial bearing that number. The accompanying lower jaw, numbered NMNH 84021, seems to match the cranium perfectly. In another vial, labelled NMNH 84021, is a cranium bearing that number and a lower jaw numbered NMNH 37329. These also seem to match perfectly, which is significant, because the two skulls in question differ in size. The vial holding NMNH 84021 is also labelled "formerly 7842" which would make it the paratype of *R. parvula.* It appears that the lower jaws were switched before the skulls were numbered. In any case NMNH 37329 (cranium) is obviously of the species now occurring in eastern México, and should be regarded as the holotype. The holotypes of *R. tumida* and *R. t. riparia* were compared with KU 29886 from Veracruz, TCWC 19756 from Nicaragua, UNM 27545 from Oaxaca, and AMNH 91234 from Yucatán (holotype of *R. p. aeneus*), among others. Handley (*in litt.*) compared the holotype of *R. io* with NMNH 374017, *R. tumida* from Urama, Venezuela, and J. E. Hill (*in litt.*) compared the holotypes of *R. io* and *R. velilla* with each other. Handley also compared the holotype of *R. velilla* with NMNH 312113, *R. tumida* from Ft. Kobbe, Panamá. Measurements are in table 3.

Description.—A small to moderate-sized *Rhogeessa* with short ears and nearly bare uropatagium; otherwise highly variable. Distal one third of dorsal hairs Fuscous-Black to Pinkish Cinnamon, except in Venezuela and Guyana, where darkest specimens Brussels Brown, and palest specimens somewhat darker than those from other parts of the species' range; bases usually buffy gray to buffy yellow, and may or may not contrast sharply with tips; ventrally, tips Buffy Brown to Light Ochraceous-Buff, concolor to somewhat paler at bases; fur 3-4 (rarely 5); sparse hairs on dorsum of uropatagium rarely extend as far as knees; sagittal crest present in approximately half of all specimens examined, but present in only one fourth of specimens from Colombia, Venezuela, Trinidad, and Guyana; i3 usually smaller than i2, but may equal i2; even when i3 equals i2, i3 has less well-developed cusps; lingual cingulum of C1 with two small cusps, sometimes only a suggestion of cusps present; skull small to moderate in size; forehead slope slight; "helmet" often present in North American specimens, rarely in South America.

Bacula.—Twenty-nine bacula of North American specimens have dimensions as follows: length, 0.65 (0.50-0.80); depth, 0.19 (0.12-0.28); and width, 0.52 (0.36-0.84). In fourteen specimens from South America, means are: length, 0.66 (0.48-0.80); depth, 0.19 (0.14-0.24); width, 0.60 (0.44-0.74). The only apparent difference between the two groups is in width, and this is not statistically significant.

In shape, both individual and geographic variation are apparent (Fig. 2F-L). Generally, as compared to bacula of *parvula,* the bacula of *tumida* possess wider shafts, wider spreading (laterally), and wider (distal-proximal) proximal knobs; their width exceeds one half their length. In Central America the bacula of *tumida* tend to be Y-shaped, due to deeper indentation between ends of proximal knobs. The distal free portion of shaft is shorter than that portion from which knobs extend. In some, additional widening of shaft results in a roughly triangular shape. In Colombia, Y-shaped, triangular, and intermediate specimens appear; whereas in Venezuela, Guyana, and Trinidad, the Y-shape is rare, and in some the proximal knobs extend laterally at an angle of 90° to the shaft.

Comparisons.—In the Isthmus of Tehuantepec *R. tumida* differs from *R. parvula* as outlined under the account of that species. In general, the bare uropatagium and relatively large i3 of *tumida* distinguish all *tumida* from all *parvula.* Other characters tend to be geographically variable and thus will not separate consistently the two species. In northwestern Venezuela and adjacent Colombia, where *tumida* apparently occurs sympatrically with *minutilla, tumida* is larger on the average, and has proportionately greater postorbital width (Table 2). *Rhogeessa tumida* is always darker in color (both fur and membranes). It has a greater difference in length between forearm and third metacarpal, and the tibia is shorter. Toothwear is rarely heavy. In most of the extensive range of *tumida* there is no other species of *Rhogeessa* present.

The discriminant function analysis correctly identified 194 of 212 specimens as *tumida* (Table 4). Two were misidentified as *minutilla,* one as *gracilis,* and 15 as *parvula.* In the pooled sample of 75 from Central America, a region where a bewildering amount and kind of geographic variation occurs, only 15 were correctly identified as being from Central America. The value of the other multivariate analyses is discussed under *parvula.* It is noteworthy that the canonical scattergram (Fig. 12) seems to separate *tumida* in South America surprisingly well from *minutilla.*

Distribution and geographic variation.—Tamaulipas, south in Caribbean lowlands, including the Yucatan Peninsula, to Pacific versant in Chiapas, throughout Central America, and South America, locally south to southern Brazil, Bolivia, and Ecuador (Fig. 9). Sea level to 1500 m in North America, with the higher elevations from Chiapas through Costa Rica; sea level to 1200 m in South America. A large majority of all specimens were collected from below 500 m. *Rhogeessa tumida* seems to be known from virtually every major vegetational association in tropical North America and northern South America, within the limits imposed by elevational restrictions. It is difficult to generalize in terms of geographic variation in size, since clines are poorly developed and skin and skull measurements do not indicate the same kinds of trends. Mexican specimens (excluding Yucatán) tend to be the largest, followed by specimens from Central America (excluding Caribbean coast) and then specimens from South America (including Yucatán, but excluding Pacific coast of Colombia).

The SS-STP analyses for forearm and greatest length of skull (Fig. 13) illustrate geographic changes in size. Note that specimens from Costa Rica (interior), from Nicaragua (Caribbean lowlands), and from eastern México have the largest forearms, with the intermediate sized bats being from the Pacific versant of Central America (including Chiapas) and southern Campeche. Most of the smallest specimens are from South America, but those from the northern Yucatan Peninsula are the most diminutive of all. Based on greatest length of skull, the same group of samples (with the addition of Chiapas) is largest in size, but they are arranged in a different sequence. The middle-sized group is similar except for sequence and the loss of the El Salvador-Nicaragua (Pacific versant) sample which drops to a position among the South American samples. The Colombian sample also drops significantly in the standings. However, two specimens from the Pacific coast of Colombia are as large as specimens from Nicaragua (Caribbean) and are not included in the sample from Colombia.

The distance coefficients (Fig. 14) differ substantially in value in various parts of the range and support my contention that variation is essentially non-clinal. The largest values in the conterminous portion of the range are those between southern Campeche and Veracruz, and between Campeche and Pacific coastal Chiapas. Values between Campeche and Guatemala, El Salvador, and Honduras are much lower, however. Few specimens are available from the Yucatan Peninsula, but it appears that a South-North cline of decreasing size is operative, resulting in specimens from Yucatán and Quintana Roo which are more like South American specimens in size than like those from adjacent areas. From Honduras south and east through western Panamá, it appears that clines from small to large and pale to dark operate along a Pacific-Caribbean axis. Two specimens from the Pacific coast of Colombia are also large and dark. It seems probable that the large, dark population of Caribbean Central America extends across Panamá in the far east to join the large, dark bats of Colombia, but no specimens are available

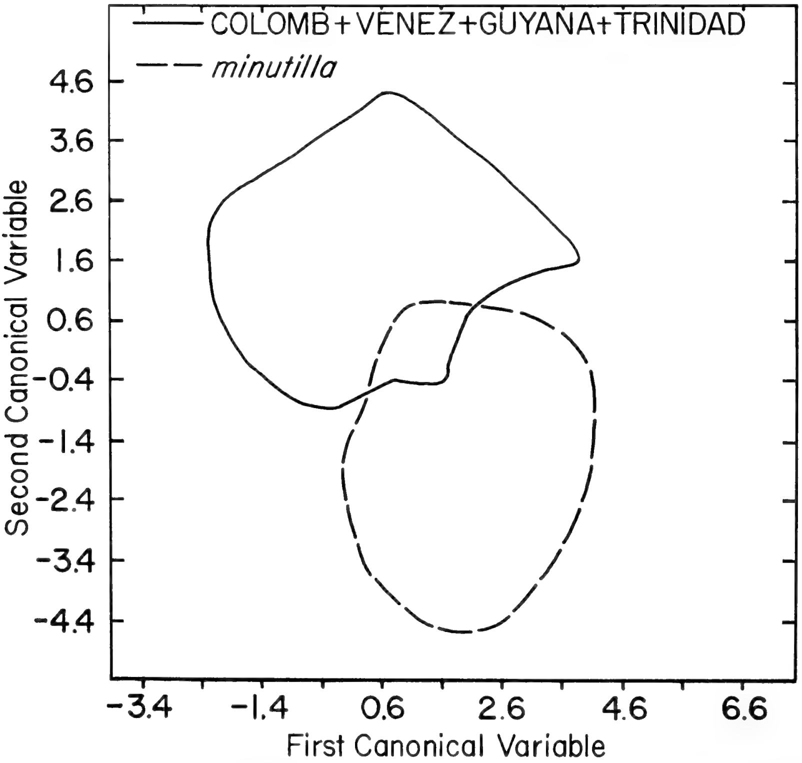
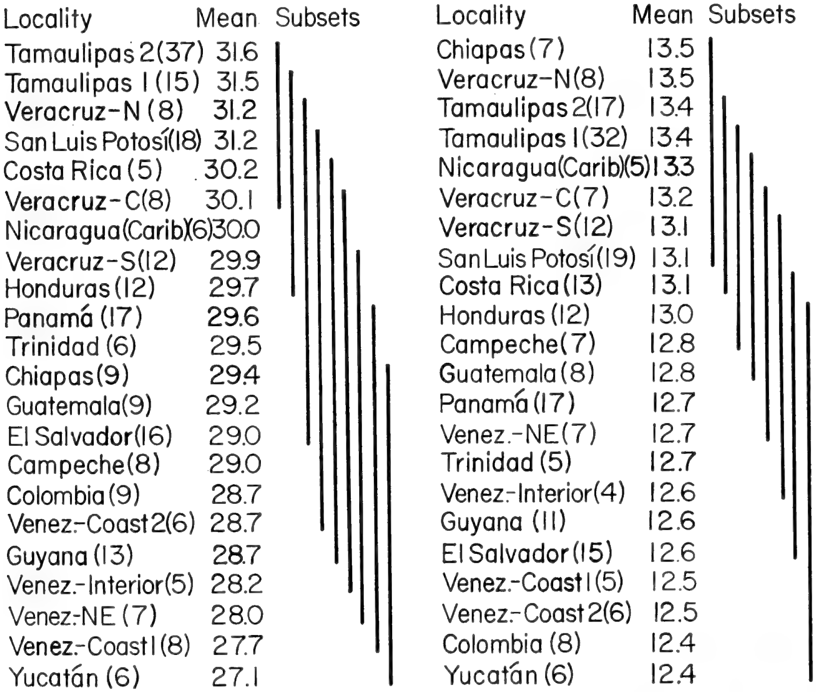


FIG. 12. Scatter diagram from first two canonical variables for *Rhogeessa tumida* (4 pooled samples) and *R. minutilla* in South America. The following numbers of dots are enclosed by the lines: COLOMB + VENEZ + GUYANA + TRINIDAD, 49; *minutilla*, 62.

to support that hypothesis. If true, it will pose some rather interesting systematic problems.

Farther south along the Pacific Coast of South America, two specimens known from Puna Island, Ecuador, are both very small in size, and are similar to specimens from the Caribbean coast of Colombia and Venezuela. Two specimens from Brazil are very much like specimens from Chiapas and Guatemala, in size and color. I was not able to examine the single specimen from Bolivia in the Field Museum of Natural History. South of Venezuela and central Colombia, *R. tumida* is represented by so few specimens that it is not possible to speculate on geographic variation or even on the limits of geographic distribution. Because of the absence of specimens among large collections of bats from some parts of Brazil, Perú, Bolivia, Paraguay, and Uruguay, I believe that *R. tumida* is truly a rare species in much of South America, and may be only locally distributed.

Color is both individually variable, based on age of pelage, and geographically variable. Eastern Mexican specimens tend to be closer to the red and yellow end of the spectrum, with little contrast



Locality	Mean
Tamaulipas 2(37)	31.6
Tamaulipas 1(15)	31.5
Veracruz-N (8)	31.2
San Luis Potosí(18)	31.2
Costa Rica (5)	30.2
Veracruz-C(8)	30.1
Nicaragua(Carib)(6)	30.0
Veracruz-S(12)	29.9
Honduras (12)	29.7
Panamá (17)	29.6
Trinidad (6)	29.5
Chiapas(9)	29.4
Guatemala(9)	29.2
El Salvador(16)	29.0
Campeche(8)	29.0
Colombia (9)	28.7
Venez.-Coast 2(6)	28.7
Guyana (13)	28.7
Venez.-Interior(5)	28.2
Venez.-NE (7)	28.0
Venez.-Coast 1 (8)	27.7
Yucatán (6)	27.1

Locality	Mean
Chiapas(7)	13.5
Veracruz-N(8)	13.5
Tamaulipas 2(17)	13.4
Tamaulipas 1(32)	13.4
Nicaragua(Carib)(5)	13.3
Veracruz-C(7)	13.2
Veracruz-S(12)	13.1
San Luis Potosí(19)	13.1
Costa Rica (13)	13.1
Honduras (12)	13.0
Campeche(7)	12.8
Guatemala (8)	12.8
Panamá (17)	12.7
Venez.-NE(7)	12.7
Trinidad (5)	12.7
Venez.-Interior(4)	12.6
Guyana (11)	12.6
El Salvador(15)	12.6
Venez.-Coast 1 (5)	12.5
Venez.-Coast 2(6)	12.5
Colombia (8)	12.4
Yucatán (6)	12.4

FIG. 13. SS-STP analysis showing geographic variation in forearm (left) and in greatest length of skull (right) of *Rhogeessa tumida*.

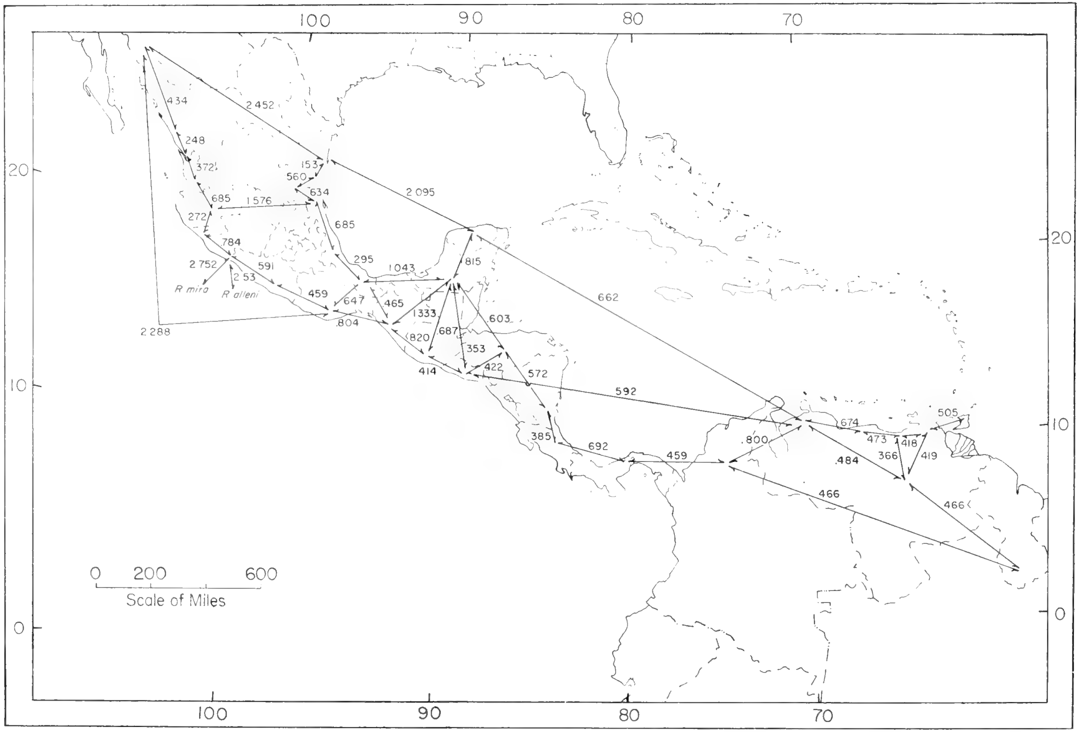


FIG. 14. Map showing selected distance coefficients from the distance matrix between localities and pooled samples of five species of *Rhogeessa*. The lines diverging from northwestern Venezuela all show distance coefficients between *R. minutilla* and *R. tumida*. *Rhogeessa gracilis* is not represented on the map.

between bases and tips. Specimens from the Yucatan Peninsula, Chiapas, Caribbean coast of Nicaragua and Panamá, and Pacific coast of Colombia tend to have buffier bases and darker brown or black tips, which contrast strongly with bases. Specimens from the Pacific coast of Central America tend to resemble eastern Mexican specimens in color. In South America, most of the color combinations known from North America occur, but many redder and yellower specimens also occur, with differing combinations of base and tip color. Throughout the range, males tend to be darker than females; however, this observation may represent an artifact, because many series of specimens have been collected during early summer, when males have probably recently molted and females have not.

Based on the data obtained in this study, I have been unable to divide the wide-ranging *R. tumida* into sympatric species, allopatric species, or into subspecies, although one or more of these actions ultimately may be necessary. The preliminary karyotypic studies of R. J. Baker (pers. com.) indicate that animals having at least four different karyotypes exist within the geographic range of *R. tumida.* Two different karyotypes are represented among animals from southern Chiapas, and individuals from the Caribbean lowlands of Nicaragua, and from Trinidad, differ karyotypically from specimens collected in Pacific coastal Central America. At this point it is not possible to evaluate these karyotypic trends in terms of the systematics of *R. tumida.*

Reproduction and molt.—Relatively few preparators of *Rhogeessa* specimens have recorded data on reproductive condition. More information is available on *tumida* than the other species, even though much of it is negative. Pregnant females were taken in May in Tabasco. Nine bats caught in Guatemala, El Salvador, Honduras, and Nicaragua were pregnant in the period from 14 February through 28 April. Gravid females were taken in Costa Rica on 9 March, and in Panamá on 25 February. A pregnant individual from Venezuela was captured on 23 March, and another, possibly pregnant, on 12 October. Lactating females were collected on various dates from 24 May to 20 June in Tamaulipas and 30 April to 12 June in Veracruz. Others were taken on 12 June in Oaxaca, May in Tabasco, 18 July in Nicaragua, and 29 March and 7 May in Costa Rica. Bats recorded as not pregnant, or as not lactating, were caught in most months of the year, but few of these were from the spring or early summer months.

Based on these data, it appears that gestation, parturition, and lactation extend from mid-February through mid-July. Obviously, there is variation in dates for reproductive events among females. To what extent this is geographically correlated cannot be determined, however. Of ten specimens for which the number of embryos was recorded, three had but one embryo, and the remainder two. Juveniles were taken on 23 dates scattered during the period 21 May through 27 August. One Venezuelan juvenile was caught on 4 October. Because this individual was captured at a locality within 5°N of the equator, it seems possible that a somewhat different breeding cycle prevails at that latitude.

Males with enlarged testes (6-7) were taken during September, November, December, and January. Bats from other months had testes ranging in size from 2 to 5, suggesting that maximum production of spermatozoa may occur during the autumn and early winter, as in Temperate Zone vespertilionid bats. Five males were molting in late May and June, and three females in July, suggesting coordination with reproductive cycles.

Remarks.—Included in the synonymy are five names applied to subspecies of either *tumida* or *parvula* by Goodwin (1958). *Rhogeessa io* Thomas and *R. t. riparia* Goodwin are names applied to Venezuelan specimens. There is little geographic variation in this area, and, although the holotype of *riparia* is a larger individual than the holotype of *io,* it would be pointless to apply these names to subspecies. There is no sharp break in Panamá or Colombia which would tend to validate the recognition of a distinct South American subspecies.

Rhogeessa velilla Thomas, based on a specimen from Ecuador, may be applicable to a subspecies, but the specimens which might show a pattern of geographic variation deserving of nomenclatural recognition have not yet been collected. The holotype of *velilla* does not differ in size from the holotype of *io,* and J. E. Hill (*in litt.*) noted that they were almost identical. The holotype of *R. bombyx,* from the Pacific coastal lowlands of Colombia, is typical of the large individuals which seem to occur along the Caribbean versant of Central America (from Nicaragua southward) and the west coast of Colombia. At present I choose not to recognize *bombyx* as a species or subspecies because of the apparent clinal transition from small pale individuals on the Pacific coast of Central America to large, dark individuals on the Caribbean coast. The substantial gaps in eastern Panamá and Colombia suggest that subsequent collecting may reveal a more accurate rendition of variation in this region.

Rhogeessa parvula aeneus Goodwin is a name applied to small individuals from Yucatán and northern Quintana Roo. According to my notes "This skull [holotype of *tumida*] is almost identical to AMNH 91234, holotype of *aeneus* . . . (although latter is smaller)." The size of specimens from various localities in Campeche, southern Quintana Roo, and Belice suggests a clinal change. I prefer not to give nomenclatural recognition to various segments of a cline, especially when the dividing line would be of necessity arbitrary.

Rhogeessa (Rhogeessa) minutilla G. S. Miller

Rhogeessa minutilla G. S. Miller, 1897:139 [Holotype.—NMNH 63216 from Margarita Island, Venezuela; Lt. Wirt Robinson, collector].
Rhogeessa parvula minutilla—Goodwin 1958:7.

Holotype.—National Museum of Natural History 63216, adult male, skin and skull. This specimen was compared with 98 other specimens of *minutilla* from Venezuela and Margarita in the NMNH, as well as with 51 specimens of *tumida* from Venezuela and Trinidad. Measurements of holotype appear in table 3.

Description.—Essentially as in description of Venezuelan *tumida.* Major differences will be noted under "Comparisons." Distal one third of dorsal hairs Cinnamon Buff to near Sudan Brown; basal two-thirds contrasting with tips, Light Buff in most specimens; ventrally, Warm Buff to Light Ochraceous-Buff to Cinnamon Buff; fur 4-5; sagittal crest present in 26 of 76 skulls.

Bacula.—Mean dimensions of eleven bacula from specimens of *minutilla* (all from northwestern Venezuela) are: length, 0.50 (0.40-0.60); depth, 0.17 (0.12-0.22); width, 0.50 (0.40-0.62). As compared to bacula of South America *tumida,* the bacula of *minutilla* are shorter and narrower; lateral knobs extend at a higher angle from shaft, and approach a right angle in some specimens (Figs. 2M and 2N). Some *minutilla* bacula resemble closely those of some *tumida.*

Comparisons.—Despite their great similarity, there are some consistent differences between *tumida* and *minutilla.* The two species are compared in tables 2 and 5.

Univariate analyses give poor separation of *tumida* and *minutilla* in South America, but the multivariate analyses allow a somewhat different perspective. The plot of the second and fourth principal components (Fig. 4) and of the first and second canonical variables (Fig. 12) show remarkably good separation between these two species. The discriminant function table (Table 4) indicates that 42 of 62 specimens of *minutilla* were correctly identified. Ten specimens of the 12 misidentified as *tumida* were identified as *tumida*

TABLE 5. A comparison of major characters which distinguish *Rhogeessa tumida* and *R. minutilla* in northwestern Venezuela.

R. tumida	*R. minutilla*
Fur and membranes darker	fur and membranes paler
"helmet" rarely present	"helmet" usually present
POW greater	POW less
tibia shorter	tibia longer
heavy toothwear rare	heavy toothwear common
tragus shorter	tragus longer
third metacarpal at least 1 mm shorter than forearm	third metacarpal about 0.5 mm shorter than forearm

from Yucatán, and eight as *parvula.* Only two were misidentified as *tumida* from South America.

Distribution.—Arid lowlands of Margarita Island, northwestern Venezuela, and adjoining portion of the Guajira Peninsula of Colombia (Fig. 9) *Rhogeessa minutilla* occurs from sea level to 500 m. Virtually all of this region is vegetated by desert scrub and thorn forest. Although there appear to be minor differences in size and color among the samples examined, there are no obvious trends that might suggest geographic variation.

Reproduction and molt.—No pregnant females have been recorded; however, numerous specimens collected in June and July were recorded as being not pregnant. Juveniles were taken from late June through mid-July. Five males from June and July had small testes, measuring 2-3. Molting females were taken on 30 June, 17 July, and 18 July; a single molting male was recorded from 16 July.

Remarks.—The type locality (Margarita Island) is approximately 500 km east of the main range of *minutilla;* its separation by an area where only *tumida* seems to occur is a strangely anomolous situation. Yet the three specimens from Margarita can be easily matched by bats from northwestern Venezuela. It seems probable that during a more arid (interglacial?) period the range of *minutilla* was continuous along the northern coast of South America, and reached at least one of the offshore islands. On the other hand, the lowered sea levels characteristic of periods of glaciation may have facilitated a crossing from the mainland to Margarita, or vice versa. Arid habitat in the areas occupied by *minutilla* today is separated by areas of more mesic vegetation. No specimens of *minutilla* seem to have been taken in areas where *tumida* is common, but a few specimens of *tumida* have come from within or very near the main range of *minutilla.*

DISCUSSION

The multivariate statistical analyses (utilizing only mensural characters) were undertaken with the intent of illustrating the degree to which dots representing sample means or individual specimens would cluster in multidimensional space. I hoped these analyses would give some clue to evolutionary (and thus systematic) relationships, as well as demonstrate geographic variation.

The results of the multivariate analyses (Figs. 4, 6, 7, 8, 12 and 14) were helpful, but hardly conclusive; in some cases results were confusing or even contradictory. In general, they seem to indicate that *R. alleni* is phenetically distant from the other species of *Rhogeessa,* thus supporting my subgeneric separation of that species. Although *Rhogeessa gracilis* and *R. mira* are closer phenetically to the other species than is *alleni,* the degree of phenetic separation varies among the different analyses. *Rhogeessa gracilis* seems to be closer to the others than *R. mira.* However, when one examines characters not included in the statistical analyses, the reverse seems to be true; *i.e., mira* is closely related to *parvula,* and *gracilis* seems very distinct from all other species.

Rhogeessa parvula, R. tumida, and *R. minutilla,* on the other hand, are shown to be closely related by both the multivariate statistics and the other characters discussed in the species accounts. Thus it appears that there are four closely related species, which probably evolved by isolation from a common ancestor, plus two peripheral species (*alleni* and *gracilis*) which were separated from the common ancestor of the other four at a much earlier point in time. It is also possible that the genus is polyphyletic and that *alleni,* and even more likely, *gracilis* are similar to *Rhogeessa* only by convergence. When *gracilis* is karyotyped, some light may be shed on this question.

Because four species occur sympatrically in western México, it seems safe to assume that *Rhogeessa* evolved there from a primitive vespertilionine bat, which perhaps also gave rise to *Eptesicus* and *Pipistrellus.* These latter two genera, however, are almost cosmopolitan, and encompass many species. If we therefore postulate a much longer evolutionary history for them, then *Rhogeessa* is either much younger as a genus, or has been blocked in its efforts to expand its distributional range and diversify into additional species by such factors as competitive exclusion by other insectivorous species, or by other evolutionary and zoogeographic problems.

Periodic climatic changes before and during the Pleistocene probably led to periods of isolation between lowland populations on the western and eastern coasts of México, making possible the occurrence of separate but similar species (*tumida* and *parvula*) on the coasts. The eastern population spread southward throughout Central America and northern South America, finding climates much like those in eastern México. In order for speciation to have occurred in northwestern Venezuela, producing *R. minutilla,* ancestral *R. tumida* must have reached South America before or during the Pleistocene, so that the climatic changes necessary to isolate a population there could have taken place. Presently, *R. tumida* may be in the process of invading central and southern South America, where it seems to be rare and local in distribution.

In western México the lowland population must have been broken into two segments at one point in time, to allow speciation of *R. mira* from *R. parvula.* How and when this might have occurred is not clear. Because *alleni* and *gracilis* normally are found at higher elevations than *parvula* or *mira,* it can be speculated that geographic isolation of different mountain masses and associated contrasts in climate and vegetation led to their speciation at an early date, and that these same factors have maintained the present restricted distributional ranges of these two species.

Figures 4, 5, and 14 tell us something about multidimensional geographic variation. Because the dots are not in a straight line, figure 4 demonstrates that the rate of clinal change differs among variables, and figure 14 shows that the rate of clinal change differs among samples in different portions of the species' geographic ranges. Figure 4 shows increasing size from upper right to lower left, and figure 5 groups samples of similar size.

KEY TO THE SPECIES OF *RHOGEESSA*

1. Greatest length of skull more than 14.5; i3 unicuspid, 1/6 to 1/8 cross-sectional area of i2; ratio of third metacarpal to first phalanx of third digit averaging 2.20 to 1 .... Subgenus *Baeodon; R. alleni*

   Greatest length of skull less than 14.5; i3 often bicuspid, having cross-sectional area greater than 1/6 that of i2; average ratio of third metacarpal to first phalanx of third digit more than 2.20 to 1 .... Subgenus *Rhogeessa,* 2

2. Ears averaging 18; dorsal fur obviously 3-banded, darker at bases .... *R. gracilis*

   Ears averaging 15 or less; dorsal fur 2-banded, paler at bases 3

3. Greatest length of skull averaging 11.4; lingual cingulum of C1 smooth, lacking cusps .... *R. mira*

   Greatest length of skull averaging 11.9 to 13.5; lingual cingulum of C1 not smooth, usually with cusps 4

4. Uropatagium sparsely to heavily furred from base to point halfway from knees to foot; i3 usually much smaller than i2 .... *R. parvula*

   Uropatagium furred only at base; i3 usually only slightly smaller than i2 5

5. Color pale; helmet usually present; POW averaging 2.9 or 3.0; third metacarpal averaging 0.5 mm shorter than forearm .... *R. minutilla*

   Color dark; helmet usually absent; POW averaging 3.1 or 3.2; third metacarpal at least 1 mm shorter than forearm .... *R. tumida*

SUMMARY

More than 650 specimens of bats of the Neotropical genera *Rhogeessa* and *Baeodon* were examined to determine the number of genera and species that should be recognized, as well as to evaluate geographic variation within each species. In addition to the usual morphological characters, large numbers of bacula were measured and compared, and hairs were examined by scanning electron microscopy. The preliminary results of a study of karyotypic variation in *Rhogeessa* by R. J. Baker and associates were taken into account. Both multivariate and univariate statistical methods were utilized.

One species, *Rhogeessa alleni,* is assigned to the subgenus *Baeodon,* and is a large-skulled form restricted to western México. The remaining five species are assigned to the subgenus *Rhogeessa. Rhogeessa parvula,* restricted to western México, is characterized by a hairy uropatagium. *Rhogeessa gracilis,* also restricted to western México, possesses much larger ears than do the other species. A new species, *R. mira,* is presently known only from two localities in Michoacán, and is substantially smaller than the other three species inhabiting western México. *Rhogeessa tumida,* an extremely variable (and perhaps composite) species, ranges from Tamaulipas to Brazil and Bolivia. *Rhogeessa minutilla,* a pale desert species, is restricted to Margarita Island, northwestern Venezuela, and the adjoining Guajira Peninsula of Colombia.

RESUMEN

Con el fin de determinar el número de géneros y especies que deben ser reconocidos y también analizar la variación dentro de cada especie, se examinaron mas de 650 especímenes de murciélagos neotropicales do los géneros *Rhogeessa* y *Baeodon.* Además de los caracteres morfológicos usualmente empleados, se midieron y compararon los báculos, y se examinaron los pelos por medio de un microscopio electrónico de "scanning." Fueron tomados además en consideración, el estudio hecho por R. J. Baker y compañeros, sobre la variación en los kariotipos de *Rhogeessa;* y finalmente para el análisis estadístico se usó los métodos de univarianza y multivarianza.

Una de las especies, *Rhogeessa alleni,* una forma de craneo grande, restringida a el Occidente de México, es asignada al subgénero *Baeodon.* Las otras cinco especies son asignadas a el subgénero *Rhogeessa. Rhogeessa parvula,* restringida a México occidental, está caracterizada por tener un uropatagio cubierto de pelo. *Rhogeessa gracilis,* también restringida a México occidental, tiene orejas que son mas grandes que las de las otras especies. Una especie nueva, *R. mira,* conocida solamente de dos localidades de Michoacán, es la mas pequeña de las quatro especies en México occidental. *Rhogeessa tumida,* una especie extremadámente variable y posiblemente un "composite species" (compuesta de mas de una especie), se extiende desde Tamaulipas hasta Brasil y Bolivia. *Rhogeessa minutilla,* una especie de color pálido, encon-

trada en áreas desérticas, es restringida a la Isla Margarita, el Noroeste de Venezuela, y la península de la Guajira de Colombia y Venezuela.

SPECIMENS EXAMINED

For each species, countries are listed from north to south, and from west to east. States, departments and provinces are given in the same sequence following each country, and individual localities are listed in the same manner following each state, department or province. Localities which have not been precisely located on a map are placed in quotation marks. Abbreviations for museums given with specimen numbers are those listed in the Acknowledgments section of this paper. Localities from which specimens were examined are represented on the distribution maps only insofar as space permits. Many map spots cover several (as many as five) localities.

Rhogeessa alleni

MÉXICO: *Jalisco:* Piedra Gorda, *ca.* 8 km NW Soyatlán del Oro, 1600 m, UA 10292. *Michoacán:* 20 km N El Infiernillo, UNAM 8597; 7 km N El Infiernillo, *ca.* 125 m, KU 97307. *Puebla:* 10 mi W Acatlán, 6000 ft, TCWC 8480. *Oaxaca:* 2 mi NNW Tamazulapan [=Tamazulapám], 1990 m, KU 61170-1; Cuicatlán, 590 m, KU 29439; 2 mi N, 6 mi W Nejapa, KU 68773.

Rhogeessa gracilis

MÉXICO: *Jalisco:* 5 mi NE Huejuquilla, 6200 ft, KU 108976; 10 mi SE Talpa de Allende, 5350 ft, KU 97050; 17 km SE Talpa de Allende, 5200 ft, KU 92951. *Puebla:* Piaxtla, about 1100 m, NMNH 70691, 70694. *Oaxaca:* Valero Taujano, 2 mi W Tomallim [=Tomellin?], MVZ 78315-6; Cerro San Felipe, San Felipe del Agua, about 1700 m, AMNH 186901; "Isthmus of Tehauntepec," NMNH 38294.

Rhogeessa parvula

MÉXICO: *Sonora:* Estero Tastiota, sea level, MVZ 85290; 28 mi E Mazatán, 500 m, UNM 18587; W Side Alamos, KU 24853-4; near Alamos, UA 2717; Casa Las Delicias, Alamos, UA 2969; La Aduana, LACM 13247; 8 mi (by road) S Río Alamos, Alamos, about 200 m, UA 16956, 16981-3; 11.3 mi SSE Alamos, Río Cuchijaga, UA 14270; "Rancho Guirocoba," LACM 9700. *Sinaloa:* 1 mi S El Cajón, 1800 ft, KU 100401; 16 km NNE Choix, 1700 ft, KU 90752, 90754; 1 mi S, 6 mi E El Carrizo, KU 105563; 7 mi ESE Sanalona, 600 ft, KU 100402; La Cruz, 30 ft, KU 90755, 90757; Elota, sea level, UA 6358, LACM 19011; ½ mi E Piaxtla, sea level, KU 61163-8; km marker 1289 on Mex. hwy. 15, 9 km W Río Piaxtla, sea level, UA 15991-3, 17189-90; 14 mi N Mazatlán, sea level, UA 13477, 13978, LSU 10431-3; Punta de Cauca, 11 mi N, 2.5 mi E Mazatlán, LACM 12498-500; Mazatlán, LACM 16531; Chupaderos, on Río Panuco, about 26 mi NE Villa Unión, 800 ft, UA 9725, LACM 19080-1; 2 mi E Palmito, KU 97078-81; 5 mi NE Concordia on Mex. hwy. 40, 100 m, UA 11059; 12 km N Villa Unión, 400 ft, KU 95878; Escuinapa, 100 ft, TCWC 14471; 5 mi WSW Plomosas, 800 ft, KU 97082, 97084. *Durango:* Santa Ana, 12 km E Cosalá, Sinaloa, 1300 ft, KU 90759. *Nayarit:* Huajicori, Río del Bajar, 120 m, UA 9724, LACM 19079; 4 km S Playa Novilleros, sea level, UA 11037; about 40 mi E Acaponeta, La Cuchara, LACM 13821; Tres Marías Islands, San Juanito Island, AMNH 180543-4; Tres Marías Islands, María Madre Island, AMNH 180522, NMNH 92413; "Tres Marias Islands," NMNH 84021, ANSP 1832; 5 mi NE San Blas, ¼ mi N Singaita, sea level, UA 18552-3; 8 mi E San Blas, about 200 m, UA 8278-9; LACM 12503-5, 12507, 13244-6, 13436-41; ½ mi E San Blas, 10 ft, KU 39723-5; 4 mi S, 5 mi E San Blas, UNM 16858. *Jalisco:* 9 mi N Guadalajara, 4000 ft, KU 107493-4; 2 mi S La Cuesta, 1500 ft, KU 111613-5; Piedra Gorda, about 8 km NW Soyatlán del Oro, about 1600 m, UA 10294; El Salitre, about 4 km N Soyatlán del Oro, about 1600 m, UA 10590, 10602; Río de Aguacate, about 4 km E Soyatlán del Oro, about 1300 m, UA 10307; about 4 km S Soyatlán del Oro, about 1500 m, UA 10319-20; Cuitzamala, 25 ft, KU 105564; 2 mi N Tenacatita, 25 ft, KU 105565-6; 10 mi NNE Pihuamo, 3500 ft, KU 108974-5. *Colima:* Rancho Tavernillas, about 35 km NW Pueblo Juárez, 350 m, UA 8838, LACM 19082; Tabarnillas, 6 km N Agua Zarca, UNAM 6321-3; Pueblo Juárez, 330 m, UNAM 5643; 2 km N Tlapeixtes, near Manzanillo, sea level, UA 10676; 1 km N Tlapeixtes, near Manzanillo, sea level, UA 10686; Colima, about 500 m, NMNH 52065-6, 52102; "4 mi S Cerro de Ortega," UA 3299; 2 mi E Cuyutlan, LACM 11271-7; 5 mi SE Armeria, LACM 11729-30. *Michoacán:* 20 km N El Infiernillo, UNAM 8592; 7 km N El Infiernillo, ENCB 990-7. *Guerrero:* "Guerrero," NMNH 187713; 4.3 km N Teloloapan, 1480 m, UNAM 8864-7; Ojo de Agua, 3.4 km N Mexicapán, 1480 m, UNAM 9984-5, 10684-5; El Ojo de Agua de Chapa [7 km SSE Teloloapan], UNAM 1990-2; 8 km SW Teloloapan, 1300 m, UNAM 11869; Agua del Obispo, 3300 ft, TCWC 6351; Xaltianguis, about 500 m, NMNH 269315-6. *Morelos:* Río Oaxtepec, 1 km S Oaxtepec, 890 m, UNAM 9706. *Oaxaca:* Santo Domingo, NMNH 73269; San Carlos Yautepec, San Bartolo Yautepec, 800 m, AMNH 167467, 175263; 9 mi NW Tehauntepec, near sea level, UNM 27545; Tehauntepec, sea level, AMNH 178744; 8 km NW Salina Cruz, ENCB 3487-8; 20 mi W Tapanatepec, sea level, UA 13440-2; Río Ostuta, 4 mi W Zanatepec, sea level, AMNH 186406.

Rhogeessa mira

MÉXICO: *Michoacán:* 20 km N El Infiernillo, UNAM 8593-6; 7 km N El Infiernillo, ENCB 998-1007.

Rhogeessa tumida

MÉXICO: *Tamaulipas:* Santa María, 870 m, AMNH 148196; 4 mi N La Pesca, sea level, KU 55192; 3 mi N La Pesca, sea level, KU 55191, 55193, 55208; 2 mi N La Pesca, sea level, KU 55198-208; 1 mi N La Pesca, KU 55194-7; 2 mi S, 10 mi W Piedra, Sierra de Tamaulipas, 1200 ft, KU 55152-63; 55165-89; 3 mi S, 16 mi W Piedra, Sierra de Tamaulipas, 1400 ft, KU 55190; 30 mi N El Mante, Río Cielito, TCWC 25679. *San Luis Potosí:* 10 mi WSW Ebano, LSU 4047; 19 km SW Ebano, LSU 4942-53; 3 km N Taninul, 650 ft, LSU 4936-41. *Veracruz:* 25 mi W Tampico, KU 82922; El Higo, 6 km NNW Ejido El Chote, about 75 m, UNAM 11063; 12.5 mi N Tihuatlán, 300 ft, KU 88427-34; Boca del Río, 10 ft, KU 29886; Río Blanco, 20 km W Piedras Negras, 400 ft, KU 19231; 24 mi S Veracruz, near sea level, AMNH 203917; San Andrés Tuxtla, 360 m, UNAM 9485; 9 mi ENE Catemaco, *ca.* 200 m, UNAM 7751-2; 24 mi S Santiago Tuxtla, Los Tuxtlas, TCWC 9488; Mirador, sea level, NMNH 37329 (skull) + ANSP 1831 (skin of NMNH 37329); Achotal, FMNH 14149; 2.3 km W, 3 km SSW, 2.5 km SW, and 4.1 km S Tenochtitlán, 50 m, UM 116286-91, 116293-98. *Oaxaca:* 3 km W Estación Vicente, Municipio de Acatlán, 60 m, UNAM 11492-3. *Tabasco:* Rancho El Tumbo, 4 km E F.F.C.C. El Zapote, Macuspana, UNAM 1717, 1959-60. *Chiapas:* Rancho San Fernando, 42 km W Cintalapa, 500 m, UA 15711; 32 mi SW Cintalapa, Rancho San Miguel, TTU 11274-5; 2 mi SW

Las Cruces, about 600 m, KU 61169; Finca San Salvador, 15 km SE San Clemente, 1000 m, KU 102619; 11.9 mi SE Tres Picos, Puente El Mosquito, TTU 11354-5; Pijijiapan, 10 m, UM 96523-4; 5 km SE Pijijiapan, 100 ft, TCWC 14466-9; Prusia, 1000 m, UM 88196-8; Huehuetán, 35 m, NMNH 78600; 7 mi ENE Tapachula, about 300 m, KU 68772; 3.8 mi SW Tapachula, TTU 11133; 14 km SW Tapachula, 50 m, KU 120535. *Yucatán:* 10 mi W Progresso, LACM 18167; Piste, 10 m, KU 92000; Chichén-Itzá, AMNH 91234, UNAM 1808, MCZ 10807, 32868, UM 79938. *Campeche:* 5 km S Champotón, 10 m, KU 92007-9; La Tuxpeña, NMNH 170858; Isla del Carmen, 1 km S Puerto Real, 3 m, KU 92010; Balchacaj [=Balchacah?], Laguna de Terminos, FMNH 47394; 65 km S, 128 km E Escárcega, KU 93536. *Quintana Roo:* 4 km WSW Puerto Juárez, 5 m, KU 92001; Pueblo Nuevo X-Can, 10 m, KU 92002-3; Isla Cozumel, 4 km N San Miguel, KU 92004-5; 4 km NNE Felipe Carrillo Puerto, 30 m, KU 92006.

GUATEMALA: "Moca Guatalon," MCZ 28144. *El Petén:* La Libertad, 170 m, AMNH 144697. *San Marcos:* Finca [El] Porvenir, FMNH 50063. *Quetzaltenango:* Finca Los Pirineos, near Santa María de Jesús, *ca.* 1500 m, FMNH 50062. *Suchitepequez:* Mocá, about 1000 m, FMNH 41649, 41828-30, 41856-7. *Santa Rosa:* Finca Santa Isabel, about 200 m, FMNH 74012; Astillero, 25 ft, KU 64992-3.

BELICE: *Belize:* Turneffe Island, Calabash Cay, LSU 7148.

HONDURAS: "Patuca River," NMNH 36062. *Cortez:* 23 mi by road N San Pedro Sula, *ca.* sea level, TTU 13297. *Yoro:* Portillo Grande, 4100 ft, MCZ 33869. *Copán:* Copán, 660 m, TCWC 19752. *Santa Bárbara:* 12 km N Santa Bárbara, TTU 13295-6; 7 mi N Santa Bárbara, 120 m, TCWC 19753-5. *Olancho:* 10.3 mi by road SSW Dulci Nombre de Culmi, TTU 13298, 13300-1. *Comayagua:* 3 km W Comayagua, 580 m, TCWC 21106-7. *Distrito Central:* La Flor Archaga, *ca.* 800 m, MCZ 28976; Comayaguela, 1000 m, MCZ 28975. *La Paz:* El Pedrero, 3000 ft, AMNH 126901-4. *Francisco Morazán:* 2 mi S El Zamorana, *ca.* 1200 m, TCWC 11017; Escuela Agricola Panamericana, MCZ 45401. *El Paraiso:* Chichicaste, 480 m, TCWC 22108.

EL SALVADOR: *Chalatenango:* San José del Sacare, 3600 ft, MVZ 130998; 20 km W Chalatenango, 250 m, TCWC 19751. *Cuscatlán:* Colima, MVZ 130990-1. *Usulatan:* Puerto del Triunfo, sea level, MVZ 130994-5. *San Miguel:* Río San Miguel, 13° 25′ N, 225 ft, MVZ 130991-3.

NICARAGUA: *Matagalpa:* 6 km N Tuma, 550 m, TCWC 24126-7; Uluce [=Uluse?], AMNH 29863; 1 km NE Esquipulas, 420 m, KU 115148. *Chinandega:* 6.5 km N, 1 km E Cosiguina, 10 m, KU 115145-7; Hda. Bellavista, 720 m, Volcán Casita, KU 106284; Chinandega, about 20 m, AMNH 28996. *Boaco:* Santa Rosa, 17 km N, 15 km E Boaco, 300 m, KU 111233-4. *Carazo:* 3 km N, 4 km W Diriamba, 600 m, KU 111235-6. *Zelaya:* 10 km W Rama, 40 m, TCWC 19756; 4.5 km NW Rama, TTU 13313; 3 km NW Rama, TTU 13317-8. *Rivas:* 6.9 mi E San Juan del Sur, TTU 13320.

COSTA RICA: "Pacific Coast," AMNH 4966. "Finca San Miguel," FMNH 67305-6. *Alajuela:* San Torte, between San Carlos and Altamira, ROM 60464. *Guanacaste:* Sámara [=Samari?], LACM 26669. *Puntarenas:* Boca del Barranca, LACM 23767, 25258. *San José:* Río Corrogres, about 2 km NW Santa Ana, 820 m, LSU 12989-93; Finca Lornessa, about 2 km NW Santa Ana, 850 m, LSU 14750-7.

PANAMÁ: "Panamá," MCZ 33525. *Bocas del Toro:* 7 km SSW Changuinola, sea level, NMNH 315776; Almirante, sea level, NMNH 315774-5; Isla Bastimentos, sea level, NMNH 335419. *Chiriquí:* Bugaba, about 200 m, MCZ 10446; 8 mi SE Progresso, sea level, NMNH 363107. *Coclé:* 3 mi W Churubé, 300 ft, NMNH 331910; Santa Clara, sea level, NMNH 296265. *Los Santos:* Guanico Arriba, about 200 m, NMNH 323605. *Canal Zone:* Ft. Sherman, sea level, NMNH 396406; Summit Gardens, about 100 m, NMNH 304930; San Pablo, NMNH 171212-3, 223330; Curundu, NMNH 309219; Ft. Kobbe, sea level, NMNH 309220; Ft. Kobbe Beach, sea level, NMNH 312108-13, 313777-82; Ancon, MCZ 28100; Tapia, AMNH 140472. *Darién:* La Palma de Darién, sea level, MVZ 113936.

COLOMBIA: *Magdalena:* "San Alberto," LACM 16781; Río Guaimaral, Valledupar, 168 m, NMNH 281310; Colonia Agrícola Caracolicito, Santa Marta, about 200 m, NMNH 281921. *Bolívar:* Catiral Upper Río San Jorge, FMNH 69526. *Norte de Santander:* 10 mi N Cueta [=Cúcuta], FMNH 18725-6. *Tolima:* Honda, Las Margaritas, ROM 49045, 49048; Guamo, about 300 m, UAB 426. *Cundinamarca:* Mesitas de Colegio, 1200 m, AMNH 207922, LACM 19064-5. *Valle:* Río Raposo, about 100 m, NMNH 334744. *Huila:* 16 km NE Villavieja, 1600 ft, MVZ 113936.

VENEZUELA: *Zulia:* 30 mi E Maracaibo, sea level, NMNH 260191; Perija, Río Cogollo, sea level, FMNH 21984; 48 km WNW Encontrados, 54 m, NMNH 441790; 38 km WNW Encontrados, 37 m, NMNH 441791. *Trujillo:* 23 km NW Valera (nr. Agua Santa), 90 m, NMNH 372488. *Mérida:* Sta. Elena, Río Guachi, FMNH 21985. *Yaracuy:* 8 km N, 18 km W San Felipe, near Minas de Aroa, 400 m, NMNH 441773-5; 19 km NW Urama, km 40, 100 m, NMNH 372487, 372489, 374016-8. *Aragua:* nr. Rancho Grande, sea level, NMNH COH7876-7. *Miranda:* 5 km S, 5 km E Caracas, Encantados, 570 m, NMNH 441776; 1 km E Río Chico, sea level, NMNH 387738; 5 km E Río Chico, nr. Puerto Tuy, sea level, NMNH 387736-7. *Sucre:* Takal, 11 km SSW Cumaná, about 200 m, KU 119074; 2.5 km SW Cumaná, 5 m, KU 119072; Cuchivano, 700 ft, AMNH 69968; 4 km S, 25 km E Carúpano (nr. Manacal), 170 m, NMNH 409487. *Guárico:* Calabozo, Est. Biol., NMNH UCV4871. *Monagas:* Jusepín, about 100 m, KU 119073; 54 km SE Maturin, Mata de Bejuco, 18 m, NMNH 441792-4; 60 km SE Maturin, LACM 14355. *Apure:* 60 km NE Pto. Paéz, Hato Cariben, La Villa, 76 m, NMNH 374019-20; 8 km NW Pto. Paéz, Cerro de los Murciélagos, 76 m, NMNH 374021. *Amazonas:* 65 km SSW Puerto Ayacucho, Morocoy, 161 m, NMNH 409488.

TRINIDAD: "Trinidad," NMNH 141885. *St. George:* Maracas Valley, TTU 5409, 5457; Maracas, 500 ft, AMNH 183163; Maracas Valley, Waterfalls Rd., about 1100 ft, AMNH 176379, ROM 31438-9, 31453; Port of Spain, sea level, FMNH 51157-8. *St. Patrick:* San Rafael Rancho Estate, Santa María [=St. Mary's?], TTU 5257; Siparia, about sea level, AMNH 179965-6, 182924, 183861.

GUYANA: *Rupununi:* Dadanawa House, ROM 32348; Cotanrib. Isl., 5 mi above Dadanawa, left bank Rupununi River, ROM 59709-10; nr. Shea v. Kuitaro, ROM 43093; Tacatu R. area, 40 mi SW Dadanawa, ROM 58843; (remaining localities not precisely located, but near four previously listed localities) Ikoui Tau, ROM 40764, 40766-7; Kuitaro River, ROM 32783, 46211; Raa Wau, ROM 40798; Tamtoon, ROM 36842; Weri More, ROM 44527.

ECUADOR: *Puná:* Puna Island, San Ramón, sea level, AMNH 66824.

BRASIL (not mapped): *Maranhao:* Alto Parnahyha? [Alto Parnaiba, 9° 06′ S, 45° 57′ W?], FMNH 26465. *Mato Grosso:* 264 km (by road) N Xavatina, Serra do Roncador, 12° 51′ S, 51° 46′ W, 1750 ft, NMNH 393759.

Rhogeessa minutilla

COLOMBIA: *Guajira:* 119 km N, 32 km W Maracaibo, Venezuela, 15 m, NMNH 441781-2.

VENEZUELA: *Zulia:* 114 km N, 32 km W Maracaibo, 12 m, NMNH 441777; 114 km N, 28 km W Maracaibo, 15 m, NMNH 441778-80, 441783-9; Río Aurare, sea level, FMNH 18711; Empeladi Savanna, FMNH 18742-5. *Falcon:* Capatárida, 55 m, NMNH 441795-9, 441801, 441819-36; 6 km SSW Capatárida, Santa Rosa, NMNH 441771-2, 441800, 441802-13, 441815-18.

Lara: Río Tocuyo, 500 m, AMNH 130671-2, 130674-6, 130711-4, 131192; 10 km N El Tocuyo, Caserío Boro, 528 m, NMNH 443183, 443186, 455992, 455994, 455997-9, 456000-1, 456009-15, 456020-24, 456028-9, 456031-2, 456035-7, 456039. *Margarita Island:* "Margarita Island," NMNH 63216, 113497; Nueva Esparta, 2 km N, 30 km W Porlamar (nr. Teatas de María Guevara), 10 m, NMNH 405828.

APPENDIX 1

To plot unknown specimens on any of the three canonical scattergrams (Figs. 7, 8, and 12), first make the nine standard measurements outlined in the section on materials and methods, and substitute into the following formulae:

$$X_{axis}\ \text{(First canonical variable)} = (-0.46)(FA-29.04) - 0.16(3MC-28.28) + 0.47(GLS-12.90) - 0.94(DB-4.66) - 2.09(POW-3.14) + 0.05(MW-6.78) - 1.44(M2M2-5.20) - 0.21(C1C1-3.66) - 1.64(MAX-4.48).$$

$$Y_{axis}\ \text{(Second canonical variable)} = 0.08(FA-29.04) + 0.42\ (3MC-28.28) + 0.58(GLS-12.90) - 0.11(DB-4.66) + 5.59(POW-3.14) - 1.47(MW-6.78) + 0.95(M2M2-5.20) - 0.42\ (C1C1-3.66) - 5.12(MAX-4.48).$$

The two coordinates thereby obtained can then be plotted on the appropriate scattergram in the usual manner.

LITERATURE CITED

Allen, H.
1866. Notes on the Vespertilionidae of tropical America. Proc. Acad. Nat. Sci. Philadelphia, 18:279-288.

Alvarez, T. and C. E. Aviña
1965. *Baedon [sic] alleni, Rhogeessa tumida major* and *R. p. parvula* newly reported for Michoacan, with notes on the qualitative differentiation of the two rhogeessas. Southwest. Nat., 10:75-76.

Anderson, S.
1960. The baculum in microtine rodents. Univ. Kansas Publ. Mus. Nat. Hist., 12:181-216.

Baker, R. J. and J. L. Patton
1967. Karyotypes and karyotypic variation of North American vespertilionid bats. J. Mamm., 48:270-286.

Benedict, F. A.
1957. Hair structure as a generic character in bats. Univ. California Publ. Zool., 59:285-548.

Blackith, R. E. and R. A. Reyment
1971. Multivariate morphometrics. Academic Press, London, vii+412 pp.

Brown, R. E., H. H. Genoways and J. K. Jones, Jr.
1971. Bacula of some Neotropical bats. Mammalia, 35:456-464.

Dobson, G. E.
1878. Catalogue of the Chiroptera in the . . . British Museum. London, xlii+567 pp.

Goodwin, G. G.
1958. Bats of the genus *Rhogeëssa.* Amer. Mus. Novitates, 1923:1-17.

GOODWIN, G. G. and A. M. GREENHALL
1961. A review of the bats of Trinidad and Tobago. Bull. Amer. Mus. Nat. Hist., 122:187-302.
HALL, E. R.
1952. Taxonomic notes on Mexican bats of the genus Rhogeëssa. Univ. Kansas Publ. Mus. Nat. Hist., 5:227-232.
HALL, E. R. and K. R. KELSON
1959. The mammals of North America. Ronald Press, New York, 1:xxx+546+79 pp.
HAMILTON, W. J., JR.
1949. The bacula of some North American vespertilionid bats. J. Mamm., 30:97-102.
HANDLEY, C. O., JR.
1959. A revision of American bats of the genera Euderma and Plecotus. Proc. U. S. Nat. Mus., 110:95-246.
JONES, J. K., JR., J. D. SMITH and R. W. TURNER
1971. Noteworthy records of bats from Nicaragua, with a checklist of the chiropteran fauna of the country. Occas. Pap., Mus. Nat. Hist. Univ. Kansas, 2:1-35.
KOOPMAN, K. F. and E. L. COCKRUM
1967. Bats, pp. 109-150, *in* Recent mammals of the World, a synopsis of families (S. Anderson and J. K. Jones, Jr., eds.), Ronald Press, New York, viii+453 pp.
LAVAL, R. K.
1973. A revision of the Neotropical bats of the genus *Myotis*. Bull. Los Angeles Co. Mus. Nat. Hist., 15:1-54.
MILLER, G. S.
1897. Revision of the North American bats of the family Vespertilionidae. N. Amer. Fauna, 13:1-135.
1897. Description of a new bat from Margarita Island, Venezuela. Proc. Biol. Soc. Washington, 11:139.
1906. Twelve new genera of bats. *Ibid.*, 19:83-86.
PINE, R. H., D. C. CARTER and R. K. LAVAL
1971. Status of *Bauerus* Van Gelder and its relationships to other nyctophiine bats. J. Mamm., 52:663-669.
QUAY, W. B.
1970. Integument and derivatives. Pp. 1-56, *in* Biology of bats (W. A. Wimsatt, ed.), Academic Press, New York, 2:xiii+477 pp.
RIDGWAY, R.
1912. Color standards and color nomenclature. Privately published, Washington, D. C.
SIMPSON. G. G.
1945. The principles of classification and a classification of mammals. Bull. Amer. Mus. Nat. Hist., 85:1-350.
SMITH, J. D.
1972. Systematics of the chiropteran family Mormoopidae. Misc. Publ., Mus. Nat. Hist. Univ. Kansas, 56:1-132.
TATE, G. H. H.
1942. Results of the Archbold Expeditions. No. 47. Review of the vespertilionine bats, with special attention to genera and species of the Archbold Collections. Bull. Amer. Mus. Nat. Hist., 80: 221-297.
THOMAS, O.
1892. Description of a new Mexican bat. Ann. Mag. Nat. Hist., (6) 10: 477-478.
1903. Two South American forms of *Rhogeessa*. *Ibid.*, (7) 11:382-383.
1913. New mammals from South America. *Ibid.*, (8) 12:567-574.

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A NEW GENUS AND SPECIES OF MICROHYLID FROG FROM ECUADOR

By

CHARLES F. WALKER[1]

Two tiny frogs were collected in the Oriente of Ecuador in 1962, and were presumed, at the time, to be juveniles. Subsequent dissection of these specimens revealed them to be adults of an undescribed microhylid. Additional specimens of this frog have been secured more recently by William E. Duellman and his associates at The University of Kansas. He generously has made this material available and has encouraged me to describe the creature.

Syncope new genus

Type species.—Syncope antenori, new species.

Diagnosis.—Seven presacral vertebrae, the first two partially or completely fused (Fig. 1); coccyx articulating with sacrum by two narrowly separated condyles; a small tympanum distinctly differentiated; foot with only four toes evident externally.

The first of these character states alone serves to distinguish the new genus from other American microhylids, the second from the African genus *Breviceps* which shares the vertebral count, and the third and fourth afford convenient external means of recognition. Among the American genera only *Otophryne* possesses a tympanum and in this genus the structure is relatively huge, about equal to the orbit in diameter; although the inner toe of *Otophryne* is small, it is quite distinct. Other osteological features of *Syncope* are:

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[1] Curator, Division of Herpetology, Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48104.

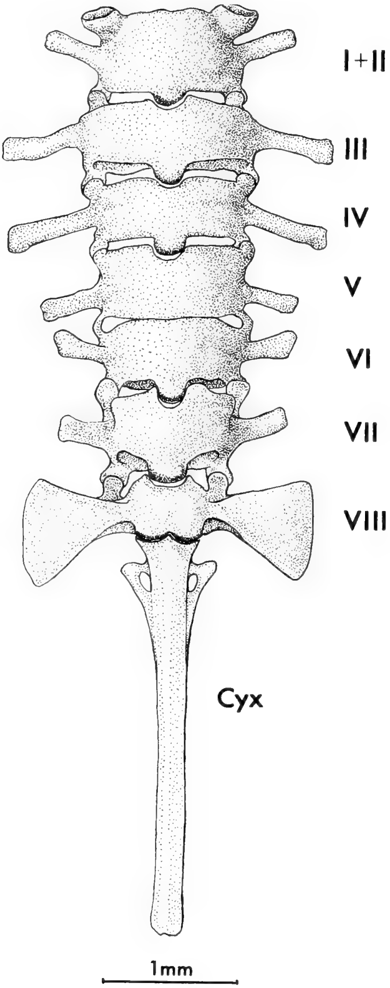

FIG. 1. Vertebral column of *Syncope* in ventral aspect.

vertebrae procoelous; sacral diapophyses expanded; coccyx with basal transverse processes, vestigial or well developed; procoracoid cartilage and clavicle present but reduced, the latter curved, meeting the coracoid in its distal third; omosternum absent; ethmoids paired (*sensu* Parker, 1934); quadratojugal absent, the maxillary arch incomplete; edentulous; premaxilla with notched palatal shelf; maxilla thin, bladelike, with no palatal shelf posteriorly; inner nares bordered anteromedially by a narrow crescentic anterior prevomer; posterior prevomer well developed, medially fused with ethmoid (Fig. 2); no discrete palatine; pterygoid with long anterior ramus

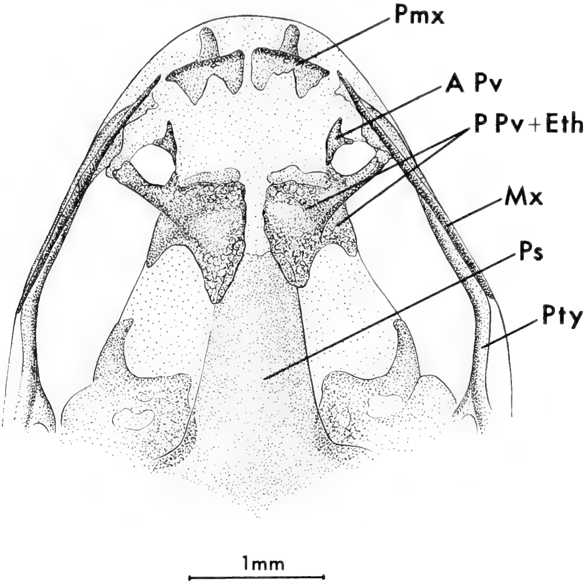

FIG. 2. Anterior cranial elements of *Syncope* in palatal aspect.

articulating with maxilla; anterior ramus of squamosal vestigial; nasals and frontoparietals closely approximated in midline; phalangeal formula of hand 2, 2, 3, 3, of foot 1, 2, 3, 4, 3, the terminal phalanges of inner finger and of inner and outer toes reduced to minute but discrete nodules.

Syncope antenori new species

Holotype.—University of Kansas Museum of Natural History (KU) 124009, an adult female collected on 18 July 1968 by W. E. Duellman and Linda Trueb at Puerto Libre, Río Aguarico, 570 m, Provincia Napo, Ecuador.

Paratypes.—KU 124001-08, 124010-11, all from the type locality, July 1968.

Allotype.—University of Michigan Museum of Zoology (UMMZ) 131699, a male, 7 August 1962, C. F. Walker, 9 km E of Puyo, Provincia Pastaza, Ecuador.

Description of Holotype.—Viewed from above, snout somewhat truncate, interorbital width twice that of eyelid; canthal area rounded; loreal region oblique; head skin smooth; no postorbital fold. In lateral aspect, snout strongly projecting over lower jaw, nostril much closer to snout than to eye; tympanum distinct, its diameter nearly half that of eye. Fingers bluntly rounded at tips, 3>2>4>1, 1 and 4 rudimentary, 3 much the longest, all margined with fleshy web; palms smooth, subarticular tubercles absent. Foot with only four toes evident, small but distinct disks at tips, 4>3>5>2, the normal first toe not developed externally; soles smooth except for a feeble, rounded inner metatarsal tubercle. Tongue elongate, oval, extensively free posteriorly; two low, rounded, transverse palatal dermal ridges, the posterior the longer. Color dark brown above and below, flecked with small white spots, more numerous and larger ventrally than dorsally. Snout-vent length 12.3, tibia 6.0, foot 4.9, head width 4.2, tympanum 0.8 mm.

Variation.—The largest specimen, an adult female paratopotype, is 13.2 mm in length; the male allotype is 11.2 mm in length with well developed testes, and shows no external sexual dimorphism in structure or color. No vocal sac is apparent nor are there any apertures present indicative of an internal sac. The membrane covering the testes is lightly pigmented.

The vertebral number, as shown by X-ray photographs, is constant throughout the series of 13 specimens, as is also some degree of fusion of the first two vertebrae. In those individuals in which the fusion of vertebrae I and II is complete (Fig. 1), there are only six functionally independent presacral elements. Thus the reduction of the column has been achieved in part by fusion, a frequent occurrence among anurans, and in part by elision, a much rarer event. The partial fusion of vertebrae V and VI of the figured specimen represents an individual variation. The coccygeal processes vary from mere vestiges to the maximum shown in the figure, which is approached by only one other individual. The forward tilt of the processes supplies evidence that the shortening of the column has been achieved by the incorporation of a former vertebral element into the coccyx, concurrent with the transfer of the sacral function from vertebra IX to vertebra VIII. A parallel situation has been described by Tihen (1960) in the African bufonid genus *Mertensophryne*, and may be inferred in certain species of the American bufonid genus *Rhamphophryne* (Trueb, 1971) which exhibit seven presacral vertebrae with no evidence of fusion. The coccygeal processes of *Syncope* are thus not strictly homologous with those of discoglossids and ascaphids. Their presence is to be interpreted as a derived rather than primitive condition.

It has been remarked frequently that departures from the standard foot structure, four fingers and five toes, are rare among anurans. Most of the exceptions seem to occur among diminutive species. In the African bufonid genus *Didynamipus*, with a maximum recorded length of 18 mm, only three toes are apparent externally. Still smaller is the Neotropical brachycephalid *Psyllophryne didactyla* (♀ 10.2 mm, ♂ 8.6 mm) recently described by Izecksohn (1971), in which only two fingers and three toes are obvious. The phalangeal formula of these genera is not of record. In *Syncope* the phalangeal formula reveals that suppression of the inner toes has not been complete, nor has it in *Geobatrachus*, a genus of disputed familial relationship, which also lacks an externally evident inner toe and shares with *Syncope* the pedal formula: 1, 2, 3, 4, 3. Dwarfing seems to have been accompanied by paedomorphosis affecting the foot structure independently in these four unrelated lines.

Although patently specialized in most respects, *Syncope* retains two primitive character states, distinct tympanum and posterior prevomer. Derived states include loss of a presacral vertebra, reduction of clavicle, absence of palatine, quadratojugal, externally evident inner toe, and diminutive size. Examination of Table 1, in which the principal character states of the American microhyline genera are presented, shows clearly that *Syncope* could not have evolved from any existing genus. Presumably it has arisen from a

TABLE 1. Occurrence of Character States among American Genera of Microhylid Frogs

	Included taxa	Presacral vertebrae	No. of toes	Tympanum	Clavicle A to scapula B not to scapula	Posterior prevomer	Palatine	Maxillary arch complete, incomplete	Premaxillary notch	Coccygeal process
*Arcovomer**	1	8	5	—	B	+	—	I	+	—
Chiasmocleis	11	8	5	—	B	—	—	C	+	+, —
Ctenophryne	1	8	5	—	—	—	—	C	+	—
Dasypops	1	8	5	—	B	—	—	I	+	—
Dermatonotus	1	8	5	—	A	—	—	C	—	—
Elachistocleis	2	8	5	—	B	—	—	C	+	—
Gastrophryne	5	8	5	—	—	—	—	C	+	—
Glossostoma	2	8	5	—	—	+	+	C	+	—
Hamptophryne	1	8	5	—	B	+	—	C	+	—
Hypopachus	14	8	5	—	A	—	—	C	+	—
Hyophryne	1	?	5	—	B	+	+	C	+	—
*Myersiella***	1	8	5	—	—	—	—	I	—	+
Otophryne	2	8	5	+	A	—	—	C	+	—
Relictovomer	1	8	5	—	B	+	—	I	+	—
Synapturanus	1	8	5	—	—	—	—	C	—	—
Stereocyclops	1	8	5	—	A	+	+	C	+	—
Syncope	1	7	4	+	B	+	—	I	+	+

* Unique in its T-shaped terminal phalanges

** Presacral vertebra VIII procoelous.

relatively primitive stock prior to the loss of the tympanum and posterior prevomer. This same stock may have given rise subsequently to *Chiasmocleis*, *Elachistocleis*, *Hamptophryne*, and other more advanced genera.

In Parker's (1934) monograph, which relies heavily on condition of the pectoral girdle, the new species keys out to *Chiasmocleis*, and that structure indeed is so similar to the girdle of *Chiasmocleis albopunctata* (Parker, 1934:117) as to obviate the need of an additional figure. In Carvalho's (1954) key to the American genera, one is balked at the first couplet because the combination of a differentiated tympanum and a reduced clavicle was unknown to that author.

Etymology.—The generic name, a word of Greek origin, is common to English and most European languages (with only minor variations in orthography) as a figure of speech denoting a shortening by elision. In the present context it alludes to the loss of one presacral element from the vertebral column. The specific name acknowledges the notable contributions of Antenor Leitão de Carvalho to our knowledge of the morphology and biology of the American microhylids.

Remarks.—The specimens in the Kansas collection, 124001-124011, were taken at Puerto Libre on the north bank of the Río Aguarico, just below the mouth of the Río Cofanes. All were collected at night, from litter on the forest floor or from leaves of low herbs and ferns. The two frogs in the Michigan collection, UMMZ 131699, were flushed from a large patch of low terrestrial bromeliads in humid forest about 9 km E of Puyo. Several small groups of eggs in early stages of development were found in these bromeliads. An effort to rear some of these eggs was unsuccessful, and no evidence exists that the eggs were indeed those of *Syncope* other than the treacherous evidence of propinquity of eggs and adults. In two mature, unspawned females the complement of well-yoked follicles is 3 and 4 respectively. One ovulated egg, free in the coelom, is about 1.2 mm in diameter and is heavily pigmented.

Acknowledgments.—Thanks are due Alice G. C. Grandison, British Museum (Natural History) and Richard Zweifel, American Museum of Natural History for the loan of three species not otherwise available to me, and to Martha Lackey for her painstaking care with the figures.

Resumen.—Syncope antenori, se llama el nuevo genero y especie de ranas microhylid del este Ecuatoriano. *Syncope* se diferencia de otros microhylids americano porque tiene siete vertebras presacrales, el coxis articulado con el sacro por dos condilos angostos y separados, un timpano pequeño claramente visible, y tiene solo cuatro dedos en las patas posteriores.

Material Examined.—Arcovomer passarellii: KU 93232-6, 92237 (cl. & st.), Brasil. *Chiasmocleis albopunctata:* UMMZ 63972, 104324, Bolivia; *C. bassleri:* UMMZ 68197, Bolivia; *C. hudsoni:* BMNH 1947.2.11.93, Guyana; *C. panamansis:* UMMZ 126775, Panamá; *C. ventrimaculata:* KU 126668, Ecuador. *Ctenophryne geayi:* AMNH 44787, Brasil; 42887, Perú. *Dasypops schirchi:* UMMZ 115660, Brasil. *Dermatonotus muelleri:* UMMZ 105318, 105321, Brasil. *Elachistocleis bicolor:* UMMZ 66534, Bolivia. *Gastrophryne olivacea:* UMMZ S-2643 (skeleton), Texas; *G. usta:* UMMZ S-1068 (skeleton), Guatemala. *Glossostoma aterrimum:* UMMZ 123591, Costa Rica; *G. aequatoriale:* AMNH 17553, 17562, Ecuador. *Hamptophryne boliviana:* UMMZ 63966, Bolivia. *Hypopachus aquae:* UMMZ S-1032 (skeleton), Guatemala; *H. oxyrrhinus:* UMMZ 128077 (skeleton), 128550 (cl. & st.), Nayarit, México; *H. cuneus:* UMMZ S-2314 (skeleton), Tamaulipas, México; *H. inguinalis:* UMMZ S-2927 (skeleton), Guatemala. *Hyophryne histrio:* none examined; data from Carvalho (1954). *Myersiella subnigra:* KU 93264 (cl. & st.), Brasil. *Otophryne robusta:* UMMZ 85137-40, Venezuela. *Relictovomer pearsei:* UMMZ 45569, 45573, Colombia. *Synapturanus microps:* UMMZ 85143, Venezuela. *Stereocyclops incrassatus:* UMMZ 115659, Brasil; cranial data from Carvalho (1948). *Syncope antenori:* KU, UMMZ, type material, listed above, Ecuador.

LITERATURE CITED

CARVALHO, A. L. DE
1948. Sobre a validez de *Stereocyclops incrassatus* Cope 1871 e *Hypopachus mülleri* (Boettger) 1885. Bol. Mus. Nacional, Rio de Janeiro, Zoologia, 84:1-13, 6 figs.
1954. A preliminary synopsis of the genera of American microhylid frogs. Occ. Papers Mus. Zool. Univ. Michigan, 555:1-19, 8 figs.

IZECKSOHN, E.
1971. Novo genero e nova especie de Brachycephalidae do estado do Rio de Janeiro, Brasil. Bol. Mus. Nacional, Rio de Janeiro, Zoologia, 280:1-12, 16 figs.

PARKER, H. W.
1934. A monograph of the frogs of the family Microhylidae. London: British Museum. xiii + 208 pp., 67 figs.

TIHEN, J. A.
1960. Two new genera of African bufonids, with remarks on the phylogeny of related genera. Copeia, 1960(3):225-233.

TRUEB, L.
1971. Phylogenetic relationships of certain Neotropical toads with the description of a new genus. Los Angeles County Museum Contributions in Science, 216:1-40, 11 figs.

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NEW NORTH AMERICAN ERINACEINE HEDGEHOGS (MAMMALIA: INSECTIVORA)

By

THOMAS H. V. RICH[1] AND DONALD L. RASMUSSEN[2]

Modern hedgehogs, members of the subfamily Erinaceinae, first appeared in the fossil record of Asia and Europe approximately 35 million years ago during the Oligocene. Today the subfamily continues to thrive on those two continents as well as Africa, where they are known to have occurred first 20 million years ago near the beginning of the Miocene.

Although now extinct in North America, members of the subfamily first appeared on that continent approximately 23 million years ago near the beginning of the Miocene. At that time, three erinaceine species, belonging to as many different genera, made their appearance in the fossil record. Two of the species are closely related to forms known in Oligocene deposits of Asia and Europe and hence, apparently immigrated into North America shortly after their appearance there in the fossil record. No known erinaceids in the pre-Miocene fossil record of either the Eastern or Western Hemisphere are closely related to the third species. Therefore the question of whether this third species is a newly arrived immigrant into North America or a descendant from an Oligocene endemic form remains unresolved.

The Erinaceinae persisted in North America until the latter part of the Miocene about 10 million years ago. During the interval of their presence on that continent, only one additional erinaceine

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[1] Department of Geology, Columbia University; Department of Vertebrate Paleontology, the American Museum of Natural History. Present address: The Museum, Texas Technological University, Lubbock, Texas 79409.

[2] Department of Geology and Museum of Natural History, The University of Kansas, Lawrence, Kansas 66045.

genus and species appeared after the initial, nearly simultaneous appearance of the three forms that marked the beginning of the episode. Otherwise, the group did not undergo any noticeable change in North America other than the extinction of its members.

Previously, the North American history of the Erinaceinae had been documented by the description of fewer than two dozen specimens of which less than half were correctly recognized as erinaceines. In an attempt to further elucidate the history of the Erinaceinae, this report will describe a similar number of new North American erinaceine specimens and review those previously mentioned ones which are referred to the same taxa.

ACKNOWLEDGMENTS

For the loan of specimens we are deeply indebted to Mr. Morris F. Skinner and Dr. Malcolm C. McKenna, Department of Vertebrate Paleontology, and Dr. Sydney Anderson, Department of Mammalogy, American Museum of Natural History; Dr. Larry D. Martin, Museum of Natural History, University of Kansas; Dr. Robert W. Wilson, Museum of Geology, South Dakota School of Mines and Technology; Dr. Peter Robinson, University of Colorado Museum; Dr. Robert W. Fields, Department of Geology, University of Montana; the late Dr. Claude W. Hibbard, Museum of Paleontology, University of Michigan; and Dr. Elwyn L. Simons, Peabody Museum of Natural History, Yale University. We also thank Drs. Craig C. Black, Malcolm C. McKenna, and Larry D. Martin for criticizing the manuscript and making several suggestions for improvement.

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Ranchers Dean Tavenner and Marvin Radtke graciously gave permission to collect specimens on their properties.

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METHODS AND ABBREVIATIONS

The primary geochronologic units employed in this report are the North American and European Land-Mammal Ages. Also given are the approximate epoch and radiometric age equivalents based on data summarized in Berggren (1971) and Van Couvering (1972).

Figure 1 illustrates the method employed for making measurements of teeth discussed in this report, and figure 11 illustrates how angular measurements of lower jaws were taken.

Museum abbreviations used with catalogue numbers are as follows:

AMNH	Department of Vertebrate Paleontology, American Museum of Natural History
AMNH (M)	Department of Mammalogy, American Museum of Natural History
F:AM	Frick American Mammals, Department of Vertebrate Paleontology, American Museum of Natural History
KU	Museum of Natural History, University of Kansas
MPUM	Department of Geology, University of Montana
SDSM	South Dakota School of Mines and Technology
UCM	University of Colorado Museum
UMMP	Museum of Paleontology, University of Michigan
YPM	Yale Peabody Museum

HISTORICAL RESUMÉ

Established by Koerner in 1940, *Parvericius montanus* was the first erinaceine species to be recognized and named in North America. The new species was based on a single specimen, consisting of a maxillary fragment with $M^{1\text{-}3}$ and the buccal regions of $P^{3\text{-}4}$, from the Miocene Deep River Formation of Meagher County, Montana. Koerner regarded the species as an erinaceine and considered it to be more closely related to *Erinaceus* than to any other member of that subfamily, devoting the generic diagnosis to an enumeration

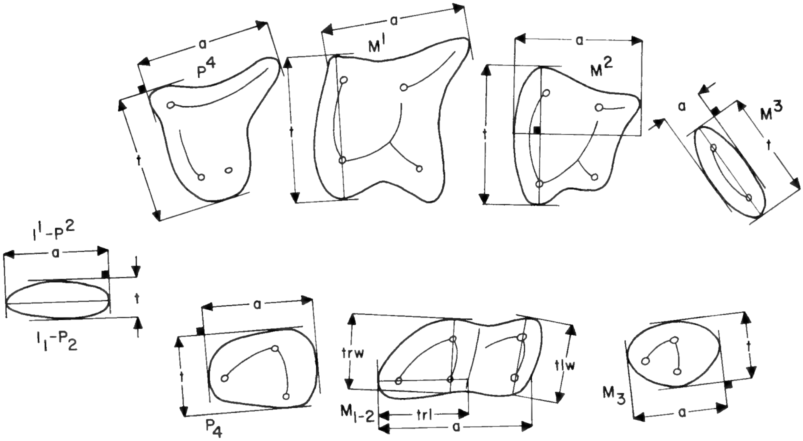

FIG. 1. Occlusal view of erinaceine dentition showing points between which tooth measurements were taken. Abbreviations: *a,* anterorposterior diameter; *t,* transverse diameter; *tl w,* talonid width; *tr l,* trigonid length; *tr w,* trigonid width. For I^1-P^4, M^3, I_1-P_4, and M_3, the transverse diameter, *t,* is defined as the greatest distance from the buccal to the lingual borders of the tooth measured perpendicular to the anteroposterior diameter, *a,* but not necessarily on a single line. For M^2, the anteroposterior diameter, *a,* is defined as the greatest distance from the anterior to the posterior borders of the tooth measured perpendicular to the transverse diameter, *t,* but not necessarily on a single line.

of eleven differences he considered significant between the two (Koerner, 1940:841).

Although Butler (1948:490) suggested that *Parvericius* might belong to the tribe Erinaceini (subfamily Erinaceinae), he tentatively placed it in the Brachyericini (subfamily Neurogymnurinae) in his classification of the Erinaceidae (1948:488). Butler (loc. cit.) regarded the M^1 as more transverse and the M^3 more reduced in *Parvericius montanus* than in *Amphechinus edwardsi*. Examination of Koerner's illustration of the upper dentition of *P. montanus* (see also Fig. 12a, this paper) and Hürzeler's of *A. edwardsi* reveals that the M^3 transverse width is equal to the distance from the buccal edge of the M^2 opposite the metacone to the buccal side of the hypocone on both specimens (Koerner, 1940:Pl. 1, Fig. 1a; Hürzeler, 1944: Fig. 4). Direct examination of the type of *P. montanus* (YPM 13956) confirms this relationship in that specimen. In the same way, the anteroposterior dimensions of the M^3 on the two specimens appear to be proportionally the same, and morphologically the two teeth are quite similar. Therefore, it cannot be said generally that *P. montanus* has a more reduced M^3 than is found on *A. edwardsi*.

In 1960, R. W. Wilson identified an isolated lower molar from the Hemingfordian lower Pawnee Creek Formation of northeastern Colorado as an M_2 of *Metechinus marslandensis*. This specimen now appears to be an M_1 of either *Parvericius* or *Stenoechinus*, new genus.

Friant (1961) placed *Parvericius* in her broadly defined Erinaceinae.

Van Valen (1967:273) synonymized *Parvericius* with *Amphechinus* for three reasons. At the time, Val Valen regarded it likely that material referred to *Metechinus marslandensis* was the otherwise unknown lower dentition of *Parvericius montanus*. On this basis, he assumed that *Parvericius* was similar to *Amphechinus* in possessing an enlarged lower incisor. Subsequently, however, the material referred to *M. marslandensis* has been shown to be the lower dentition of *Brachyerix macrotis*, an erinaceid quite unlike *P. montanus* (Rich and Rich, 1971:12-13). Secondly, Van Valen thought that both *Metechinus* (a genus he thought to have been derived from *Parvericius*) and *Amphechinus* had foreshortened skulls. However, comparison of figures of the skulls of *Amphechinus* and other erinaceines such as *Erinaceus*, reveals that the skull of *Amphechinus* is as elongated, if not more so, than those of other members of the Erinaceinae (cf. Viret, 1938: Fig. 1). Finally, Van Valen regarded the teeth of *Amphechinus* and *Parvericius* as quite similar. Although the available teeth of *Parvericius* do resemble those of *Amphechinus*, they show equally strong resemblances to other known erinaceines.

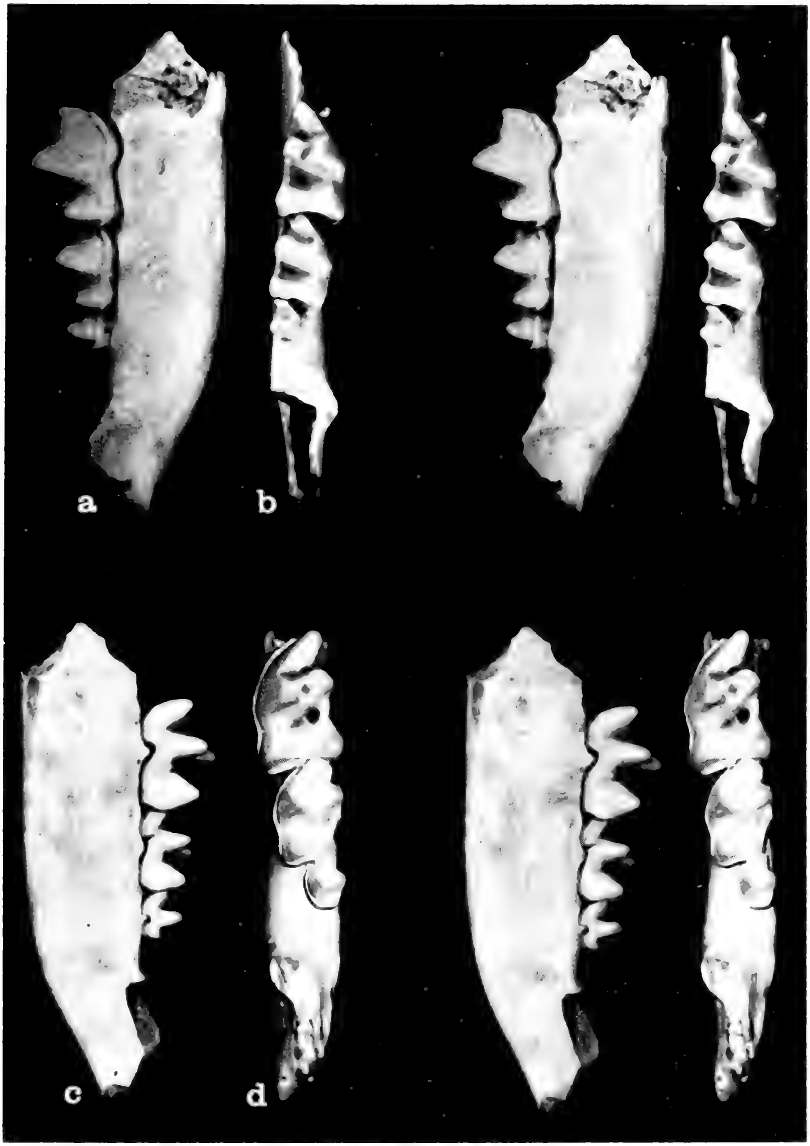

FIG. 2. *Stenoechinus tantalus,* n. gen. and n. sp. A. Lateral view; B. Occlusal view; C. Lingual view of holotype, KU 18001, right mandible, from the late Arikareean, upper Cabbage Patch beds, Tavenner Ranch locality 2 (KU-Mt-21), NW ¼, NW ¼, SW ¼, SW ¼, sec. 11, T 8 N, R 10 W, Powell Co., Montana (= locality 1, Wood and Konizeski, 1965:462). D. Occlusal view of KU 18406, left mandible, from the medial Arikareean, middle Cabbage Patch beds, Cabbage Patch locality 13 (KU-Mt-46), CSW ¼, SE ¼, sec. 1, T 10 N, R 12 W, Granite Co., Montana (= MV6547, Rasmussen, 1969:132). ×6.

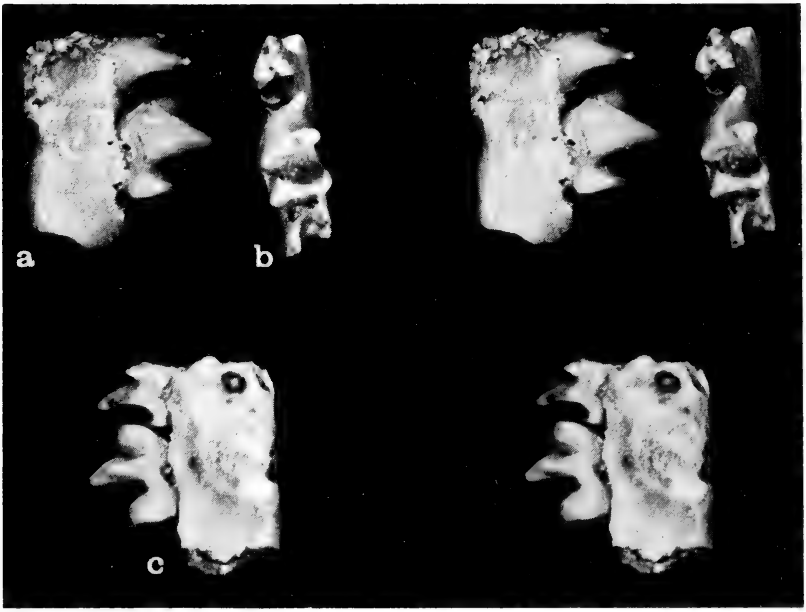

FIG. 3. *Stenoechinus tantalus,* n. gen. and n. sp., KU 18002, left mandible. A. Lateral view. B. Occlusal view. C. Lingual view. From the late Arikareean, upper Cabbage Patch beds, Tavenner Ranch locality 2 (KU-Mt-21), NW ¼, NW ¼, SW ¼, SW ¼, sec. 11, T 8 N, R 10 W, Powell Co., Montana (= locality 1, Wood and Konizeski, 1965:462). ×6.

Mandibles of *Parvericius montanus* described here for the first time support the placement of this species in a genus other than *Amphechinus.* Although the two genera share the elongate I_1 that has so impressed previous workers, this new material demonstrates that the M_1 trigonid of *Parvericius* is anteroposteriorly compressed rather than being anteroposteriorly expanded as in *Amphechinus.* Although but a single difference, in a group as highly uniform as the Erinaceinae, we consider it of generic significance.

Palaeoerinaceus minimus Bohlin (1942) was described first from Taben-buluk, Kansu, China; recently, additional material from Nareen Bulak, Mongolia, has been assigned tentatively to that species by Sulimski (1970) under the designation *Amphechinus* (*Palaeoerinaceus*) cf. *minimus.* Both localities have yielded faunas regarded as somewhat younger than that from the Hsanda Gol Formation of Mongolia and medial or late Oligocene in age (Mellett, 1968:9; Sulimski, 1970:69). Although *P. minimus* apparently has the enlarged I_1 characteristic of all members of *Amphechinus,* the M_1 trigonid is not anteroposteriorly expanded; therefore, this species is transferred to *Parvericius* with which it agrees in both characters. Furthermore, the few mandibles of *Parvericius minimus* can be distinguished from the few of *Parvericius montanus* only by the greater depth of the latter, a difference probably due to ontogenetic stage of development. Therefore, *P. minimus* is regarded here as a junior synonym of *P. montanus*.

Despite the removal of *Parvericius montanus* from *Amphechinus,* the latter genus still is known in North America because *Palaeoerinaceus horncloudi* J. R. Macdonald (1970) from the early Arikareean Monroe Creek Formation of South Dakota may be assigned to *Amphechinus* following Butler's action synonymizing the two genera (Butler, 1948:473). J. R. Macdonald (1970:21) distinguished *A. horncloudi* from other species of the genus by the talonid having a greater width than the trigonid on P_4 and the shorter trigonid on M_1. However, the latter character does not appear valid when figures of other species of *Amphechinus* are compared to the type specimen of *A. horncloudi.* (For example, compare figures of the following species of *Amphechinus:* 1) *A. horncloudi,* Macdonald, 1970: Fig. 5; this paper: Fig. 9; 2) *A. edwardsi,* Hürzeler, 1944: Fig. 13; 3) *A. intermedius,* Viret, 1938: Fig. 9; and 4) *A. arvernensis,* Viret, 1929: Pl. 28, Fig. 1b.) Relative to either the width of the trigonid or the length of the tooth, the anteroposterior length of the M_1 trigonid is as great or greater on *A. horncloudi* as on any other species in the genus.

From the same lithic unit and general area that yielded the type specimen of *Amphechinus horncloudi,* L. J. Macdonald (1972) recently has reported the presence of additional specimens of that species (under the name *Metechinus marslandensis*) together with specimens of *Parvericius montanus.*

SYSTEMATIC ACCOUNTS

Class Mammalia Linnaeus, 1758
Order Insectivora Illiger, 1811
Superfamily Erinaceoidea Fischer von Waldheim, 1817
Family Erinaceidae Fischer von Waldheim, 1817
Subfamily Erinaceinae Fischer von Waldheim, 1817

Stenoechinus new genus

Type Species.—Stenoechinus tantalus new species.

Known Distribution.—Late Arikareean (22.5-21 my, early Miocene), North America.

Diagnosis.—Distinguished from *Aethechinus, Amphechinus, Atelerix, Dimylechinus, Erinaceus, Gymnurechinus, Hemiechinus, Mioechinus, Paraechinus, Parvericius,* and *Postpalerinaceus* by the greater width of the M^1 relative to its length; from *Amphechinus, Dimylechinus, Mioechinus, Palaeoscaptor,* and *Postpalerinaceus* by an anteroposteriorly compressed M_1 trigonid; from *Aethechinus, Amphechinus, Atelerix, Erinaceus, Hemiechinus, Mioechinus, Para-*

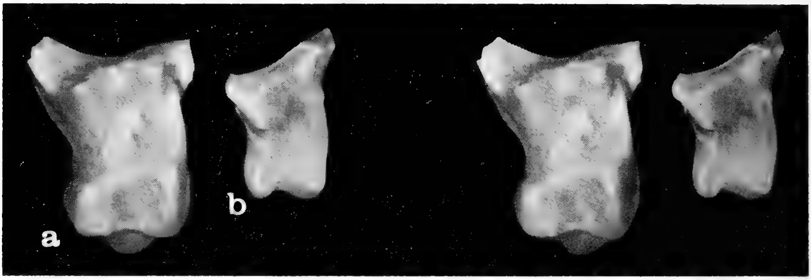

FIG. 4. *Stenoechinus tantalus,* n. gen. and n. sp., occlusal view. A. KU 18359, right M^1. B. KU 18098, right M^2. Same locality as in figure 3. ×12.

echinus, Parvericius, and *Postpalerinaceus* by the presence of a prominent postcingulum on M_3; from *Palaeoscaptor* by a talonid on M_3 reduced to a prominent postcingulum; and from *Dimylechinus* by presence of M_3.

Etymology.—Stenos, Greek, meaning narrow, referring to the proportions of the M^1, M^2, M_1 trigonid, and M_3 talonid; *echinos,* Greek, meaning hedgehog.

Stenoechinus tantalus new species

Figures 2-4

Holotype.—KU 18001, right manible fragment with M_{1-3}, lacking ascending ramus and horizontal ramus anterior to M_1 except for the medial wall of the horizontal ramus that has traces of four alveoli immediately anterior to M_1.

Type Locality and Stratigraphic Position.—Upper Cabbage Patch beds, Tavenner Ranch locality 2 (KU-Mt-21), NW ¼, NW ¼, SW¼, SW ¼, sec. 11, T 8 N, R 10 W, Powell Co., Montana (= Locality no. 1, Wood and Konizeski, 1965:462).

Diagnosis.—Only known species of genus.

Etymology.—Tantalos, Greek, mythological character symbolic of eternal torment.

Referred Material.—KU 18002, left mandible fragment with P_4, M_1, and that part of the mandible immediately below these two teeth. KU 18003, right mandible fragment with M_2, alveolus for M_3, and lacking horizontal ramus anterior to M_2, ascending ramus, and angle. KU 18004, isolated left M_1. KU 18098, isolated right M^2, heavily worn. KU 18342, edentulous left mandible fragment with alveoli for M_{2-3}, and lacking horizontal ramus anterior to M_2 alveoli, ascending ramus, and angle. KU 18354, isolated right M_1. KU 18356, left mandible fragment with M_1 and alveoli for M_{2-3}, lacking horizontal ramus anterior to M_1 and all of mandible behind M_3 alveolus. KU 18359, isolated right M^1. KU 18404, isolated right M_1 trigonid. All the material referred to in this paragraph was collected at the same locality as the type specimen.

KU 18406, left mandible fragment with M_{1-3}, lacking ascending ramus and horizontal ramus anterior to M_1. Found in the middle Cabbage Patch beds, Cabbage Patch locality 13 (KU-Mt-46), CSW ¼, SE ¼, sec. 1, T 10 N, R 12 W, Granite Co., Montana (= MV6547, Rasmussen, 1969:132).

TABLE 1. Measurements (mm) of the Upper Dentition of *Stenoechinus tantalus* and *Palaeoscaptor acridens*

	S. tantalus KU 18098	*S. tantalus* KU 18359	*P. acridens* AMNH 22080
M^1 anterorposterior diameter	----	1.7	2.2
M^1, transverse diameter	----	2.2	2.6
M^2, anteroposterior diameter	1.2	----	1.6
M^2, transverse diameter	1.9	----	2.2

Lower Dentition.—(Figs. 2 and 3) Only indirect data are available to give an indication of the dental condition anterior to P_4. In transverse section, the horizontal ramus of KU 18001 has a medial and a lateral layer of compact bone with a space in between. On the internal side of the medial wall of this specimen, immediately anterior to the M_1, are preserved traces of the partitions between the next four anterior alveoli (Fig. 2a). The most posterior of these alveoli were occupied by the roots of P_4 (Fig. 3a, c). Although the forward wall of the most anterior alveolus preserved is absent, enough of that alveolus is preserved to indicate that it probably had a significantly greater anteroposterior diameter than the one immediately behind. A similar size relationship exists between the same alveoli on a specimen of another small erinaceine, *Palaeoscaptor* cf. *acridens* (AMNH 22082). On that mandible, the more posterior of these two alveoli was occupied by the rear root of P_3 and the more anteroposteriorly elongated anterior alveolus was occupied by the forward root of P_3 and the single root of P_2 (Fig. 5). If there was a bony partition between the forward root of P_3 and the root of P_2, it has been lost without a trace on both KU 18001 and AMNH 22082 and must have been much thinner than the other alveolar walls, for these two roots are quite close to one another on AMNH 22082.

The most anterior alveolar wall preserved on the medial wall of the mandible of KU 18001 extends nearly to its ventral border. In erinaceids such as *Amphechinus? rectus* (AMNH 22084), which have an enlarged I_1 root alveolus extending posteriorly to the region immediately in front of the anterior root of P_4, the alveolar borders of the C_1-P_3 may be traced on the internal side of the medial wall of the ramus from the dorsal lip of their respective alveoli only halfway to the ventral border of the mandible. At that point, the alveolar walls of C_1-P_3 are cut off by the alveolar wall of I_1 because

TABLE 2. Measurements (mm) of P_4-M_3 of *Stenoechinus tantalus* and *Palaeoscaptor acridens*

				S. tantalus					*P. acridens*
	KU 18001	KU 18002	KU 18003	KU 18004	KU 18354	KU 18356	KU 18404	KU 18406	AMNH 22080
P_4, anteroposterior diameter	----	1.5	----	----	----	----	----	----	2.0
P_4, transverse diameter	----	0.9	----	----	----	----	----	----	1.0
M_1, anteroposterior diameter	2.2	2.1	----	2.0	2.1	2.0	----	2.5	2.7
M_1, trigonid length	1.2	1.1	----	1.1	1.1	1.1	1.2	1.4	1.6
M_1, trigonid width	1.5	1.3	----	1.2	1.3	1.1	1.2	1.6	1.5
M_1, talonid width	1.6	1.3	----	1.3	1.4	1.1	----	1.7	1.6
M_2, anteroposterior diameter	1.8	----	1.8	----	----	----	----	----	1.9
M_2, trigonid length	0.9	----	1.0	----	----	----	----	1.1	1.1
M_2, trigonid width	1.3	----	1.3	----	----	----	----	1.4	1.4
M_2, talonid width	1.2	----	1.3	----	----	----	----	----	1.2
M_3, anteroposterior diameter	1.0	----	----	----	----	----	----	1.1	----
M_3, trigonid width	0.7	----	----	----	----	----	----	0.8	----

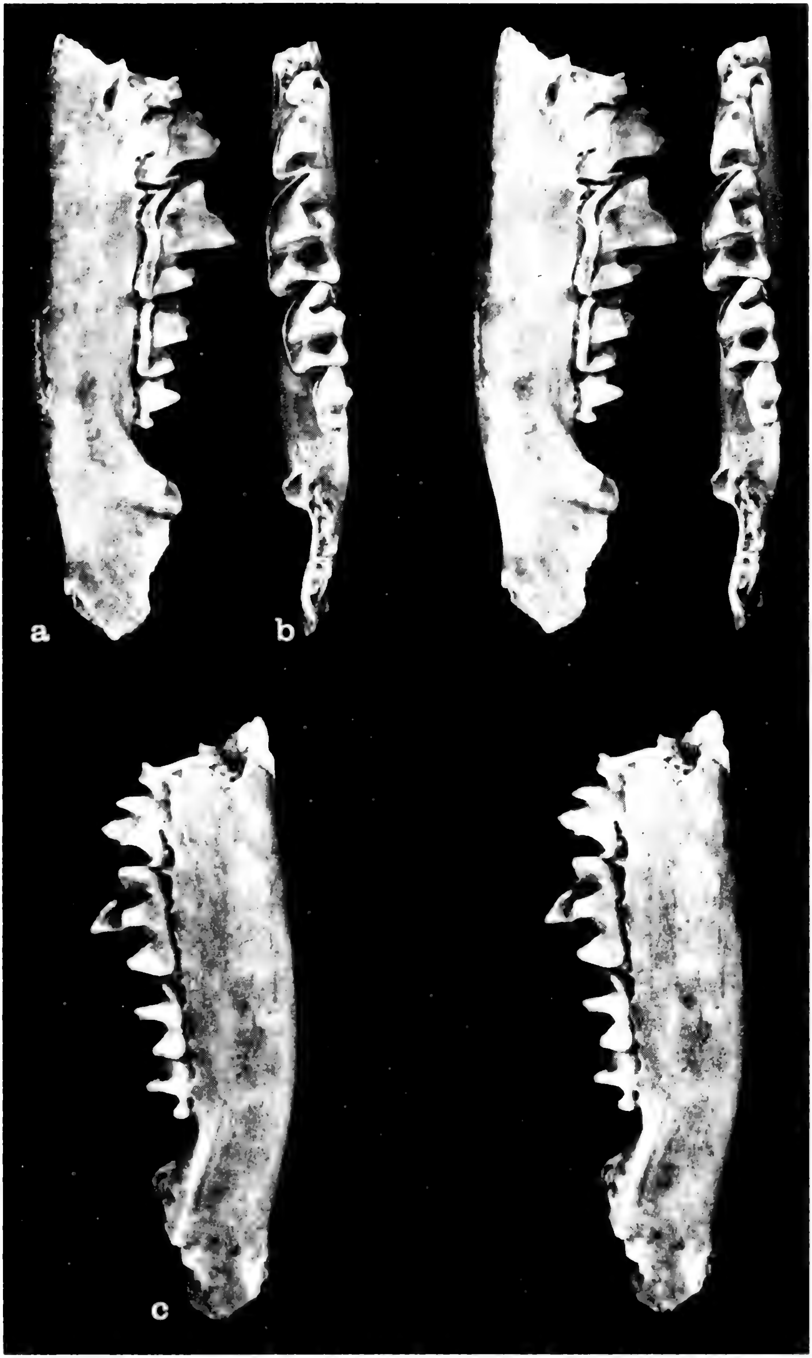

FIG. 5. *Palaeoscaptor cf. acridens,* AMNH 22082, left mandible. A. Lateral view. B. Occlusal view. From the medial Oligocene, Hsanda Gol Formation, Tsagan Nor Basin, Mongolia. ×6.

the root of I_1 passed medial to the roots of C_1-P_3. Hence, the root of I_1 in *Stenoechinus tantalus* did not extend as far posteriorly and was probably closer in relative size to the more reduced I_1 found in the living *Erinaceus europaeus.*

P_4.—Tallest cusp on the tooth, the slender protoconid is half again as high as the paraconid above the base of the enamel, the height of the protoconid being one and one-fourth times the length of the tooth. On the single specimen in which the protoconid is preserved (KU 18002), the lingual third of that cusp has been lost; thus, the casual observer might believe that the metaconid is placed well away from the protoconid base, whereas the bases of the two cusps are actually quite close together. The paraconid is only slightly lower than the metaconid and is situated on the midline of the tooth at its anterior edge; the cusp lies so far forward that its base projects forward beyond the anterior root of the tooth. Along the rear margin of the tooth is a well developed posterior cingulum that dips steeply ventrobuccally. Continuous with this posterior cingulum is a weak buccal cingulum that is developed along the entire length of the tooth.

M_1.—The length of the trigonid is slightly more than half that of the tooth. The trigonid is slightly shorter than wide; the protoconid is the tallest of the trigonid cusps and has the greatest basal dimensions. Intermediate in height, the metaconid is anterolingual to the protoconid; the two cusps are linked by a protolophid that has an acute V-shaped profile in posterior view. The paralophid links the protoconid with the paraconid, the lowest cusp on the trigonid. In lateral view the paralophid has a V-shaped profile; the angle between the two segments of the V is obtuse but close to a right angle. The lingual segment of the paralophid is nearly horizontal. The paraconid lies at the anterolingual corner of the tooth. In lingual view, the paraconid axis is either vertical and parallel to the metaconid axis, or anterodorsally inclined and forms an angle as great as 30 degrees with respect to the metaconid axis.

Width of the talonid is equal to, or slightly greater than that of the trigonid, with the entoconid and hypoconid at the extreme posterior corners of the tooth. The entoconid is the taller of the talonid cusps and is intermediate between the paraconid and metaconid in height. The entoconid is posterior to the metaconid and the hypoconid lies slightly more labial than the protoconid. In anterior view, the buccal margin of both the protoconid and hypoconid are buccally convex. Extending anteriorly from the hypoconid, the cristid obliqua abuts against the posterior wall of the trigonid at a point slightly buccal to the tip of the protoconid. A low entocristid closes the talonid basin lingually. A well developed but narrow cingulum extends along the entire buccal side of the tooth from a point below the paraconid to the base of the hypoconid where it passes into the posterior cingulum; the latter is directed dorsomedially so that it terminates lingually, midway between the hypoconid and entoconid just below the crest of the postcristid. In the region of transition between the buccal and posterior cingula, adjacent to the hypoconid base, these narrow cingula are even narrower.

No specimen is available with the alveoli of this double-rooted tooth exposed.

M_2.—Because this tooth is quite similar to M_1 in general morphology, a detailed description is unnecessary, but a few points of difference are noted.

In length and width, this tooth is about four-fifths as large as the M_1. No distinct paraconid is present; the paralophid terminates lingually without any noticeable swelling. The protoconid and metaconid are equal in height.

The entoconid is only slightly lower in height than the metaconid and markedly taller than the lingual region of the paralophid where the paraconid would be expected if developed. Despite the fact that the talonid is slightly narrower, not equal to, or slightly wider than the trigonid, the hypoconid position is still somewhat more buccal than that of the protoconid. The buccal cingulum is developed as extensively as on the M_1, and terminates anteriorly at the forward edge of the prevallid.

Although the alveoli of this double-rooted tooth are equivalent in width, the posterior alveolus is nearly circular and about twice as long anteroposteriorly as the elliptical anterior alveolus.

M_3.—This double-rooted tooth is markedly different than the more anterior molars; it lacks a well developed talonid, having only a wide postcingulum. The trigonid is anteroposteriorly expanded to the extent that it is slightly longer than wide. Of the two well developed trigonid cusps, the protoconid is the taller and has greater basal dimensions. Its base and that of the lower, smaller metaconid are in close juxtaposition; thus, the protolophid between the two cusps is short. A small, obtuse, V-shaped notch is present near the middle of the protolophid when viewed from the rear. The lingual end of the paralophid lacks a swelling marking the presence of the paraconid. As in the more anterior molars, the paralophid in lateral view has a V-shaped profile; the two limbs of the V meet at nearly right angles with the lingual segment nearly horizontal. A well-developed, continuous, and narrow basal cingulum is present along the buccal margin of the tooth; the basal cingulum passes into a much wider postcingulum that lies along the entire posterior side of the trigonid. This postcingulum is widest midway between the protoconid and metaconid, and tapers to minima at both the lingual and buccal margins of the tooth.

The M_3 is double-rooted in the holotype (KU 18001), but in two other specimens (KU 18003 and KU 18356) where alveoli of this tooth are known, only a single, anteroposteriorly elongated root is indicated; thus, suggesting the condition of the root of M_3 may vary from specimen to specimen. On one of these specimens where the alveolus is exposed, a single elongated root is preserved just below the alveolar lip (KU 18356).

Mandible.—(Figs. 2 and 3) The preserved fragments of the mandible indicate that it is slightly deeper below M_1 than M_3. Between those two areas, the ventral border is nearly straight, but behind the M_3 the ventral border curves sharply upward. The posterior border of the mental foramen is preserved on KU 18002 adjacent to the anterior root of P_4, midway between the dorsal and ventral margins of the mandible. Beneath the M_1 of KU 18001 there is a slight ridge on the buccal side of the mandible near its ventral border. Presumably, this is the lateral border of the diagastric fossa. No diastema are developed between P_2 and M_3.

Upper Dentition.—Two isolated upper molars from Tavenner Ranch locality 2 probably represent the otherwise unknown M^1 and M^2 of *Stenoechinus tantalus* (KU 18359 and KU 18098, respectively). The relative dimensions of these two upper molars are similar to those of the homologous teeth on a specimen of *Palaeoscaptor acridens* from the Hsanda Gol Formation of Mongolia in which the left jaw was found in occlusion with the skull (AMNH

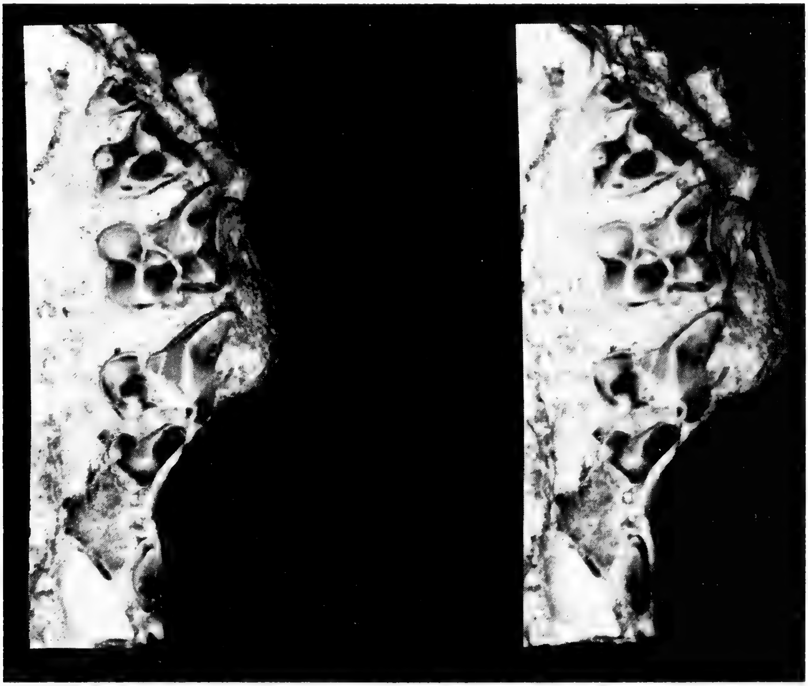

FIG. 6. *Palaeoscaptor acridens*, AMNH 22080, partial skull, occlusal view of right upper dentition. From the medial Oligocene, Hsanda Gol Formation, Tsagan Nor Basin, Mongolia. ×6.

22080), (Table 1). In addition, when the dimensions of the upper and lower teeth on this specimen of *P. acridens* are compared, the ratios are found to be similar to those between the lower teeth of *S. tantalus* and these two upper molars (compare Tables 1 and 2). In morphology, the M^1 is similar to that of *P. acridens* (compare Figs. 4a and 6). Extensive wear during life all but obliterated the cusps and trigon basin on the M^2; however, enough remains to show that in outline this tooth is similar to the M^2 of *P. acridens.* A further reason for associating these upper molars with the lowers in the type specimen of *S. tantalus* is that no other erinaceid is known from Tavenner Ranch locality 2 except the much larger *Amphechinus horncloudi.*

M^1.—(Fig. 4a) The length of this tooth is about three-fourths its width. Of the four principal cusps on the tooth, the metacone is the tallest, its height being slightly more than half the length of the tooth. The protocone and paracone are equal to one another in height and both are equal to the metacone in basal dimensions. Lowest of the four principal cusps and smallest in basal dimensions is the hypocone. The protocone is slightly forward of a point directly lingual to the paracone; the hypocone is lingual to the metacone. A line passing through the paracone and metacone is parallel to one drawn through the protocone and hypocone. The parastylar spur is directed anteriorly away from the main body of the tooth; the metastylar spur is directed posterobuccally. In occlusal view, the lingual, buccal, and posterior borders of the tooth are markedly concave, whereas the anterior border is broadly convex. Close to the convex anterior border are the preprotocrista and preprotoconule crista which grade imperceptibly into one another, because no paraconule is developed. This crest extends from the anterobuccal side of the protocone to the vicinity of the anterior side of the paracone base from which it is separated by a shallow notch. In anterior view, this loph has a profile reminiscent of an inverted, broad, truncated letter V; the margins are formed by the steeply sloping sides of the two cusps and the horizontal midsection is formed by the crest between them. The postprotocrista is directed posterobuccally from the protocone. This crista divides at a point lingual to the anterior edge of the metacone; one branch extends posterolingually to the hypocone and the other extends buccally to the metacone. No trace of a metaconule is present. Developed along the anterior edge of the tooth, the narrow precingulum curves apically at its buccal end, there joining the anterior terminus of the short paracrista. The posterior terminus of the paracrista is at the base of the paracone. A short centrocrista links the bases of the paracone and metacone. From the metacone, the metacrista extends in a buccal and slightly posterior direction along the posterior edge of the metastylar spur for a distance approximately equal to one-fourth the length of the tooth. Along the buccal margin of the

tooth between the paracone and metacone is an extremely weak ectocingulum. Three roots are developed on this tooth—one above the paracone-paracrista region; a second over the metacone-metacrista region; and the third lingual root over the protocone-hypocone region. The anterior and posterior borders of the third lingual root converge toward its dorsal tip in contrast to other erinaceines in which the borders are parallel.

M^2.—(Fig. 4b) In basic outline, the tooth is a right triangle in which the hypotenuse represents the anterior margin. The narrow parastylar spur projects buccally and slightly anteriorly away from the main body of the tooth. The metastylar spur projects posteriorly and the base of the hypocone forms a third spur that projects posterolingually away from the main body of the tooth. A narrow ectocingulum lies buccal to the paracone; as it passes posteriorly, buccal to the metacone, the ectocingulum narrows. A short metacingulum is developed behind the metacone. A precingulum is developed along the anterior side of the tooth. The precingulum extends from the buccal region of the protocone base to a point slightly lingual to the paracone where a prominent wear facet on the parastylar spur has obliterated it. Three roots are developed on this tooth—one above the paracone-paracristra region, a second above the metacone-metacrista region, and a third over the protocone.

Comparisons.—*Stenoechinus tantalus* differs from *Palaeoscaptor acridens* found in the medial Oligocene of Mongolia in five important characters: M_3 talonid reduced to a prominent postcingulum; M_1 trigonid less anteroposteriorly expanded; P_4 paroconid markedly lower than the protoconid; P_4 protoconid height less than tooth length; and I_1 root not extending as far posteriorly. Sulimski (1970: 63) characterized *Palaeoscaptor* as having a more reduced I_1 than *Amphechinus* (= *Palaeoerinaceus* of Sulimski's usage).[1] However, examination of an X-ray photograph of the only known mandible of *P. acridens* containing an I_1 (AMNH 22080) shows that both the

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[1] Following Butler (1948), Sulimski (1970:63) placed *Palaeoerinaceus* Filhol (1879) and *Palaeoscaptor* Matthew and Granger (1924) in *Amphechinus* Aymard (1850). In addition, he formally divided *Amphechinus* into two subgenera: *Palaeoerinaceus* and *Palaeoscaptor*. The basis for this division was the relative size of the I_1 and single-rooted and reduced talonid condition of the M_3. Although a re-examination of specimens of *Palaeoscaptor* in the American Museum of Natural History which were unavailable to Sulimski indicates that all species included by him in *Amphechinus* shared an enlarged I_1, the second criterion, condition of the M_3, continues to appear valid. By this valid criterion, the type species of *Amphechinus*, *A. arvernensis*, clearly belongs in the subgenus *Palaeoerinaceus* for the M_3 is single-rooted and possesses a reduced talonid. According to article 44(a) of the International Code of Zoological Nomenclature (Stoll *et al.*, 1961), if a genus is divided into subgenera, the subgenus containing the type species must be placed in a subgenus with the same name as the genus. For this reason, the name for the subgenus *Palaeoerinaceus* should be changed to *Amphechinus*.

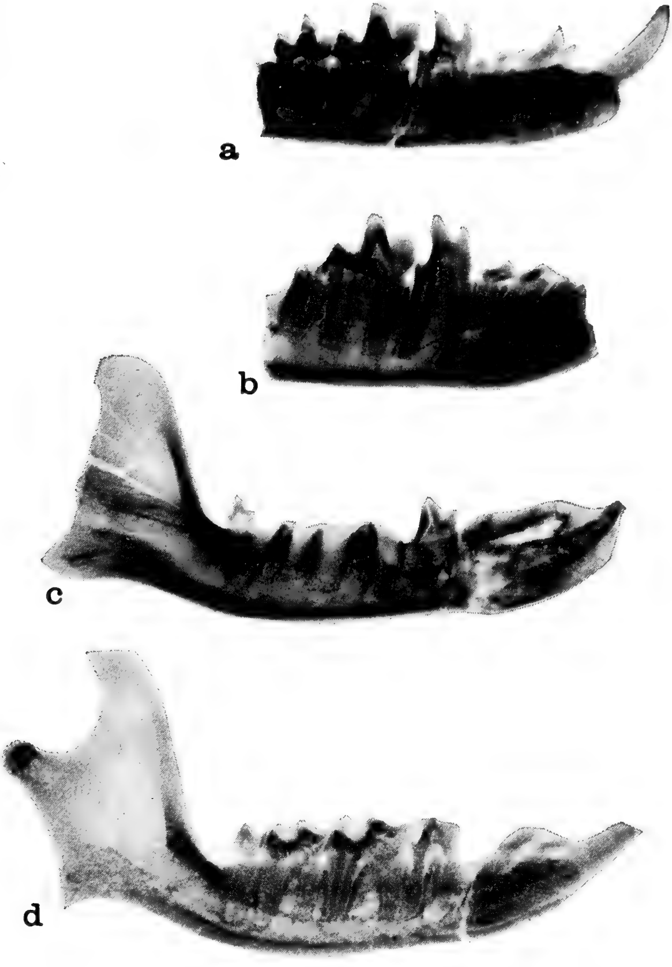

FIG. 7. X-rays of mandibles in lateral view. A. *Palaeoscaptor acridens,* AMNH 22080, reversed left mandible, from the medial Oligocene, Hsanda Gol Formation, Tsagan Nor Basin, Mongolia. ×4. B. *Amphechinus horncloudi,* SDSM 62113, type, right mandible, from the Arikareean, Monroe Creek Formation, T 39 N, R 42 W, Shannon Co., South Dakota. ×3. C. *Amphechinus horncloudi,* KU 18162, right mandible, from the medial Arikareean, middle Cabbage Patch beds, Cabbage Patch locality 3 (KU-Mt-11), SE ¼, NE ¼, SE ¼, SE ¼, SW ¼, sec. 7, T 10 N, R 11 W, Powell Co., Montana (= MV6617, Rasmussen, 1969:140). ×3. D. *Parvericius montanus,* UMMP V56569, reversed left mandible, from the late Barstovian, Egelhoff Quarry, from an unnamed lithic unit beneath the Valentine Formation and overlying the Rosebud Formation, SW corner of NE ¼, SW ¼, sec. 29, T 33 N, R 23 W, Keya Paha Co., Nebraska. ×4. X-rays taken by Dr. Howard K. Bloomfield, DDS.

crown and root are as extensively developed in that species as in the various species of *Amphechinus* (compare figures 7a and 7b, this paper and Hürzeler, 1944: Fig. 7). Except for the features mentioned above, the molars of *S. tantalus* and *P. acridens* are quite similar in morphology, relative proportions, and size.

The species of *Amphechinus* from the Oligocene and Miocene of Europe, Asia, Africa, and North America differ from *Stenoechinus tantalus* by having an anteroposteriorly expanded trigonid on M_1. Together with *Parvericius montanus,* the species of *Amphechinus* differ further in having an enlarged I_1 with a root that extends posteriorly to the region immediately anterior to the forward root of P_4; P_4 paraconid nearly as tall as the protoconid; P_4 protoconid height subequal to the tooth length; complete absence of a talonid on M_3; and M^1 and M^2 more expanded anteroposteriorly.

The species of *Gymnurechinus* from the Miocene of East Africa described by Butler (1956, 1969) are approximately twice as large

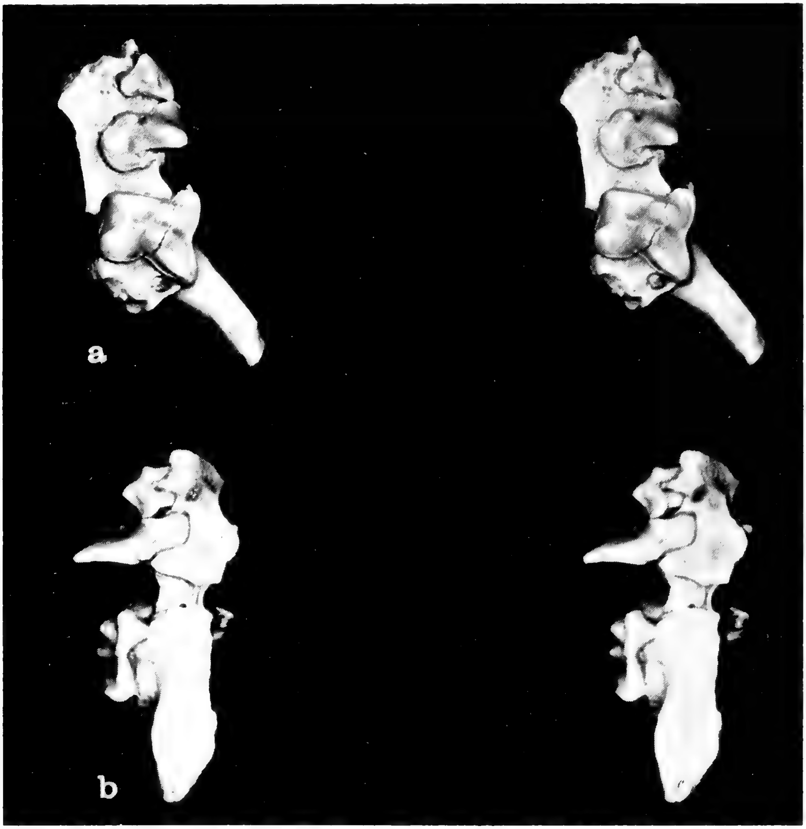

FIG. 8. *Amphechinus horncloudi,* KU 18097, left maxilla fragment. A. Occlusal view. B. Lateral view. From same locality as in figure 3. ×3.

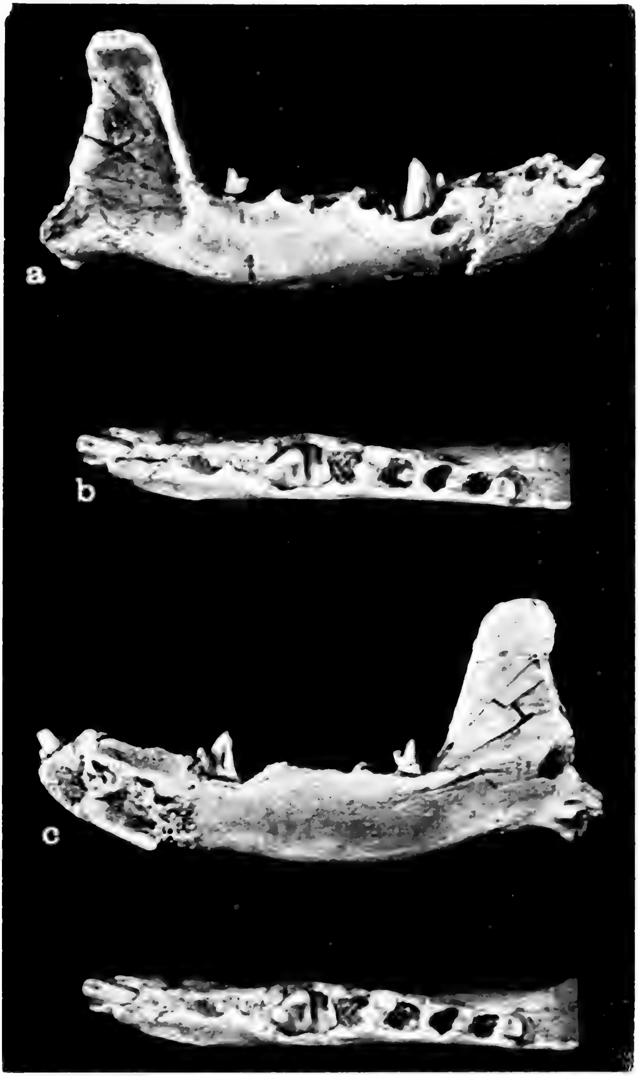

FIG. 9. *Amphechinus horncloudi,* KU 18162, right mandible. A. Lateral view. B. Occlusal view. C. Lingual view. From the medial Arikareean, middle Cabbage Patch beds, Cabbage Patch locality 3 (KU-Mt-11), SE ¼, NE ¼, SE ¼, SE ¼, SW ¼, sec. 7, T 10 N, R 11 W, Powell Co., Montana (= MV6617, Rasmussen, 1969:140). ×3.

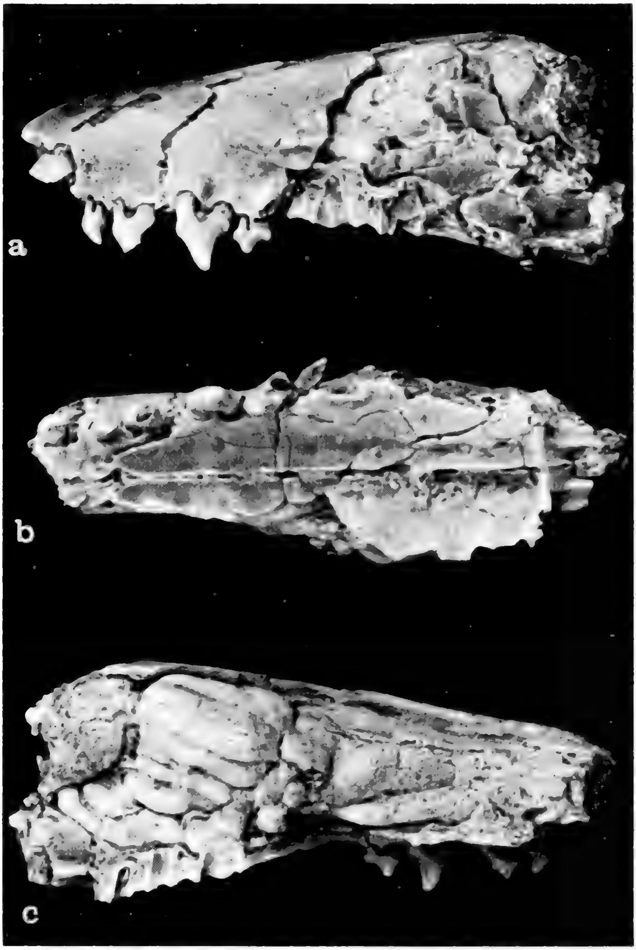

Fig. 10. *Amphechinus horncloudi,* KU 18163, skull fragment. A. Left lateral view. B. Palatal view. C. Right lateral view. From the medial Arikareean, middle Cabbage Patch beds, Cabbage Patch locality 2 (KU-Mt-9), SE ¼, NW ¼, SW ¼, SE ¼, sec. 1, T 10 N, R 12 W, Granite Co., Montana (= MV6504-5, Rasmussen, 1969:131-132). ×3.

as *Stenoechinus tantalus.* In addition, the African species differ in that the paraconid is large and nearly as tall as the protoconid on P_4; and the M^1 and M^2 are expanded more anteroposteriorly.

The anteroposteriorly expanded condition of the lower molar trigonids indicates that *Stenoechinus tantalus* is too advanced or derived to be considered a member of the Adapisoricidae as Van Valen (1967) constituted that group. Among late Mesozoic and early Tertiary insectivores including the adapisoricids, the lower molar trigonid is characteristically anteroposteriorly compressed as compared with the condition commonly observed among several geologically younger groups of insectivores; *e.g.* Erinaceidae, Talpidae, and Soricidae.

Within the Erinaceidae, *Stenoechinus tantalus* is more closely allied with the Erinaceinae than Galericinae due to the reduction of the talonid on M_3 to a prominent postcingulum, a condition rarely encountered among other insectivores and hence considered derived. However, if *S. tantalus* is assigned correctly to the Erinaceinae, it is the most primitive member of that subfamily because its P_4 paraconid lacks the prominence that is the unique derived character state which distinguishes every other member of the subfamily from all other insectivores.

If *Stenoechinus tantalus* is the most primitive known member of the Erinaceinae, the known forms most closely related to that species' immediate ancestors are presumably members of the Adapisoricidae. Found in Europe, Asia, and North America, this family ranges temporally from Paleocene to Oligocene. For this reason, it is not possible to select between the hypotheses that the stock that gave rise to *S. tantalus* was part of the general Arikareean invasion of North America or that the lineage had a prior Oligocene history in North America.

Amphechinus Aymard 1850

Type Species.—Amphechinus arvernensis (deBlainville 1838).

Known Distribution.—Stampian?—Vindobonian (?35—14 my, early? Oligocene—medial Miocene), Europe; Aquitanian—Vallesian (20—11 my, early to late Miocene), Africa; 32—31 my (medial Oligocene), Asia; medial Arikareean—medial Barstovian (23—14 my, early to medial Miocene), North America.

Diagnosis.—Distinguished from *Palaeoscaptor* by absence of a metacone on M^3; from *Palaeoscaptor* and *Stenoechinus* by the greater length of the M^1 relative to its width; from *Aethechinus, Atelerix, Erinaceus, Gymnurechinus, Hemiechinus, Mioechinus, Paraechinus, Postpalerinaceus,* and *Stenoechinus* by presence of an enlarged I_1; from *Aethechinus, Atelerix, Erinaceus, Gymnurechinus, Hemiechinus, Paraechinus, Parvericius,* and *Stenoechinus* by an anteroposteriorly elongated trigonid on M_1; from *Gymnurechinus, Palaeoscaptor,* and *Stenoechinus* by absence of a talonid or postcingulum on M_3; and from *Dimylechinus* by presence of M_3 and M^3.

Amphechinus horncloudi (J. R. Macdonald, 1970)
New Combination
Figures 7b-c, 8-10

Palaeoerinaceus horncloudi J. R. Macdonald 1970:20.

Holotype.—SDSM 62113, fragment of right mandible with P_2-M_1, damaged C_1, roots of I_{1-2}, and anterior root of M_2.

Type Locality and Stratigraphic Position.—Collected from the Monroe Creek Formation in T 39 N, R 42 W, Shannon Co., South Dakota (SDSM V6229; more precise locality information is on file at the South Dakota School of Mines and Technology, Museum of Geology).

Diagnosis.—Distinguished from other species of *Amphechinus* by the talonid being greater in width than the trigonid on P_4.

Referred Material.—KU 18097, left maxilla fragment with P^3, P^4 (except metacrista), M^1 and anterior alveoli of M^2. KU 18405, right P^4 fragment. From the upper Cabbage Patch beds, Tavenner Ranch locality 2 (KU-Mt-21), NW ¼, NW ¼, SW ¼, SW ¼, sec. 11, T 8 N, R 10 W, Powell Co., Montana (= locality 1, Wood and Konizeski, 1965:462).

KU 18162, right mandible with partially erupted I_1, P_4, fully erupted M_3, alveoli for I_2, C_1, P_2, and M_{1-2}, missing region posterior to base of angle. Found in the middle Cabbage Patch beds, Cabbage Patch locality 3 (KU-Mt-11), SE ¼, NE ¼, SE ¼, SE ¼, SW ¼, sec. 7, T 10 N, R 11 W, Powell Co., Montana (= MV6617, Rasmussen, 1969:140).

KU 18163, anterior half of skull with broken right I^1; complete right I^2-P^2; missing lateral part of left palate and lateral part of

Table 3. Measurements (mm) of the Upper Dentition of *Amphechinus horncloudi*

	KU 18097	KU 18163
I^2, anteroposterior diameter	----	1.1
I^2, transverse diameter	----	0.9
I^3, anteroposterior diameter	----	2.0
I^3, transverse diameter	----	1.1
C^1, anteroposterior diameter	----	2.6
C^1, transverse diameter	----	1.2
P^2, anteroposterior diameter	----	1.7
P^2, transverse diameter	----	0.9
P^3, anteroposterior diameter	2.1	----
P^3, transverse diameter	1.7	----
P^4, anteroposterior diameter	3.5[a]	----
P^4, transverse diameter	3.3	----
M^1, anteroposterior diameter	3.4	----
M^1, transverse diameter	3.7	----

[a] Posterior limit of tooth estimated by assuming contact with parastylar spur on M^1.

TABLE 4. Measurements (mm) of the Lower Dentition of *Amphechinus horncloudi*

	type, SDSM 62113	KU 18162
Mandible depth below M_1 anterior root	4.0	3.3
Mandible depth below M_2 posterior root	----	3.9
P_4, anteroposterior diameter	2.5	2.7
P_4, transverse diameter	2.0	1.9
M_3, trigonid length	----	1.1
M_3, trigonid width	----	0.9

right palate behind P^2; casts of olfactory bulbs, chambers for ethmoturbinals, and left maxillary sinus exposed. Found in the middle Cabbage Patch beds, Cabbage Patch locality 2 (KU-Mt-9), SE ¼, NW ¼, SW ¼, SE ¼, sec. 1, T 10 N, R 12 W, Granite Co., Montana (= MV6504-5, Rasmussen, 1969:131-132).

Lower Dentition.—(Fig. 9) *I_1.*—Near the tip of this tooth, its cross section is crudely circular with noticeable flattening on the medial and anterior sides. The crown is anterodorsally inclined.

I_2, C_1.—In dorsal view, the outline of the single alveolus for each of these teeth is an oval with the broad end posterior and the major axis directed anteroposteriorly. The maximum length and width of the alveolus for I_2 are 1.0 and 0.5 mm respectively; similar dimensions for C_1 are 1.6 and 0.9 mm. Both alveoli are anterodorsally inclined.

P_2.—The single alveolus for this tooth is too damaged to allow meaningful statements concerning its outline or dimensions. It seems to have been about the size of the alveolus for I_2.

P_4.—Of the trigonid cusps, the protoconid is tallest and largest in basal dimensions. The paraconid is anteromedial to the protoconid, from which it is separated by a distinct notch. In height, the paraconid is equal to the metaconid, but in basal dimensions, the paraconid is much larger. The protolophid is directed lingually from the posteromedial corner of the protoconid. At the site of the metaconid at the lingual end of this lophid, there is no swelling to mark the presence of the cusp. The talonid is a narrow ridge along the posterior border of the tooth with its highest point behind the protoconid. The maximum transverse diameter of this tooth occurs in the talonid region.

M_1.—The forward alveolus for this double-rooted tooth is trapezoidal in outline; the base of the trapezoid is formed by the medial wall of the alveolus. The maximum anteroposterior measurement of this alveolus is 1.3 mm and the maximum mediolateral measurement is 1.1 mm. The shape of this alveolus may not accurately reflect the condition that would be found in a fully mature individual, because the unerupted P_4 talonid forms the anterior border, and no bony partition is preserved between the tooth and alveolus. The posterior

alveolus is roughly rectangular in outline; the anterioposterior length is 1.2 mm and the mediolateral width is 1.3 mm. The bony partition between the forward and rear alveoli displays the paired bony ridges common in erinaceids.

M_2.—In outline, the two alveoli for this tooth are crudely circular except in the area of the bony partition which separates them from one another; here they are straight or actually concave in the case of the anterior alveolus. Their diameters are approximately 1.0 mm. As on the M_1, the bony partition between the two alveoli has bony ridges.

M_3.—The prevallid is expanded anteriorly, the length of the trigonid being about 10 percent greater than the width. No distinct paraconid is developed at the anterior end of the paralophid; this region is markedly lower than the posterior area. Along the rear of the trigonid is a tall protolophid. At the lingual and buccal ends of this crest there are slight swellings that represent the metaconid and the slightly taller protoconid, respectively. No talonid is developed, but a narrow postcingulum is present that is continuous with a buccal cingulum that extends to the anterior extremity of the tooth.

Upper Dentition.—(Figs. 8 and 10) *I^1*.—The single root of this mediolaterally flattened tooth passes posteriorly above the roots of the succeeding incisors and terminates near the premaxilla-maxilla suture. Although broken off at the base of the crown, this tooth is clearly much larger than the posterior incisors.

I^2-C^1.—Morphologically, these three teeth are quite similar, but there is a marked progressive increase in size posteriorly. In outline, each tooth is crudely elliptical with the major axis directed anteroposteriorly. I^3 and C^1 are double—rooted but I^2 has only one root; however on the buccal side of the I^2 root there is a clear division into anterior and posterior lobes. On the crown of all three teeth there is a single, tall cusp, the height of which is nearly equal to or slightly greater than the length of the respective teeth. The anterior edge of this cusp dips posteroventrally and the posterior edge is nearly vertical. The tip of the cusp is ventral to the posterior root on the I^3 and C^1 and to the posterior lobe on the single root on the I^2. Extending posteriorly from the base of the cusp along the midline of each tooth is a short crest which slopes posterodorsally.

P^2.—Two roots are present on this small tooth. As on I^2-C^1, the outline of the tooth is crudely elliptical and there is a single, prominent cusp, but its height is only two-thirds the length of the tooth. Moreover, the tip of the cusp is further forward than on I^2-C^1 for it is ventral to the anterior root. The posterior edge of the cusp dips anteroventrally. Extending anteriorly from the base of the cusp is a short crest on a precingulum which projects forward of the anterior root. Extending posteriorly from the base of the cusp is a second, much longer crest that terminates at a small

cuspule on a cingulum which projects posteriorly beyond the rear root.

P^3.—In occlusal view, the straight buccal border of the tooth is directed anteromedially; the anterior and posterior borders are concave, and the lingual border is convex. The prominent metacrista extends posterobuccally from the paracone along the midline of the well developed metastylar spur to the posterior tip of that structure. The protocone is somewhat less than half the height of the paracone, and anteromedial to it. Behind the protocone is a flat surface that dips posterodorsally. This surface lacks any trace of a hypocone. A narrow cingulum extends along the anterior side of the base of the paracone. Three roots are developed on this tooth, one above the protocone, another over the paracone, and a third over the metacrista.

P^4.—This tooth is several times larger than the preceding P^3. The height of the paracone, the tallest and most prominent cusp on the tooth, is subequal to the tooth length. The metastylar spur projects posteriorly and somewhat laterally away from the buccal side of the main body of the tooth; thus, the main body of the tooth is more anteroposteriorly elongated buccally than lingually. One—third the height of the paracone, the protocone is located lingual and slightly anterior to that cusp, as in modern hedgehogs. The hypocone is equal in basal dimensions to the protocone but lower. Linking these two cusps is a low crest. A similar crest extends anterolaterally from the protocone to the base of the paracone. On the anteromedial side of the hypocone base are two cuspules. Posterior to the hypocone is a small planar surface that dips steeply anteroventrally. Along the posterior and medial edges of this surface is a weak cingulum. Although no distinct parastyle is present, a prominent parastylar spur is developed on the anterior side of the base of the paracone. Along the margin of the parastylar spur is a distinct cingulum. Three roots are developed on this tooth, one about the protocone-hypocone, a second above the metacrista, and the third above the paracone-parastylar spur.

M^1.—Although this tooth is slightly shorter anteroposteriorly than the P^4, it is markedly broader. The paracone and metacone are subequal in height, their heights being about one-half the length of the tooth. The paracone is anterobuccal to the metacone. Third tallest cusp on the tooth, the protocone is lingual and slightly anterior to the paracone. Posterolingual to the protocone is the lowest of the four principal cusps, the hypocone. Unlike modern erinaceines, the protocone and paracone are no closer to one another than the hypocone and metacone. Because no protoconule is developed, the preprotocrista and preprotoconule crista grade imperceptibly into one another. Linking the protocone and paracone, this loph extends along the anterior border of the tooth and in anterior view has a broad U-shaped profile. The postprotocrista

and postmetaconule crista grade imperceptibly into one another because no metaconule is present. They form a loph which extends posterobuccally from the protocone and gradually turns so that it is convex posteromedially and directed mediolaterally at its termination near the base of the metacone. This loph lacks any connection with the hypocone, for not even a weak crest is developed between them. A weak paracrista linking the paracone and precingulum is developed on the small parastylar spur, which, despite its name, lacks any trace of a distinct parastyle. From the metacone, the metacrista extends posterobuccally for a distance equal to two-fifths the tooth length, and terminates in a weak metastyle. Except for the posterior tip of the metastylar spur, the entire margin of the tooth is bounded by a weak cingulum. In occlusal view, the anterior and medial borders are nearly straight and the buccal and posterior borders, concave. The metastylar spur forms a prominent projection posterobuccally away from the body of the tooth while the parastylar spur is a much weaker anterior projection. Three roots are developed—one above the paracone-paracrista region, a second above the metacone-metacrista region, and a third above the protocone-hypocone region.

M^2.—The circular alveolus above the paracone-parastylar region is approximately 0.8 mm in diameter. Posteromedial to this alveolus is the alveolus above the metacone-metastyle region and medially is the one above the protocone-hypocone region. Only the anterior part of the rims of these latter two alveoli are preserved. Judging from the placement of the three alveoli, the angle formed by the buccal edge of this tooth with that of the M^1 appears to have been about 135°, and the width of this tooth was slightly less than that of the M^1.

Face.—As is typical of erinaceids, the nasals are long and narrow, their posterior ends contacting the frontals. Due to extensive damage on the specimen available, it is not clear how far forward the nasals extended relative to the premaxilla or if there was direct contact between the frontal and premaxilla. The maxilla-premaxilla suture begins ventrally between the C^1 and I^3 and forms an irregular arc that curves upward and backward. The supraorbital crest and the region posterior to it are not preserved.

Palate.—Most of the palate is formed by the maxilla, the premaxilla contributing only in the area immediately adjacent to the upper incisors. The anterior border of the maxilla extends as far forward as the anterior side of the I^2. The palatine fissure is developed on the maxilla-premaxilla suture close to the midline of the palate. The palate extends for a short distance behind the transverse crest, as in the Erinaceinae. Becaues the lateral margin of the palate has been destroyed in the region of the transverse crest on all

TABLE 5. Degree of Elongation of Palate (mm)

Taxa	Specimen number or literature source	*A* Distance from anterior edge of maxilla to transverse crest	*B* Width of palate at P^2	Degree of elongation of palate: A/B
Amphechinus horncloudi	KU 18163	20.0	8.3[a]	2.41
Amphechinus edwardsi	Fig. 4 *in* Hürzeler (1944)	19.0	8.7[a]	2.30
Amphechinus edwardsi	Fig. 7 *in* Viret (1938)	18.0	7.5	2.40
Amphechinus ruingensis	Fig. 16 *in* Butler (1956)	16.0	6.7	2.39
Erinaceus europaeus	AMNH(M) 42562	29.4	15.0	1.96
Erinaceus europaeus	AMNH(M) 160470	26.7	13.4	1.99
Erinaceus europaeus	AMNH(M) 149412	24.6	13.0	1.89
Atelerix albiventris	AMNH(M) 187230[b]	18.2	9.9	1.84
Paraechinus hypomelas	AMNH(M) 166942	22.6	12.3	1.84

[a] Width of left half of palate doubled.

[b] Immature.

specimens available, the presence or nature of posterior palatine foramina in that crest cannot be determined.

A slight groove is developed on either side of the midline at the anterior end of the palatine; it extends posteriorly to a small foramen. Presumably this groove is homologous to the similar one found in galericines, in which the palatine nerve and artery lie. Midway between the aforementioned foramen and the transverse crest is a smaller palatine foramen. The bones of the palate are as thick and solid as those of the living galericines. No vacuities typical of the modern erinaceines are present in the palate.

Although the snout is more elongate than in living erinaceines, the molars are more posterior relative to the zygomatic arch. The elongation is reflected in the high length-to-width ratio of the palate (Table 5). On KU 18163 this ratio is 2.41, on species of *Amphechinus edwardsi* it is from 2.30 to 2.40, and in a sample of recent erinaceines it ranges from 1.84 to 1.99. The location of the base of the zygomatic arch, mainly opposite the M^1, is indicative of the degree of posterior displacement of the molars; however, a small segment of the base lies opposite the M^2. In most modern erinaceines the base of the arch is equally developed above both molars.

Mandible.—(Fig. 9) The mental foramen lies below the anterior root of P_4. A wide groove extends anterodorsally from the mental foramen and terminates below the partition between the alveoli for P_2 and C_1. In the region beneath P_2-M_2, the mandible depth is nearly uniform. Moving away from this region in either direction, the depth gradually decreases.

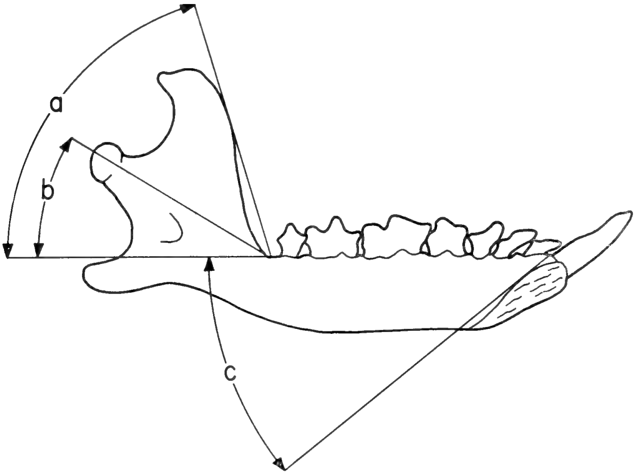

FIG. 11. Method of measuring the elevation of the anterior edge of the ascending ramus ($\angle a$), elevation of the condyle ($\angle b$), and inclination of the dorsal border of the midline symphysis ($\angle c$) on the lower jaw.

Extending forward from beneath P_2, the unfused symphysis occupies the ventral three-quarters of the mandibular surface. The dorsal border of the symphysis is convex dorsally and roughly parallel to the ventral border, dipping posteriorly at an angle of 25° (∠ c in Fig. 11).

The ascending ramus lies slightly labial to the midline of the mandible. Due to damage sustained by the only mandible available, the anteroposterior length of the ascending ramus, precise position of the condyle, and extent of the angle cannot be determined. The straight anterior border of the ascending ramus is posteriorly inclined at an angle of 76° (∠ a in Fig. 11). This angle is the same as Butler's (1948:469-470) "elevation of anterior edge of coronoid process." Contact between the dorsal and anterior edges of the ascending ramus is at a gently rounded corner. A strong lateral flange on the leading edge of the ascending ramus forms the anterior margin of the masseteric fossa. There is a ridge near the base and on the medial side of the ascending ramus. It extends posterordorsally from the anterior edge of the ascending ramus, passes immediately above the mandibular foramen (which is level with the tooth row), and continues a short distance further before being abruptly cut off by the damage described above. Because ridges similar to this are directed at the condyle on complete erinaceine mandibles, it appears that the condyle was quite low, with an angle of elevation (∠ b in Fig. 11) of about 15°. This angle is the same as the "elevation of the condyle" as defined by Butler (*loc. cit.*). On the medial side of the angle can be seen the most anterior part of the inflected ridge which is directly below the mandibular foramen.

Comparisons.—Each of the three specimens from Montana identified as *Amphechinus horncloudi* are from different localities and stratigraphic positions in the Cabbage Patch beds. All are of the proper size to be parts of the unknown dentition, jaw, or skull of *Amphechinus horncloudi* originally described from South Dakota. However, with the exception of KU 18162, there is no reason other than geographic proximity to regard these specimens as conspecific with *A. horncloudi* rather than the slightly larger *Amphechinus edwardsi* of Europe or slightly smaller *Amphechinus rusingensis* of Africa. See Butler (1956: Tables 4 and 7) and Hürzeler (1944:461) for measurements of the dentitions of these two species.

KU 18097, a maxilla fragment with P^3-M^1, is similar to the species of *Amphechinus* in the proportions of the upper molars. Molars of modern erinaceines, *Gymnurechinus, Mioechinus,* and *Postpalerinaceus* are all more anteroposteriorly elongate. *Palaeoscaptor* and *Stenoechinus* have much smaller molars.

KU 18162, a mandible with I_1, P_4, and M_3 is similar to other species of *Amphechinus* and unlike other erinaceines except *Palaeoscaptor* and *Gymnurechinus.* The P_4 is similar to that of the type of

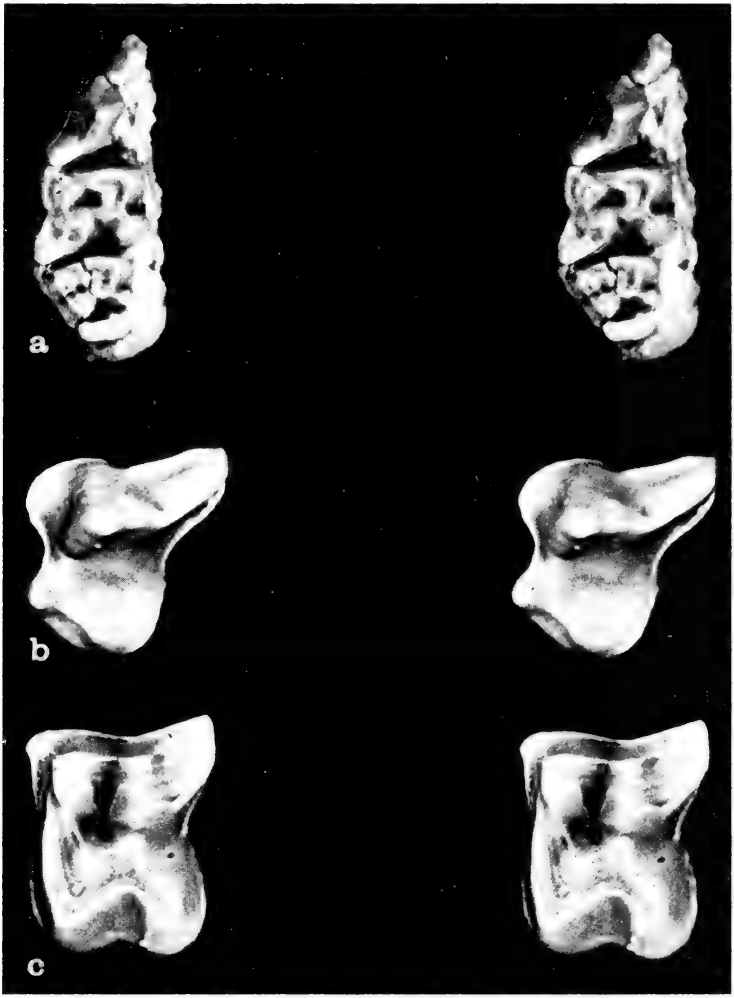

FIG. 12. *Parvericius montanus.* A. YPM 13956, type, right maxilla fragment, occlusal view, from Arikareean or Hemingfordian, Deep River beds, sec. 3, T 10 N, R 5 E, Meagher Co., Montana. ×6. B. UMMP V61033, right P^4, occlusal view, from late Barstovian, Egelhoff Quarry, from an unnamed lithic unit beneath the Valentine Formation and overlying the Rosebud Formation, SW corner of NE ¼, SW ¼, sec. 29, T 33 N, R 23 W, Keya Paha Co., Nebraska. ×12. C. UMMP V61026, right M^1, occlusal view, same locality as B. ×12.

Amphechinus horncloudi (SDSM 62113) and unlike any other known species of the genus in that the maximum transverse diameter is in the talonid region, not further forward across the trigonid.

KU 18163, a partial skull with I^1-P^2, resembles *Amphechinus edwardsi* and *Amphechinus rusingensis* in the presence of an en-

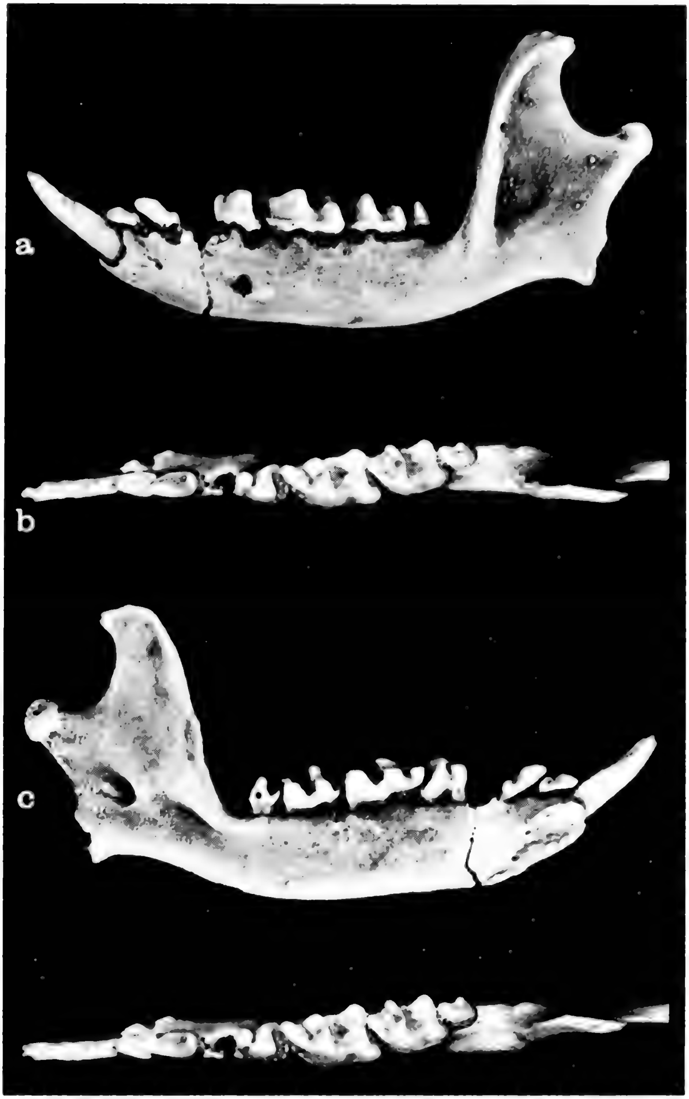

FIG. 13. *Parvericius montanus,* UMMP V56569, left mandible. A. Lateral view. B. Occlusal view. C. Lingual view. From the late Barstovian, Egelhoff Quarry, from an unnamed lithic unit beneath the Valentine Formation and overlying the Rosebud Formation, SW corner of NE ¼, SW ¼, sec. 29, T 33N, R 23 W, Keya Paha Co., Nebraska. ×4.5.

larged I^1. Among the other genera of Erinaceinae, only the much smaller *Palaeoscaptor* is known to possess as enlarged an I^1 (Trofimov, 1960:38 and Fig. 1).

Parvericius Koerner 1940

Type Species.—*Parvericius montanus* Koerner 1940.

Known Distribution.—?32—?31 my (medial? Oligocene) Asia; medial Arikareean—late Barstovian (23—12.5 my, early to medial Miocene), North America.

Diagnosis.—Distinguished from *Palaeoscaptor* and *Stenoechinus* by the greater length of the M^1 relative to its width; from *Palaeoscaptor* by absence of a metacone on M^3; from all other erinaceines except *Palaeoscaptor* and *Amphechinus* by the presence of an enlarged I_1; from *Stenoechinus* by a prominent paraconid taller than the metaconid on P_4; from *Amphechinus, Dimylechinus, Mioechinus, Palaeoscaptor,* and *Postpalerinaceus* by the anteroposteriorly compressed M_1 trigonid; from *Gymnurechinus, Palaeoscaptor,* and *Stenoechinus* by absence of a talonid or postcingulum on M_3; and from *Dimylechinus* by presence of M_3 and M^3.

Parvericius montanus Koerner 1940

Figures 7d, 12-15

Parvericius montanus Koerner 1940:841.
Palaeoerinaceus minimus Bohlin 1942:23.
Amphechinus (*Palaeoerinaceus*) cf. *minimus* Sulimski 1970:64.

Holotype.—YPM 19356, right maxilla fragment with P^3-M^3 complete except for lingual halves of P^{3-4}.

Type Locality and Stratigraphic Position.—Collected from the Deep River beds in sec. 3, T 10 N, R 5 E, Meagher Co., Montana.

Diagnosis.—Only known species of genus.

Referred Material.—MPUM 1551, right mandible with highly worn P_4-M_3, tip of I_1 root, fragment of C_1, P_3 alveolus, horizontal ramus complete from C_1 to base of leading edge of the ascending ramus. Found in the middle Cabbage Patch beds, Bert Creek locality 2 (MV6504-2), NW ¼, NE ¼, SW ¼, SE ¼, sec. 1, T 10 N, R 12 W, Granite Co., Montana (Rasmussen, 1969:131-132).

UCM 29507, isolated left M_1. Found in the Split Rock Formation, SW ¼, NW ¼, sec. 36, T 29 N, R 90 W, Fremont Co., Wyoming.

UCM 29853, isolated right M_1. UCM 29955, left mandible with M_{1-3}, posterior half of rear alveolus of P_4, horizontal ramus complete from rear alveolus of P_4 to base of leading edge of ascending ramus. Found in the Split Rock Formation, NE ¼, NE ¼, NW ¼, sec. 36, T 29 N, R 90 W, Fremont Co., Wyoming.

F:AM 76704, complete left mandible, edentulous except for P_4. UMMP V56569, left mandible lacking only P_2 and the angle. UMMP V57331, left mandible fragment lacking the region posterior to the alveolus for the forward root of M_2 with I_1, C_1, P_4 and alveoli for I_2, P_3, M_1 and anterior alveolus for M_2. UMMP V61029, isolated left M_1 (this specimen appears to have been etched by acid). UMMP V61031, isolated right M_2. UMMP V61027, isolated right M_2. UMMP V61033, isolated left P^4. UMMP V61034, isolated right M^1. UMMP V61026, isolated left M^1. Found at Egelhoff Quarry in the SW corner of NE ¼, SW ¼, sec. 29, T 33 N, R 23 W, Keya Paha Co., Nebraska, in an unnamed lithic unit that unconformably overlies the Rosebud Formation and is unconformably overlain by the Valentine Formation.

UMMP V61022, isolated left M_1. Found at Norden Bridge Quarry in the SE ¼, SW ¼, sec. 33, T 33 N, R 23 W, Brown Co., Nebraska, in the same lithic unit as Egelhoff Quarry described in the previous paragraph.

Upper Dentition.—(Fig. 12) *P^3*.—Only the buccal half of this tooth is preserved on the single specimen available. The paracone is the largest and tallest cusp preserved on the tooth. The anterior side of the paracone is straight and the posterior side, concave. Wear has blunted the tip of the paracone, but, when unworn, the apical height of this cusp was probably no more than two-thirds the crown length. Directed posteriorly from the metacone, the metacrista abruptly turns in a buccal direction at the posterior border of the tooth, but no metastyle or other cuspules are developed there. On the anterior side of the paracone base there is a narrow precingulum with a weak paracrista which extends ventrally

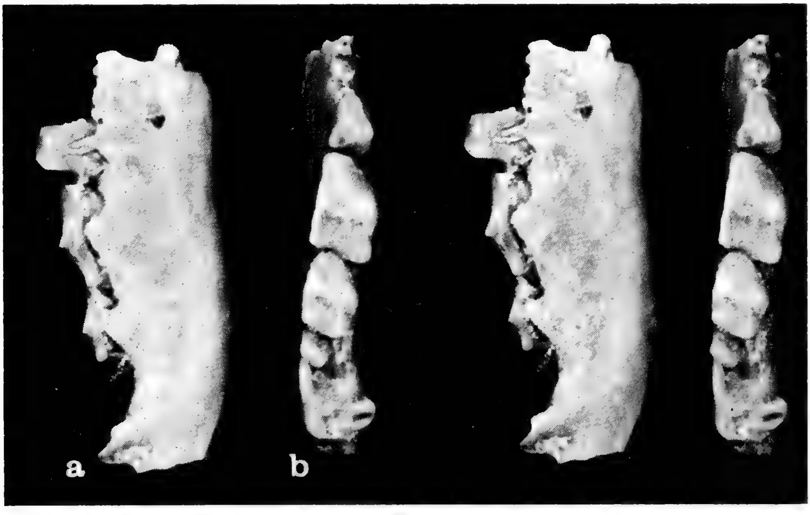

FIG. 14. *Parvericius montanus,* MPUM 1551, right mandible. A. Lateral view. B. Occlusal view. From the medial Arikareean, middle Cabbage Patch beds, Bert Creek locality 2 (MV6504-2), NW ¼, NE ¼, SW ¼, SE ¼, sec. 1, T 10 N, R 12 W, Granite Co., Montana (Rasmussen, 1969:131-132). ×6.

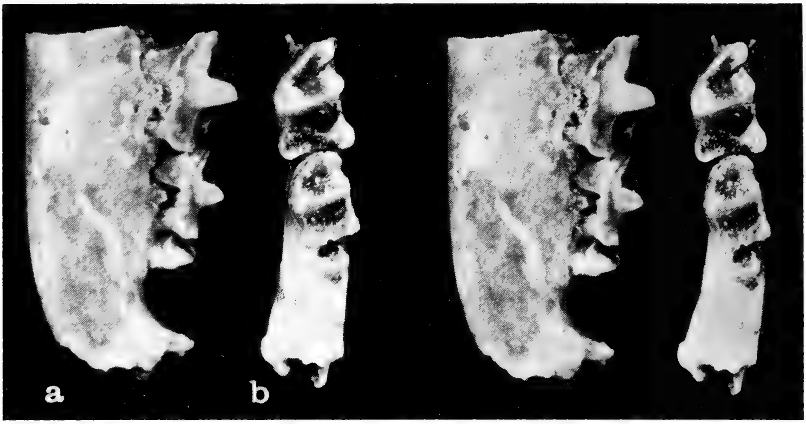

FIG. 15. *Parvericius montanus,* UCM 29955, left mandible. A. Lateral view. B. Occlusal view. From the Hemingfordian, Split Rock Formation, NW ¼, sec. 36, T 29 N, R 90 W, Fremont Co., Wyoming. ×6.

from the cingulum toward, but not reaching, the apex of the cusp. Examination of the broken surface where the lingual half of the tooth broke away suggests that it was markedly shorter anteroposteriorly than the buccal half; thus, the metastylar spur projected away from the body of the tooth as on the P^4. On the buccal side of the tooth along the base of the paracone is a weakly developed cingulum. Two prominent roots are preserved, one above the parastylar region, the other over the metacrista. If a third root were present above the missing lingual region of the tooth, all trace of it has been lost.

P^4.—This tooth is several times larger than the preceding P^3. The height of the paracone, tallest cusp on the tooth, is about five-sixths of the tooth length. Two-fifths the height of the paracone, the protocone is lingual and slightly anterior to the cusp, as in living hedgehogs. Equally as large in basal dimensions, the hypocone is

TABLE 6. Measurements (mm) of the Upper Dentition of *Parvericius montanus*

	YPM 13956 type	UMMP V61033	UMMP V61026	UMMP V61034
P^3, anteroposterior diameter	1.1	----	----	----
P^4, anteroposterior diameter	2.1	2.2	----	----
P^4, transverse diameter	----	2.2	----	----
M^1, anteroposterior diameter	2.1	----	2.0	2.2
M^1, transverse diameter	2.5	----	2.4	2.6
M^2, anteroposterior diameter	1.6	----	----	----
M^2, transverse diameter	1.8	----	----	----
M^3, anteroposterior diameter	0.4	----	----	----
M^3, transverse diameter	1.1	----	----	----

lower than the protocone and posterolingual to it. Although these two lingual cusps are linked together by a low crest, neither cusp is joined to the buccal structure of the tooth by a crest. Between the hypocone and the base of the metastylar spur is a planar surface that slopes posterodorsally. A small parastyle is present on the well-developed precingulum anterior to the base of the paracone. Although no paracrista is present, the prominent metacrista is directed posterobuccally away from the paracone and terminates posteriorly without a distinct metastyle. Likewise, the metastylar spur projects posterobuccally away from the body of the tooth so that its lingual half is narrower anteroposteriorly than the buccal half. Continuous with the precingulum is a weaker cingulum along the buccal side of the tooth. The three roots of the tooth lie above the protocone and hypocone, paracone, and metacrista, respectively; all are subequal in length and diameter.

M^1.—Largest tooth in the skull, the M^1 is somewhat broader but subequal in length to the P^4. The height of the paracone, third tallest and third largest of the four principal cusps, is half the length of the tooth. The paracone is anterior to the metacone and their bases are confluent. Subequal in height and basal dimensions, the metacone and protocone are the tallest and largest of the four principal cusps. The anterior side of the metacone is steep; the posterior side is more gently dipping. The protocone is lingual and slightly anterior to the paracone. The hypocone is the lowest and smallest of the four principal cusps. The hypocone and metacone are as close to one another as the protocone and paracone. Linking the anterobuccal corner of the protocone and the anterolingual corner of the paracone are the well-developed preprotocrista and preprotoconule crista which grade imperceptibly into each other in the absence of a paraconule. In anterior view this loph has a broad, inverted V-shaped profile. The postprotocrista is directed posterobuccally from the protocone. This crista divides at a point lingual to the anterior edge of the metacone; one branch extends posterolingually to the hypocone whereas the other, the postmetaconule crista, extends buccally to the metacone. No metaconule is developed on this tooth. A short paracrista crosses the precingulum and terminates against the base of the paracone at the anterobuccal corner of the tooth. No parastyle is present. The metacrista extends posterobuccally from the metacone for a distance equal to one-half the tooth length. A cingulum is developed along the entire margin of the tooth except at the posterior tip of the metastylar spur. In outline the tooth is approximately square, with prominent excavations on the posterior and lingual side. A well-developed metastylar spur projects posterobuccally away from the body of the tooth, and a much smaller parastylar spur projects anteriorly. Three roots are present—one above the paracone-paracrista region, a second

TABLE 7. Measurements (mm) of the lower dentition of *Parvericius montanus*

	MPUM 1551	UCM 29507	UCM 29853	UCM 29955	UMMP V56569
P_4, anteroposterior diameter	1.2	----	----	----	1.5
P_4, transverse diameter	0.9	----	----	----	1.2
M_1, anteroposterior diameter	1.9	2.4	2.2	2.2	2.5
M_1, trigonid length	1.1	1.2	1.2	1.2	1.3
M_1, trigonid width	1.3	1.3	1.6	1.4	1.6
M_1, talonid width	1.3	1.5	1.7	1.5	1.8
M_2, anteroposterior diameter	1.5	----	----	1.7	2.0
M_2, trigonid length	0.9	----	----	0.9	1.0
M_2, trigonid width	1.2	----	----	1.2	1.5
M_2, talonid width	1.0	----	----	1.2	1.4
M_3, anteroposterior diameter	0.7	----	----	0.7	1.0
M_3, trigonid width	0.6	----	----	0.6	0.8

TABLE 7. (continued)

	UMMP V57331	UMMP V61031	UMMP V61029	UMMP V61027	F:AM 76704	UMMP V61022
P_4, anteroposterior diameter	1.4	----	----	----	1.5	----
P_4, transverse diameter	1.1	----	----	----	1.0	----
M_1, anteroposterior diameter	----	----	2.5	----	----	2.5
M_1, trigonid length	----	----	1.5	----	----	1.3
M_1, trigonid width	----	----	1.4	----	----	1.5
M_1, talonid width	----	----	1.6	----	----	1.6
M_2, anteroposterior diameter	----	1.8	----	2.0	----	----
M_2, trigonid length	----	1.0	----	1.0	----	----
M_2, trigonid width	----	1.4	----	1.5	----	----
M_2, talonid width	----	1.2	----	1.4	----	----
M_3, anteroposterior diameter	----	----	----	----	----	----
M_3, trigonid width	----	----	----	----	----	----

above the metacone-metacrista region, and a third above the protocone-hypocone region.

M^2.—Although smaller, the M^2 is basically similar to the M^1. The protocone and paracone are subequal in height and basal dimensions, being the tallest and largest of the four principal cusps. The lingual region of the M^2 is the same as the M^1; however, the buccal region, particularly the posterobuccal area, is different. The metacone has shifted position so that it is posterolingual to the paracone, not posterior. The metastylar spur projects posteriorly, not posterobuccally, and is reduced. The buccal border of the tooth is not subparallel to the midline of the skull, but is directed posteromedially. Similarly, the parastylar spur has shifted so that it projects anterobuccally rather than anteriorly. Narrow cingula are developed on all sides except the lingual. Only the two buccal roots of the tooth can be observed; relative to structures on the crown, their positions are the same as on the M^1.

M^3.—This tooth is basically a mediolaterally elongated blade with a protocone at the lingual end and an equally large and tall paracone at the buccal end; the two cusps are joined together by a short, straight crest. A weak precingulum is developed along the anterior margin of this tooth. Two roots are developed on this tooth—one above the protocone and a second over the paracone.

Lower Dentition.—(Figs. 13-15) *I_1.*—In morphology and size, this tooth is quite distinct from the incisor behind (I_2). It is elongated, extends forward, and curves slightly upward from the anterior end of the mandible for a distance about equal to the I_2-P_3 length, or 3.7 mm on the least worn specimen (UMMP V56569). Posteriorly, the root extends beneath and medial to the roots of I_2-P_3 to terminate just in front of the anterior root of P_4. In cross-section at the alveolar border, the tooth is a slightly distorted, dorsoventrally elongated oval with the blunt end dorsal and the medial side straight rather than curved. The tooth is mediolaterally compressed so that its dorsoventral diameter is about half again as great as its mediolateral diameter. At its alveolar border, the tooth is nearly as wide and deep as the mandible itself. Further posterior, beneath the canine, the dorsoventral diameter of the tooth is equal to about half the height of the mandible.

I_2.—This tooth and the somewhat larger canine behind are more similar in form to one another than either is to the I_1. Presumably, the same could be said for the P_2, although the tooth is known only by its alveolus in this species. The single root of the I_2 dips posteriorly at a shallow angle. Overlapping the I_1 ahead, the crown of the I_2 projects forward from the root. Along the midline is a low crest with two prominent swellings. The anterior swelling lies slightly forward of the midpoint of the tooth and is the protoconid; the second swelling lies at the posterior margin of the short talonid. The length of the tooth is about twice the width.

C_1.—In addition to its somewhat larger size, the C_1 differs from the I_2 primarily in the relative sizes of protoconid and talonid cusp, which are slightly taller relative to the length and width of the tooth.

P_2.—This tooth is known in this species only by its single alveolus. The P_2 was probably similar in size and morphology to the I_2, because the alveoli of the two teeth are of similar dimensions; in other erinaceines, they are similar in morphology. The posterior dip of the P_2 alveolus is steeper than in I_2 or C_1.

P_4.—This tooth is markedly larger than the three immediately anterior to it. The protoconid is most prominent of the cusps; its height is nearly as great as the length of the tooth. Anteromedial to the protoconid is the lower paraconid, a well-developed cusp. In lateral view the paralophid linking the two cusps has a deep, acute V-shaped profile. The protolophid is directed medially from the protoconid and has a slight swelling on the lingual end, but no distinct metaconid. Along the buccal border of the tooth is a weak cingulum. This cingulum passes into the narrow talonid which is developed for the full width of the trigonid.

On no specimen were the alveoli of this double-rooted tooth visible.

M_1.—The length of the trigonid is four-fifths its width and approximately equal to half the length of the tooth. Lowest of the trigonid cusps, the paraconid is anterior to the metaconid; the bases of the two cusps are separated by a deep cleft. The protoconid is posterobuccal to the paraconid; the two cusps are linked by a paralophid. In lateral view, the paralophid has a V-shaped profile that is acute but nearly a right angle, whereas in occlusal view, the paralophid is somewhat buccally convex. The protoconid is the tallest cusp on the tooth and has the greatest basal dimensions. On the least worn specimen (UCM 29853), the height of the protoconid is equal to 85 percent of the tooth length. The protolophid joins the metaconid and protoconid; when viewed posteriorly, it has an acute, V-shaped profile. The metaconid is intermediate in height between the protoconid and paraconid.

Ten percent wider than the trigonid, the talonid has only two cusps, one in each posterior corner. The entoconid is the taller of these two cusps and is intermediate in height between the metaconid and paraconid. The entoconid is directly posterior to the metaconid and the hypoconid is slightly more buccally placed than the protoconid. In anterior view, the buccal margin of the protoconid is nearly straight and that of the hypoconid, convex. Between the entoconid and that part of the posterior wall of the trigonid beneath the apex of the metaconid is a low entocristid which encloses the talonid basin lingually. Directed anteriorly and slightly lingually from the hypoconid, the cristid obliqua abuts against the postvallid immediately behind the protoconid. A continuous, well-developed, narrow cingulum extends along the entire buccal side of the tooth. At the base of the hypoconid, the buccal cingulum passes into the posterior cingulum which is directed dorsomedially so that it terminates lingually midway between the hypoconid and entoconid just below the crest of the postcristid. In the region of transition between the buccal and posterior cingula, these narrow cingula are even narrower.

The partition between the alveoli of this double-rooted tooth has twinned vertical ridges characteristic of erinaceids. On the posterior wall of the rear alveolus is a single vertical ridge. The anterior alveolus is nearly circular with the posterior side slightly flattened. Its diameter is approximately 0.7 mm. The larger, posterior alveolus is roughly rectangular with an anteroposterior length of 0.8 mm and width of 0.9 mm.

M_2.—Although the M_2 is only four-fifths as large as the M_1, in other respects the teeth are quite similar. Therefore, only differences between these teeth will be noted in the following two paragraphs.

The trigonid length is only two-thirds as great as its width. The paraconid is not developed as a distinct cusp but rather is a small swelling at the anterolingual end of the paralophid. The anterolingual quarter of the protolophid is at an abrupt angle with respect to the remainder of that crest, being oriented mediolaterally rather than anterolingually.

The entoconid is more buccally placed on the tooth than the metaconid. When viewed anteriorly, the buccal margin of the protoconid is buccally convex. No buccal cingulum is developed on the most anterior quarter of the prevallid.

M_3.—This tooth differs from the two anterior molars in several ways: markedly smaller size; complete absence of a talonid; more anteroposteriorly expanded trigonid, its length being one-fourth greater than its width; and a single anteroposteriorly elongated root that may be weakly bifurcated. Only two distinct cusps are present on the trigonid—the protoconid and metaconid. The protoconid is taller and somewhat larger in basal dimensions than the metaconid; the bases of the two cusps are so close to one another that only a narrow notch separates them. No swelling is present at the lingual end of the paralophid to mark the presence of a distinct paraconid. Only the worn base of the paralophid remains on the best available specimen of this tooth. A well-developed, continuous, narrow basal cingulum is present along the buccal margin of the tooth, but no cingulum is present along the posterior side of the trigonid.

Oval in outline, the single alveolus of this tooth departs slightly from the vertical so as to dip posteriorly. The length of the oval is 0.9 mm and the width, 0.5 mm.

Mandible.—(Figs. 13-15) Circular in outline, the mental foramen lies below the middle of P_4, midway between the dorsal and ventral borders of the ramus. Beneath P_3-M_2, the mandible is of a uniform depth; it gradually decreases in depth posteriorly and abruptly anteriorly. The angle of the jaw protrudes ventrally and posteriorly away from the body of the mandible and is slightly inflected. The unfused midline symphysis of the mandible extends posteriorly to a point beneath the C_1-P_3 juncture. The dorsal boundary of the symphysis dips posteriorly at an angle of 25° with respect to the dorsal edge of the mandible ($\angle$ c in Fig. 11). Beneath I_1, the symphysis covers the entire medial surface of the mandible; posteriorly it covers a progressively decreasing amount. Parallel and adjacent to the ventral margin of the midline symphysis is a faint depression which opens posteriorly and may have been the site for the insertion of the geniohyoideus muscle.

The ascending ramus lies slightly labial to the midline of the mandible. Its anteroposterior width, measured from the condyle, is twice the maximum depth of the jaw. The anterior border of the ascending ramus departs slightly from the vertical and dips an-

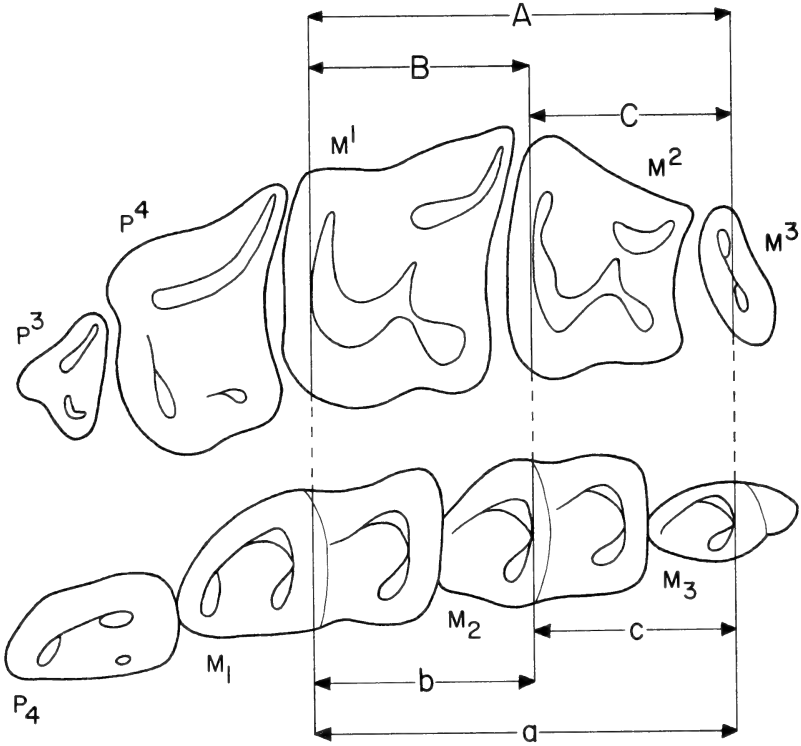

FIG. 16. Method of measuring distances between occluding surfaces. Corresponding measurements on the upper and lower teeth are indicated by the same letter of the alphabet, capital letters for the upper teeth and small letters for similar measurements on the lower teeth.

teriorly; the angle of elevation ($\angle$ a in Fig. 11) is 80°. Near its dorsal end, the anterior edge curves slightly posteriorly and dorsally and passes smoothly into the convex dorsal edge of the ascending ramus. On the leading edge of the ascending ramus, there is a sharp lateral flange that forms the anterior margin of the masseteric fossa. The prominence of this flange decreases dorsally. There is a ridge on the medial side of the ascending ramus. Beginning in the anteroventral corner of the ascending ramus immediately behind the tooth row, the ridge extends posterodorsally for a distance less than one-fourth the width of the ascending ramus. To the rear, the ridge terminates somewhat anterior to the mandibular foramen; between that point and the condyle, there is no ridge developed on the medial side of the mandible. The mandibular foramen is midway between the anterior and posterior borders of the ascending ramus and level with the tooth row. The condyle is well above the level of the tooth row, the angle of elevation ($\angle$ b in Fig. 11) being about 35°. In posterior view, the margin of the mandible has a knife-edge thinness except immediately below the condyle. The posterior border of the ascending ramus curves anterodorsally from the condyle and meets the dorsal edge of the ascending ramus at a sharp angle.

Comparisons.—In a living erinaceine such as *Erinaceus europaeus*, the distances between adjacent occlusal surfaces of the upper dentition are found to be close to those of the corresponding occlusal surfaces of the lower dentition. For example, the distance from the prevallum of M^1 to that of M^2 is nearly the same as that from the postvallid of M_1 to that of M_2. Because the prevallum of M^1 is adjacent to the postvallid of M_1 when the two teeth are in occlusion and likewise, the prevallum of M^2 is adjacent to the postvallid of M_2 in the same circumstances; this result is hardly surprising. See figure 16 for a diagramatic explanation and table 8 for a set of measurements in a sample of five recent specimens of *E. europaeus*.

If the distances between the prevalla of the upper molars of *Parvericius montanus* (YPM 13956, Fig. 12a) are compared to the

TABLE 8. Measurements (mm) of the distances between occlusal planes in *Erinaceus europaeus* (See Fig. 16 and text for explanation)

	AMNH(M) 34820	AMNH(M) 34821	AMNH(M) 149412	AMNH(M) 160470	AMNH(M) 164391
A	8.9	9.2	8.4	9.1	8.8
a	8.7	9.1	8.6	8.6	8.6
B	4.6	4.9	4.4	4.6	4.5
b	4.6	4.8	4.7	4.6	4.5
C	4.3	4.3	4.0	4.5	4.3
c	4.1	4.3	3.9	4.0	4.1

TABLE 9. Measurements (mm) of the distances between occlusal planes in *Palaeoscaptor*, *Parvericius*, and *Stenoechinus* (See Fig. 16 and text for explanation)

	Palaeoscaptor acridens AMNH 22080	*Parvericius montanus* type, YPM 13956	*Parvericius montanus* UCM 29955	*Parvericius montanus* UMMP V56569	*Stenoechinus tantalus* type, KU 18001
A	3.9	3.2	----	----	----
a	----	----	3.5	4.0	3.4
B	2.2	1.8	----	----	----
b	2.1	----	2.0	2.1	1.9
C	1.7	1.4	----	----	----
c	----	----	1.5	1.9	1.5

distances between the postvallids of the mandible fragment presumed to be that of *P. montanus* from the Split Rock Formation (UCM 29955, Fig. 5), the corresponding measurements are found to be similar to the degree found between individuals of *Erinaceus europaeus* of slightly different size (compare Tables 8 and 9). In addition, these upper and lower dentitions have been modified in the characteristic erinaceine pattern; M^3 reduced to a straight blade between the protocone and paracone; M_3 diminished to a trigonid lacking a talonid. These specializations of the most posterior upper and lower molars are functionally correlated with one another and are not known to occur singly.

On the basis of the above evidence only, it could be postulated that the mandibles of *Stenoechinus tantalus* were the previously unknown lower jaws of *Parvericius montanus.* The distances between the corresponding occlusal surfaces are nearly the same (Table 9); and, although the M_3 of *S. tantalus* does have a wide postcingulum, it conceivably did occlude with an M^3 similar to that on *P. montanus.* However, the M^1 and M^2 referred to *S. tantalus* (found at the same locality as the majority of known lower dentitions of that species) appears to be quite unlike those of *P. montanus;* thus, the possibility of taxonomic synonymy seems improbable. The material from Egelhoff Quarry further supports the assignment of the lower dentions, here inferred to belong to *P. montanus,* with the upper dentition on which the species is based. At that locality only one form of small erinaceine tooth is known for each position of the dental series represented, suggesting that all such teeth belong to a single species. The isolated P^4 and two M^1's from Egelhoff Quarry are quite similar to those of the type of *P. montanus,* whereas the lower teeth from there are 10 percent larger than those of the Split Rock mandible.

Dentitionally, specimens of *Parvericius montanus* from Taben-buluk (originally described as *Palaeoerinaceus minimus* Bohlin, 1942), and from Nareen Bulak (originally described by Sulimski, 1970, as *Amphechinus* (*Palaeoerinaceus*) *cf. minimus*), are similar to specimens of *P. montanus* from North America. On the basis of dimensions of the teeth, this Asian material is most similar to older, smaller Arikareean and Hemingfordian North American specimens of *P. montanus.* There is a marked difference in the depth of the mandible; the North American specimens are about half again as deep as the Asiatic ones (Bohlin, 1942: Fig. 3d, d′, Plate 1, Fig. 4; Sulimski, 1970: Fig. 2d-f; Plate 19, Figs. 5-7). Besides *P. minimus,* Bohlin described another species in 1942 from Taben-buluk, *Palaeoerinaceus kansuensis* Bohlin (1942). This species is based on an incomplete edentulous mandible fragment. The mandibular depth is closer to the North American *P. montanus* than *P. minimus,* being only one-fifth larger. Furthermore, based on the alveoli, the molars appear to have been about as large as the later, larger Barstovian North American specimens of *P. montanus.*

Comparisons with *Stenoechinus tantalus* were made on p. 18.

Direct comparison of the type and referred specimen of *Amphechinus horncloudi* (SDSM 62113, and 6278; J. R. Macdonald, 1970: Fig. 5) together with the descriptions and figures of *Amphechinus edwardsi* in Viret (1938: Figs. 4, 8, and Plate I, Fig. 2) and Hürzeler (1944: Figs. 7, 10, 13) and of *Amphechinus arvernensis* in Viret (1929: Plate 28, Figs. 1-2), reveals two significant differences between these three species and *Parvericius montanus.* The corresponding dimensions of the teeth are only about one-half to three-fifths as large, and the trigonid of M_1 is anteroposteriorly compressed on *Parvericius montanus.*

Erinaceinae genus and species *indet.*

Figure 17

Material.—KU 18396, isolated right M^2. Found in the middle Cabbage Patch beds, Cabbage Patch locality 4 (KU-Mt-12), SW ¼, SE ¼, SW ¼, SE ¼, sec. 1, T 10 N, R 12 W, Granite Co., Montana (= MV6504-4, Rasmussen, 1969:131-132).

M^2.—(Fig. 17) Length of the tooth is only two-thirds the width (length = 1.5 mm, width = 2.4 mm). Few signs of wear mark the surface of the tooth. Tallest of the four principal cusps, the paracone is anterobuccal to the metacone and their bases are confluent. Second tallest of the cusps, the metacone has more gently sloping anterior and posterior sides than the paracone. Nearly equal in height to the metacone, the protocone is approximately lingual to the paracone. The base of the protocone projects medially beyond the body of the tooth. Posterolingual to the protocone is the lowest of the four principal cusps, the hypocone. The base of the hypocone projects posterolingually away from the body of the tooth. The hypocone and metacone are nearly as far apart as the protocone

FIG. 17. Erinaceinae, genus and species indet., KU 18396, right M^2, occlusal view. From the medial Arikareean, middle Cabbage Patch beds, Cabbage Patch locality 4 (KU-Mt-12), SW ¼, SE ¼, SW ¼, SE ¼, sec. 1, T 10 N, R 12 W, Granite Co., Montana (= MV6504-4, Rasmussen, 1969:131-132). ×15.

and paracone. Linking the anterobuccal corner of the protocone and the paracrista are the well-developed preprotocrista and preprotoconule crista which grade imperceptibly into one another, in the absence of a paraconule. In anterior view, this loph has a broad inverted V-shaped profile. The postprotocrista is directed posterobuccally from the protocone and terminates posteriorly lingual to the metacone. A short crest is directed from the posterior tip of the postprotocrista posterolingually toward the hypocone. However, the length of the crest is only about one-third of that necessary to link the postprotocrista to the hypocone; therefore, the cusp is isolated. A similar gap exists between the postprotocrista and the metacone because the postmetaconule crista extends buccally from the cusp but does not reach the crest. No metaconule is developed on this tooth. Along the straight anterior margin is a well-developed precingulum that buccally becomes progressively wider and curves ventrally until it merges with the paracrista buccal to the paracone. Together the precingulum and paracrista extend further buccally to the margin of the prominent parastylar spur. No distinct parastyle is developed. From the metacone, the metacrista extends posterobuccally for about two-thirds of its length and then turns to an anterobuccal direction to terminate finally without development of a distinct metastyle. A well-developed ectocingulum is present between the paracrista and metacrista. Along the posterior margin of the base of the metacone is a similarly well-developed postcingulum.

Comparisons.—This specimen differs from the upper molars of all other erinaceids possessing a distinct metacrista in that the buccal third of that crest is directed anterobuccally rather than posterobuccally.

In general form, this tooth is quite similar to the M^2 of *Palaeoscaptor acridens* and *Parvericius montanus,* although it is about 10 to 15 percent larger in every dimension and possesses a more prominent parastylar spur. In contrast to *P. acridens,* the postprotocrista and postmetaconule crista are not parts of one continuous crest, but instead form two short crests quite distinct from one another. Unfortunately, the M^2 of the only specimen of *P. montanus* is too worn to discern the condition of these crests in that species.

The M^2's of *Amphechinus, Neurogymnurus, Mioechinus, Postpalerinaceus,* and the modern Erinaceinae are markedly longer relative to their respective widths and larger in size than this specimen. With the exception of *Postpalerinaceus* and some specimens of *Amphechinus,* this group also differs from this isolated M^2 in that the base of the hypocone does not project away from the main body of the tooth.

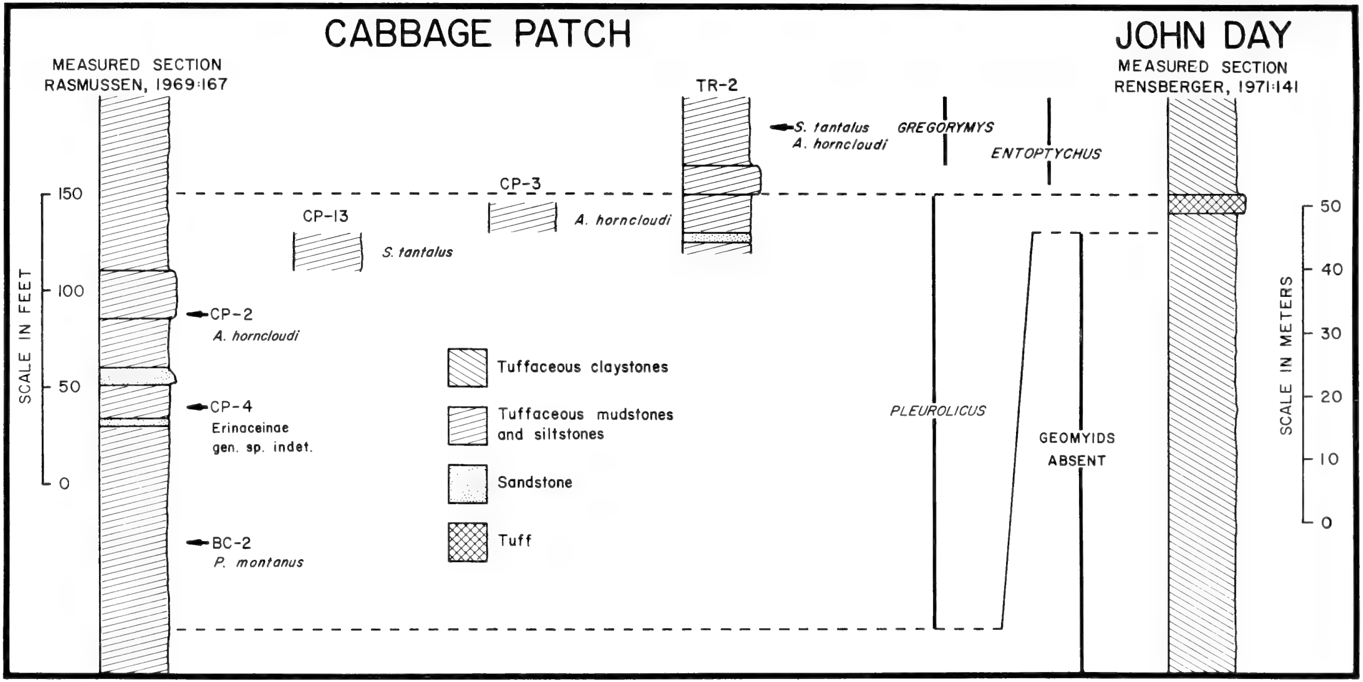

FIG. 18. Generalized stratigraphic sections of Cabbage Patch beds showing stratigraphic positions of hedgehogs from Montana discussed in this report. Correlation to a section measured in the John Day Formation is based on the highest and lowest occurrence of *Pleurolicus* and the lowest occurrence of *Gregorymys* (Cabbage Patch beds) and *Entoptychus* (John Day Formation).

STRATIGRAPHIC RELATIONSHIPS

Stratigraphic positions of the erinaceine insectivores discussed in this paper from Granite and Powell Counties, Montana, are illustrated in figure 18. Cabbage Patch beds shown in this figure range in age from medial to late Arikareean (late Oligocene and early Miocene), as based on correlations of the enclosed Cabbage Patch faunas to Arikareean faunas in the John Day of Oregon and Great Plains of South Dakota, Nebraska, and Wyoming. Cabbage Patch localities 2 (KU-Mt-9) and 4 (KU-Mt-12) and Bert Creek locality 2 (MV6504-2) occur within a single measured section. Cabbage Patch locality 13 (KU-Mt-46) occurs not far from this measured section and can be directly correlated into it. Because of poor exposures, erosional gaps, and distances up to several kilometers, correlation of Cabbage Patch locality 3 (KU-Mt-11) and Tavenner Ranch locality 2 (KU-Mt-21) to the measured section discussed above is difficult, but each can be approximately correlated using the stratigraphic position of the range zone of the gopher *Pleurolicus*. Thus, each locality is correlated by recording whether it occurs above, within, or below the *Pleurolicus* range zone. Likewise, an approximate correlation of this biostratigraphic zone can be made to the *Pleurolicus* range zone in the John Day Formation of Oregon (Rensberger, 1971:141, Fig. 69).

Ten of the eleven specimens of *Stenoechinus tantalus* occur at a single horizon and locality (Tavenner Ranch locality 2) in the upper Cabbage Patch beds above the *Pleurolicus* range zone. Although several rich fossil localities above and below this stratigraphic position of Tavenner Ranch locality 2 have been extensively searched and large bulk samples have been washed from some of them, only one other specimen of *Stenoechinus* has been found (at Cabbage Patch locality 13 which lies within the *Pleurolicus* range zone in the middle Cabbage Patch beds). Also occurring at Tavenner Ranch 2 is a partial maxillary (KU 18097) and partial isolated tooth (KU 18405) of *Amphechinus horncloudi.* Other mammals found at this locality include *Nanodelphys, Peratherium, Domnina, Proscalops, Meniscomys, Niglarodon, Paciculus, Leidymys, Plesiosminthus, Gregorymys, Mookomys, Paleocastor, Archaeolagus, Nothocyon, Leptomeryx,* and oreodonts, and will be reported on in a later paper by Rasmussen.

Two additional specimens of *Amphechinus horncloudi* have been found within the *Pleurolicus* range zone in the middle Cabbage Patch beds (Fig. 18)—KU 18162 from Cabbage Patch locality 3, and KU 18163 from Cabbage Patch locality 2. Each was found associated with a fauna that is less varied but similar to that accompanying *A. horncloudi* at Tavenner Ranch locality 2, except that *Pleurolicus* is present and *Gregorymys* is absent.

An upper second molar of a small erinaceine (KU 18346) was found at Cabbage Patch locality 4 within the *Pleurolicus* range zone in the middle Cabbage Patch beds. Although more than one ton of matrix has been washed from this locality and several hundred specimens have been recovered, this is the sole record of a hedgehog in the fauna other than the genus *Ocajila.* Mammals from the locality include *Peratherium,* a mole, *Ocajila, Domnina, Allomys, Niglarodon, Pleurolicus, Mookomys,* a beaver, *Eutypomys, Archaeolagus,* an ochotonid, and *Diceratherium.*

A lower jaw of a small hedgehog (MPUM 1551) referred to *Parvericius montanus* was found in the middle Cabbage Patch beds in association with *Peratherium,* a beaver, *Pleurolicus,* and *Archaeolagus* at Bert Creek locality 2. The *Pleurolicus* specimens collected at this locality are among the most primitive in the Cabbage Patch beds, indicating this locality is near the base of the *Pleurolicus* range zone.

Several specimens of *Stenoechinus* have been found at Tavenner Ranch locality 2 in the Cabbage Patch beds and were not found at other localities stratigraphically above and below (except the single specimen from Cabbage Patch locality 13). Even at localities which were intensively sampled, the absence of *Stenoechinus* may be due to paleoecological differences among the various localities. The type locality of *Stenoechinus* (Tavenner Ranch locality 2) is uniquely rich in terrestrial gastropods, whereas all other localities where hedgehogs were found (including Cabbage Patch locality 13) have very numerous freshwater gastropods. The scarcity of freshwater gastropods and other aquatic organisms and the abundance of terrestrial animals at Tavenner Ranch locality 2 suggests that the area was relatively remote from aquatic environments during most of the episode of deposition of this particular bed. The sediment at Tavenner Ranch locality 2 is composed almost entirely of silt-sized glass shards with little clay and sand, and may have been partially wind-blown into the site of deposition. Root burrows are extremely common, indicating abundant vegetation. A grassy or wooded habitat in an area free from frequent flooding or standing water is indicated. Thus *Stenoechinus* may have lived in habitats which were drier than those indicated at the other localities where other types of hedgehogs have been found.

Two isolated lower molars and a mandibular fragment of *Parvericius montanus* were found in Fremont Co., east central Wyoming, in the upper porous sandstone sequence of the Split Rock Formation in association with mammals of the Split Rock local fauna considered to be of Hemingfordian age, medial Miocene (Love, 1961:24; Munthe and Lander, 1973:497). All these specimens were found at or near locality 11-V of Love (1970).

Two mandibles, three isolated lower teeth, and three isolated upper teeth of *Parvericius montanus* were found at Egelhoff Quarry in Keya Paha Co., north-central Nebraska, in an unnamed lithic unit that unconformably overlies the Rosebud Formation and in turn is unconformably overlain by the Valentine Formation (R. H. Tedford, pers. com., 1972). In the same lithic unit and about 2 km southeast of Egelhoff Quarry, is the Norden Bridge Quarry in Brown Co., Nebraska, where an isolated M_1 of *P. montanus* was found. Both local faunas are regarded as Barstovian in age (C. W. Hibbard, pers. com., 1972).

The type of *Parvericius montanus* Koerner (1940), a maxilla fragment, was found in Meagher Co., central Montana, in the Deep River beds. Unfortunately, Koerner never published a complete faunal list for the Deep River beds. However, the oreodont material he collected and described (Koerner, 1940), together with his rodent and lagomorph specimens described by Black (1961), indicate that some parts of the unit (as Koerner conceived it) are of Arikareean age and other parts Hemingfordian. In other areas of North America, *Promerycochoerus* and *Paciculus* are known from Arikareean deposits while *Hypolagus* and *Monosaulax* are known from Hemingfordian or later deposits (Schultz and Falkenbach, 1949; Black, 1961; Dawson, 1958; R. W. Wilson, 1960).

CONCLUSIONS

In the Arikareean (latest Oligocene and earliest Miocene), a general faunal interchange of mammals, particularly small forms, took place between the Old World and North America after an extended interval of almost no interchange during the medial and late Oligocene (R. W. Wilson, 1968). It is at that time, and presumably as part of that episode of widespread interchange, that the North American history of the Erinaceinae appears to have begun with an invasion from Asia by at least two species. These are documented by the presence of two erinaceine species in Arikareean deposits of North America—*Amphechinus horncloudi* and *Parvericius montanus.* Each species appears to be more closely related to known Oligocene species of Europe or Asia than to any other North American erinaceines. The Arikareean appearance of *Stenoechinus tantalus* n. gen. and n. sp. in North America may be the result of yet another invasion immediately prior to the Arikareean. Or it is equally as likely that *S. tantalus* could represent the first record of a lineage endemic to North America through the Oligocene. Because no earlier species in either the Western or Eastern Hemisphere closely resembles *S. tantalus,* it is not possible at the present time to strongly support one alternative over the other. A poorly known species described here as "Erinaceinae, genus and species indet." may be congeneric with one of the three other species.

Largest of the North American erinaceine species, *Amphechinus horncloudi* can be readily allied with the early Oligocene to early

Miocene European group *Amphechinus cayluxi, Amphechinus arvernensis,* and *Amphechinus edwardsi.* The three European species and *A. horncloudi* are all quite similar to one another in size and morphology; apparently little change took place in this group during the time of its existence.

Except for a somewhat deeper mandible, *Parvericius montanus* from North America is nearly identical to medial or late Oligocene east Asian specimens originally described by Bohlin (1942) as *Palaeoerinaceus minimus. Parvericius* would seem to be most similar and closely allied to *Amphechinus* among the known erinaceine genera but more primitive in the shorter length of the M^1 and M^2 relative to their respective widths and in the more anteroposteriorly compressed M_1 trigonid.

The M^2 described as "Erinaceinae, genus and species indet." appears to be yet another distinct species, because it is too large to be the M^2 of either *Parvericius montanus* or *Stenoechinus tantalus* and much too small to be the M^2 of *Amphechinus horncloudi.* In addition, it is distinguished from the M^2 of *Paleoscaptor acridens* in having a more prominent parastylar spur, and the postprotocrista and postmetaconule crista developed as two distinct ridges rather than as one continuous ridge.

One of the three erinaceine genera described here has a post-Arikareean record in North America and a second one may. *Parvericius* survived until the late Barstovian; this genus has been found in the samples of that age collected at Egelhoff and Norden Bridge Quarries in north-central Nebraska. Rich will describe these specimens in a future paper. John Storer is describing three molar talonids of a large erinaceid of the proper size to be *Amphechinus,* collected at the medial Barstovian Kleinfelder Farm locality in southern Saskatchewan. Although none of the genera discussed here endured in North America after the Barstovian, the Erinaceinae were represented on this continent until at least Clarendonian time as attested by the presence of a single, isolated lower molar belonging to a member of this subfamily in the WaKeeney local fauna of Kansas (see R. L. Wilson, 1968: Fig. 12a-b).

SUMMARY

The history of the Erinaceinae in North America begins in the Arikareean (latest Oligocene and earliest Miocene) with the appearance of four species: *Amphechinus horncloudi, Parvericius montanus, Stenoechinus tantalus* n. gen. and n. sp., and Erinaceinae, genus and species indet. The first two species listed are more closely related to various species known from Oligocene deposits of Europe and Asia than to any North American ones; hence, at least two separate erinaceine groups appear to have invaded North America. Presumably these invasions took place immediately prior to the

first record of these species in North America and were part of an episode of renewed, widespread interchange of mammals between North America and the Old World that occurred at that time (R. W. Wilson, 1968). *Stenoechinus tantalus* is not closely related to any known earlier forms; therefore, the Arikareean record of this species may be either the first discovery of a lineage whose unknown Oligocene history was in North America, or the descendant of yet another group that invaded North America from Asia in the Arikareean. The fourth, poorly known species may have been derived from one of the stocks that gave rise to one of the first three mentioned species, or it may represent yet another lineage with an independent history extending well back into the Oligocene.

LITERATURE CITED

Aymard, Auguste
    1850. (No title.) Ann. Soc. Agric. Puy, 14:104-114.
Berggren, W. A.
    1971. Neogene chronostratigraphy, planktonic foraminiferal zonation and the radiometric time scale. Hungar. Geol. Soc. Bull., 101:162-169, 3 tables.
Black, C. C.
    1961. Rodents and lagomorphs from the Miocene Fort Logan and Deep River Formations of Montana. Postilla, (48):1-20, 6 figs.
de Blainville, H. M. D.
    1838. Recherches sur l'ancienneté des mammifères insectivores à la surface de la terre; précédées de l'historie de la science à ce sujet, des principes de leur classification et de leur distribution géographique actuelle. C. R. Acad. Sci. Paris, 6:738-744.
Bohlin, B.
    1942. The fossil mammals from the Tertiary deposit of Taben-buluk, western Kansu. Part I: Insectivora and Lagomorpha. *In* Hedin, Sven, Reports from the scientific expedition to the northwestern provinces of China. Stockholm. Vertebrate Paleontology. 6 (3): 1-113, 32 figs., 1 pl.
Butler, P. M.
    1948. On the evolution of the skull and teeth in the Erinaceidae, with special reference to fossil material in the British Museum. Proc. Zool. Soc. London, 118:446-500, 28 figs.
    1956. Erinaceidae from the Miocene of East Africa. Brit. Mus. Nat. Hist., Fossil Mamm. Afr., (11):1-75, 18 figs., 4 pls., 16 tables.
    1969. Insectivores and bats from the Miocene of East Africa: New material. *In* Leakey, L. S. B., ed., Fossil Vertebrates of Africa. Academic Press, New York and London. 1:1-37, 13 figs.
Dawson, M. R.
    1958. Later Tertiary Leporidae of North America. Univ. Kansas Paleont. Contrib., Vertebrata, (art. 6):1-75, 39 figs., 2 pls., 14 tables.
Filhol, Henri
    1879. Étude des mammifères fossiles de Saint Gerand le Puy (Allier). Ann. Sci. géol. (Paris), 10:1-253, 30 pls.
Friant, M.
    1961. Les insectivores de la famille des Erinaceidae. L'evolution de leurs molaries au cours des temps géologiques. Ann. Soc. Géol. Nord. 81:17-30, 6 figs., 2 pls.

HÜRZELER, J.
1944. Über einem dimyloiden Erinaceiden (*Dimylechinus* nov. gen.) aus dem Aquitanien der Limagne. Eclog. Geol. Helvetiae. 37 (2):460-467, 13 figs.

KOERNER, H. E.
1940. The geology and vertebrate paleontology of the Fort Logan and Deep River formations of Montana. Part I: New vertebrates. Amer. Jour. Sci. 238 (12):837-862, 7 pls.

LOVE, J. D.
1961. Split Rock Formation (Miocene) and Moonstone Formation (Pliocene) in central Wyoming. U. S. Geol. Surv. Bull. (1121-I):1-39, 6 figs., 3 tables.
1970. Cenozoic geology of the Granite Mountains area, central Wyoming. U. S. Geol. Surv. Prof. Paper (495-C): viii+154 pp., 61 figs., 13 tables.

MACDONALD, J. R.
1970. Review of the Miocene Wounded Knee faunas of southwestern South Dakota. Bull. Los Angeles Co. Mus. Nat. Hist. (8):1-82, 32 figs., 53 tables, 2 maps.

MACDONALD, L. J.
1972. Monroe Creek (early Miocene) microfossils from the Wounded Knee area, South Dakota. South Dakota Geol. Surv. Rept. Invests. 105: iii+43 pp., 14 figs.

MATTHEW, W. D., and WALTER GRANGER
1924. New insectivores and ruminants from the Tertiary of Mongolia, with remarks on the correlation. Amer. Mus. Novitates (105):1-7, 3 figs.

MELLET, J. S.
1968. The Oligocene Hsanda Gol Formation, Mongolia: a revised faunal list. Amer. Mus. Novitates (2318):1-16, 4 figs., 2 tables.

MUNTHE, JENS, JR. and E. BRUCE LANDER
1973. A reevaluation of the age of the Split Rock vertebrate fauna, Wyoming. Geol. Soc. Amer. Abs. with Programs 5(6):497.

RASMUSSEN, D. L.
1969. Late Cenozoic geology of the Cabbage Patch area, Granite and Powell Counties, Montana. Univ. Montana unpubl. M.A. thesis: 1-188, 15 figs., 10 plates, 3 tables.

RENSBERGER, J. M.
1971. Entoptychine pocket gophers (Mammalia, Geomyidae) of the Early Miocene John Day Formation, Oregon. Univ. Calif. Publ. Geol. Sci. 90:1-209, 76 figs., 22 pls., 15 tables.

RICH, T. H. V. and P. V. RICH
1971. *Brachyerix,* a Miocene hedgehog from western North America with a description of the tympanic regions of *Paraechinus* and *Podogymnura.* Amer. Mus. Novitates (2477):1-58, 22 figs., 4 tables.

SCHULTZ, C. B. and C. H. FALKENBACH
1949. Promerycochoerinae, a new subfamily of oreodonts. Bull. Amer. Mus. Nat. Hist. 93 (art. 3):69-198, 26 figs., 8 tables, 6 charts.

STOLL, N. R., et al., eds.
1961. International Code of Zoological Nomenclature. International Trust for Zoological Nomenclature. London: xviii+176 pp.

SULIMSKI, A.
1970. On some Oligocene insectivore remains from Mongolia. Palaeont. Polonica. (21):53-70, 2 figs., 2 pls., 6 tables.

TROFIMOV, B.
1960. [The insectivore genus *Palaeoscaptor* from the Oligocene of Asia.] Trudy Pal. Inst. Akad. Nauk SSSR 77:35-40, 3 figs., (Russian).

Van Couvering, J. A.

1972. Radiometric calibration of the European Neogene. *In* W. W. Bishop and M. A. Miller, eds., Calibration of Hominoid Evolution. Edinburgh, Scottish Academic Press:247-271, 2 figs., 2 tables.

Van Valen, L.

1967. New Paleocene insectivores and insectivore classification. Bull. Amer. Mus. Nat. Hist. 135(art. 5):217-284, 7 figs., 2 pls., 7 tables.

Viret, J.

1929. Les faunes de mammifères de l'Oligocène supérieur de la Limagne Bourbonnaise. Ann. Univ. Lyon, (n. s. 1), (fasc. 47): viii+328 pp., 32 figs., 32 pls.

1938. Étude sur quelques Erinacéidés fossiles spécialement sur le genre *Palaerinaceus*. Trav. Lab. Géol. Univ. Lyon, (fasc. 34, Mém. 28): 1-32, 12 figs., 1 pl.

Wilson, R. L.

1968. Systematics and faunal analysis of Lower Pliocene vertebrate assemblage from Trego County, Kansas. Contrib. Mus. Paleo., Univ. Mich. 22(7):75-126, 17 figs., 20 tables.

Wilson, R. W.

1960. Early Miocene rodents and insectivores from Northeastern Colorado. Univ. Kansas Paleont. Contrib., Vertebrata, (art. 7):1-92, 131 figs.

1968. Insectivores, rodents, and intercontinental correlation of the Miocene. XXIII International Geological Congress 10:19-25, 1 table.

Wood, A. E. and R. L. Konizeski

1965. A new eutypomyid rodent from the Arikareean (Miocene) of Montana. Jour. Paleontology. 39(3):492-496, 2 figs., 2 tables.

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A SYSTEMATIC REVIEW OF THE MARSUPIAL FROGS (HYLIDAE: *GASTROTHECA*) OF THE ANDES OF ECUADOR

By

WILLIAM E. DUELLMAN[1]

Many species of marsupial frogs, genus *Gastrotheca,* occur in the Andes and associated cordilleras from western Venezuela southward to northern Argentina. Because of the paucity of specimens of many of the named taxa and confusing variation exhibited by some species, the taxonomy of the marsupial frogs has been chaotic. Duellman and Fritts (1972) reviewed the species occurring in the Andes to the south of the Huancabamba Depression in northern Perú and delimited seven species there as members of the *Gastrotheca marsupiata* group. These frogs differ in cranial characters from the species in the Huancabamba Depression and northward, all of which were referred to the *Gastrotheca argenteovirens* group by Duellman and Fritts (1972).

The Ecuadorian species included in the latter group were: *G. lojana* Parker, 1932; *G. monticola* Barbour and Noble, 1920; *G. plumbea* (Boulenger, 1882); and *G. riobambae* (Fowler, 1913). Colombian and Venezuelan species assumed to belong to the same group were: *G. argenteovirens* (Boettger, 1892); *G. aureomaculata* Cochran and Goin, 1970; *G. helenae* Dunn, 1944; *G. medemi* Cochran and Goin, 1970; *G. mertensi* Cochran and Goin, 1970; and *G. nicefori* Gaige, 1933. It now seems apparent that these frogs are treated best as two distinct species groups. The Ecuadorian species listed above and two species named in this paper can be referred to as the *Gastrotheca plumbea* group, and the Colombian and Venezuelan species, as the *Gastrotheca argenteovirens* group. When better known, *G. williamsoni* Gaige, 1922, and an unnamed species related to *G. plumbea* from Antioquia and Cundinamarca, Colombia,

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[1] Curator, Division of Herpetology, Museum of Natural History, University of Kansas.

may be referable to the *Gastrotheca argenteovirens* and *plumbea* groups, respectively.

Thus, this paper is a review of the *Gastrotheca plumbea* group. The purpose of the present paper is to provide a synthesis of accumulated information and in so doing, 1) define the species, 2) assign names to taxonomically recognizable populations, and 3) summarize data on geographic variation, distribution, ecology, and life history. The results presented here, together with the synthesis of the southern Andean frogs by Duellman and Fritts (1972), will provide a basis for a future systematic assessment of the *Gastrotheca argenteovirens* group.

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MATERIALS AND METHODS

I have examined 1125 preserved frogs (including type specimens of all taxa), 24 skeletons, and 50 lots of tadpoles referable to the species discussed in this paper, and I have studied each of the species in the field. Terminology follows that of Duellman (1970), except for two additional measurements: length of third finger is the distance from the proximal edge of the palmar tubercle to the tip of the finger; length of thumb is the distance from the proximal edge of the prepollical tubercle to the tip of the thumb. Throughout the text, specimens are listed by their catalogue numbers preceded by the appropriate museum abbreviations, as follows:

AMNH	American Museum of Natural History
ANSP	Academy of Natural Sciences of Philadelphia
BMNH	British Museum (Natural History)
CAS	California Academy of Sciences
CAS-SU	Stanford University Collection (in California Academy of Sciences)
FMNH	Field Museum of Natural History
FSM	Florida State Museum
KU	University of Kansas Museum of Natural History
MCZ	Museum of Comparative Zoology, Harvard University
MJP	Museo Javier Prado, Lima, Perú
MNCN	Museo Nacional de Ciéncias Naturales, Madrid
MNHN	Museum National d'Histoire Naturelle, Paris
NHMW	Naturhistorisches Museum, Wien
NHRM	Naturhistoriska Riksmuseet, Stockholm
SMF	Senckenbergische Museum, Frankfurt
TNHC	Texas Natural History Collection
UMMZ	University of Michigan Museum of Zoology
USNM	United States National Museum
UZM	Universitets Zoölogiske Museum, Copenhagen
ZMB	Zoölogisches Museum, Berlin

THE *GASTROTHECA PLUMBEA* GROUP

Species comprising this group have short to moderately long legs, narrow to moderately wide heads, relatively large hands, moderate to extensive exostosis of the dermal roofing bones, broad frontoparietals expanded into lateral flanges, the frontoparietal fontanelle covered by the frontoparietals, and a long cultriform process of the parasphenoid. All species have aquatic tadpoles.

In contrast, members of the *Gastrotheca argenteovirens* group have long legs, broad heads, large hands, extensive exostosis of the dermal roofing bones and in some species co-ossification and casquing, and at least in some species a short cultriform process. Insofar as known, all species in this group have aquatic tadpoles, but at least in *G. argenteovirens,* the tadpoles hatch at an advanced stage, and the larval period is short. Members of the *Gastrotheca marsupiata* group have short legs, narrow heads, small hands, no exostosis of the dermal roofing bones, small narrow frontoparietals not roofing the frontoparietal fontanelle, and a long cultriform process. Three species have aquatic tadpoles; in the other four development is completed in the maternal pouch.

ACCOUNTS OF SPECIES

In the following accounts, each taxon is diagnosed; the variation is discussed, and the distribution of each species is annotated. Pertinent measurements and proportions are given in Table 1, and the frogs are illustrated in figures 1 and 2. Maximum snout-vent lengths are given in the diagnoses.

TABLE 1. Measurements and proportions of Andean *Gastrotheca*.
(First line, mean ± 1 SDX̄; second line, range)

Species and Sex		*N*	Snout-Vent Length (SVL)	Tibia Length/ SVL	Foot Length/ SVL	Interorbital/ Head Width	Eye-Nostril/ Head Length	Tympanum/ Eye
G. cavia	♂	6	54.4±4.435	0.414±0.013	0.462±0.26	0.290±0.016	0.265±0.015	0.539±0.055
			46.2—58.5	0.401—0.435	0.427—0.491	0.276—0.316	0.246—0.278	0.481—0.632
	♀	14	63.3±2.940	0.415±0.017	0.474±0.023	0.286±0.012	0.256±0.013	0.621±0.042
			57.5—67.2	0.392—0.452	0.440—0.509	0.265—0.309	0.223—0.281	0.561—0.695
G. lojana	♂	5	53.4±2.230	0.479±0.012	0.450±0.011	0.351±0.022	0.303±0.010	0.609±0.020
			50.5—56.0	0.469—0.500	0.437—0.464	0.333—0.377	0.294—0.315	0.587—0.636
	♀	3	58.5	0.511	0.466	0.396	0.297	0.501
			50.7—67.4	0.497—0.522	0.454—0.479	0.390—0.406	0.263—0.319	0.480—0.530
G. monticola	♂	4	55.0	0.468	0.458	0.285	0.267	0.594
			46.0—60.0	0.446—0.527	0.432—0.500	0.273—0.294	0.247—0.280	0.540—0.682
	♀	4	66.8	0.505	0.455	0.418	0.302	0.695
			61.6—77.0	0.468—0.529	0.434—0.475	0.387—0.435	0.278—0.323	0.564—0.759
G. plumbea	♂	9	57.4±3.150	0.478±0.012	0.470±0.010	0.313±0.013	0.301±0.014	0.630±0.026
			52.2—62.3	0.457—0.492	0.452—0.483	0.294—0.337	0.280—0.321	0.600—0.667
	♀	3	64.5	0.497	0.476	0.348	0.296	0.634
			59.7—68.0	0.489—0.509	0.456—0.510	0.305—0.403	0.279—0.308	0.568—0.691
G. psychrophila	♂	8	49.6±1.769	0.492±0.020	0.467±0.022	0.353±0.011	0.263±0.008	0.650±0.037
			46.0—51.5	0.472—0.524	0.442—0.493	0.341—0.374	0.246—0.272	0.579—0.700
	♀	2	60.9	0.509	0.510	0.362	0.248	0.707
			60.8—61.0	0.502—0.515	0.505—0.515	0.358—0.365	0.244—0.252	0.704—0.709
G. riobambae	♂	15	43.4±3.043	0.383±0.021	0.416±0.021	0.259±0.010	0.239±0.016	0.577±0.039
			38.8—48.7	0.357—0.410	0.362—0.434	0.245—0.283	0.213—0.272	0.532—0.644
	♀	9	47.8±3.429	0.412±0.016	0.442±0.017	0.308±0.013	0.285±0.012	0.567±0.031
			41.0—51.2	0.373—0.434	0.416—0.478	0.241—0.275	0.218—0.268	0.549—0.739

Gastrotheca cavia new species

Holotype.—KU 148532, an adult female, 64.0 mm, from Isla Pequeña, Laguna Cuicocha, Provincia Imbabura, Ecuador, 2890 m; one of a series collected on 31 October 1971 by William E. Duellman and John E. Simmons.

Paratopotypes.—KU 138216-20, 24 July 1970, Thomas H. and Patricia R. Fritts; 139137-9, 30 January 1971, William E. Duellman; 143094, 148530-1, 148533-36, 31 October 1971, William E. Duellman and John E. Simmons; 148537-40, 30 January 1971, William E. Duellman.

Diagnosis.—1) Body robust, 58.5 mm in males, 67.2 in females; 2) snout round in dorsal view, rounded above and anteroventrally inclined in profile; 3) canthus rounded; 4) loreal region shallowly concave; 5) tympanum vertically elliptical; 6) supratympanic fold moderately heavy; 7) subarticular tubercles on hand large, round; 8) supernumerary tubercles on hand low, round; 9) palmar tubercle bifid; 10) fingers not webbed; 11) toes one-third webbed; 12) tarsal fold low, extending one-third length of tarsus; 13) inner metatarsal tubercle low, ovoid, visible from above; 14) outer metatarsal tubercle low, flat; 15) subarticular tubercles on foot large, round; 16) supernumerary tubercles on foot small, low; 17) discs round; 18) dorsal skin shagreened, tubercular in tympanic region; 19) dorsum green or tan with or without small irregular black spots; narrow bronze dorsolateral stripe usually present; 20) facial area uniform green or tan; canthal and labial stripes absent; 21) flanks tan with numerous small black spots; 22) dorsal surfaces of limbs plain or with small black spots; 23) posterior surfaces of thighs cream with black mottling; 24) venter cream with black mottling; 25) squamosal exostosed, in broad contact with maxillary; 26) temporal arcade complete in large individuals; 27) prevomers abutted medially; 28) transverse processes on eighth presacral vertebra slightly inclined anteriorly.

Gastrotheca cavia resembles *G. riobambae* in having short legs, a narrow interorbital distance, and a short snout. It differs from *G. riobambae* in having a distinct dorsolateral light stripe, small black flecks on the flanks, and dorsal markings comprised of small black spots. *Gastrotheca riobambae* lacks a dorsolateral light stripe and has large dark spots on the flanks and a dorsal pattern consisting of paired elongate dark marks; the dorsal pattern is shared with *G. lojana* and *monticola*. *Gastrotheca plumbea* and *psychrophila* have unmarked dorsal surfaces and uniformly dark flanks and venters. The venter in *G. cavia* is cream with small dark spots.

Variation.—Whereas some individuals have only a few black flecks on the posterior part of the dorsum, others have more flecks over the entire dorsum; in more heavily flecked specimens, flecks on the shank tend to form transverse bars. In life, adults are green;

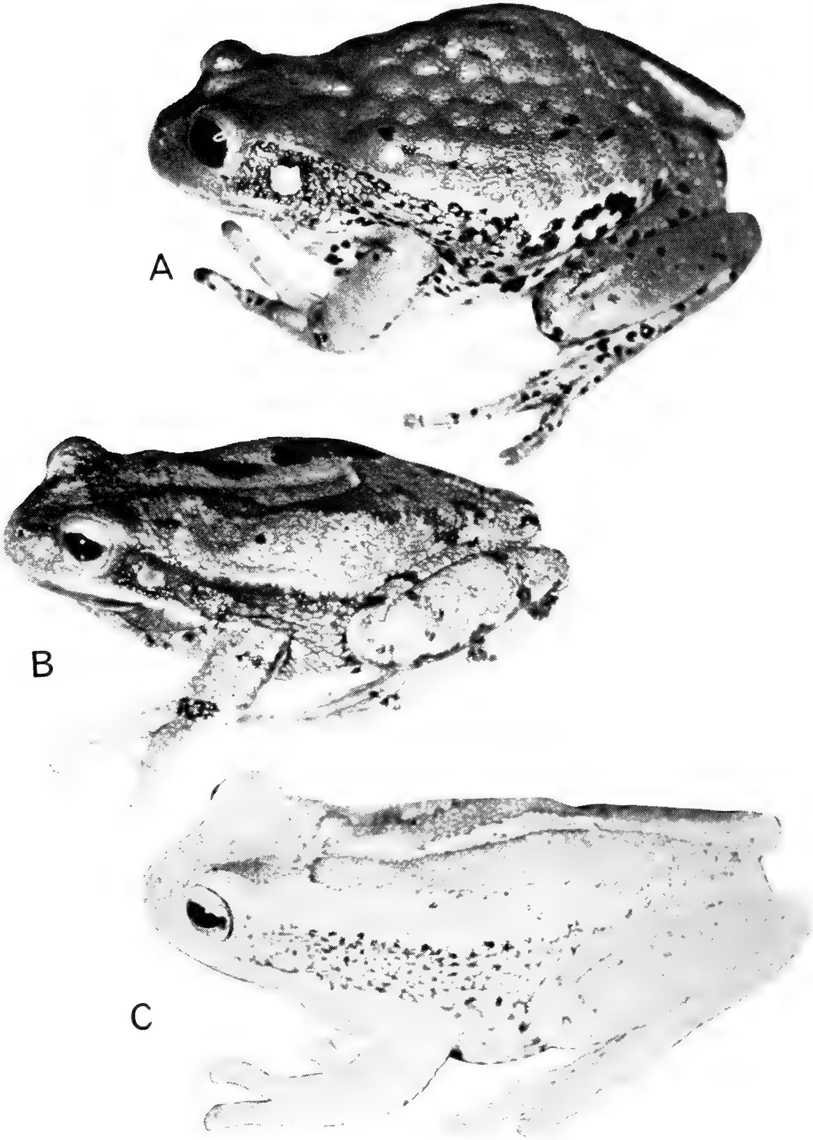

Fig. 1. A. *Gastrotheca cavia,* ♀, SVL 60.0 mm, KU 139139. B. *G. lojana,* ♂, SVL 56.5 mm, KU 148549. C. *G. monticola,* ♀, 65.0 mm, KU 148568.

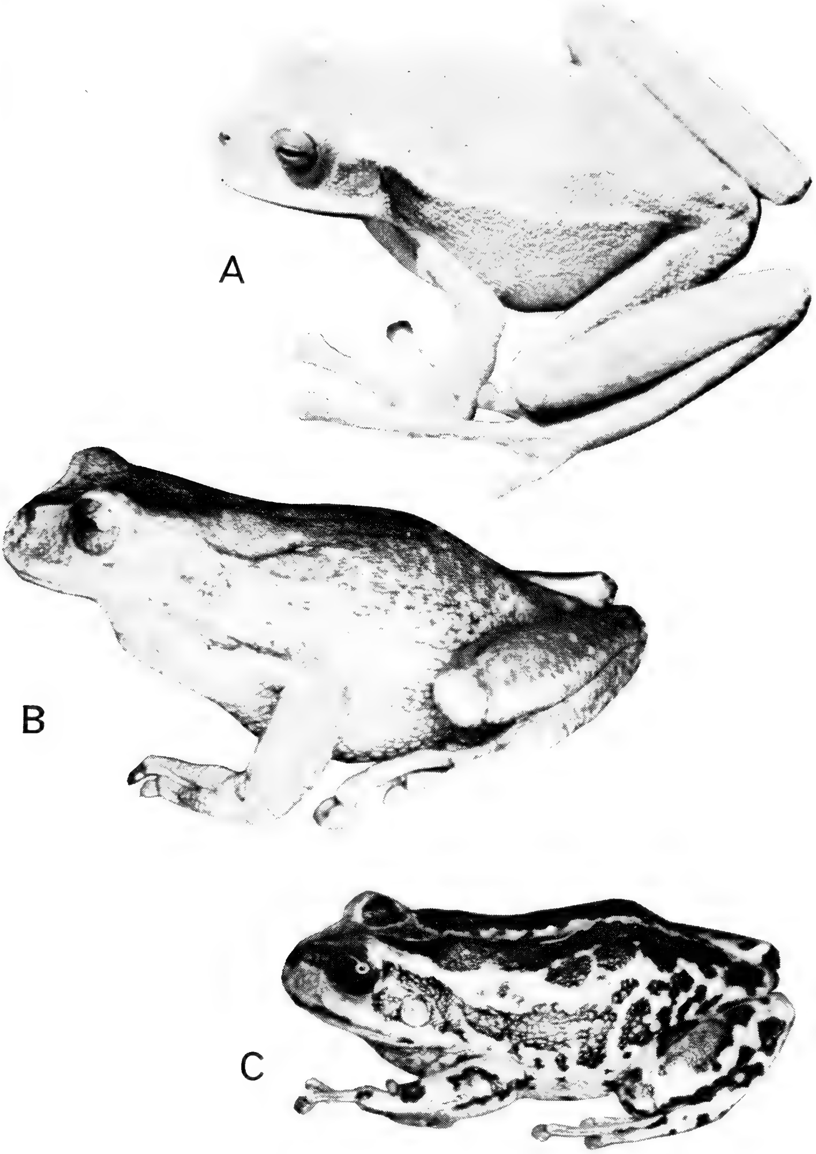

FIG. 2. A. *Gastrotheca plumbea*, ♂, SVL 55.3 mm, KU 142614. B. *G. psychrophila*, ♀, SVL 61.0 mm, KU 120650. C. *G. riobambae*, ♂, 46.5 mm, KU 120725.

the flanks are cream or bronze with black flecks, fused into reticulations in some individuals. The groin and posterior surfaces of the thighs are pale blue with black flecks. The dorsolateral stripe, extending from the posterior edge of the eye to the groin, usually is bronze and distinct. In some individuals, the stripe is narrow and fragmented by black flecks; in others it is cream, and in one female it is absent. The throat is pale yellow; the rest of the venter is dull grayish white with small black spots. The iris is dull bronze, heavily marked with brown spots and black flecks. Juveniles are pale green or bronze-tan; the flanks and hidden surfaces of the limbs are pale greenish yellow with black spots, and the venter is pale yellow with or without black reticulations. Although most males and all females are green, three males are tan.

Distribution.—This species is known definitely from only two localities in the Cordillera Occidental in northwestern Ecuador (Fig. 3). The species is abundant on two rocky islands in a crater lake, Laguna Cuicocha, at an elevation of 2890 m on the south slope of Volcán Cotacachi. The other locality, Hacienda San Nicolas is at an elevation of 2000 m on the Pacific slope of the Cordillera Occidental. Two specimens from "Western Ecuador" (BMNH 1860.6.16.124-125) and one from Ibarra (?) (BMNH 1898.4.28.156) are referred to this species.

Remarks.—Many adults were found in large terrestrial bromeliads in July, 1970, January and October, 1971. At the time of the last two visits, some adults were found beneath rocks. Brooding females were obtained in January and July, but not in October. Tadpoles were found in the lake surrounding the island in January, and at the same time two metamorphosing young were observed on reeds in the lake. Tadpoles have two upper and three lower rows of denticles.

Superficially, *Gastrotheca cavia* resembles *G. argenteovirens* Boëttger; I have examined the type of the latter (SMF 2676) and have compared living and preserved specimens of *argenteovirens* with *cavia.* In comparison with *G. cavia, G. argenteovirens* has proportionately longer legs (ratio of tibia length to snout-vent length 0.488-0.514, $\bar{x} = 0.498 \pm 0.010$, $N = 5$ ♂ ♂; 0.486-0.514, $\bar{x} = 0.501 \pm 0.012$, $N = 4$ ♀ ♀) and broader interorbital distance (ratio of interorbital distance to head width 0.335-0.371 $\pm$ 0.014, $\bar{x} = 0.358$, $N = 5$ ♂ ♂; 0.369-0.395 $\bar{x} = 0.383 \pm 0.011$, $N = 4$ ♀ ♀). The flanks and posterior surfaces of the thigh are mottled with dark blue, and the dorsum lacks black flecks. Furthermore, the cultriform process of the parasphenoid is short, and in large individuals there is integumentary-cranial co-ossification.

Etymology.—The specific name is the same as the generic name for the guinea pig (Caviidae), called *cui* in Quecchua the domi-

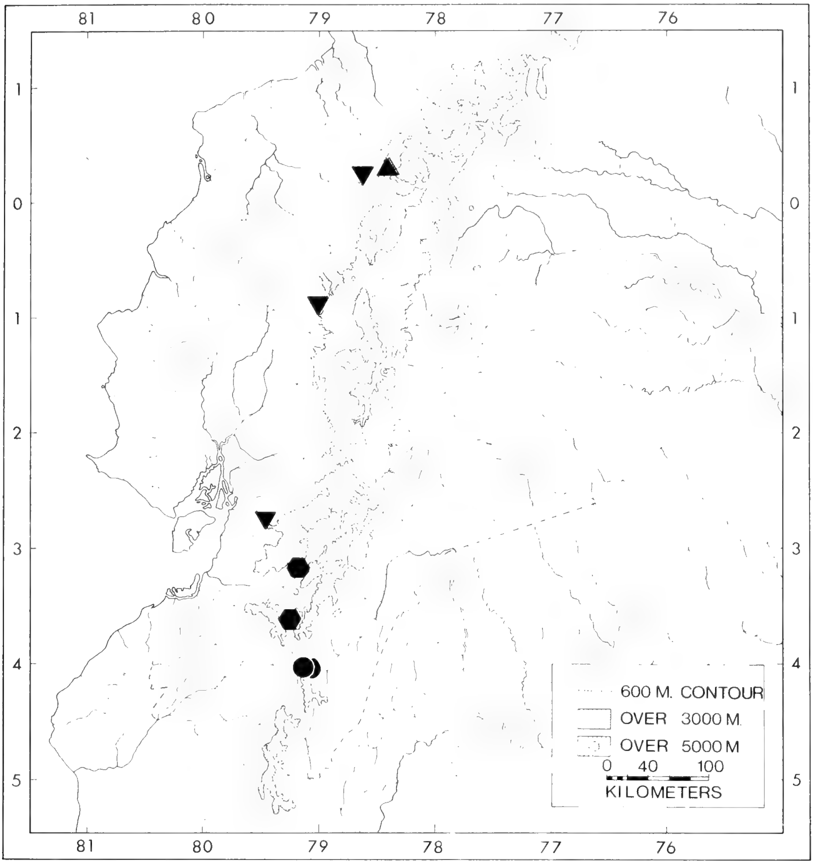

FIG. 3. Distributions of *Gastrotheca cavia* (triangles), *G. monticola* (hexagons), *G. plumbea* (inverted triangles), and *G. psychrophila* (circles).

nant Indian language in the Ecuadorian Andes. *Cuicocha* means lake of the guinea pig.

Gastrotheca lojana Parker
New combination

Gastrotheca marsupiata lojana Parker, 1932:25 [Holotype.—BMNH 1931.2.12.4 (RR 1947.2.31.13) from Loja, Provincia Loja, Ecuador; C. Carrion collector].

Diagnosis.—1) Body depressed, 56.0 mm in males, 60.0 in females; 2) snout round in dorsal aspect and in profile; 3) canthus rounded; 4) loreal region barely concave; 5) tympanum vertically elliptical; 6) supratympanic fold moderately heavy, angled posteroventrally behind tympanum; 7) subarticular tubercles on hand large, round; 8) supernumerary tubercles on hand small, subconical; 9) palmar tubercle bifid; 10) fingers not webbed; 11) toes one-half webbed; 12) tarsal fold low, extending one-half length of tarsus; 13) inner metatarsal tubercle low, elliptical, visible from above; 14) outer metatarsal tubercle low, round; 15) subarticular tubercles on foot large, round; 16) supernumerary tubercles on foot low, round; 17) discs round; 18) dorsal skin shagreened; 19) dorsum tan or green, with or without pair of elongate dark markings; narrow bronze or cream dorsolateral stripe present; 20) facial area green or tan; bronze canthal stripe and cream labial stripe present; 21) flanks dark brown with cream spots ventrally; 22) dorsal surfaces of limbs green or tan, with or without narrow brown transverse bars; 23) posterior surfaces of thighs heavily mottled with bluish purple; 24) chin and chest gray; belly pinkish bronze; 25) squamosal exostosed, in narrow contact with maxillary; 26) temporal arcade complete; 27) prevomers narrowly separated medially; 28) transverse processes on eighth presacral vertebra transverse.

Gastrotheca lojana resembles *G. monticola* and *riobambae* in usually having a pair of elongate dorsal markings. It differs from *G. riobambae* in having fine pale reticulations laterally or dark flanks, nearly uniformly dark posterior surfaces of the thighs, and a dorsolateral light stripe; *G. riobambae* has large spots on the flanks, mottled posterior surfaces of the thighs, and lacks a dorsolateral light stripe. *Gastrotheca monticola* has mottled posterior surface of the thighs and further differs from *G. lojana* in having a wider dorsolateral stripe and a cream venter with dark spots, whereas the venter in *G. lojana* is dark brown with creamy-white spots. The other Andean *Gastrotheca* in Ecuador lack paired dorsal markings.

Variation.—Variation in coloration can best be described by the following accounts of topotypic adult males (colors in life):

KU 148549.—Tan above with greenish suffusion dorsolaterally; dorsolateral and labial stripes bronze; flanks and dorsal markings dark brown; upper surfaces of thighs bronze-tan; upper surfaces of shanks and posterior surfaces of thighs dull green; anterior surfaces of thighs dark brown; throat brown; belly brown with white spots; ventral surfaces of thighs pinkish brown; ventral surfaces of shanks bluish white.

KU 148550.—Tan above with brown markings; face mask and anterior flanks dark brown; labial stripe creamy bronze; anterior and posterior surfaces of thighs mottled dark brown and blue; throat gray-brown; belly brown with white spots.

KU 148551.—Dorsum dull green with dark brown markings; flanks are dark brown; anterior and posterior surfaces of thighs and inner surfaces of shanks mottled dull blue and dark brown; throat dark bronze brown; belly brown with cream spots.

KU 126073.—Dorsum pale greenish brown with dark brown markings; labial and dorsolateral stripes cream; flanks gray-brown; groin and posterior surfaces of thighs creamy brown with green flecks.

KU 142603.—Dorsum dull leaf green with no distinct markings; canthal, labial, and dorsolateral stripes bronze; flanks bronze-brown; groin and anterior and posterior surfaces of thighs purplish brown; throat pinkish bronze; belly same, becoming darker brown posteriorly, with white spots.

In all specimens the iris is bronze. Four specimens from Chachapoyas, Departamento Amazonas, Perú (KU 138238-41) are colored somewhat differently: "Adults with leaf green dorsum; one with thin beige stripe from nostril through eye to inguinal region and beige spots on flanks; all with white supralabial border; posterior thigh light leaf green; anterior thigh pale leaf green with few black flecks; venter yellow-beige; iris metallic orange. Juvenile with white patch at anus; dorsum tan with light brown blotches edged with dark brown; blotch between eyes and inverted U on body with few scattered small spots posteriorly; broad rich light brown stripe from eye to midflank; groin gray-white with small black blotches; posterior thigh flesh-pink, leaf green distally; supralabial area beige-white" (T. H. Fritts, field notes, 1 May 1970).

The dorsal markings are highly variable. Some individuals lack markings except for a few scattered spots. In most individuals a pair of broad longitudinal marks extend from the scapular region to the groin. In some individuals the marks are fragmented into anterior and posterior components, whereas in others the marks are confluent anteriorly. If an interorbital mark is present, it may or may not be connected to the body markings.

Distribution.—This species occurs at moderate elevations in the Huancabamba Depression and associated interandean valleys in northern Perú and southern Ecuador, where it has been found from elevations of 2100 to 2350 m in both Atlantic and Pacific drainages (Fig. 4). A record from Zamora, Ecuador, at an elevation of 1000 m on the Amazonian slopes is highly questionable; the specimen (BMNH 1933.6.24.45) is *G. lojana*, but the locality data probably are erroneous.

Remarks.—In the Loja valley in southern Ecuador this species is found most frequently in large *Agave*, where the frogs seek shelter at the bases of the leaves by day and call by night. Individuals also have been found under rocks and in marshy meadows. At Chachapoas, Perú, they were beneath rocks and clods of earth in a cultivated field. Tadpoles were found in a grassy irrigation ditch. They are uniformly black and have two upper and three lower rows of denticles.

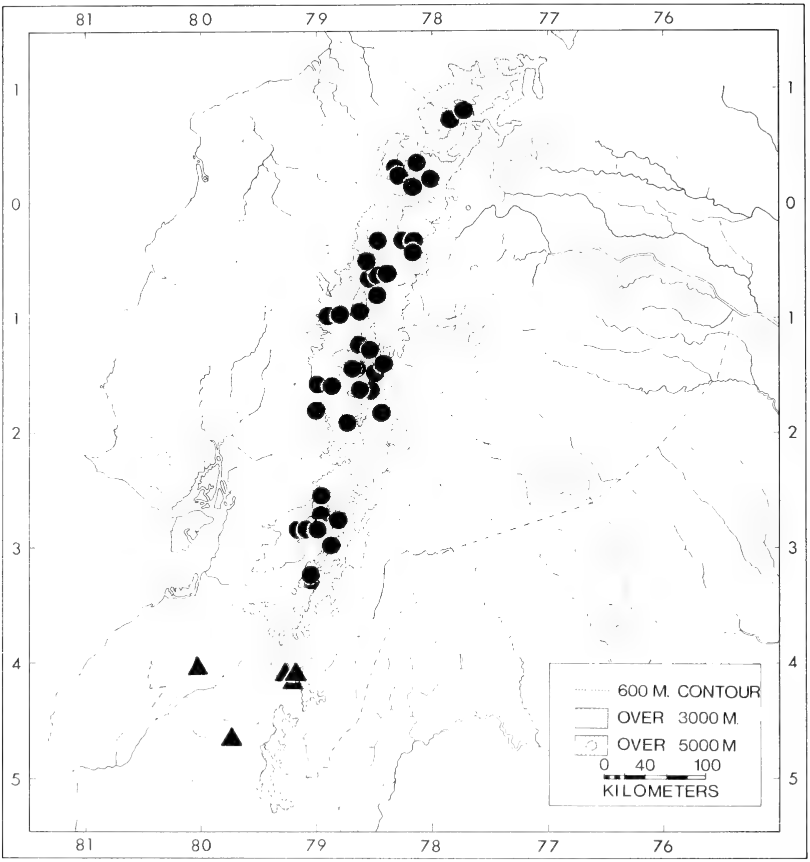

FIG. 4. Distributions of *Gastrotheca lojana* (triangles) and *G. riobambae* (circles).

One specimen (FSM 30080, an adult male having a snout-vent length of 48.5 mm) from 24 km WSW of Leimebamba, Departamento Amazonas, Perú, 3370 m tentatively is referred to *G. lojana*. This individual differs from all other *G. lojana* by having a dark brown dorsum with tan middorsal and dorsolateral stripes; the venter is mottled with dark gray. Futhermore, the locality is 1000 m higher than any other recorded for *G. lojana*.

Parker (1932:25) named *lojana* as a subspecies of *Gastrotheca marsupiata*, a name which he applied to populations now known as *G. riobambae*. As noted in the foregoing diagnosis, *G. lojana* differs from *G. riobambae* in a number of characters; there is no evidence for gene flow between the southern populations of *G. riobambae* and *G. lojana*.

Gastrotheca monticola Barbour and Noble

Gastrotheca monticola Barbour and Noble, 1920:426 [Holotype.—MCZ 5290 from Huancabamba, Departamento Piura, Perú; G. K. Noble collector].
Gastrotheca marsupiata monticola—Parker, 1932:25.
Gastrotheca monticola monticola—Vellard, 1957:39.

Diagnosis.—1) Body robust, 60.0 mm in males, 77.0 mm in females; 2) snout round in dorsal view and profile; 3) canthus rounded; 4) loreal region barely concave; 5) tympanum nearly round, slightly higher than wide; 6) supratympanic fold moderately heavy, curved posteroventrally behind tympanum; 7) subarticular tubercles on hand large, round; 8) supernumerary tubercles on hand large, conical; 9) palmar tubercle bifid; 10) fingers not webbed; 11) toes one-half webbed; 12) tarsal fold tubercular, extending full length of tarsus; 13) inner metatarsal tubercle elongate, visible from above; 14) outer metatarsal tubercle absent; 15) subarticular tubercles on feet large, round; 16) supernumerary tubercles on hands small, round, flat; 17) discs round; 18) dorsal skin shagreened; 19) dorsum green or tan, usually with paired elongate dark markings; creamy bronze dorsolateral stripe present; 20) facial area green or tan; creamy bronze canthal stripe pesent; 21) flanks brown with cream and black flecks; groin blue; 22) dorsal surfaces of limbs green or tan with or without darker transverse bands; 23) posterior surfaces of thighs blue; 24) throat gray; chest and belly creamy gray with gray spots; 25) squamosal weakly exastosed, in moderately broad contact with maxillary; 26) temporal arcade complete in large individuals; 27) prevomers narrowly separated medially; 28) transverse processes on eighth presacral vertebra barely inclined anteriorly.

Gastrotheca monticola differs from *G. plumbea* and *psychrophila* in having a pale venter with black spots, instead of a uniformly dark venter. *Gastrotheca cavia* resembles *G. monticola* in having a broad dorsolateral stripe and mottled posterior surfaces of the thighs, but *G. cavia* lacks paired longitudinal dark marks on the dorsum, characteristic of *G. monticola, lojana,* and *riobambae.* The latter species differs from *G. monticola* in having large dark spots, instead of fine reticulations, on the flanks, and in lacking a dorsolateral stripe. *Gastrotheca monticola* is most like *G. lojana,* from which it differs in having a pale venter with dark spots (dark with white spots in *lojana*), broader dorsolateral stripe, and more mottling on the flanks and thighs.

Variation.—The dorsum is green with paired longitudinal dark markings on the body; a large dark spot on the head, including the eyelids, is present in some individuals. The longitudinal marks extend from the eyelids or occipital region to the groin. In some individuals the marks are confluent anteriorly. The marks are green, usually darker than the dorsal ground color, and outlined with brown. The flanks are brown with or without bronze flecks. The dorsolateral and labial stripes are bronze-tan to metallic cream. The groin and hidden surfaces of the thighs vary from pale green to blue with cream and black mottling. The venter is creamy tan to creamy yellow with brown flecks; the vocal sac is gray. The iris is pale bronze.

Comparison of specimens from Saraguro, Ecuador, with the type series from Huancabamba, Perú, revealed slight differences. The Peruvian specimens have less ventral spotting and more dark pigment on the posterior surfaces of the thighs. One Peruvian specimen (UMMZ 57747A), a male, has a highly fragmented dorsal pattern.

Distribution.—Gastrotheca monticola occurs at elevations of 1600-2500 m on the Pacific slopes and associated intermontane valleys in northern Perú and southern Ecuador (Fig. 3). The Cordillera Occidental in that region is dissected by many broad, dry valleys, so it is unlikely that the distribution of *G. monticola* is continuous.

Remarks.—At Saraguro, Ecuador, adults were found beneath rocks in a pasture and in and along a vegetation-choked drainage ditch. At Girón, Ecuador, adults were in *Agave* plants by day. Tadpoles were found in the ditch at Saraguro. The body is dull green above and greenish silver below; the tail is tan with green lichenous markings. The tadpoles have two upper and three lower rows of denticles.

Parker (1932:25) considered *G. monticola* to be a subspecies of *G. marsupiata* (= *riobambae*). The differences noted in the diagnosis obviate such an arrangement in the absence of evidence indicating genetic interchange. Cochran and Goin (1970:185) used the combination *Gastrotheca monticola argenteovirens.* Boettger named *argenteovirens* in 1892, whereas the name *monticola* dates from Barbour and Noble (1920). Moreover, the two taxa are considerably different and certainly not conspecific.

Gastrotheca plumbea (Boulenger)

Nototrema plumbeum Boulenger, 1882:417 [Holotype.—BMNH 78.1.25.22 (RR 1947.2.31.19) from Intac, Provincia Pichincha, Ecuador; Mr. Buckley collector].

Gastrotheca plumbeum—Peters, 1955:346.

Diagnosis.—1) Body robust, 62.3 mm in males, 68.0 mm in females; 2) snout round in dorsal view, angular above and inclined anteroventrally in profile; 3) canthus rounded; 4) loreal region barely concave; 5) tympanum vertically elliptical; 6) supratympanic fold weak; 7) subarticular tubercles on hand moderate, round; 8) supernumerary tubercles on hand small, round; 9) palmar tubercle bifid; 10) fingers webbed basally; 11) toes one-half webbed; 12) tarsal fold round, extending one-third length of tarsus; 13) inner metatarsal tubercle elliptical, visible from above; 14) outer metatarsal tubercle absent; 15) subarticular tubercles on foot moderate, round; 16) supernumerary tubercles on foot small, conical; 17) discs round; 18) dorsal skin shagreened; 19) dorsum green with narrow bronze dorsolateral stripe; 20) facial area green with bronze canthal and labial stripes; 21) flanks brown; 22) dorsal surfaces of limbs green, mottled or not with tan; 23) posterior surfaces of thighs bronze-tan; 24) venter greenish yellow; 25) squamosal not exostosed, in moderately broad contact with maxillary; 26) temporal arcade incomplete; 27) prevomers abutted medially; 28) transverse processes on eighth presacral vertebra strongly inclined anteriorly.

Gastrotheca plumbea differs from all other Andean *Gastrotheca*, except *G. psychrophila*, in having a uniformly pigmented venter and a green iris. Like *G. psychrophila*, it also lacks dorsal markings, but it differs from *G. psychrophila* in having paler venter, a dorsolateral light stripe, a green, instead of brown dorsum, and a green, instead of copper, iris.

Variation.—The dorsum invariably is unmarked bright green to tannish green. The canthal, labial, dorsolateral, and anal stripes are yellow. The loreal region, flanks, and posterior surfaces of the thighs are bronze, and the dorsal surfaces of the limbs are greenish bronze. The venter is yellowish tan with a greenish tint on the throat, and the ventral surfaces of the shanks are blue. A diffuse blue spot is present in the grain; the iris is green.

Distribution.—*Gastrotheca plumbea* is known from moderate elevations (1300-2350 m) on the Pacific slopes of the Cordillera Occidental in Ecuador (Fig. 3). Although the range of the species may extend northward into Colombia, it is doubtful if the species ranges into Perú; the dry valleys of the Huancabamba Depression probably are a barrier to southward dispersal.

Remarks.—At Pilaló, Provincia Cotopaxi, Ecuador, where there are remnants of cloud forest, individuals were found in bromeliads in trees and on a cliff by day; males called from bromeliads at night.

Gastrotheca psychrophila new species

Holotype.—KU 120760, an adult female, 61.0 mm, from the ridge between Loja and Zamora, 2850 m, 13-14 km E (by road) of Loja, Provincia Zamora-Chinchipe, Ecuador; obtained on 10 June 1968 by John D. Lynch.

Paratopotypes.—KU 120761, 10 June 1968, John D. Lynch; 141586, 21 May 1971, Richard R. Montanucci; 142631-7, 21-23 July 1971, William E. Duellman.

Diagnosis.—1) body depressed, 51.5 mm in males, 61.0 mm in females; 2) snout pointed with vertical rostral keel, in profile rounded above and anteroventrally inclined; 3) canthus angular; 4) loreal region flat; 5) tympanum slightly higher than wide; 6) supratympanic fold heavy, curved downward behind tympanum; 7) subarticular tubercles on hand large, round; 8) supernumerary tubercles on hand large, round; 9) palmar tubercle trifid; 10) fingers webbed basally; 11) toes slightly less than one-half webbed; 12) tarsal fold curved, two-thirds length of tarsus; 13) inner metatarsal tubercle elliptical, visible from above; 14) outer metatarsal tubercle low, round; 15) subarticular tubercles on foot large, round; 16) supernumerary tubercles on foot large, conical; 17) discs round; 18) dorsal skin shagreened; 19) dorsum uniform dark brown to grayish tan or dull green; 20) facial area colored like dorsum; bronze labial stripe in females; 21) flanks bluish black; 22) dorsal surfaces of limbs dark brown to grayish tan; 23) posterior surfaces of thighs bluish black; 24) venter grayish brown; 25) squamosal exostosed, in broad contact with maxillary; 26) temporal arcade incomplete; 27) prevomers abutted medially; 28) transverse processes on eighth presacral vertebra strongly inclined anteriorly.

Gastrotheca psychrophila differs from all other Andean *Gastrotheca,* except *G. plumbea,* in having a dark venter. It also is like *G. plumbea* in lacking dorsal blotches, but *G. psychrophila* differs from *G. plumbea* in lacking a dorsolateral light stripe and in having a darker venter, usually a primarily brown dorsum (green in *G. plumbea*) and a copper iris (green in *G. plumbea*).

Variation.—Individuals of this species are capable of considerable metachrosis. When frogs were found in bromeliads they were dark brownish black above and below; the flanks and posterior surfaces of the thighs were dark bluish black. Later the dorsum changed to copper or bronze-tan with or without diffuse pale green blotches or streaks. The flanks are orange-brown or dark brown. The axilla, groin, and hidden surfaces of the limbs are bluish gray or bluish purple. The lips are dull bronze, and the iris is copper with black flecks.

Distribution.—This species is known only from the ridge between Loja and Zamora, Ecuador (Fig. 3). Most individuals have been found on the upper eastern slope between 2750 m and the crest at 2850 m.

Remarks.—The Loja-Zamora ridge is exceedingly wet; cold winds blow from the east. The vegetation near the crest consists of grasses and dense bushes. Large bromeliads are abundant on the ground and in the bushes. Adult *G. psychrophila* were found in the bromeliads and under rocks. Tadpoles were obtained from a grassy pond on the west side of the ridge. The tadpoles are black and have two upper and three lower rows of denticles.

Etymology.—The specific name is from the Greek *psychros,* meaning cold, and *philos,* meaning having an affinity for; the name is used in allusion to the climate at the type locality.

Gastrotheca riobambae (Fowler)

Hyla riobambae Fowler, 1913:157 [Holotype.—ANSP 16161 from Riobamba, Provincia Chimborazo, Ecuador; S. N. Rhoads collector].
Hyla quitoe Fowler, 1913:159 [Holotype ANSP 18238 from Quito, Provincia Pinchincha, Ecuador; S. N. Rhoads collector].
Chorophilus olivaceus Andersson, 1945:85 [Holotype.—NHRM 1965 from "Rio Napo, 400 m." (= ? Baños, Provincia Tungurahua), Ecuador; William-Clarke MacIntyre collector].
Gastrotheca m[arsupiata] ecuadoriensis Vellard, 1957:43 [*Nomen nudum*].
Gastrotheca riobambae—Duellman and Fritts, 1972:11.

Diagnosis.—1) Body robust, 48.7 mm in males, 51.2 in females; 2) snout rounded in dorsal view and in profile; 3) canthus rounded; 4) loreal region shallowly concave; 5) tympanum round; 6) supratympanic fold weak, curved posteroventrally behind tympanum; 7) subarticular tubercles on hand large, round; 8) supernumerary tubercles on hand small, subconical; 9) palmar tubercle bifid; 10) fingers not webbed; 11) toes one-fourth webbed; 12) tarsal fold curved, extending full length of tarsus; 13) inner metatarsal tubercle elliptical, visible from above; 14) outer metatarsal tubercle absent; 15) subarticular tubercles on foot large, subconical; 16) supernumerary tubercles on foot small, round; 17) discs round; 18) dorsal skin shagreened, with scattered pustules, tubercular in tympanic region; 19) dorsum green or tan, usually with pair of large elongate dark spots; 20) facial area green or brown; canthal and labial stripes absent; 21) flanks green, blue, or tan with dark brown or black spots; 22) dorsal surfaces of limbs green or tan, usually with elongate dark mark on thigh and irregular blotches or transverse bars on shank; 23) posterior surfaces of thighs dark brown with cream flecks; 24) venter cream with brown or gray mottling on chest and belly; 25) squamosal exostosed in large individuals, in moderately broad contact with maxillary; 26) temporal arcade incomplete; 27) prevomers abutted or narrowly separated medially; 28) transverse processes on eighth presacral vertebra transverse or slightly inclined anteriorly.

Gastrotheca riobambae is like *G. cavia* in having short legs, a short snout, and a narrow interorbital distance, but it differs from *G. cavia* by having paired longitudinal dorsal marks, large spots on the flanks, and no dorsolateral light stripe. The dorsal color patterns of *G. lojana* and *monticola* are similar to that of *G. riobambae,* but both *G. lojana* and *G. monticola* have reticulated or plain flanks and dorsolateral light stripes. *Gastrotheca plumbea* and *psychrophila* have no dorsal markings and uniformly colored flanks; the former has a dorsolateral light stripe.

Variation.—The preceding diagnosis is based principally on topotypic material. Considerable variation, especially in coloration, obtains in this species. Five aspects of coloration are worthy of discussion (Table 2):

1. Dorsal ground color: The dorsum is either green or brown, varying to grayish tan in some individuals. The proportions of green to brown individuals is highly variable in local samples. At Papallacta on the high Amazonian slopes of the Cordillera Oriental, all individuals are green. The same is true at Guaranda on the Pacific slopes of the Cordillera Occidental. Approximately one-half of the frogs from the Cuenca Basin are green. At Riobamba, in the upper reaches of the Río Pastaza drainage, 97 percent of the frogs are brown; at Baños, lower in the Río Pastaza valley, 89 percent are brown.

2. Dorsal markings: Most specimens have dark dorsal blotches. In green frogs these are usually darker green, but in some the blotches are brown. The same variation occurs in brown frogs, with the addition of green blotches that are dark brown peripherally and bordered or not by cream. The blotches usually are in the form of a pair of broad, irregular marks extending from the eyelid or occiput to the rump. In a few individuals the blotches are fragmented into a row of spots; in others they are expanded so as to cover most of the dorsum. With the exception of the series from Riobamba, all large samples contain some individuals lacking dorsal blotches. Plain individuals make up less than one-third of each sample, except that from Guaranda, in which one-half of the specimens lack blotches. Most *Gastrotheca riobambae* lack definite dorsolateral light stripes, but these stripes are present in some specimens from Guaranda and the Cuenca Basin.

3. Thigh coloration: In most samples the posterior surfaces of the thighs are brown, gray, or tan (frequently with a green suffusion) with black flecks or small spots. In specimens from Riobamba and Guano the posterior surfaces of the thighs are tan or green with small cream flecks. The thighs are uniform dull blue in specimens from Papallacta and Biblian, bluish green from Cuenca, and blue with black flecks from Mulaló and Guaranda.

4. Flank coloration: The flanks are tan, green, gray, or blue, usually with black or dark brown spots. In specimens from Papallacta and Biblian the flanks are uniform blue.

5. Ventral coloration: Specimens from Papallacta are uniformly gray below. In all other samples the belly is cream; the belly is marked with black, gray, or dark brown flecks, spots, blotches, or reticulations in all other samples, except those from the Cuenca Basin, in which the belly is uniformly cream.

In all specimens the iris is deep bronze to copper with black reticulations; males in all samples have dark brown to gray vocal sacs.

Table 2. Geographic variation in *Gastrotheca riobambae*.

Locality	*N* ♂; ♀	Green: Brown	Blotched: Plain	Posterior Thighs	Flanks	Belly	Max. SVL (mm) ♂; ♀
Imbabura: Otovalo-Quiroga	23;8	12:19	23:8	Tan-green; black flecks	Blue gray; black spots	Black blotches	50;49
Pichincha: Quito	7;10	3:14	15:2	Brown-green; black flecks or plain	Blue-green; black spots	Small black spots	52;57
Napo: Papallacta	13;2	15:0	12:3	Blue	Blue	Gray	53;63
Cotopaxi: Mulaló	6;10	8:8	12:4	Blue; black flecks	Blue; black flecks	Small black flecks	42;47
Tungurahua: Baños	39;13	6:46	50:2	Gray-green; black spots	Gray-green; black spots	Black spots	49;56
Tungurahua: Mocha	15;2	5:12	15:2	Green	Green; black flecks	Black flecks	47;52
Chimborazo: Riobamba-Guano	48;14	2:60	62:0	Tan-green; cream flecks	Blue-green; black spots	Black reticulations	50;55
Bolivar: Guaranda	6;6	12:0	6:6	Blue; black flecks	Blue; black flecks	Black flecks	50;57
Canar: Biblian	5;4	5:4	7:2	Blue	Blue	Cream	54;58
Azuay: Cuenca	26;7	16:17	25:8	Blue-green	Blue-green	Cream	55;58

There are some correlations between some of the aspects of coloration. Only three of the 37 plain specimens incorporated in table 2 are brown. The color of the flanks generally is the same as the dorsum in green frogs, but in many brown frogs the flanks are green. Apparently the development of blue color on the flanks (most prevalent in the groin) is independent of dorsal color, but uniformly blue flanks are most prevalent in green frogs. The color of the flanks and posterior surfaces of the thighs usually are the same, but the markings on these surfaces are not necessarily the same.

When the variation in coloration is examined with respect to geography, two things are evident: 1) Samples containing only green frogs are from the outer slopes of the Andes (Papallacta and Guaranda); all samples from the inner slopes and interandean valleys contain both green and brown frogs. 2) Samples from the Cuenca Basin (Cuenca and Biblian) lack spots on the flanks, thighs, and venter. Other samples are more alike than any is to the four mentioned above. Because the population in the Cuenca Basin may be isolated genetically from more northern populations, it may represent a distinct taxon. Likewise, the populations on the outer Andean slopes may be isolated genetically from those in the interandean valleys. The populations at Guaranda and Papallacta are widely separated topographically with different phenons occurring in the intervening area.

If the variation in *Gastrotheca riobambae* is examined with respect to genetic polymorphism, it can be conjectured that the polymorphs at any given locality represent a balanced polymorphism resulting from selection for fitness to a particular environment (Levins, 1968). Data from the samples incorporated in Table 2 were analyzed with respect to climatic variables (mean annual temperature, mean annual rainfall, minimum and maximum monthly rainfall, and number of rainy days). Comparisons of percentages of green versus brown frogs, plain versus blotched frogs, and blue versus non-blue flanks and thighs with each of the climatic variables resulted in no correlations.

Jameson and Pequegnat (1971) demonstrated that similar color polymorphism in *Hyla regilla* is correlated with seasonal and microecological differences in vegetation color. The samples of *G. riobambae* containing only green frogs are from areas where the vegetation is in leaf and green throughout the year. The population containing the highest percentage of brown frogs (Riobamba) is from an area having sparse deciduous vegetation. At these and other localities, there was no planned sampling at different seasons; at those localities sampled at different seasons there is no significant difference in the frequency of different morphs in the samples.

Distribution.—*Gastrotheca riobambae* has a broad geographic and altitudinal range in Ecuador (Fig. 4). It occurs on the upper Pacific slopes of the Cordillera Occidental ($>$ 2600 m) and Amazonian slopes of the Cordillera Oriental ($>$ 1800 m), and in interandean valleys ($>$ 2300 m) as far south as the slopes of Cerro Tinajillas in Provincia Azuay. The species occurs at elevations of 3860 m in the Páramo de Apagua, 3960 m at Paso de Guamani, and 4135 m on Volcán Antisana. The species occurs in extreme southern Colombia, but specimens resembling *G. riobambae* from Bogotá, Departamento Cundinamarca, and San Pedro, Departamento Antioquia, apparently are not conspecific.

Remarks.—Gastrotheca riobambae occurs in a variety of habitats ranging from wet montane meadows to dry rocky hillsides. The species frequents ruderal situations—drainage and irrigation ditches, *Agave,* and corn fields. On cloudy or rainy days individuals are active, and males commonly call by day. Despite low temperatures (as low as 2-4° C), adults are most active at night. Tadpoles develop in still water. In large ponds the tadpoles aggregate in shallow water, but upon the slightest disturbance, they rapidly flee to deep water.

As noted in the preceding discussion of variation, some populations currently assigned to *Gastrotheca riobambae* may be specifically distinct. I suggest that biochemical and karyological investigations might be fruitful approaches to the taxonomy of this complex.

DISCUSSION

Apparent evolutionary trends in the Andean marsupial frogs are confusing. Members of the *Gastrotheca marsupiata* group are the most terrestrial and live in what seem to be suboptimal environmental conditions—dry interandean valleys. On the other hand, members of the *Gastrotheca argenteovirens* group and some members of the *Gastrotheca plumbea* group are arboreal and live in what seem to be more optimal anuran environments—cloud forest and wet páramo.

Within the *Gastrotheca plumbea* group, two species (*plumbea* and *psychrophila*) inhabit cool moist environments. *Gastrotheca plumbea* lives in arboreal and terrestrial bromeliads in cloud forest, and *G. psychrophila* inhabits terrestrial bromeliads in wind-swept subparamo (Fig. 5). The other species in the *Gastrotheca plumbea* group principally inhabit drier interandean valleys and Pacific slopes of the Andes. In these areas the frogs live in páramo, *Agave,* and cultivated fields; *G. cavia* inhabits bromeliads in scrubby subparamo (Fig. 6).

Among the members of the *Gastrotheca plumbea* group, *G. riobambae* is most like members of the *Gastrotheca marsupiata*

FIG. 5. Type locality of *Gastrotheca psychrophila,* ridge east of Loja Ecuador. Note terrestrial bromeliads in foreground.

group in having a relatively narrow head, least developed lateral flanges on the frontoparietals, and relatively small hands. The color pattern of *G. riobambae* is similar to that of *G. peruana,* the northernmost species in the *Gastrotheca marsupiata* group. I consider the *Gastrotheca plumbea* group to have been derived from the *Gastrotheca marsupiata* group and *G. riobambae* to be the most primitive member of the *Gastrotheca plumbea* group. All other members of the group have more extensive cranial ossification and exostosis.

The major phyletic line in the *Gastrotheca plumbea* group has dorsolateral light stripes and moderately long snouts. Two members (*G. lojana* and *monticola*) of this line retain the paired dorsal blotches of *G. riobambae,* whereas the dorsum is plain in *G. plumbea,* a species most like members of the Colombian *Gastrotheca argenteovirens* group. The nearly unicolor *G. psychrophila* and the flecked *G. cavia,* each apparently represent independent derivatives from a *G. riobambae*-like stock.

Vuilleumier (1971) documented Pleistocene changes in the flora and avifauna in the Andes. Her summary of geological, climatic, and biogeographic evidence demonstrates two glaciations in the Ecuadorian Andes. During glacial periods snow line was lowered as much as 700 m, and temperatures were depressed 4-11° C. The patterns of speciation and distribution of the *Gastrotheca plumbea* group are compatible with Vuilleumier's paleobiogeographic hy-

FIG. 6. Type locality of *Gastrotheca cavia,* Isla Pequeña, Laguna Cuicocha, Provincia Imbabura, Ecuador. Note bromeliads in scrubby trees in middle of picture.

pothesis. *Gastrotheca lojana* and *monticola* are relictual populations of warm-dry interglacial periods now isolated in lower and drier areas than other members of the group. During climatic depression in glacial periods, populations were isolated in interandean basins and the outer slopes of the Andes; thus, *G. riobambae, plumbea,* and *psychrophila* differentiated in the intermontane valleys, Pacific slopes, and Amazonian slopes, respectively. A *riobambae*-like stock apparently was isolated from more southern populations by uninhabitable environments in the Nudo de Mojanda during a glacial period and differentiated into *G. cavia.* Conceivably, the differentiation of the six species occurred at the time of the first glacial period. If so, the differentiation within *G. riobambae* and southward migration of *G. lojana* and *monticola* into northern Perú could be coincidental with the second glaciation. This proposed speciation model is similar to that suggested by Montanucci (1973) for the Andean microteiid genus *Pholidobolus,* a group of lizards inhabiting the same areas as *Gastrotheca.*

SUMMARY

The marsupial frogs of the genus *Gastrotheca* inhabiting the Andes and interandean valleys of Ecuador form a phylogenetic unit (*Gastrotheca plumbea* group) that is intermediate between the more southern *Gastrotheca marsupiata* group and the more northern *Gastrotheca argenteovirens* group. The *Gastrotheca plumbea* group is characterized by a supraorbital flange on the frontoparietals and extensive exostosis, but no co-ossification, of the cranial roofing bones. Apparently all species in the group have free-swimming tadpoles.

The *Gastrotheca plumbea* group contains six species: *G. lojana* Parker, *G. monticola* Barbour and Noble, *G. plumbea* (Boulenger) and *G. riobambae* (Fowler). In addition, two new species are named herein: *G. cavia* from Laguna Cuicocha, Provincia Imbabura, Ecuador, and *G. psychrophila* from the ridge east of Loja, Ecuador. *Gastrotheca riobambae* is highly variable; some populations may represent distinct species.

The *Gastrotheca plumbea* group seems to have been derived from the *Gastrotheca marsupiata* group, and *G. riobambae* probably is the most primitive member of the group. Speciation within the group evidently occurred through isolation of populations due to climatic fluctuation during the Pleistocene.

RESUMEN

Las ranas marsupiales del género *Gastrotheca* que habitan los Andes y valles interandinos del Ecuador forman una unidad filogenetica (el grupo *Gastrotheca plumbea*) que es un grupo intermediano entre el grupo *Gastrotheca marsupiata* del sur y el grupo *Gastrotheca argenteovirens* del norte. El grupo *Gastrotheca plumbea* se caracteriza por tener una protuberencia supraorbital en los frontoparietales y prominencias extensas pero no co-ossificación de los huesos que forman la cubierta craneal. Parece que todas las especies del grupo tienen renacuajos acuaticos.

El grupo *Gastrotheca plumbea* tiene seis especies: *G. lojana* Parker, *G. monticola* Barbour and Noble, *G. plumbea* (Boulenger), y *G. riobambae* (Fowler). Además dos especies nuevas son nominadas aquí: *G. cavia* de la Laguna Cuicocha, Provincia Imbabura, Ecuador, y *G. psychrophila* de la cordillera al este de Loja, Ecuador. *Gastrotheca riobambae* es muy variable; algunas poblaciones pueden representar especies distintas.

El grupo *Gastrotheca plumbea* parece dirivarse del grupo *Gastrotheca marsupiata*, y probablemente *G. riobambae* es la especie más primitiva de este grupo. La diferenciación en el grupo ocurre evidentemente como resultado del aislamiento de poblaciones debido las fluctuaciones climaticas durante el Pleistoceno.

SPECIMENS EXAMINED

Gastrotheca cavia

"Western Ecuador," BMNH 1860.6.16.124-125. Imbabura: Hacienda San Nicolas, 2000 m, UMMZ 92269, 92278-9, 92289-98; Ibarra, 2300 m, BMNH

(898.4.28.156; locality?); Laguna Cuicocha, 2890 m, KU 138216-20, 139136-9, 139439 (tadpoles), 139440 (young), 143094, 143537 (tadpoles), 148530-42, 148543-4 (skeletons), 148545-7 (tadpoles), 148548 (young).

Gastrotheca lojana

Loja: Celica, 2130 m, BMNH 1931.11.3.3-4; Loja, 2150 m, BMNH 1931. 2.12.10-13, 1933.6.24.18-44, 1935.11.3.26-32, 1947.2.31.6-18, KU 120673-4; 2 km N Loja, 2100 m, KU 142846 (tadpoles); 5 km N Loja, 2150 m, 138235-6, 138237 (skeleton); 2 km E Loja, 220 m, KU 120675; 9 km E Loja, 2660 m, KU 121387 (tadpoles); 2 km S Loja, CAS 93898; 3 km W Loja, 2150 m, KU 138233; 5.5 km W Loja, 2330 m, KU 142603-8, 148549-51; 10 km W Loja, 2500 m, KU 138234.

Zamora-Chinchipe: Zamora, 1000 m, BMNH 1933.624.45 (locality?).

PERÚ: *Amazonas:* Chachapoyas, 2340 m, KU 138238-41; 24 km WSW Leimebamba, 3370 m, FSM 47216 (ID?). *Cajamarca:* Cajamarca, MJP 204. *Piura:* Ayabaca, MJP 702 (2).

Gastrotheca monticola

Azuay: Girón, 2240-2500 m, KU 138401-3. *Loja:* Saraguro, 2500 m, KU 138404-9, 138410 (skeleton), 138769 (tadpoles), 141565, 142609-13, 142847 (tadpoles), 148563-8, 148569-70 (skeletons), 148571 (tadpoles).

PERÚ: *Cajamarca:* Bellavista, BMNH 1947.2.22.47-8, 1947.2.25.77-8; Querocotilla, MCZ 5328-20. *Piura:* Huancabamba, AMNH 7551, MCZ 5290-3, 5296-7, 5299-300, 5302, 5304-7, 5309, 5312-15, 5317, 5319, 5328-30, SMF 2677, UMMZ 55747.

Gastrotheca plumbea

Azuay: Molleturo, 2350 m, ZMB 30057. *Carchi:* Atal, near San Gabriel, UMMZ 83655. *Cotopaxi:* Pilaló, 2320 m, KU 132413-22, 132423 (skeleton), 142614. *Pichincha:* Intac, 1200 m, BMNH 1947.2.31.19.

Gastrotheca psychrophila

Loja: 10 km E Loja, 2570 m, KU 142855 (tadpoles). *Zamora-Chinchipe:* 13-15 km E. Loja, KU 120760-2, 141585 (skeleton), 141586, 141595, 142631-7.

Gastrotheca riobambae

Province Unknown: No specific locality, MNHN 965, 6227-9 (8), 9595; Andes, BMNH 58.7.25.21, 58.7.25.23, 58.7.25.25, 58.7.25.27-8, 58.7.25.31-3; Western Ecuador, BMNH 60.6.16.17, 60.6.16.127. *Azuay:* Bestion, AMNH 13967; Cuenca, 2540 m, CAS 85172, KU 120676-723, 129797-8, SMF 2669-75, USNM 61757-60, USNM-JAP 2345, 2347-8, 2350; 6 km N Cuenca, AMNH 71588-600; 9 km N Cuenca, CAS 85339-40, 93884-94; 18 km N Cuenca, CAS-SU 21851; 4 km E Cuenca, 2540 m, KU 138587-613, 138622-3 (skeletons), 138773 (tadpoles); 8 km SW Cuenca, AMNH 71601-2; 8.8 km NW Cuenca, 2620 m, KU 141583-4, 141594 (tadpoles); 9 km S Cumbe, 3300 m, KU 132536 (tadpoles); 10 km S Cumbe, 3350 m, KU 132392; 28.6 km S Cumbe, 3190 m, KU 142853 (tadpoles); 0.8 km S Cutchil, 2535 m, KU 141582; 2.1 km S Cutchil, 2720 m, KU 141572; 3.5 km S Cutchil, 2785 m, KU 141579-81; 8.5 km S Cutchil, KU 141577-8; Lago de Sarogucho, 20 km W Cuenca, CAS 94114; Laguna de Zurucuchu, 3200 m, KU 121388 (tadpoles); Narihuina, MNHN 06-283; Río Matadero, 8 km E. Cuenca, CAS-SU 21845-6; Río Matadero, 9 km E Cuenca, CAS 94217 (tadpoles), 94218-22, CAS-SU 21847-8; Río Matadero, 12 km E Cuenca, KU 129779-96; Sinicay, 2560 m, AMNH 17451-7, 17459-63, 17465-8, 17552, 17567. *Bolivar:* Guaranda, 2640 m, KU 132403-12, 132531 (tadpoles), 132540 (young); 27.3 km

E Guaranda, 3800 m, KU 142850 (tadpoles); 2.5 km S Guaranda, 2650 m, KU 142616-9, 142851 (tadpoles), 142852, 148573; Guaranda-Riobamba road at Chimborazo border, 3700 m, KU 132541, 132542 (young). *Cañar:* 3 km S Azogues, 2500 m, KU 138624-7, 138774 (tadpoles); Biblian, 2620 m, KU 141570-1, 141573, 142620-4, 147113; 8 km NW Biblian, 3420 m, KU 132537 (tadpoles); Cañar, NHMW 6476, 6480, 2.8 km S Cañar, 3150 m, KU 141574-6; km 94, Guayaquil-Cuenca railroad, CAS 93899-900. *Carchi:* El Carmelo (El Pun), 2750 m, USNM-JAP 4946-7; Quebrada de Piedras, 20 km S Tulcan, 3400 m, KU 118120 (tadpoles); Tulcan, 3000 m, KU 117978-9, 118119 (tadpoles). *Chimborazo:* No specific locality, BMNH 1932.10.2.86; Guamote, USNM 33863; 1 km S Guano, 2500 m, KU 132354-89, 148581, 148582-4 (skeletons), 148592; Hacienda Alao, 15 km SE Pungala, 3100 m, KU 132543 (tadpoles); Laguna de Colta, 15 km SE Riobamba, 3400 m, NSNM-JAP 1728, 1730-3; Riobamba, 2780 m, ANSP 16161, KU 120732, MNHN 02-62(2), 02-350(2); 10 km N Riobamba, 2730 m, KU 138547-73, 138574-6 (skeletons); 15 km E Riobamba, 2600 m, KU 120725-31, 120758-9, 121389 (tadpoles); Rosario, NHMW 6485; San Juan, 3160 m, KU 142615; 10 km W San Juan, 3160 m, KU 120724; 20 km SW Santa Rosa, 3700 m, KU 132348-9; Urbina Railroad Station, 3609 m, KU 132350-3; Volcán Chimborazo, USNM 103268-74. *Cotopaxi:* El Porvenir, 2 km W Campamento Mariscal Sucre, 3620 m, KU 124167 (tadpoles); Guilo, 8 km E Pilaló, 3500 m, KU 132538 (tadpoles); Laguna de Limpios, N base Volcán Cotopaxi, 3890 m, KU 122593; 4 km S Latacunga, USNM 164337; 6 km S, 7 km E Latacunga, 2750 m, KU 127082-4; Mulaló, 2980 m, KU 141566, 146263-4, 146749-61, 146762-3 (skeletons); Páramo de Apagua, 3860 m, KU 132390-1, 132535 (tadpoles); 24.3 km E Pilaló, 3750 m, KU 142848 (tadpoles); 11.3 km W Pujili, 3500 m, KU 141567; 38.3 km W Pujili, 3350 m, KU 142849 (tadpoles); Río Pita, N base Cerro Ingaloma, 3780 m, KU 122594-9. *Imbabura:* Ibarra, 2300 m, AMNH 10569-71, BMNH 98.4.28.152-4, NHMW 6482-6; N slope Nudo de Mojanda, 3650 m, KU 132393; Nudo de Mojanda, 4 km S San Pablo, 3050 m, KU 132394; Otovalo, 2550 m, KU 68708, 138587-613, MNCN 333; Quebrada San Miguel, 1 km N Otovalo, 2560 m, KU 117980; Quiroga, 2500 m, KU 1138577-86, 148585-6 (tadpoles). *Napo:* Laguna Papallacta, 3350 m, KU 109169 (tadpoles); Papallacta, 3130 m, KU 143095-102, 143538-40 (tadpoles), 143541, 148574-7; Rio Napo, 400 m, MNRM 1965 (locality?); Santa Barbara, 2625 m, USNM-JAP 4479, 4507; 1 km NW Santa Barbara, 2625 m, USNM-JAP 4487, 4491-3; 1 km SW Santa Barbara, 2625 m, USNM-JAP 4567; Volcán Antisana, 4135 m, AMNH 20127. *Pastaza:* Mera, 1140 m, AMNH 52852 (locality?). *Pichincha:* Intac, 1200 m, BMNH 78.1.25.20, FMNH 3607, NHMW 6481 (6) (locality?); Llave Pongo, AMNH 20140; Machachi, 2950 m, SMF 2667-8, UMMZ 47216; Paso de Guamani, 20 km E Pifo, 3960 m, KU 111626, 112316-7 (tadpoles), 127081, 127134 (tadpoles); W slope Paso de Guamani, 3940 m, KU 109170 (tadpoles), 109334-5; Quito, 2840 m, AMNH 20438-41, 20447-50, 20471-90, 60631; ANSP 18235, CAS-SU 2274, 11436-7, KU 94403, 111613-25, 112313-5 (tadpoles), 148416-28, 148578-80, 148587-91 (tadpoles), 148593-9, NMCN 156 (2), 158 (6), MNHN 34 (2), 1662 (2), 4878 (4), USNM 57804, USNM-JAP 1570-2, 1574, 1576-7, 1579, 1584, 1586-7, 1593, 1595, 1620-4, 1666, 1669, 1686, 2248-50, 2254, 2487, 2506-8; UZM 1474, 1477-8, 14424-93; between Río Arturo and Taldadas, NE Cayambe, 3450 m, CAS-SU 8281; Río Chiche, Valle de los Chillos, 2535 m, KU 152147-8; Santo Domingo de los Colorados, 500 m, AMNH 20147 (locality?). *Tungurahua:* Ambato, 2700 m, KU 120733-40, 121390 (tadpoles), USNM 164302; Baños, 1800 m, CAS-SU 5082, FMNH 28091-2, 173661-80, KU 99123, 99124-9 (skeletons), 99130-84, UIMNH 65539-675, USNM-JAP 5834-6, 6010-12, 6014, 6019-20; Chambo Grande, 7.6 km SE Pelileo, 2340 m, KU 141568-9, 142625-6, 146261-2; 10 km W Cotaló, 3300 m, KU 132400-2; 1 km W Juan Benigno Vela, 3080 m, KU 132395-6; Llanganati, near Río Jorge, 3000 m, CAS-SU 17426-7; 4 km N Mocha, 3140 m, KU 120757; 10 km SW Mocha, 3700 m, KU 120741-56; Pelileo, 2600 m, MNHN 03/211; 3 km SSW San Miguelito, 2620 m, KU 132399; 12 km SW Santa Rosa, 3400 m, KU 132397-8.

COLOMBIA: *Cundinamarca:* Bogotá, BMNH 1919.3.6.37 (locality?). *Narino:* Cuaspud, TNHC 40564-5.

LITERATURE CITED

ANDERSSON, L. C.
1945. Batrachians from east Ecuador collected 1937, 1938 by Wm. Clarke-MacIntyre and Rolf Blomberg. Arkiv Zool., 37A (2):1-88.

BARBOUR, T. and G. K. NOBLE
1920. Some amphibians from northwestern Peru, with a revision of the genera Phyllobates and Telmatobius. Bull. Mus. Comp. Zool., 63:395-427.

BOULENGER, G. A.
1882. Catalogue of the Batrachia Salientia s. Ecuadata in the collection of the British Museum, ed. 2 London, xvi + 503 pp.

COCHRAN, D. M. and C. J. GOIN
1970. Frogs of Colombia. Bull. U.S. Natl. Mus., 288: xii + 655 pp.

DUELLMAN, W. E.
1970. The hylid frogs of Middle America. Monog. Mus. Nat. Hist. Univ. Kansas, 1:xi + 753 pp.

DUELLMAN, W. E. and T. H. FRITTS
1792. A taxonomic review of the southern Andean marsupial frogs (Hylidae: *Gastrotheca*). Occas. Papers Mus. Nat. Hist. Univ. Kansas, 9:1-37.

FOWLER, H. W.
1913. Amphibians and reptiles from Ecuador, Venezuela, and Yucatan. Proc. Acad. Nat. Sci. Philadelphia, 55:153-176.

JAMESON, D. L. and S. PEQUEGNAT
1971. Estimation of relative viability and fecundity of color polymorphisms in anurans. Evolution, 25:180-194.

LEVINS, R.
1968. Evolution in changing environments. Princeton Univ. Press, Princeton, ix + 120 pp.

MONTANNUCI, R. R.
1973. Systematics and evolution of the Andean lizard genus *Pholidobolus* (Sauria: Teiidae). Misc. Publ. Mus. Nat. Hist. Univ. Kansas, 59:1-52.

PARKER, H. W.
1932. Some new or rare reptiles and amphibians from southern Ecuador. Ann. Mag. Nat. Hist., (10) 9:21-26.

PETERS, J. A.
1955. Herpetological type localities in Ecuador. Rev. Ecuatoriana Ent. Parasit., 2 (3-4):335-352.

VELLARD, J.
1957. Estudios sobre batracios andinos IV. El genero Gastrotheca. Mem. Mus. Hist. Nat. Javier Prado, 5:1-47.

VUILLEUMIER, B. S.
1971. Pleistocene changes in the fauna and flora of South America. Science, 173 (3999):771-780.

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SPECIATION IN FROGS OF THE *HYLA PARVICEPS* GROUP IN THE UPPER AMAZON BASIN

By

William E. Duellman[1] and Martha L. Crump[2]

As our knowledge of the amphibians in the upper Amazon Basin in South America increases, it becomes evident that the richness of the frog fauna is due to the occurrence there of representatives of many species groups and in some cases to the occurrence of several sympatric species belonging to one group. The latter phenomenon is especially noticeable in the *Hyla leucophyllata* and *Hyla parviceps* groups with five and three species, respectively. The present paper deals only with the latter group.

The primary purposes of this paper are to present analyses and interpretations of the morphological features of adults and tadpoles, mating calls, breeding behavior, and ecological relationships of the three species at Santa Cecilia in Amazonian Ecuador. However, as in most Amazonian frogs, some taxonomic problems must be dealt with before the biological problems can be discussed effectively. Thus, we also present here a systematic review of the entire *Hyla parviceps* group, as presently understood.

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[1] Curator, Division of Herpetology, Museum of Natural History, The University of Kansas, Lawrence, Kansas 66045.

[2] Research Assistant, Division of Herpetology, Museum of Natural History, The University of Kansas, Lawrence, Kansas 66045.

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Materials and Methods

The systematic aspects of this study are based on the examination of 720 preserved specimens, 26 cleared and stained specimens, and 19 lots of tadpoles. Recordings were made on a Uher-4000 Recorder and analyzed on a Vibralyzer (Kay Electric Company). All measurements of morphological characters and calls were taken in the manner described by Duellman (1970). Webbing formulae were determined in the manner described by Savage and Heyer (1967). Tadpoles were staged according to Gosner's (1960) system.

All specimens are referred to by the following abbreviations:

AMNH	American Museum of Natural History
BMNH	British Museum (Natural History)
CAS	California Academy of Sciences
CM	Carnegie Museum
FMNH	Field Museum of Natural History
KU	University of Kansas Museum of Natural History
LG	Lescure-Guiana (Jean Lescure, Paris)
LSU	Louisiana State University Museum of Zoology
NHMB	Naturhistorisches Museum Basel
SMF	Senckenbergische Museum Frankfurt
UIMNH	University of Illinois Museum of Natural History
UMMZ	University of Michigan Museum of Zoology

USNM-GOV	United States National Museum (Gustavo Orcés V. collection)
WCAB	Werner C. A. Bokermann, São Paulo, Brasil
ZMB	Zoologisches Museum Berlin

SYSTEMATICS

The *Hyla parviceps* Group

Definition.—1) Great sexual dimorphism in size; snout-vent lengths to 25 mm in males, 32 mm in females; 2) snout short, blunt; 3) tympanum visible, but tympanic ring indistinct or absent; 4) hands and feet moderately webbed; 5) axillary membrane abbreviated; 6) thoracic glands absent; 7) calcars, ulnar and tarsal folds absent; 8) males having single, median, subgular vocal sac and no nuptial excrescences; 9) dorsum tan or brown with dark brown markings, with or without dorsolateral light stripes; 10) pale, vertical suborbital bars present; 11) thighs marked with cream, yellow, or orange spots; 12) anal, ulnar, and tarsal stripes absent; 13) iris pale gray with red ring around pupil; 14) nasals small, abutting or slightly overlapping sphenethmoid; 15) tectum nasi and septum nasi perichondrally ossified and synosteotically united with sphenethmoid; 16) frontoparietal fontanelle covered, or nearly so, by frontoparietals; 17) squamosals articulating with prootics; 18) quadratojugal reduced to small spur, or absent, not articulating with maxillary; 19) prevomerine teeth on posteromedially directed dentigerous processes between choanae; 20) presacral vertebrae nonimbricate, lacking neural crests, having transverse processes decreasing in length posteriorly (3,6 perpendicularly transverse; 4,5 inclined posteriorly; 7,8 inclined anteriorly); 21) sacral diapophyses expanded 53-77°, with convex edges; 22) tadpoles having ovoid bodies and xiphicercal tails with moderately deep fins not extending onto body; 23) larval mouths anteroventral with one row of large labial papillae laterally and ventrally, robust serrate beaks, and no more than one row of denticles; 24) mating call consisting of short, high-pitched notes, followed or not by shorter secondary notes; 25) diploid chromosome number 30.

Content.—Six species: *Hyla bokermanni* Goin, 1960; *H. brevifrons* new species; *H. luteocellata* Roux, 1927; *H. microps* Peters, 1872; *H. parviceps* Boulenger, 1882; *H. subocularis* Dunn, 1934.

Distribution.—The Amazon Basin, coastal lowlands and slopes of southeastern Brasil, northern South America from French Guiana to Colombia, and eastern Panamá.

Comment.—The *Hyla parviceps* group is one of four groups of small Neotropical frogs that share many of the characters noted above. The other groups are—the *Hyla leucophyllata* group with about six species in South America and one in Central America, the *Hyla microcephala* group with perhaps a dozen species in South and Central America, and *Hyla minuta*, a widespread South American "species" (see Cochran and Goin, 1970, for taxonomic comments). The *Hyla leucophyllata* and *microcephala* groups were defined by Duellman (1970).

Twelve of the 25 species in these four groups have a diploid number of 30 chromosomes (Duellman, 1970; Bogart, 1973); the chromosome numbers in the others are unknown. All known tadpoles (18 species) have xiphicercal tails and reduced mouth parts. In addition, the species in the four groups are consistent in characters 4, 7, 8, 18, 19, 20, and 22. Members of the *Hyla parviceps* group differ from all of the other three groups by having (numbers correspond to statements in preceding definition): 1) more pronounced sexual dimorphism in size; 2) shorter snout; 3) tympanic ring indistinct or absent; 5) much less extensive axillary membrane; 9) sexual dimorphism in width of dorsolateral stripes; 10) suborbital bars; 11) thighs patterned; 13) iris color; 15) more perichondral ossification in the tectum nasi and solum nasi; 17) squamosals articulating with prootics.

Although tadpoles of all of the groups have reduced mouth parts, there are consistent differences among the groups. Members of the *Hyla parviceps* and *minuta* groups have anteroventral mouths; there is one row of papillae in *parviceps* and two in *minuta*. Tadpoles of the *Hyla parviceps* group have no, or one, row of denticles below the beaks; *minuta* has one row. Tadpoles of the *Hyla leucophyllata* and *microcephala* groups have terminal mouths lacking rows of denticles; labial papillae are present in the former, absent in the latter.

The mating calls of members of the *Hyla leucophyllata* and *microcephala* groups, and *H. bokermanni* in the *parviceps* group consist of primary and secondary notes; the calls of *Hyla minuta* and other members of the *Hyla parviceps* group consist of series of short notes.

Cochran (1955) and Bokermann (1964) included *Hyla microps* in the *Hyla marmorata* group, although Bokermann (1964) defined the group in a more strict sense to include only four species (*Hyla acreana, marmorata, melanargyrea,* and *senicula*). These frogs differ from the groups discussed above by having more extensive webbing, well-developed ulnar and tarsal folds, less cranial ossification, and different kinds of mating calls. They are like the other groups in general larval and karyological features.

Other named taxa might be associated with the *Hyla parviceps* group or one of the other three groups; however, these species are too poorly known at the present time to be assigned to any group. These include:

Hyla schubarti Bokermann, 1963.—Rondônia, Brasil, and Amazonian lowlands of Perú.

Hyla leali Bokermann, 1964.—Rondônia, Brasil, and Amazonian lowlands of Ecuador and Perú.

Hyla grandisonae Goin, 1966.—Guyana.

Hyla oliveae Cochran and Goin, 1970.—Leticia, Colombia.

Hyla riveroi Cochran and Goin, 1970.—Amazonian Colombia, Ecuador and Perú.

Duellman (1969) named *Hyla carnifex* from the Pacific slopes of the Andes of Ecuador and placed the species in the *Hyla parviceps* group. Although there are superficial similarities in adult structure and coloration, tadpoles, and mating calls, *Hyla carnifex* seems to be related to *Hyla columbiana* and *variabilis* in Colombia and is now excluded from the *Hyla parviceps* group.

ANALYSIS OF CHARACTERS

Three categories of characters were analyzed in adult frogs—morphometric, structural, and coloration. In addition, characters of the mating calls and tadpoles were utilized.

Morphometric Characters

Seven measurements were taken on representative samples of the six species. From these, five proportions were calculated (Tables 1 and 2). Analyses of variance showed highly significant differences ($P \leqq .001$) in both sexes among species for the following: snout-vent length, tibia length/snout-vent length, and head width/snout-vent length. Equally significant differences exist for head length/snout-vent length in females and for tympanum/eye in males. Significant differences ($P \leqq .01$) were found for foot length/snout-vent length in males. The differences among species in foot length/snout-vent length and tympanum/eye in females, and in head length/snout-vent length in males were not significant.

Statistical comparisons of the sexes of three species revealed significant differences in snout-vent length between males and females of all three and in different proportions in different species (Table 1). Adult females of all six species are much larger than adult males; this is especially noticeable in *Hyla parviceps,* in which the smallest gravid females are larger than the largest males.

Structural Characters

The species comprising the *Hyla parviceps* group are alike in most structural features; those features that are constant, or nearly so, are listed in the definition of the group. The tongue is cordiform in all species, deeply notched posteriorly in *H. microps,* and shallowly notched in the others. Ulnar and tarsal tubercles are absent in all species, except females of *H. parviceps* and both sexes of *H.*

TABLE 1.—Measurements and proportions of three species of the *Hyla parviceps* group. All samples from Santa Cecilia, Ecuador.

Character	Males				Females				t
	Range	$\bar{X}$	SD	SE	Range	$\bar{X}$	SD	SE	
	Hyla brevifrons 25 ♂♂, 11 ♀♀								
Snout-vent length (SVL)	17.00-21.40	18.570	0.970	0.190	20.1 -23.2	21.68	1.090	0.330	0.001
Tibia length/SVL	0.46- 0.51	0.484	0.015	0.003	0.45- 0.51	0.473	0.020	0.006	NS
Foot length/SVL	0.35- 0.46	0.416	0.027	0.005	0.38- 0.45	0.415	0.023	0.007	NS
Head length/SVL	0.28- 0.35	0.324	0.016	0.003	0.27- 0.34	0.315	0.018	0.005	NS
Head width/SVL	0.29- 0.33	0.308	0.012	0.002	0.29- 0.33	0.301	0.013	0.004	NS
Tympanum/Eye	0.36- 0.50	0.410	0.036	0.007	0.34- 0.44	0.379	0.033	0.010	0.05
	Hyla bokermanni 25 ♂♂, 25 ♀♀								
Snout-vent length (SVL)	20.00-22.70	21.420	0.750	0.150	20.4 -25.6	23.48	1.300	0.260	0.001
Tibia length/SVL	0.46- 0.56	0.502	0.024	0.005	0.45- 0.53	0.494	0.023	0.005	NS
Foot length/SVL	0.38- 0.48	0.428	0.022	0.004	0.34- 0.46	0.420	0.028	0.006	NS
Head length/SVL	0.30- 0.38	0.329	0.018	0.004	0.29- 0.34	0.309	0.014	0.003	0.001
Head width/SVL	0.26- 0.32	0.298	0.017	0.003	0.27- 0.32	0.293	0.012	0.002	NS
Tympanum/Eye	0.33- 0.44	0.391	0.035	0.007	0.33- 0.56	0.413	0.056	0.011	NS
	Hyla parviceps 25 ♂♂, 25 ♀♀								
Snout-vent length (SVL)	15.20-18.30	16.740	0.720	0.140	21.6 -26.1	23.45	0.970	0.190	0.001
Tibia length/SVL	0.44- 0.55	0.494	0.022	0.004	0.46- 0.55	0.506	0.025	0.005	NS
Foot length/SVL	0.38- 0.47	0.425	0.017	0.003	0.38- 0.46	0.424	0.021	0.004	NS
Head length/SVL	0.30- 0.35	0.328	0.014	0.003	0.28- 0.32	0.299	0.012	0.002	0.001
Head width/SVL	0.28- 0.33	0.308	0.012	0.002	0.26- 0.31	0.288	0.012	0.002	0.001
Tympanum/Eye	0.25- 0.45	0.328	0.042	0.008	0.34- 0.52	0.392	0.042	0.008	NS

TABLE 2.—Measurements and proportions of males of Non-Ecuadorian species in the *Hyla parviceps* group.
(See Table 1 for comparable statistics for Ecuadorian species.)

Character	Range	X̄	SD	SE
Hyla luteocellata 9 ♂♂				
Snout-vent length (SVL)	20.00-23.10	21.720	1.260	0.420
Tibia length/SVL	0.47- 0.50	0.483	0.014	0.005
Foot length/SVL	0.39- 0.45	0.417	0.017	0.006
Head length/SVL	0.31- 0.35	0.326	0.013	0.004
Head width/SVL	0.31- 0.33	0.319	0.008	0.003
Tympanum/Eye	0.36- 0.45	0.397	0.035	0.012
Hyla microps 25 ♂♂				
Snout-vent length (SVL)	18.30-23.20	21.110	1.340	0.270
Tibia length/SVL	0.45- 0.55	0.499	0.025	0.005
Foot length/SVL	0.41- 0.46	0.437	0.018	0.004
Head length/SVL	0.30- 0.34	0.320	0.014	0.003
Head width/SVL	0.29- 0.34	0.318	0.014	0.003
Tympanum/Eye	0.37- 0.52	0.454	0.037	0.007
Hyla subocularis 25 ♂♂				
Snout-vent length (SVL)	20.50-23.10	21.720	0.730	0.150
Tibia length/SVL	0.48- 0.55	0.509	0.015	0.003
Foot length/SVL	0.38- 0.45	0.426	0.018	0.004
Head length/SVL	0.29- 0.34	0.320	0.011	0.002
Head width/SVL	0.32- 0.34	0.328	0.007	0.001
Tympanum/Eye	0.26- 0.44	0.365	0.041	0.008

microps. In the latter, small tubercles are present on the eyelid in most specimens (see Lutz, 1973, for discussion of variation).

The webbing is slightly variable within all species (Table 3); *H. parviceps* has slightly more webbing than any of the others. Females generally have slightly more webbing than do males; this is especially noticeable in *H. parviceps,* which has the greatest sexual dimorphism in size.

Coloration

Five aspects of color pattern were analyzed on 408 preserved adults, representing both sexes of all species, except *H. luteocellata* and *microps,* for which only males were used. However, partial data were utilized for two female *H. microps*; the pattern of female *H. luteocellata* was described by Rivero (1969).

Dorsal Body Pattern.—This is the most intraspecifically variable pattern character (Table 4). *Hyla bokermanni* is the most variable species.

Dorsolateral Stripes.—These stripes are absent in *H. microps* and *parviceps,* and most males of *H. brevifrons.* In males of the other species a narrow cream or pale yellow stripe extends from

TABLE 3.—Variation in webbing in members of the *Hyla parviceps* group. (Roman numerals = digits; Arabic numerals = number of free phalanges.)

Species	*N*	Hand	Foot
H. bokermanni	20	II(1½-2^-)-(2¾-3)III(2^+-2¾)-(2^--2¼)IV	I(1½-2)-(2-2^+)II(1-1½)-2 III(1^+-1½)-2 IV(1½-2)-(1-1½)V
H. brevifrons	20	II(2^--2)-(2½-2¾)III(2¼-2¾)-(2^--2)IV	I(2^--2)-(2-2^+)II(1¼-1½)-(2-2¼)III(1^+-1½)-2 IV 2-(1¼-1½)IV
H. luteocellata	5	II 2^--(2¾-3^-)III 2½-(2-2^+)IV	I(1¾-2)-(2^--2)II(1^+-1½)-2 III(2^+-2¼)-(2-2½)IV(2-2½)-(1¼-1½)V
H. microps	8	II(2^--2½)-(2½-3)III(2½-3)-2 IV	I(1¼-2)-(2^--2^+)II(1^+-1¼)-(2^--2¼)III(1-1½)-(2-2^+)IV(2^--2^+)-(1¼-1½)V
H. parviceps	20	II(1½-2^-)-(2¼-3^-)III(2^--2^+)-(2^--2^+)IV	I(1¼-1¾)-(2-2^+)II(1-1½)-(2^--2^+)III(1-1½)-(2^--2^+)IV(2^--2¼)-(1-1½)V
H. subocularis	20	II(1¾-2^+)-(2¾-3)III(2^+-2½)-(2^--2^+)IV	I(1¾-2^-)-(2^--2^+)II(1^--1½)-(1½-2½)III(1-2)-(2-2^+)IV(2^--2^+)-(1-1½)V

the eyelid or supratympanic region to the sacral region. In females of these species the stripe is broad and well defined; the stripe angles posterolaterally onto the flank in *H. brevifrons* but continues posteriorly in the other species.

TABLE 4.—Variation in dorsal color pattern in the *Hyla parviceps* group. (Numbers are percentages.)

Pattern	*H. bokermanni*	*H. brevifrons*	*H. luteocellata*	*H. microps*	*H. parviceps*	*H. subocularis*
N	93	111	9	25	114	56
Plain	20	----	----	36	----	18
Flecks	19	3	----	----	----	----
Longitudinal marks	11	----	----	----	----	----
Median blotch anteriorly; paired marks posteriorly	9	----	----	----	----	----
Transverse bars	41	97	----	----	----	----
X anteriorly; paired spots posteriorly	----	----	100	----	----	----
λ-shaped mark	----	----	----	----	76	----
Median blotch anteriorly; trans. bar posteriorly	----	----	----	----	24	----
X anteriorly	----	----	----	----	----	20
X anteriorly; transverse bar posteriorly	----	----	----	----	----	62
Irregular dashes	----	----	----	64	----	----

Head Markings.—All species have vertical, cream or yellow suborbital bars, although the bars are absent in 5 percent of the *H. parviceps*. Normally there are two bars in *H. bokermanni, brevifrons,* and *subocularis,* and only one bar in the other species. The bars are much broader in *H. microps* than in the other species. Canthal and rostral stripes are absent in *H. microps* and *parviceps.* Stripes are present in varying percentages of the other species (Table 5). The stripes are cream or pale yellow. A canthal stripe

TABLE 5.—Variation in head stripes in the *Hyla parviceps* group. (Numbers are percentages.)

	H. bokermanni	*H. brevifrons*	*H. luteocellata*	*H. subocularis*
N	93	111	9	56
Canthal only	41	8	----	29
Canthal & rostral	51	30	----	62
Rostral only	----	29	100	----
None	8	33	----	9

extends along the canthal ridge from the anterior corner of the orbit to the nostril; in some individuals the stripes meet on the snout or fuse with the upper end of the vertical rostral keel on the snout.

Hind Limb Markings.—Important interspecific differences are evident in the coloration of the thighs. All individuals of *H. luteocellata* and *subocularis* and 80 percent of the *H. bokermanni* have a large black-bordered, deep yellow spot on the anterior surface of the thigh. The anterior surfaces of the thighs are unmarked in all *H. brevifrons* and *microps* and in 20 percent of the *H. bokermanni* and 11 percent of the *H. parviceps*; in the rest of the *H. parviceps* (89%) there are one or two small cream spots on the anterodorsal surface of the thigh, which otherwise is black. The dorsal surface of the thigh is dark brown or black with 1-3 small cream or yellow spots in *H. bokermanni* (91%), *brevifrons* (94%), *luteocellata* (100%), *parviceps* (3%), and *subocularis* (91%); in all *H. microps,* 97 percent of the *H. parviceps* and less than 10 percent of the other species, pale spots are absent. The posterior surface of the thigh is dark brown in *H. brevifrons,* black with or without small cream spots in *H. parviceps,* and usually yellow or tan with or without black mottling in *H. bokermanni, luteocellata,* and *subocularis.* On the posterior surface of the thigh in *H. microps* there is a large black-bordered, orange spot. The dorsal surface of the shank has transverse dark markings. These consist of 3-4 narrow bars in the *H. bokermanni*; 3 broad bars in *H. brevifrons, microps, subocularis,* and *parviceps* (median bar wider than others), or faint lines in *H. luteocellata.*

Ventral Coloration.—In *H. parviceps* the venter is dark gray fading to white medially on the throat and anterior belly; the ventral surface of the shank is gray with a bright orange spot proximally. In the other species the venter is cream; gray flecks are present on the anterior edge of the chin in *H. brevifrons* (75%), *luteocellata* (100%), and *microps* (100%), and gray flecks are present on the belly in 32 percent of *H. microps.*

Mating Calls

We have analyzed tape recordings of four species (Table 6), and Rivero (1969) provided an audiospectrogram of *H. luteocellata.* The call of *H. microps* has not been analyzed, but Lutz (1973) described the call as “the chirping of a cricket.” The calls of all of the species consist of short, high-pitched, insect-like notes. The call of *H. parviceps* is much higher pitched than the others, and the call of *H. bokermanni* is distinctive in having secondary notes (Fig. 1). The release call of *H. luteocellata* illustrated by Rivero (1969) may be a series of secondary notes.

TABLE 6.—Comparison of mating calls of members of the *Hyla parviceps* group. (*N* = individuals/notes; means in parentheses below ranges.)

Species (*N*)	Note Repetition Rate	Duration (secs)	Pulses per Second	Secondary Notes	Dominant Frequency (Hertz)
H. bokermanni	5-19	0.23-0.28	100-190	2-5	4000-4652
(4/12)	(12.2)	(0.259)	(132.5)	(3.3)	(4478)
H. brevifrons	26-46	0.43-0.49	30- 40	0	4152-5115
(9/25)	(36.8)	(0.467)	(38.9)		(4625)
H. parviceps	54.5	0.12-0.14	140	0	6072-6341
(1/3)		(0.13)			(6221)
H. subocularis	3-20			0	
(2/4)		(0.53)	(43)		2200

Tadpoles

The tadpoles of *H. luteocellata* are unknown. The tadpole of *H. microps* was described by Bokermann (1963b) and that of *H. subocularis* by Duellman (1970). The mouthparts of the tadpoles are alike in having robust, finely serrated beaks, bare upper lips and one row of labial papillae laterally and ventrally. In *H. bokermanni* and *subocularis* the papillae lateral to the mouth are partially fused in the form of a vertical fold. The mouth is small and directed anteroventrally; the body is ovoid with blunt snout in dorsal view. The caudal fin does not extend onto the body, and the tail is xiphicercal (Fig. 2). The spiracle is sinistral and lateral, and the anal tube is dextral. Rows of denticles are absent in all except *H. microps,* which has a single row of small denticles below the lower beak.

Tadpoles of this group are brightly colored and patterned. Longitudinal cream stripes are present on the dorsal surface of the body of *H. microps* and *subocularis,* and on the snout of *H. bokermanni.* Two broad cream transverse bars are present on the body of *H. parviceps,* and broad yellowish-tan dorsolateral stripes on the body and a red streak on the dorsal fin characterize the tadpole of *H. brevifrons.*

KEY TO THE SPECIES

1. Dorsolateral light stripe absent 2
   Dorsolateral light stripe present, narrow in males, broad in females 4
2. Venter gray, white medially; small orange spot proximally on ventral surface of shank .... *Hyla parviceps*
   Venter cream or white, with or without small gray flecks; no orange spot on ventral surface of shank 3

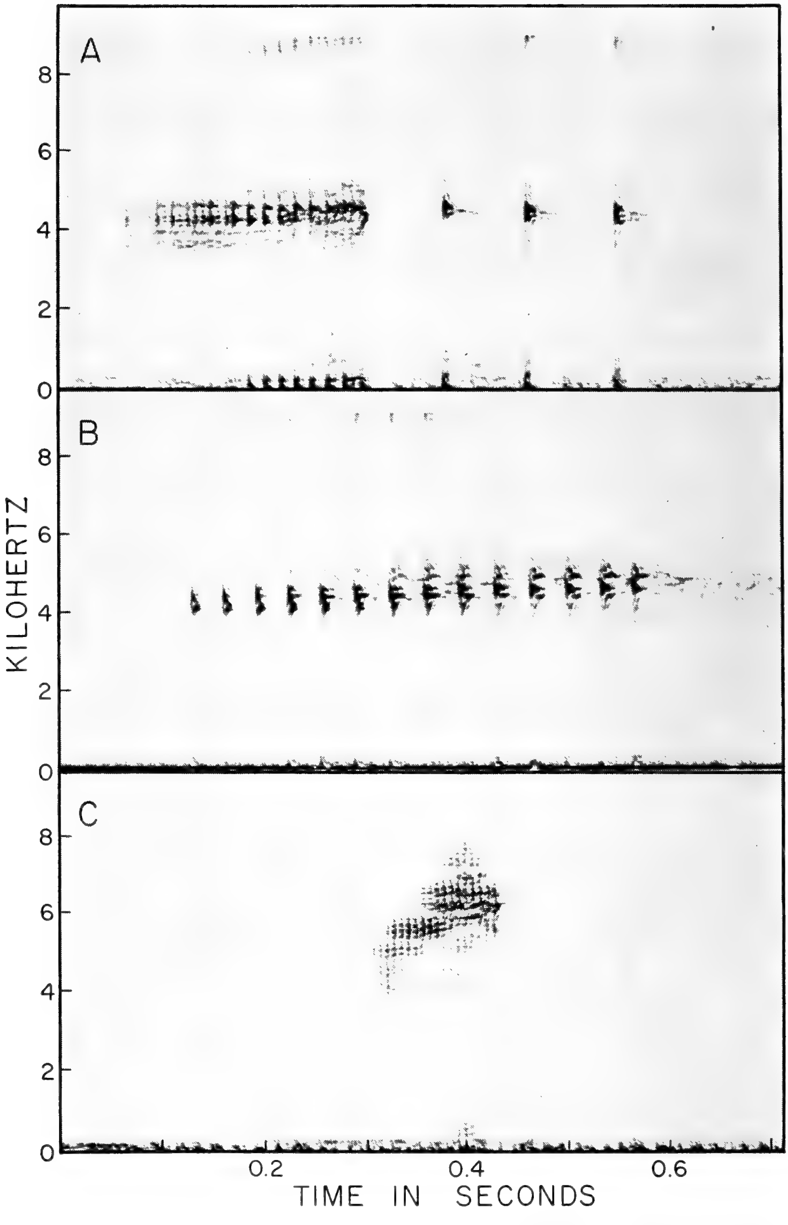

Fig. 1. Audiospectrograms of mating calls of members of the *Hyla parviceps* group at Santa Cecilia, Ecuador. A. *Hyla bokermanni* (KU Tape 688). B. *H. brevifrons* (KU Tape 1176). C. *H. parviceps* (KU Tape 1178).

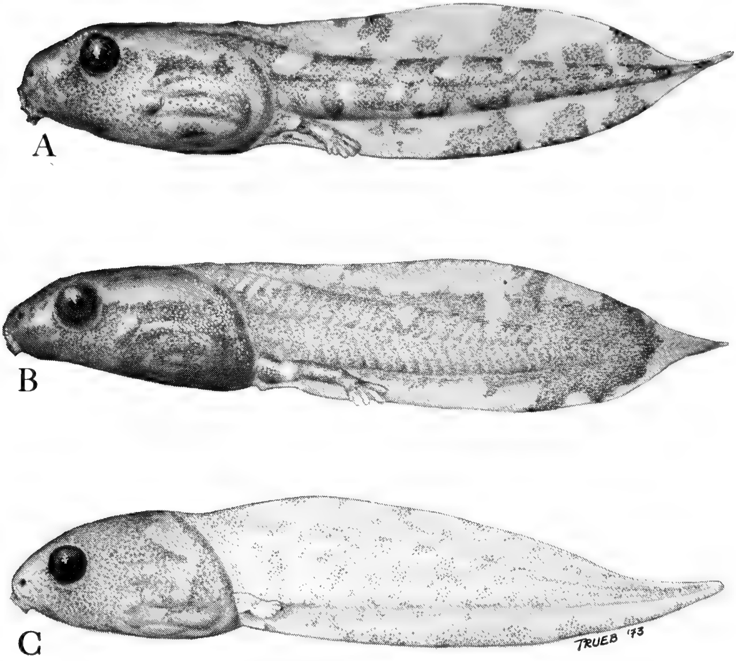

FIG. 2. Tadpoles of members of the *Hyla parviceps* group at Santa Cecilia, Ecuador. A. *Hyla bokermanni* (KU 124193). B. *H. brevifrons* (KU 125899). C. *H. parviceps* (KU 146791). ×5.

3. No spots on dorsal surface of thigh; large orange spot on posterior surface of thigh .... *Hyla microps*
Two small creamy yellow spots on dorsal surface of thigh; no large orange spot on posterior surface of thigh .... *Hyla brevifrons* (♂♂)

4. Anterior surface of thigh dark .... *Hyla brevifrons* (♀♀)
Anterior surface of thigh tan, usually with large, black-bordered spot 5

5. One suborbital white bar .... *Hyla luteocellata*
Usually two suborbital white bars 6

6. Dorsum plain, flecked, or usually marked with large median dark blotch or transverse bar anteriorly .... *Hyla bokermanni*
Dorsum marked with a dark X-shaped pattern anteriorly .... *Hyla subocularis*

SPECIES ACCOUNTS

In the following accounts, the major distinguishing features are enumerated in the diagnoses. Sizes given in diagnoses are maximum snout-vent lengths. With the exception of one new species, detailed descriptions are omitted. Variation of characters is treated in the preceding analysis of characters. Colors are of living frogs and tadpoles. The statements of distribution are based on the localities in the list of specimens examined.

Hyla bokermanni Goin
(Figure 3)

Hyla bokermanni Goin, 1960:721 [Holotype.—WCAB 2881 from Tarauacá, Territorio do Acre, Brasil; W. C. A. Bokermann collector].

Hyla rondoniae Bokermann, 1963a:247 [Holotype.—WCAB 7845 from Rondônia, Territorio do Rondônia, Brasil; A. Machado collector]. New synonym.

Diagnosis.—1) Snout-vent length 22.7 mm in males, 25.6 mm in females; 2) webbing on hand II 2^{-}-3^{-} III 2^{+}-2 IV, on foot I 2^{-}-2 II 1¼-2 III 1¼-2 IV 2-1^{+} V; 3) ulnar and tarsal tubercles absent; 4) canthal and rostral stripes (50%) or canthal stripes only (41%) present; 5) two suborbital bars (98%); 6) dorsum plain, flecked, or marked with three transverse bars or one blotch anteriorly and one bar posteriorly; 7) dorsolateral light stripe present, broad in females; 8) thigh usually (80%) having large black-bordered yellow spot anteriorly and 1-3 small yellow spots dorsally; 9) all ventral surfaces uniform cream.

Hyla bokermanni, luteocellata, and *subocularis* all have dorsolateral light stripes and large yellow spots on the anterior surfaces of the thighs. *Hyla bokermanni* differs from *H. luteocellata* in usually having canthal stripes and two, instead of one, suborbital bars; *H. subocularis* differs from *H. bokermanni* by having an X-shaped pattern anteriorly on the dorsum, instead of a large blotch, transverse bar, or no markings.

Coloration.—At night, the dorsum is pale yellowish tan; the dorsal markings and dorsolateral stripes are barely discernable. By day, the dorsum is tan, and the dorsal markings are dark brown. The dorsolateral stripe is creamy yellow in males and creamy white in females. The large spot on the anterior surface of the thigh is bright yellow, and the small spots on the dorsal surface of the thigh are creamy yellow. The iris is silvery gray with a narrow red ring around the pupil. Males have a yellow vocal sac; otherwise the venter is creamy white.

Tadpoles.—A tadpole in stage 36 has a body length of 7.2 mm and a total length of 19.8 mm. The body is dark brown with two short, broad, longitudinal yellowish tan bars on the snout. Prox-

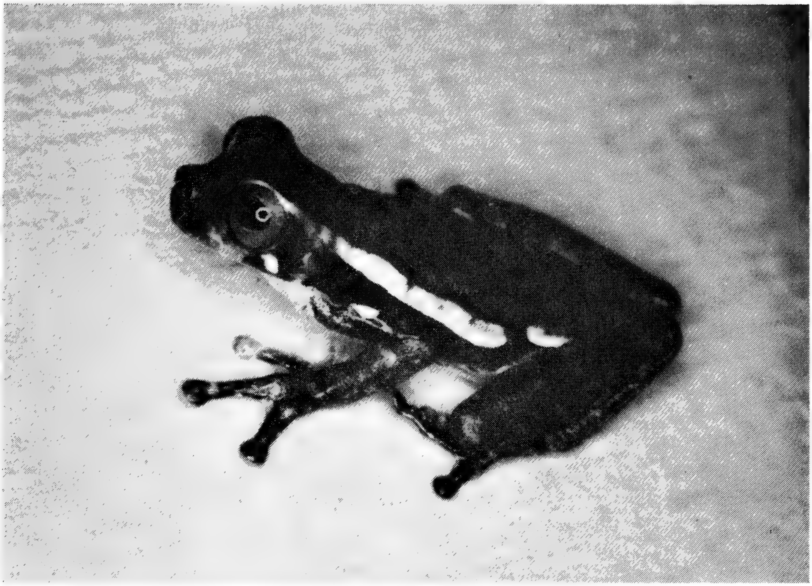

FIG. 3. *Hyla bokermanni,* female, 24.4 mm SVL (KU 126552).

imally the caudal musculature and fins are pale orange, unpigmented distally, except for broad gray vertical marks. The iris is red medially and silver peripherally.

Distribution.—Lowlands (< 1000 m) of upper Amazon Basin in Ecuador and extreme western Brasil, and presumably in the intervening area of northeastern Perú.

Remarks.—We have examined the holotype of *H. rondoniae* (WCAB 12148) and compared it with the figure of the holotype of *H. bokermanni* and series of specimens from Ecuador. As suggested by Rivero (1969), the name *H. bokermanni* is based on a female and *H. rondoniae* on a male of the same species.

Hyla brevifrons new species
(Figures 4 & 5)

Holotype.—KU 126370, an adult male, from Santa Cecilia, Provincia Napo, Ecuador, obtained on 16 May 1969, by William E. Duellman and Linda Trueb.

Allotype.—KU 126371, an adult female, same data as holotype.

Paratopotypes.—KU 111786-802, 123049-50, 123059, 123072-88, 126342-61, 126363-69, 126546, 126548-51, 136298, 143189, 146281-87, 146413, 146415-18.

Diagnosis.—1) Snout-vent length 21.4 mm in males, 23.2 mm in females; 2) webbing on hand II 2^{-}-2½ III 2⅓-2^{-} IV, on foot I 2-2 II 1⅓-2 III 1⅓-2 IV 2-1¼ V; 3) ulnar and tarsal tubercles absent; 4) canthal and rostral stripes usually present (one or both in 66%); 5) two suborbital bars (95%); 6) dorsal pattern consisting of broad transverse bars; 7) dorsolateral light stripe absent in males, broad in females; 8) thigh dark brown anteriorly, having 1-3 small yellow spots dorsally; 9) venter uniformly cream, except for gray flecks on chin (78%).

Hyla brevifrons differs from those other members of the group having dorsolateral light stripes by lacking a large black-bordered yellow spot on the anterior surface of the thigh.

Description.—The following description is based on the holotype and allotype; where differences occur, the characters of the allotype are in parentheses. Snout-vent length 19.1 mm (23.0 mm); snout short, truncate in dorsal view, inclined posteroventrally in profile; canthus rounded; loreal region slightly concave; lips rounded; internarial area depressed; nostrils slightly protuberant anterolaterally; supratympanic fold weak; tympanic ring indistinct. Axillary membrane extending one-fourth length of upper arm; forearm lacking folds or tubercles; fingers moderately short, bearing small discs; webbing on hand II 2^{-}-2½ III 2½-2^{-} IV (II 2^{-}-2½ III 2¼-2^{-} IV); webbing on foot I 2-2^{+} II 1½-2 III 1½-2 IV 2^{-}-1½ V (I 2-2 II 1¼-2¼ III 1¼-2 IV 2-1¼ V). Anal flap short, opening at upper level of thighs; skin on belly and proximal posteroventral surfaces of thighs granular; skin on other surfaces smooth. Prevomerine teeth 2-2 (3-4) on processes posteromedially inclined between posterior margins of ovoid choanae; tongue cordiform, shallowly notched posteriorly; vocal slit extending from midlateral base of tongue to angle of jaw (absent).

Color (in alcohol): Dorsum tan (grayish tan) with brown markings—blotch in occipital region, square blotch in scapular region, and transverse blotch in sacral region extending onto flanks; dorsolateral stripe absent (distinct, broad, creamy white, extending

FIG. 4. *Hyla brevifrons*, holotype, male, 19.1 mm SVL (KU 126370).

FIG. 5. *Hyla brevifrons,* allotype, female, 23.0 mm SVL (KU 126371).

from eyelid to transverse sacral blotch and thence laterad onto flanks, bordered below by broad brown mark); one (two) suborbital white bar; forearms and shanks tan with two and three transverse brown bars; thighs pale brown with two creamy yellow spots on dorsal surfaces; venter white with brown flecks on chin.

Coloration.—The dorsum is olive-tan with brown markings and, in females, distinct creamy tan dorsolateral stripes. The thighs are dark brown; the spots on the thighs and the suborbital bars are creamy yellow. The venter is unpigmented except for the pectoral region and chin (in females), which is white; males have a pale yellow vocal sac. The iris is red medially and silvery gray peripherally.

Tadpoles.—A tadpole in stage 39 has a body length of 7.6 mm and a total length of 22.2 mm. In dorsal view the body is dark brown medially and pale brown laterally. The venter and sides of the body are dark brown with cream flecks. The tail is tan with dark brown mottling and a bright red streak on the dorsal fin. The iris is gray-bronze with a red ring around the pupil.

Distribution.—The upper Amazon Basin in Ecuador, Perú, and probably western Brasil, to elevations of about 1300 m on the eastern slopes of the Andes. Additionally, the species is known from French Guiana and Belém, Brasil; it probably occurs throughout the Amazon Basin.

Etymology.—The specific name is derived from the Latin *brevis* meaning short, and the Latin *frons,* meaning brow. The name is used in allusion to the short head of the species.

Hyla luteocellata Roux

Hyla luteo-ocellata Roux, 1927:260 [Holotype.—NHMB 3900 from El Mene, Estado Falcón, Venezuela; Kugler and Vonderschmidt collectors].

Diagnosis.—1) Snout-vent length 23.1 mm in males, 28.0 mm in females (Rivero, 1969:132); 2) webbing on hand II 2^--3^- III 2½-2 IV, on foot I 2-2 II 1½-2 III 2^+-2^+ IV 2^+-1¼ V; 3) ulnar and tarsal tubercles absent; 4) canthal stripes absent, rostral stripe present; 5) one suborbital bar; 6) dorsal pattern consisting of X-shaped mark anteriorly and pair of dashes posteriorly; 7) dorsolateral light stripe present, broad in females; 8) thigh having large black-bordered yellow spot anteriorly and 1 or 2 small yellow spots dorsally; 9) venter uniformly cream, except for gray flecks on chin.

Hyla luteocellata is like *H. bokermanni* and *subocularis* in having dorsolateral light stripes and a large yellow spot on the anterior surface of the thigh. It differs from these species by lacking canthal stripes and in having only one suborbital bar. Furthermore, it differs from *H. bokermanni* by having an X-shaped dorsal marking anteriorly, instead of a median blotch or transverse bar, and from *H. subocularis* by having paired longitudinal markings posteriorly on the dorsum instead of no markings or a transverse bar.

Coloration.—Rivero (1969:128) described the suborbital bar as cream or yellow, the spot on the anterior surface of the thigh orange, spots on the dorsal surface of the thigh greenish yellow, brownish, or dirty white.

Distribution.—Northern Venezuela from Lago Maracaibo to the Unare Depression (Rivero, 1969:130). The species also occurs near Brownsweg and in the Kayser Mountains in Surinam (M. S. Hoogmoed, pers. comm.).

Hyla microps Peters

Hyla microps Peters, 1872:682 [Holotype.—ZMB 7472 from Novo Friburgo, Estado do Rio de Janeiro, Brasil; Salmin collector].

Hyla hilli Boulenger, 1920:123 [Holotype.—BMNH 1914.3.20.9 (RR 1947.2.24.10) from Teresópolis, Estado Rio de Janeiro, Brasil; J. P. Hill collector]. Synonymy *fide* Cochran (1955:177).

Hyla giesleri Mertens, 1950:185 [Holotype.—SMF 41217 from Barro Branco, Estado do Rio de Janeiro, Brasil; P. Giesler collector]. Synonymy *fide* Bokermann (1966:51).

Diagnosis.—1) Snout-vent length 24.6 mm in males, 31.3 mm in females; 2) webbing on hand II 2¼-2¾ III 2¾-2 IV, on foot I 2^--2 II 1^+-2 IV 2-1¼ V; 3) ulnar and tarsal tubercles low in both sexes; 4) canthal and rostral stripes absent; 5) one broad suborbital bar; 6) dorsum plain or marked with irregular dashes; 7) dorsolateral light stripe absent; 8) thighs yellow anteriorly, brown dorsally, having large black-bordered orange spot posteriorly; 9) venter cream with gray flecks on chin (100%) and on belly (32%).

This species differs from all other members of the group, except *H. parviceps*, in lacking dorsolateral light stripes; it differs from *H. parviceps* by having a cream venter and a large orange spot on the posterior surface of the thigh and a black mark in the axilla. *Hyla parviceps* has a gray venter with an orange spot on the proximal ventral surface of the shank and cream spots anterodorsally on the thigh.

Coloration.—Lutz (1973:95) described specimens from Serra da Bocaina, Brasil, as brown above with darker brown dorsal markings. The spots on the thighs and the webs between the inner toes are bright orange. The axilla is black, and the belly is greenish yellow.

Tadpoles.—Bokermann (1963b) described tadpoles from Campo Grande, São Paulo, Brasil. The body is dark olive with dorsolateral and lateral light stripes.

Distribution.—Coastal lowlands and lower slopes of the highlands in southeastern Brasil from Espírito Santo to Paraná.

Remarks.—Lutz (1973) mentioned a specimen 38 mm in length from Angra dos Reis, Rio de Janeiro, Brasil. Although we have not seen the specimen, we are dubious of the identification reported by Lutz because of the reported size and coloration.

Duellman examined the holotypes of *Hyla hilli* and *Hyla giesleri* and concluded as did Cochran (1955) and Bokermann (1966) that they are representatives of *Hyla microps*. In addition to the localities given in the specimens examined, Cochran (1955) reported the species from Rio Novo, Espírito Santo, and from several localities in Rio de Janeiro and Santa Catarina.

Hyla parviceps Boulenger
(Figure 6)

Hyla parviceps Boulenger, 1882:393 [Holotype.—BMNH 80.12.5.214 (RR 1947.2.13.5) from Sarayacu, Provincia Pastaza, Ecuador; Mr. Buckley collector].

Diagnosis.—1) Snout-vent length 18.3 mm in males, 26.1 mm in females; 2) webbing on hand II 1⅔-2⅔ III 2-2 IV, on foot I 1½-2 II 1^{+}-2 III 1¼-2 IV 2-1¼ V; 3) ulnar and tarsal tubercles low on females, absent on males; 4) canthal and rostral stripes absent; 5) usually (92%) one suborbital bar; 6) dorsal markings usually (76%) a λ-shaped mark, or (24%) median blotch anteriorly and transverse bar posteriorly; 7) dorsolateral stripe absent; 8) thigh usually (92%) having one or two small cream spots anteriorly and uniform dark dorsally; 9) throat and belly gray, white medially; ventral surface of shank gray with orange spot proximally.

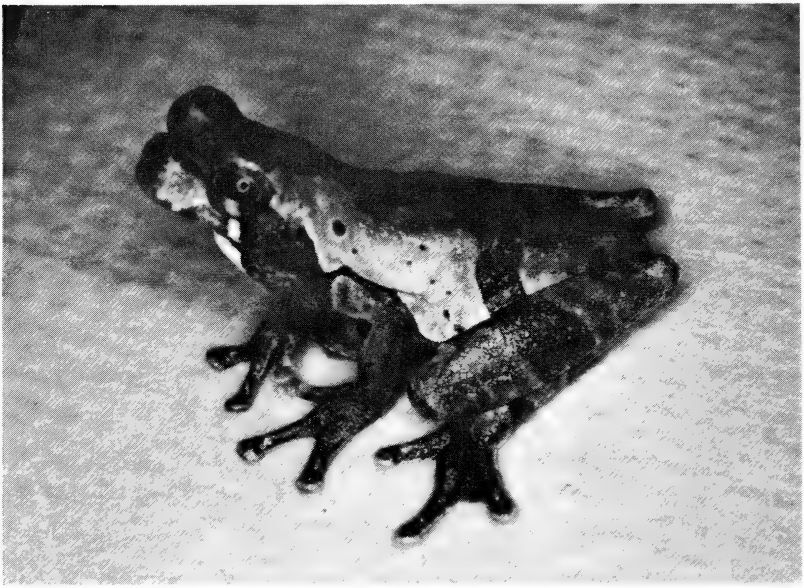

FIG. 6. *Hyla parviceps*, female, 24.5 mm SVL (KU 126476).

Hyla parviceps differs from all other species in the group, except *H. microps*, in lacking dorsolateral light stripes; it differs from *H. microps* by having a dark venter with an orange spot on the proximal ventral surface of the shank and cream spots anterodorsally on the thigh. *Hyla microps* has a cream venter and a large orange spot on the posterior surface of the thigh.

Coloration.—The dorsum is tan with faintly darker markings at night. By day the dorsum is orange-tan, reddish brown, or brown with darker brown markings. The flanks are dark brown or black and white. The thighs are dark brown or black with creamy-yellow spots. The suborbital bar is creamy white. The venter is gray or white with gray or black suffusion most prominent laterally on the throat and belly. The ventral surfaces of the limbs are gray with an elongate bright orange spot proximally on the shank. Some individuals also have a small orange spot in the axilla. The iris is red medially and silvery gray peripherally.

Tadpoles.—The body is dark brown with two broad, transverse cream bars dorsally (snout and posterior to spiracle). The tail is pinkish orange or orange-tan with dark brown mottling.

Distribution.—The upper Amazon Basin in western Brasil, southern Colombia, Ecuador, and Perú, to elevations of 1300 m on the eastern slopes of the Andes.

Remarks.—In addition to the localities given in the specimens examined, Melin (1941) reported the species from Taracuá, Amazonas, Brasil, and Cochran and Goin (1970) reported it from Río Apoporis, Amazonas, and Ceilán, Caquetá, both in Colombia, and from Acre, Brasil.

Hyla subocularis Dunn

Hyla subocularis Dunn, 1934:2 [Holotype.—AMNH 41117 from Río Chucunaque at first creek above Río Tuquesa, Provincia Darién, Panamá; Charles M. Breder collector].

Diagnosis.—1) Snout-vent length 23.1 mm in males, 26.1 mm in females; 2) webbing on hand II 2^{-}-3 III 2¼-2 IV, on foot I 2^{-}-2 II 1¼-2¼ III 1^{+}-2 IV 2^{+}-1¼ V; 3) ulnar and tarsal tubercles absent; 4) canthal and rostral stripes (64%) or canthal stripes only (29%) usually present; 5) one (14%) or two (86%) suborbital bars; 6) dorsal markings consisting of X-shaped mark anteriorly (83%) with or without transverse bar posteriorly; 7) dorsolateral light stripe present, broad in females; 8) thigh having one large black-bordered yellow spot anteriorly, and usually (91%) one small yellow spot dorsally; 9) ventral surfaces uniform cream.

Hyla subocularis is like *H. bokermanni* and *luteocellata* in having dorsolateral light stripes and a large yellow spot on the anterior surface of the thigh. *Hyla subocularis* differs from *H. luteocellata* in usually having canthal stripes and two, instead of one, suborbital bars; *H. bokermanni* differs from *H. subocularis* in having a large median dark blotch, transverse bars, or no markings anteriorly on the dorsum, instead of an X-shaped mark.

Coloration.—Duellman (1970:236) described the color of *Hyla subocularis.* The dorsum is yellowish tan with brown markings. The suborbital bars and dorsolateral stripes are creamy white or creamy yellow. The spots on the thigh are yellow. The iris is rose-pink medially and pale silver peripherally.

Tadpoles.—The tadpoles were described by Duellman (1970: 237), who noted that the body and tail are black with a dorsolateral tan stripe on the body and irregular tan vertical marks on the tail.

Distribution.—Lowlands to 800 m in Darién, Panamá, and northwestern Colombia.

ECOLOGY

All the members of the *Hyla parviceps* group inhabit wet lowland tropical forest. Information on the habitat of *Hyla luteocellata* was provided by Rivero (1969), of *H. subocularis* by Duellman (1970), and of *H. microps* by Lutz (1973). We are concerned here with the three sympatric species in the upper Amazon Basin (*H. bokermanni, H. brevifrons,* and *H. parviceps*). The following observations resulted from intensive field studies from June 1971 through July 1972 at Santa Cecilia, Provincia Napo, Ecuador. Santa Cecilia is situated at 76°58′ W, 00°02′ N at an elevation of 340 m on the northern bank of the Río Aguarico, which flows into the Río Napo, a major tributary of the Río Amazonas.

At Santa Cecilia the three sympatric species utilize different breeding sites. Males of each species occasionally were found calling in swamps in open, disturbed areas; no females were found in such habitats. *Hyla parviceps* seems to be a habitat generalist, breeding in great abundance in both forest-edge and forest swamps. This species calls and breeds sympatrically and synchronously with either of the other species. On the other hand, *H. bokermanni* and *H. brevifrons* only rarely were observed together. *Hyla bokermanni* breeds mainly in forest swamps, but occasionally in forest-edge situations. *Hyla brevifrons* breeds mainly in forest-edge swamps and only occasionally in forest swamps.

The calling sites of the three species are similar. Males call from vegetation usually 1-2 m above the water. *Hyla bokermanni* and *H. brevifrons* call from stems, branches, or leaves, whereas *H. parviceps* almost always calls from leaves. *Hyla bokermanni* usually calls from emergent vegetation, whereas the other two species also call from vegetation peripheral to the water.

There is distinct segregation in egg deposition sites. *Hyla bokermanni* and *H. brevifrons* deposit eggs in clumps on leaves overhanging the water. Egg clutches of the former were found at heights from 50 cm-160 cm ($\bar{x} = 104.0$ cm; N = 14), and those of the latter at heights from 52 cm-100 cm ($\bar{x} = 75.4$ cm; N = 5) above water. On the other hand, *H. parviceps* deposits eggs in water.

Breeding Patterns at One Study Site

The breeding patterns and relative abundances of the species were studied during 10-day intervals at a forest swamp from July 1971 to July 1972. Most observations were made between 1900 and 2400 hrs. The swamp is approximately 15 m by 50 m and is choked with large-leafed *Heliconia* plants. Twenty-two species of frogs were found at the swamp, but no more than 12 were there at any given time.

All three species of the *Hyla parviceps* group were found at the site, although *Hyla brevifrons* was observed only rarely. Several males of that species were present in August, whereas only five were present in October; none was calling. One gravid female was there in March. There were many *H. bokermanni* calling whenever *H. brevifrons* were found.

Throughout the year *H. bokermanni* and *H. parviceps* were observed calling in great numbers (more than 50 and 20 respectively).

Gravid females and/or amplectant pairs of both species were found on the same nights in November, March, and June. On only one occasion was the population of *H. parviceps* estimated to be greater than 50 individuals; in July 1972, about 100-150 calling males were present. Approximately 20 gravid females were found; this is about twice the number found on any other evening. The same evening 30-50 calling *H. bokermanni* were found; no females were observed. The water depth at this time was about 1 m in the middle of the swamp. Generally, when the two species were found calling synchronously, *H. bokermanni* was more than twice as abundant as *H. parviceps* (30-100 versus 10-35). *Hyla bokermanni* calls from *Heliconia* leaves and stems 1-2 m above the water surface. *Hyla parviceps* calls from the same sites, but usually at least one-third of them call at about the same heights from vegetation at the edge of the swamp. *Hyla bokermanni* was rarely found at the edge of the swamp.

Hyla bokermanni had two peaks of breeding activity at the swamp: October-November and February-April. These periods coincided with the times of greatest water depth in the swamp. On several occasions density of calling males was estimated between 300-500. Once in late March, the number of gravid females was estimated at 30-50; usually no more than 10-15 were found in one evening. Occasionally, when the swamp was dry, numerous egg clutches of *H. bokermanni* were hanging from the vegetation, and males were calling.

In contrast, male *H. parviceps* were observed calling only when there was at least 30 cm of water in the swamp. Generally, the more water, the greater the number of calling individuals. Breeding activity of *H. parviceps* reached a peak in October-November (coinciding with that of *H. bokermanni*) and again in June-July.

The breeding population of *H. bokermanni* generally seems to be larger than that of *H. parviceps* at any given time at the swamp. Apparently, there is no species replacement, for both species breed at the same time. This is probably due to differences in mating calls and in egg deposition sites.

Reproduction

Two modes of reproduction are represented in the *Hyla parviceps* group. *Hyla parviceps* deposits its eggs directly in the water, whereas both *H. bokermanni* and *H. brevifrons* deposit their eggs on leaves over water; upon hatching the tadpoles drop into the water where they complete development (Table 7).

The eggs of *H. parviceps* are small (1.0-1.2 mm) and heavily pigmented black and creamy white. The ovarian complement (120-395) is more than twice that of either *H. bokermanni* or *H. brevi-*

TABLE 7.—Summary of Reproductive Data for three species in the *Hyla parviceps* group at Santa Cecilia.
(Means and sample sizes are in parentheses below observed ranges.)

	H. bokermanni	*H. brevifrons*	*H. parviceps*
Snout-vent length (mm) of gravid females	22.5-25.5 (23.9, $n=29$)	18.0-23.5 (20.9, $n=15$)	20.0-25.5 (23.3, $n=101$)
Number of mature ovarian eggs	65-135 (98.3, $n=29$)	48-114 (79.1, $n=15$)	120-395 (234.1, $n=101$)
Volume (ml) of gravid female	0.9-1.1 (1.0, $n=5$)	----------	0.9-1.2 (1.1, $n=6$)
Volume (ml) of mature ovarian eggs	0.1 ($n=5$)	----------	0.1-0.2 (0.1, $n=6$)
% Egg volume of total volume of ♀	9.1-11.1 (10.5, $n=5$)	----------	8.3-22.2 (11.2, $n=6$)
Clutch size	60-196 (116.8, $n=53$)	48-91 (70.0, $n=6$)	165-385 (302.8, $n=15$)
Ovum size	1.5-1.8 (1.6, $n=53$)	1.2-1.6 (1.3, $n=6$)	1.0-1.2 (1.1, $n=15$)
Number of days until hatching	4.0-5.3 (4.4, $n=20$)	6.3 ($n=1$)	1.3-2.3 (1.9, $n=13$)
Total length (mm) of hatchling	4.0-4.5 (4.2, $n=20$)	6.0 ($n=1$)	4.0-4.5 (4.1, $n=13$)

frons. A correlation analysis was run on 112 females with mature ovarian eggs in order to determine the relationship between snout-vent length and fecundity (both variables were normally distributed). The correlation coefficient was significant at the .01 level. Therefore, on the basis of this sample, it is concluded that larger female *H. parviceps* produce more eggs at a given breeding time. *Hyla parviceps* has a slightly greater percent volume of eggs relative to its total body volume than does *H. bokermanni.* The eggs develop rapidly under laboratory conditions (1.3-2.3 days). The range of variation of total length of the hatchlings (4.0-4.5 mm) is the same as that of *H. bokermanni.* Gravid females were found in every month of the year, indicating that breeding is continuous. Of 146 females found, 125 (85.6%) were gravid.

Hyla bokermanni deposits the largest eggs (1.5-1.8 mm) of the three species. The eggs are lightly pigmented tan and cream. The ovarian complement ranges from 65-135. A correlation analysis run on 29 females of this species (both variables normally distributed) indicated no significant correlation between snout-vent length of the female and the number of mature ovarian eggs. Thus, it seems as though there is no selective advantage for female *H. bokermanni* to increase in size in order to increase fecundity. It is suggested that perhaps larger females produce larger eggs. Under laboratory conditions the eggs took from 4.0-5.3 days to hatch. As previously indicated, although the eggs are larger to begin with and require more than twice as long to hatch, the size range of the hatchlings is the same as that of *H. parviceps.* Gravid females were found October-November 1971 and throughout January-June 1972. Of 92 females found, 85 (92.4%) were gravid.

Hyla brevifrons, the smallest of the three species, deposits the intermediate-sized eggs (1.2-1.6 mm). The eggs are lightly pigmented tan and cream, similar to those of *H. bokermanni.* The species has the lowest ovarian complement (48-114). Only one clutch of eggs hatched in the laboratory; the eggs hatched in 6.3 days, and the hatchlings were 6.0 mm in length. Gravid females were found in July, October, and December 1971, and January, March, and June 1972. Of 13 females found, 10 (76.9%) were gravid.

An ovarian size factor[3] was calculated from means of egg clutches deposited in the laboratory. *Hyla parviceps* has the largest value (13.38), *H. brevifrons* the smallest (4.42), and *H. bokermanni* an intermediate value (7.05). The reproductive strategy of *H. parviceps* is to produce many small eggs, deposited in open water. The species is a habitat generalist, breeding both in forest and forest-edge situations. The other two species are more restricted; *H. bokermanni* breeds mainly in the forest, and *H. brevifrons* in forest-edge swamps and ponds. The last two species lay relatively few, large eggs, and have more specialized egg deposition sites on vegetation above the water. The nearly identical utilization of egg deposition sites perhaps explains why these species generally do not breed at the same swamps. Neither *H. bokermanni* nor *H. brevifrons* was found to be gravid throughout the year. Perhaps these factors are indicative of more critical requirements for breeding than those of *H. parviceps.* Observations on the relationship between egg deposition sites and sunlight are inconclusive. It is suggested, however, that differences in pigmentation of the eggs may be explained by their exposure to different amounts of solar radiation. The darkest eggs are those of *H. parviceps* (deposited in water); perhaps these are subject to more solar radiation than those of *H. bokermanni* and *H. brevifrons* (deposited on leaves above water) which are protected by surrounding vegetation.

Food

Stomach contents of adults of both sexes of the three species at Santa Cecilia were analyzed. Ten orders of arthropods were found in 66 stomachs. Treating males and females separately, niche over-

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[3] The ovarian size factor is calculated by the formula CS(OD)/SVL, where CS = the mean clutch size, OD = the mean ovum diameter, and SVL = the mean snout-vent length of the females depositing the clutches. This provides an index for comparing fecundity and egg size relative to adult body size.

lap scores were calculated by the method suggested by Colwell and Futuyma (1971). Niche overlap scores varied from 0.13 to 0.76 (1.0 is complete overlap). The lowest scores are those of female *H. brevifrons* in which the sample consisted of only two specimens. Analysis of variance within groups (males and females) and between groups (males versus females) revealed no significant difference. The average niche overlap scores for food is 0.451, indicating a moderate amount of overlap between sexes in a given species and between species. The niche overlap values must be considered maximal to actual overlap because 1) small sample sizes (2-23) minimize overlap, and 2) only gross identifications (to order) were made on the food items. Because of the fragmentary nature, and/or degree of decomposition, of the food, insufficient data were obtained on prey size. However, individuals of all three species, including both sexes, contained caterpillars that were nearly as long as the frogs that had eaten them.

PHYLOGENETIC RELATIONSHIPS

In deducing phylogenetic relationships, it is customary to establish criteria for primitiveness. We have relied on the criteria used by Wagner (1961) (see Kluge and Farris, 1969, and Trueb, 1973, for discussions). Utilizing these criteria, primitive character states of a particular group are: 1) likely to be present in many closely related groups; 2) more likely to be widespread within a group than is any one derived state; and 3) likely to be associated with other primitive characters.

As a basis for phylogenetic analysis, we are assuming that the small, primarily Amazonian *Hyla* having a diploid number of 30 chromosomes and tadpoles with reduced mouthparts and xiphicercal tails are more closely related to one another than any is to any other group. Thus, we recognize the *leucophyllata, microcephala, minuta,* and *parviceps* groups of *Hyla.* Eleven structural and color pattern characters that are variable within the *Hyla parviceps* group and present in the other groups were analyzed. Of these 11 characters, the primitive states of eight are present in all three of the other groups, two in two groups, and one in one group.

In the following list of characters, the primitive state is number 0; states 1 and 2 are derived in succession, except F and G, in which the advanced states (1 and 2) are probably independently derived.

A. Sexual dimorphism in size:
    0. ♂ > 90% ♀
    1. ♂ = 80-90% ♀
    2. ♂ < 80% ♀
B. Ulnar and tarsal tubercles:
    0. Absent
    1. Present

- C. Suborbital bars:
    - 0. Absent
    - 1. One
    - 2. Two
- D. Canthal stripes:
    - 0. Absent
    - 1. Present
- E. Rostral stripes:
    - 0. Absent
    - 1. Present
- F. Dorsolateral stripes:
    - 0. Absent in both sexes
    - 1. Absent in males; present in females
    - 2. Present in both sexes
- G. Anterior thigh:
    - 0. Unicolor
    - 1. Small yellow spots
    - 2. Large yellow spot
- H. Dorsal thigh:
    - 0. Unicolor
    - 1. Small yellow spots
- I. Posterior thigh:
    - 0. Unicolor
    - 1. Large orange spot
- J. Venter:
    - 0. Plain
    - 1. Patterned
- K. Denticles (larvae):
    - 0. One lower row
    - 1. Absent

The distribution of character states within the *Hyla parviceps* group reveals variation from 6 to 11 derived characters (Table 8). The greatest number of primitive states occurs in *H. microps,* followed by *H. parviceps* and *brevifrons*; *H. bokermanni, luteocellata,* and *subocularis* have the fewest primitive states.

A phylogenetic arrangement (Fig. 7) was constructed by a method proposed by Camin and Sokal (1965). The branching sequence defines one group having few derived characters (*H. microps* and *parviceps*) and another with many derived characters (*H. luteocellata, bokermanni,* and *subocularis*). *Hyla brevifrons* is intermediate between these two groups.

Although reproductive data are incomplete, the existing information supports the proposed phylogeny. *Hyla microps* and *parviceps* deposit eggs in water, whereas the other species (unknown for *H. luteocellata*) deposit eggs on vegetation above water. Quantitative data on reproduction of three species in Ecuador reveal that in most features *H. brevifrons* is intermediate between *H. bokermanni* and *parviceps.* If the reproductive mode of *H. luteocellata* is the same as that for *H. bokermanni* and *subocularis,* a phylogenetic construct based on reproductive characters would approximate the arrangement based on morphological features.

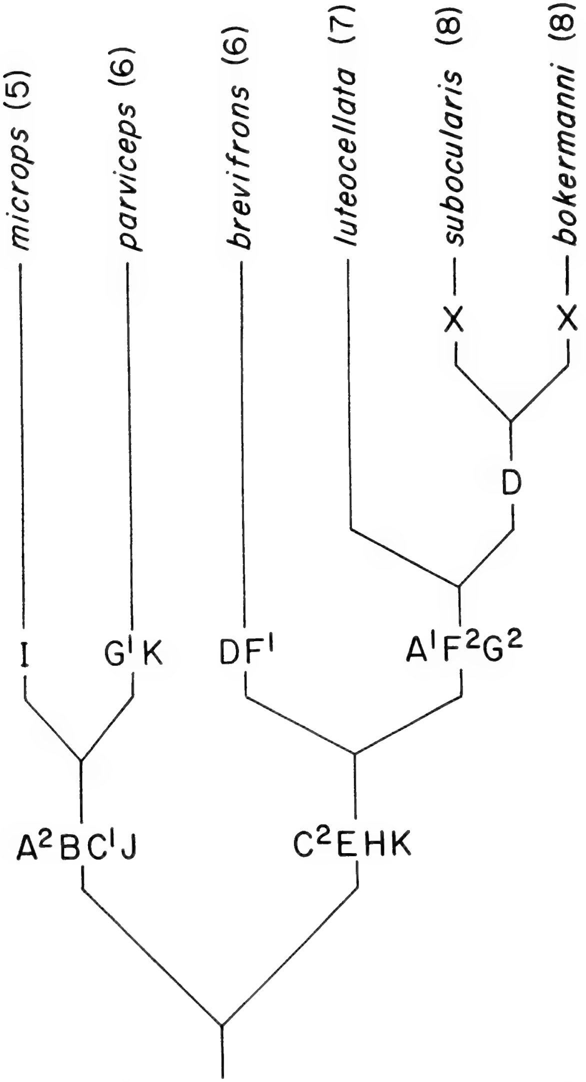

FIG. 7. Most parsimonious phylogenetic arrangement of species in *Hyla parviceps* group, based on 26 states of 11 characters. Letters indicate shifts from primitive to derived character states; superscripts indicate direction of change or degree of change in those characters represented by more than two states; X = change in dorsal pattern not accompanied by shifts in any one of the 11 characters; numbers in parentheses are numbers of evolutionary steps in each line. See Table 8 and text for character states and explanation.

TABLE 8.—Character states of 11 characters in species in the *Hyla parviceps* group.
(0 = primitive state; 1 and 2 = derived states; see text for list of characters and explanation.)

Character	*H. bokermanni*	*H. brevifrons*	*H. luteocellata*	*H. microps*	*H. parviceps*	*H. subocularis*
A	1	0	1	2	2	1
B	0	0	0	1	0.5[a]	0
C	2	2	2	1	1	0
D	1	1	0	0	0	1
E	1	1	1	0	0	1
F	2	1	2	0	0	2
G	2	0	2	0	1	2
H	1	1	1	0	0	1
I	0	0	0	1	0	0
J	0	0	0	1	1	0
K	1	1	1	0	1	1
Total	11	7	10	6	6.5	11

[a] Females only.

The presence of a row of denticles in the tadpoles of *Hyla microps* is the only larval character that can be determined as primitive in the group. Otherwise, the known tadpoles differ from one another principally in coloration. We have no bases for deducing evolutionary change in the coloration. We have incomplete data on mating calls, but the calls of *H. parviceps* and *brevifrons* consist of series of uniform notes, whereas *H. bokermanni* produces primary and secondary notes. Presumably the complex call of *H. bokermanni* is derived from the simple call of the others, a conclusion compatible with the phylogenies deduced from morphological and reproductive data.

Zoogeography

Recent works on distributional patterns in the tropical lowlands of South America emphasize Quarternary climatic fluctuations and the existence of forest refugia during times when climatic conditions were drier than present (Müller, 1968; Haffer, 1969; Vanzolini and Williams, 1970). Müller and Schmithusen (1970) and Vuilleumier (1971) summarized Pleistocene climatic changes and interglacial sea transgressions in South America. Haffer (1969) provided evidence from avian distributions and differentiation for six forest refugia in Amazonian South America. Vanzolini and Williams (1970) proposed four core areas for the differentiation of populations of *Anolis chrysolepis* and hypothesized an evolutionary model of three expansions and two contractions of forest environments resulting in isolation, differentiation, and introgression of *Anolis chrysolepis*.

Accepting the preceding phylogenetic arrangement as a reasonable approximation of the actual evolutionary sequences of morphological characters in the *Hyla parviceps* group, we can superimpose the cladistics of the frogs on the biogeographical patterns in the lowland tropics. Our paleogeographic evolutionary model of the *Hyla parviceps* group is predicated on cyclic alternation of wetter and drier climates in the Pleistocene and Holocene, resulting in expansion and contraction of lowland tropical forests, and the existence of forest refugia during the drier periods (see Moreau, 1966, for paleogeographic evidence from Africa; Vanzolini and Williams, 1970, for a survey of the literature documenting changes in South America; and Van der Hammen and Gonzalez, 1960, for dating of palynological data). Duellman (1972) and Heyer (1973) suggested probable evolutionary histories of groups of South American hylid and leptodactylid frogs with respect to vicissitudes of Quarternary climates.

The evolutionary model is outlined, as follows:

1. The prototype of the *Hyla parviceps* group was widespread in Amazonia during a wetter period. This prototype had the primitive states of the characters listed in the preceding section, aquatic eggs, and a simple mating call.

2. Climatic desiccation resulted in contraction of forests and isolation of two populations: 1) the *H. microps-parviceps* stock in an Amazonian refugium; 2) the *H. brevifrons-bokermanni-luteocellata-subocularis* stock in an upper Amazonian refugium (Napo or Peruvian refugia of Haffer). The former stock developed more sexual dimorphism in size, ulnar and tarsal tubercles in females, one suborbital bar, and gray flecks on the venter. The second stock developed two suborbital bars, rostral stripes, yellow spots on the dorsal surfaces of the thighs; retained moderate sexual dimorphism in size; and lost the larval denticles.

3. During the subsequent pluvial period both stocks spread through the Amazon Basin; the *H. microps-parviceps* group expanded into eastern and southeastern Brasil, and the other stock invaded the coastal lowlands of northern South America and eastern Panamá.

4. Climatic desiccation resulted in the isolation of two populations of the *H. parviceps-microps* group (*H. microps* in the Serra do Mar refugium of Müller in southeastern Brasil and *H. parviceps* in an Amazonian refugium). The other stock was separated into four isolates. The prototypes of *H. bokermanni* and *H. brevifrons* were isolated in separate refugia (probably Haffer's Napo and

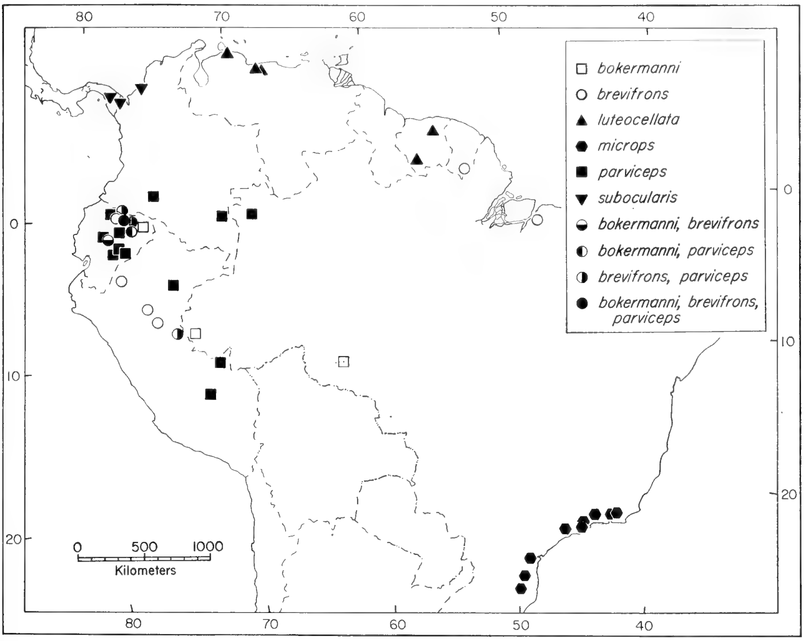

FIG. 8. Distribution of species in the *Hyla parviceps* group.

Peruvian refugia); *H. luteocellata* was isolated in the Cordillera de la Costa in northern Venezuela (a core area proposed by Vanzolini and Williams, 1970), and *H. subocularis* was restricted to one or more of the small refugia in northwestern Colombia (Chocó, Nechi, or Catatumbo refugia of Haffer, 1969).

5. The development of more equable climates resulted in the expansion of the Amazonian forests and of the ranges of the six populations of frogs. However, due to the dry *caatinga* and *cerrado* of eastern Brasil, *H. microps* remained restricted to southeastern Brasil. *Hyla luteocellata* expanded its range eastward into the Guianas, and *H. subocularis* moved into Panamá. In the Amazon Basin, the ranges of three species (*H. bokermanni, brevifrons,* and *parviceps*) expanded from their respective refugia and became sympatric in the upper part of the basin (Fig. 8).

EVOLUTION IN THE SYMPATRIC SPECIES

If we accept the proposed phylogenetic arrangement and the suggested paleogeographic model, we are forced to hypothesize that the three species now occurring in sympatry in the upper Amazon Basin evolved through geographic isolation at different times (*H. parviceps* versus *H. brevifrons* and *bokermanni*) and in different places (*H. brevifrons* and *bokermanni*). Presumably, genetic differences that evolved when the populations were isolated have been reinforced through selection in sympatric populations. Due to lack of data on any one of the species where it occurs in the absence of the other two, we are unable to determine if there is any character displacement.

According to Van der Hammen and Gonzalez (1960), the climate in northern South America has been becoming progressively wetter for the past 4000 years, thus, it is possible that the three species in the upper Amazon Basin have been sympatric for less than 4000 years, before which time they were isolated in forest refugia (Haffer, 1969).

We are concerned here with those mechanisms which are operant in maintaining the specificity of the sympatric populations. Following Müller's (1942) classification of isolating mechanisms, as modified by Fouquette (1960), we recognize three major categories of isolating mechanisms—anti-mating, courtship, and post-mating. The last category includes gametic incompatibility, hybrid inviability, and hybrid sterility; we have no information on these factors and no evidence of hybridization, so they are not considered here.

Of the five kinds of anti-mating mechanisms, one (geographic isolation) has already been accounted for by the hypothesized differentiation through geographic isolation. Data on the others can be summarized, as follows:

Habitat isolation.—Relative to breeding activities, *H. parviceps* is a habitat generalist, usually present at sites where the other species breed. *Hyla bokermanni* and *brevifrons* usually breed at different sites.

Seasonal isolation.—Synchronous breeding activity is common, but at least *H. bokermanni* and *H. parviceps* have some different periods of intense breeding activity.

Temporal isolation.—All three species are nocturnal breeders.

Climatic isolation.—All three species have a positive response to periods of heavy rainfall.

Fouquette (1960) recognized only two categories of courtship isolating mechanisms, whereas we recognize three; oviposition sites are considered:

Auditory isolation.—The mating calls of three species are distinctly different in note repetition rate and duration of notes; furthermore, the call of *H. brevifrons* is distinctive in pulse rate, that of *H. parviceps* in dominant frequency, and that of *H. bokermanni* in the presence of secondary notes (Table 6).

Mechanical isolation.—Because the females of the three species have nearly identical snout-vent lengths, difference in size might be an effective mechanical isolating mechanism only in *H. parvi-*

ceps, the males of which are much smaller than males of the other species.

Ovipositional isolation.—Hyla parviceps deposits its eggs in water and the other species place their eggs on vegetation over water. The apparent behavioral and probable physiological differences of females and eggs, respectively, are potentially important factors in isolation.

The three species broadly overlap in most categories of potential isolating mechanisms, but there are distinct differences in two categories, ethological and ovipositional. Fouquette (1960) found that the mating call was the primary isolating mechanism operant in three sympatric species of *Hyla* in Panamá. Duellman (1967) reached the same conclusion in a study of a breeding community of ten species of hylids in Costa Rica. Martof and Thompson (1958) and Littlejohn and Michaud (1959) provided experimental evidence demonstrating that females respond positively to the calls of the males and that females can discriminate between calls of males of their own and other species. Littlejohn (1964, 1965) presented evidence on evolution of differences in mating calls through geographic isolation and reinforcement of these differences in sympatric populations. We conclude that at least some of the differences in mating calls in the three species of the *Hyla parviceps* group evolved at times when the populations were geographically isolated from one another; furthermore, these differences may have been reinforced through selection upon subsequent geographical sympatry.

The differences in oviposition sites involve a modification in reproductive strategy from the presumed primitive strategy of placing eggs in water (*H. parviceps*) to a derived strategy of placing eggs on vegetation over water (*H. bokermanni* and *brevifrons*). Salthe and Duellman (1973) showed that within a given anuran reproductive mode there exist positive correlations between ovum size, clutch size and female snout-vent length, and negative correlations between clutch size and ovum size and between ovum size and rate of development. Among the three species under consideration, *Hyla parviceps* with aquatic eggs has the largest clutch size, smallest ova, and shortest duration of development (Table 7). Females of the other species are no larger than *H. parviceps*; thus, as concluded by Salthe and Duellman (1973), the achievement of a larger ovum in *H. bokermanni* and *brevifrons,* without an increase in body size of the females, was by selection for a change in the site of intraoval development, in this case vegetation over water. Larger eggs produce larger hatchlings better adapted to make the transition from leaf to water. Because the reproductive modes are different in the two lineages in the group, it is most reasonable to assume that this differentiation took place only once and that by the time the three species became sympatric in the upper Amazon Basin the differences in reproductive strategy were already in existence. However, the differences are important aspects of resource partitioning in synchronously breeding frogs within one community.

Salthe and Duellman (1973) noted that in small anurans: ". . . it seems to be more advantageous to maintain a certain minimal number of eggs in the clutch than it is to maintain the size of the hatchling. Presumably, clutch sizes are already at, or near, a lower limit allowable for the production of an adequate amount of genetic variability per unit time. Thus, in general, selection in small species seems to function by maintaining minimal clutch sizes and maximizing the sizes for relatively tiny hatchlings." Our reproductive data indicate that despite differences in mode of reproduction and ovum size, the hatchlings are about the same size in *H. bokermanni* and *parviceps,* but larger in *H. brevifrons,* which has the smallest clutches (Table 7).

The problem of production of an adequate amount of genetic variability, as related to fecundity, per unit time perhaps is an important factor in the great amount of sexual dimorphism in size in the *Hyla parviceps* group. At Santa Cecilia, the three species in the group occur in swamps inhabited by many other species, of which 17 *Hyla* are known to breed in the same ponds or swamps as do members of the *Hyla parviceps* group. All of these are larger than the species in the *Hyla parviceps* group. Selection might favor reduction in size in response to competition for food, calling sites, and oviposition sites. However, reduction in size of the females is more restricted than in males due to the limitations imposed by egg-carrying capacities. Schoener (1967, 1969, 1970) documented evidence for sexual selection in size of West Indian *Anolis,* noting that extremes of sexual dimorphism in size are reached on islands inhabited by only one species of *Anolis*; on these islands the sexes exist ecologically as two species using different resource states, such as perches and food. However, in the *Hyla parviceps* group, the presence of many other species utilizing a variety of resource states negates the hypothesis of intraspecific selection in size solely for resource partitioning and suggests that the reproductive necessities of the females balance selection for small size, which is evident in males.

SUMMARY

Among the small Neotropical *Hyla* having a diploid number of 30 chromosomes and reduced mouth parts in the tadpoles, one group of six species is characterized by great sexual dimorphism in size, more cranial ossification, and aspects of coloration (patterned thighs, suborbital bars, and iris color). Six species are included in

the group: *H. bokermanni* Goin, *H. brevifrons* new species, *H. luteocellata* Roux, *H. microps* Peters, *H. parviceps* Boulenger, and *H. subocularis* Dunn. *Hyla rondoniae* Bokermann, 1963, is placed in the synonymy of *Hyla bokermanni* Goin, 1960. The group is widespread in the Amazon Basin, southeastern Brasil, northern lowlands of South America and eastern Panamá.

Although interspecific differences exist in size, proportions, amount of webbing, and tubercles, the principal taxonomic characters are in the coloration. These include the number of pale suborbital bars, presence or absence of canthal and rostral stripes, presence and width of dorsolateral stripes, and pattern on the dorsum, venter, and especially the thighs. All of the tadpoles have one row of labial papillae. Tadpoles of *H. microps* have one row of denticles; denticles are absent in the others. The known tadpoles are brightly colored and have different patterns of transverse bars or longitudinal stripes. The mating calls consist of series of short, high-pitched notes; *H. bokermanni* produces primary notes followed by shorter secondary notes.

It is suggested that the species arose through isolation in forest refugia in the tropical lowlands during dry periods in the Pleistocene. The proposed phylogeny indicates that the two most primitive species now occupy different regions—*H. microps* in southeastern Brasil and *H. parviceps* in the upper Amazon Basin. The three most advanced species also have allopatric distributions—*H. bokermanni* in the upper Amazon Basin, *H. luteocellata* in coastal northern South America, and *H. subocularis* in eastern Panamá and northwestern Colombia.

Three species (*H. bokermanni, brevifrons,* and *parviceps*) occur at Santa Cecilia in Amazonian Ecuador. Intensive field studies there continuously for 13 months revealed slight differences in habitat and seasonal activity. One species (*H. parviceps*) lays eggs in the water, whereas the other two place eggs on vegetation over the water. Clutch size is larger and ovum size is smaller in *H. parviceps* than the others.

It is suggested that differences in mating calls and oviposition sites are the primary isolating mechanisms operating in the sympatric species. Furthermore, it is suggested that natural selection for small size in comparison with many sympatric congeners is balanced in females by the necessity for maintaining an adequate number of eggs to insure genetic variability in the population. In the absence of such pressure in the males, they have become much smaller than the females.

RESUMEN

Entre las pequeñas ranas neotropicales del género *Hyla* con un número diploide de 30 cromosomas y renacuajos con bocas de estructuras pequeñas, un grupo de seis especies se caracteriza por el gran dimorfismo sexual de su tamaño, mayor osificación craneal, y algunos aspectos de su coloración (diseños en los muslos, barras suborbitales, y color del iris). Las seis especies incluidas en el grupo son: *H. bokermanni* Goin, *H. brevifrons* nueva especie, *H. luteocellata* Roux, *H. microps* Peters, *H. parviceps* Boulenger, y *H. subocularis* Dunn. *Hyla rondoniae* Bokermann, 1963, se pone en el sinonomia de *Hyla bokermanni* Goin, 1960. Este grupo se encuentra difundido en la Cuenca Amazónica, el sureste brasileño, las tierras bajas del norte de Suramérica, y el este panameño.

Aun cuando existen diferencias interespecíficas de tamaño, proporciones, extensión de las membranas interdigitales, y tubérculos, las principales caracteristicas taxonómicas giran alrededor de la coloración. Esto incluye el número de barras suborbitales claras, la presencia o auséncia de las rayas cantales y rostrales, la presencia y ancho de las rayas dorsolaterales, y el diseño dorsal, ventral, y especialmente de los muslos. Todos los renacuajos tienen una fila de papilas labiales. Los renacuajos de *H. microps* tienen una fila de denticulos que no existe en los otros. Los renacuajos que se conocen son de coloración luminosa y tienen distintos diseños de barras transversales y rayas longitudinales. La llamada de reclamo consiste de series de notas cortas y altas; *Hyla bokermanni* produce notas primarias sequidas de notas secundarias mas cortas.

Se sugiere que estas especies surgieron como resultado de su aislamiento en refugios en la selva de la tierra tropical baja durante los períodos secos del Pleistoceno. La filogenia propuesta sugiere que las dos especies mas prímitivas ocupan ahora regiones distintas—*H. microps* ocupa el sureste brasileño y *H. parviceps* la parte superior de la Cuenca Amazónica. Las tres especies mas evolucionadas tambien tienen distribuciones alopátricas—*H. bokermanni* en la parte superior de la Cuenca Amazónica, *H. luteocellata* en la costa norte de Suramérica, y *H. subocularis* en el este panameño y noroeste colombiano.

Tres especies (*H. bokermanni, brevifrons,* y *parviceps*) se encuentran en Santa Cecilia en la Amazonia Ecuatoriana. Estudios continuos e intensivos de campo durante un período de 13 meses revelan pequeñas diferencias en su "habitat" y en la actividad estacional. Una de las especies (*H. parviceps*) pone sus huevos en el agua, mientras que las otras dos los ponen en la vegetación sobre el agua. En *H. parviceps* el número de huevos es mayor y el tamaño de los huevos es menor que en las otras especies.

Se sugiere que diferencias en las llamadas de reclamo y los lugares de oviposición son los mecanismos principales de aislamiento en las especies simpátridas. Se sugiere ademas que la selección natural a favor de un tamaño pequeño en estas especies en compariación con muchos otros congéneres simpátridos está contrarestada en las hembras por la necessidad de mantener un número adecuado de huevos con lo que asegura la variabilidad genética de la población. En la ausência de esta presión, los machos se han mantenido mas pequeños.

SPECIMENS EXAMINED

Hyla bokermanni

BRASIL: *Acre:* Cruzeiro do Sul, WCAB 12148. *Rondônia:* Rondônia, WCAB 7845.

ECUADOR: *Napo:* Limón Cocha, UIMNH 64799-800, 90069; Santa Cecilia, KU 104432-3 (skeletons), 105118-9, 105121-2, 105125-6, 105131, 105189, 109355-7, 109452, 109468, 123051-8, 123060, 123062-71, 123089-91, 124193 (tadpoles), 126362, 126541-5, 126547, 126552-5, 143131, 143188, 146288-95, 146414, 146419, 146800-1 (tadpoles), 150026-51, 152290-1 (tadpoles), 152419-28, 152535, 152750-3 (skeletons), UMMZ 129325 (4). *Pastaza:* 3 km S Puyo, KU 127087.

Hyla brevifrons

BRASIL: *Pará:* IPEAN, 5 km E Belém, KU 127846.

COLOMBIA: *Putumayo:* Santa Rosa de Sucumbios, AMNH 88068-80.

ECUADOR: *Napo:* Lago Agrio, 126556-8; Puerto Libre, KU 123092-4; Santa Cecilia, KU 105063, 105107-11, 105120, 105127-30, 105132-4, 105190, 107003-4, 109449-51, 109453-67, 111786-802, 112341 (eggs), 123049-50, 123059, 123072-88, 125899-900 (tadpoles), 126342-61, 126363-71, 126546, 126548-51, 136298, 143189, 146281-7, 146413, 146415-8, 150052-74, 152429-32, 152536-7 (tadpoles), 152754-8 (skeletons), UMMZ 129324 (2). *Pastaza:* Puyo, CAS 85142.

FRENCH GUIANA: *Inini:* Crique Eleupocigne, Upper River Oyapak, LG 1119, 1308, 1311-12.

PERÚ: *Loreto:* Pampa Hermosa, Río Cushabatay, AMNH 42358; Río Utoquinia-Río Tapiche, AMNH 43576; Tacsha Huachiyacu, Río Morona, AMNH 43045; Yurimaguas, Río Huallaga, BMNH 84.2.18.53.

Hyla luteocellata

VENEZUELA: *Aragua:* Cumboto, UMMZ 113890 (2); Monte Oscuro, BMNH 1968.73-4, KU 125861-5, UMMZ 130085-6.

Hyla microps

BRASIL: *Paraná:* Curitiba, UMMZ 104118 (2), 104129 (6), 104130, 104160. *Rio de Janeiro:* Barro Branco, SMF 41217; Novo Friburgo, ZMB 7472; Teresópolis, BMNH 1947.2.14.10. *São Paulo:* Campo Grande, Santo Andre, KU 74266-8, 74269 (skeleton), 92073-7, 92078 (skeleton); Campos de Jordão, KU 112398 (tadpoles); 10 km W Casa Grande, KU 129838. *Santa Catarina:* UMMZ 58515; Humboldt, AMNH 15573-82.

Hyla parviceps

COLOMBIA: *Putumayo:* Santa Rosa de Sucumbios, AMNH 88081-2.

ECUADOR: *Napo:* Bermejo No. 4 (well site), Sierra Umbaqui, KU 122963; Cuyabeno, UIMNH 54134-6, 54172, 59625-8, 90108-9; Dureno, KU 105113-4; Lago Agrio, KU 126480; Limón Cocha, KU 99223-8, 99229 (skeleton), UIMNH 64805, 90076; Santa Cecilia, KU 104428-31 (skeletons), 105046-62, 105064-106, 105112, 107048-9, 109433-46; 11764-84, 112339-40 (tadpoles), 122925-62, 123061, 126462-79, 143167-73, 146307-11, 146790-1 (tadpoles), 150309-56, 152303-4 (tadpoles), 152547 (tadpoles), 152759-63 (skeletons), UMMZ 129279 (9); Tena, UIMNH 59628, 90059-64; UMMZ 123903. *Pastaza:* Abitagua, UMMZ 90416-7; Chontoa, KU 120910-13, 121407; Mera, KU 120909; 3 km S Puyo, KU 127086, 127090; 25 km NNE Puyo, KU 146792 (tadpoles); Río Conambo, mouth of Río Shione, USNM-GOV 7143; Río Oglan, upper Río Curaray, USNM-GOV 9526; Sarayacu, BMNH 1947.2.13.51. *Tungurahua:* Llanganate area, FMNH 23522-3; Mirador, BMNH 99.10.30.49; Río Negro, KU 120913-14, 121408.

PERÚ: *Cuzco:* Pilcopata, KU 139228. *Loreto:* Balta, Río Curanja, LSU 25719-57; Iquitos, AMNH 42086; headwaters Río Utoquinia, AMNH 43314.

Hyla subocularis

COLOMBIA: *Córdoba:* Río Manso, CM 50447-50.

PANAMÁ: *Darién:* Laguna, KU 77348-59, 77620; Río Chucunaque, AMNH 51777; Río Chucunaque at first creek above Río Tuquesa, AMNH 41117; Rio Ucurganti, 7 km above mouth, KU 116785, 116784 (tadpoles); Tacarcuna, KU 77360-403, 77621, 77688-90 (skeletons), UMMZ 124780.

LITERATURE CITED

Bokermann, W. C. A.

1963a. Duas novas espécies de Hyla de Rondônia, Brasil (Amphibia, Salientia). Rev. Brasil. Biol., 23:247-250.

1963b. Girinos de anfíbios Brasileiros—1. (Amphibia,—Salientia). An. Acad. Brasil. Cien., 35:465-474.

1964. Notes on tree frogs of the *Hyla marmorata* group with description of a new species (Amphibia, Hylidae) Senckenberg Biol., 45:243-254.

1966. Lista anotada das localidades tipo de anfíbios Brasileiros. Impres. Serv. Documentacão, São Paulo, 183 pp.

Bogart, J. P.

1973. Evolution of anuran karyotypes. *in* Vial, J. L. (ed.) Evolutionary biology of the anurans: contemporary research on major problems. Univ. Missouri Press, Columbia: 337-349.

Boulenger, G. A.

1882. Catalogue of the Batrachia Salientia s. Ecaudata in the collection of the British Museum, ed. 2, London, xvi+503 pp.

1920. Descriptions of two new frogs from Brasil. Ann. Mag. Nat. Hist., (9)5:122-124.

Camin, J. H. and R. R. Sokal

1965. A method for deducing branching sequences in phylogeny. Evolution, 19:311-326.

Cochran, D. M.

1955. Frogs of southeastern Brazil. Bull. U.S. Natl. Mus., 206:xvi+423 pp.

Cochran, D. M. and C. J. Goin

1970. Frogs of Colombia. *Ibid.*, 288:xii+655 pp.

Colwell, R. K. and D. J. Futuyma

1971. On the measurement of niche breadth and overlap. Ecology, 52: 567-586.

Duellman, W. E.

1967. Courtship isolating mechanisms in Costa Rican hylid frogs. Herpetologica, 23:169-183.

1969. A new species of frog in the *Hyla parviceps* group from Ecuador. *Ibid.*, 25:241-247.

1970. The hylid frogs of Middle America. Monog. Mus. Nat. Hist. Univ. Kansas, 1:xi+753 pp.

1972. South American frogs of the *Hyla rostrata* group (Amphibia, Anura, Hylidae). Zool. Mededel., 47:177-192.

DUNN, E. R.
1934. Two new frogs from Darien. Amer. Mus. Novitates, 747:1-2.
FOUQUETTE, M. J., JR.
1960. Isolating mechanisms in three sympatric treefrogs in the canal zone. Evolution, 14:484-497.
GOIN, C. J.
1960. Description of a new frog of the genus *Hyla* from northwestern Brazil. Ann. Mag. Nat. Hist., 13(2):721-724.
GOSNER, K. L.
1960. A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica, 16:183-190.
HAFFER, J.
1969. Speciation in Amazonian forest birds. Science, 165:131-137.
HEYER, W. R.
1973. Systematics of the *marmoratus* group of the frog genus *Leptodactylus* (Amphibia, Leptodactylidae). Contri. Sci. Los Angeles Co. Mus., 251:1-50.
KLUGE, A. G. and J. S. FARRIS
1969. Quantitative phyletics and the evolution of anurans. Syst. Zool., 18:1-32.
LITTLEJOHN, M. J.
1964. Geographic isolation and mating call differentiation in *Crinia signifera*. Evolution, 18:262-266.
1965. Premating isolation in the *Hyla ewingi* complex (Anura: Hylidae). *Ibid.,* 19:234-243.
LITTLEJOHN, M. J. and T. C. MICHAUD
1959. Mating call discrimination by females of Strecker's chorus frog (*Pseudacris streckeri*). Texas Jour. Sci., 11:86-92.
LUTZ, B.
1973. Brazilian species of *Hyla.* Univ. Texas Press, Austin, xix+260 pp.
MARTOF, B. S. and E. F. THOMPSON
1958. Reproductive behavior of the chorus frog *Pseudacris nigrita.* Behaviour, 13:243-258.
MELIN, D.
1941. Contribution to the knowledge of Amphibia of South America. Göteborgs Kungl. Vetensk.-och Vitterh.-Sam. Handl., Ser. B, 1(4): 1-71.
MERTENS, R.
1950. Froschlurche aus Rio de Janeiro und seiner Umgebung. Wochenschr. Aquar. Terrarien, 44:173-188.
MÜLLER, H. J.
1942. Isolating mechanisms, evolution, and temperature. Biol. Symposia, 6:71-125.
MÜLLER, P.
1968. Die herpetofauna der Insel von São Sebastião (Brasilien). Saarbrucker Zeit., 68 pp.
MÜLLER, P. and J. SCHMITHÜSEN
1970. Probleme der genese südamerikanischer Biota. *in* Deutsche geographische Forschung in der Welt von Heute. Kiel:109-122.
MOREAU, R. E.
1966. The bird faunas of Africa and its islands. London, 424 pp.
PETERS, W.
1872. Über eine Sammlung von Batrachiern aus Neu-Freiburg in Brazilien. Monatsb. Akad. Wiss. Berlin, 1872:680-684.
RIVERO, J. A.
1969. On the identity and relationships of *Hyla luteocellata* Roux (Amphibia, Salientia). Herpetologica, 25:126-134.

ROUX, J.
1927. Contribution à l'érpetologie du Vénézuela. Verh. Naturf. Gesell. Basel, 38:252-261.

SALTHE, S. N. and W. E. DUELLMAN
1973. Quantitative constraints associated with reproductive mode in anurans. *in* Vial, J. L. (ed.). Evolutionary biology of the anurans: contemporary research on major problems. Univ. Missouri Press, Columbia:229-249.

SAVAGE, J. M. and W. R. HEYER
1967. Variation and distribution in the tree-frog genus *Phyllomedusa,* in Costa Rica, Central America. Beitr. Neotrop. Fauna, 5:111-131.

SCHOENER, T. W.
1967. The ecological significance of sexual dimorphism in size in the lizard Anolis conspersus. Science, 155:474-477.
1969. Size patterns in West Indian *Anolis* lizards: I. Size and species diversity. Syst. Zool., 18:386-401.
1970. Size patterns in West Indian *Anolis* lizards. II. Correlations with the sizes of particular sympatric species—displacement and convergence. Amer. Nat., 104:155-174.

TRUEB, L.
1973. Bones, frogs, and evolution. *in* Vial, J. L. (ed.). Evolutionary biology of the anurans: contemporary research on major problems. Univ. Missouri Press, Columbia:65-132.

VAN DE HAMMEN, T. and E. GONZALEZ
1960. Holocene and late glacial climate and vegetation of Páramo de Palacio (Eastern Cordillera, Colombia, South America). Geol. en Mijnb., 39:737-746.

VANZOLINI, P. E. and E. E. WILLIAMS
1970. South American anoles: the geographic differentiation and evolution of the *Anolis chrysolepis* species group (Sauria, Iguanidae). Arq. Zool., 19:1-298.

VUILLEUMIER, B. S.
1971. Pleistocene changes in the fauna and flora of South America. Science, 173:771-780.

WAGNER, W. H., JR.
1961. Problems in the classification of ferns. *in* Recent Advances in Botany. Univ. Toronto Press, Toronto:841-844.

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SYSTEMATICS AND EVOLUTION OF THE GREATER ANTILLEAN HYLID FROGS

By

LINDA TRUEB[1] AND MICHAEL J. TYLER[2]

The origins and number of ancestral stocks of the hylid fauna of the West Indies have been debated. The twelve species are now allocated to the genus *Hyla.* The Lesser Antillean treefrog fauna is depauperate, consisting only of a member of the *Hyla rubra* complex which occurs on the island of Saint Lucia. The occurrence of this small hylid on only one of the islands in the Lesser Antilles is puzzling, unless *Hyla rubra* is a relatively recent immigrant or adventive from the South American fauna, as seems probable. The species (or closely related members of the species group) is present on the continental islands of Trinidad and Tobago and is widespread on mainland South America. *Hyla squirella* has been introduced to Grand Bahama (Crombie, 1972), and *Hyla cinerea* is an apparent adventive to Puerto Rico (Albert Schwartz, pers. com.); both are common in the southeastern United States. Eight of the remaining species are endemic to either Jamaica or Hispaniola, and the ninth species is rather widespread; it occurs on Cuba and the Isle of Pines, the Bahamas, and southern peninsular Florida and recently has been introduced to Puerto Rico. Unlike *Hyla rubra* of the Lesser Antilles, *H. cinerea* of Puerto Rico, and *H. squirella* of Grand Bahama in the aforementioned nine species, there are no immediately obvious affinities between these Greater Antillean species and mainland representatives. The systematic relationships among the nine

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[1] Adjunct Curator, Division of Herpetology, Museum of Natural History, and Department of Systematics and Ecology, The University of Kansas.

[2] Honorary Associate in Herpetology of the South Australian Museum, North Terrace, Adelaide, South Australia 5000. Associate in Herpetology, Museum of Natural History, The University of Kansas.

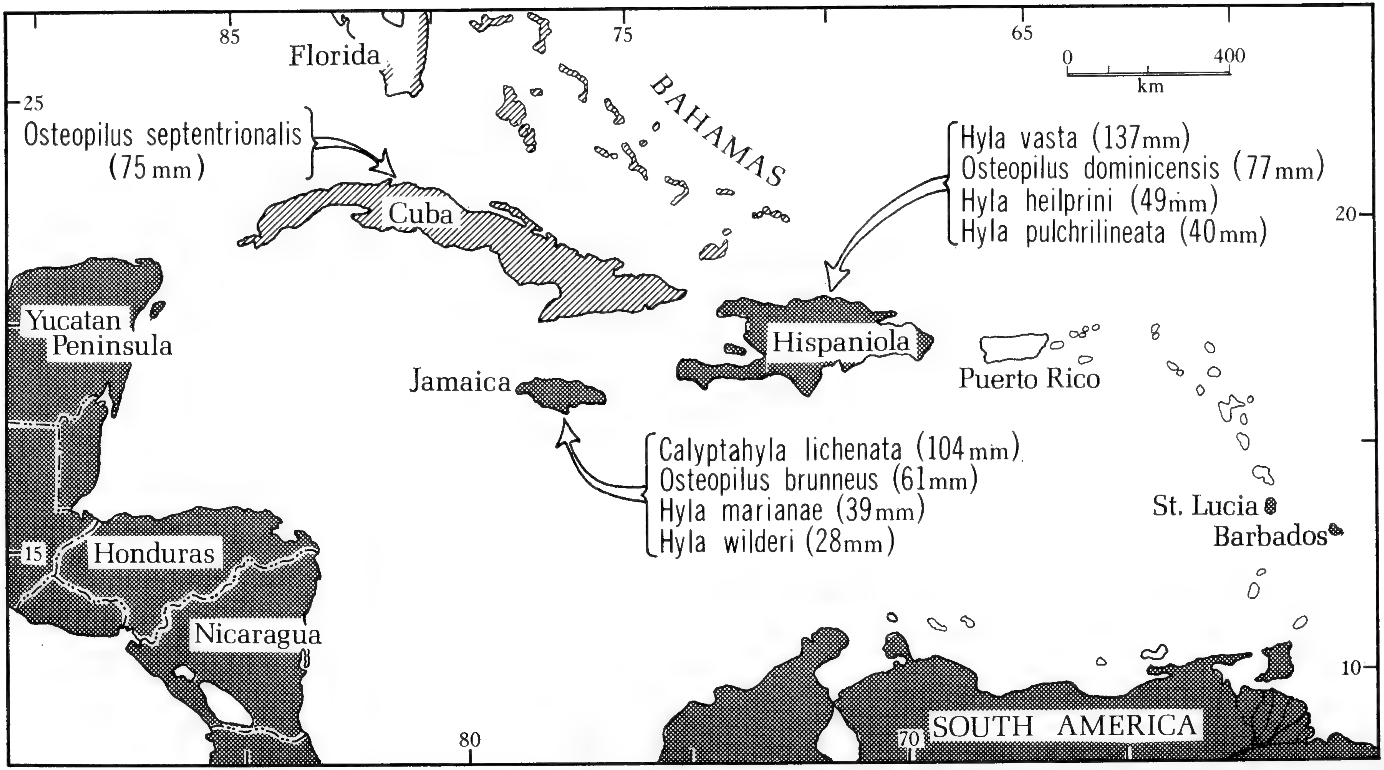

FIG. 1. Map of the West Indies showing distribution of resident hylid fauna of Greater Antilles. Distribution of *Osteopilus septentrionalis* is indicated by cross-hatching. Parenthetical numbers are average sizes of adult female frogs.

species themselves remain obscure, although they have received considerable attention in the past from Dunn and Noble, among others.

Our interest in these frogs is an outgrowth of several other morphological and systematic studies, which, in one way or another, have involved this isolated group of anurans. Because of the availability of specimens, *Hyla septentrionalis* was used by Trueb (1966) to describe the histology and development of exostosis, casquing, and integumentary-cranial co-ossification. Although the results of this research subsequently proved to be extremely useful in systematic considerations of other casque-headed, co-ossified hylids (Trueb, 1970), little was learned about the relationships of the casque-headed hylids of the Greater Antilles (*Hyla septentrionalis, H. brunea, H. dominicensis,* and *H. lichenata*). As a part of his larger study of the vocal sac structure in hylids, Tyler (1971) noted the occurrence of a unique type of throat musculature in three of the Greater Antillean frogs—*septentrionalis, brunnea,* and *dominicensis.* The accumulated morphological evidence suggested that the nine resident frogs were not so closely related as previously proposed by Dunn (1926), and prompted us to undertake this review of the taxa.

The format of the following review has been dictated by the peculiarities of the problem and our own limitations. Regrettably, neither of us has been able to observe any of these species in their natural habitat. In order to provide a general understanding of the distributions of the Greater Antillean hylids and the kinds of habitat available to them, we have provided cursory statements of the major topographical and phytogeographical features of the Greater Antilles and Bahamas. Because few species are involved, we elected to compare and contrast each of the nine species with respect to various morphological features of adults and larvae, and characteristics of breeding. The analysis of characters includes information from the literature and much new osteological and myological data. Together, these data provide a base for the critical reinterpretation of the systematics, evolution, and zoogeographic history of the Greater Antillean hylid fauna.

Acknowledgments

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Special thanks are extended to Mr. Ronald I. Crombie, who donated several specimens of *Hyla marianae* to the collections of The University of Kansas, and to Albert Schwartz and Ernest E. Williams for critical review of this manuscript. We are particularly grateful to Robert M. Mengel for his thorough editorial review, and to William E. Duellman who encouraged the preparation of this manuscript, critically reviewed it, and throughout its inception and writing served as a resourceful critic.

Materials and Methods

Measurements (Tables 1 and 2) and descriptions of external morphological features are based on examination of 140 preserved specimens. Myological observations were made on 27 preserved specimens, and osteological descriptions are based on 31 skeletal preparations.

The majority of characters analyzed are used commonly and require no special explanation other than that provided in text, and in text references. In the section dealing with osteology, several characters are discussed which should be clarified. The first group of these involve the structure of the vertebral column (Fig. 2A and B). The widths of presacral vertebrae and the sacrum were determined by measuring the linear distance between the distal tips of the transverse processes to the nearest 0.1 mm with dial calipers (Fig. 2A). Such measurements are not an index to the actual length of the transverse processes; we have gauged the overall dimension of individual vertebrae without accounting for the orientation of the transverse processes. The resulting values are useful in generating a profile of vertebral shape and only of limited use in comparing individual vertebral elements (*e. g.*, width of presacral III and sacrum). The anterior sacral angle (Fig. 2B) was determined by measuring the angle between the longitudinal axis of the vertebral column and the leading edge of the sacral diapophysis. The posterior sacral angle is that angle between the longitudinal axis and the posterior edge of the diapophysis. Sacral diapophysis expansion can be calculated by subtracting the sum of anterior and posterior angles from 180°. Camera lucida drawings of the vertebral columns were made, and the angles were measured with a protractor from these drawings.

Two characters are of particular interest in the pelvis (Fig. 2C). The first of these, relative ilial length, was determined by measuring the greatest length of the ilium and the length of the acetabular portion of the pelvis—*i.e.*, the distance from the preacetabular margin of the ilium to the posterior margin of the ischium. The pelvic angle is that angle, in lateral profile, between the acetabular

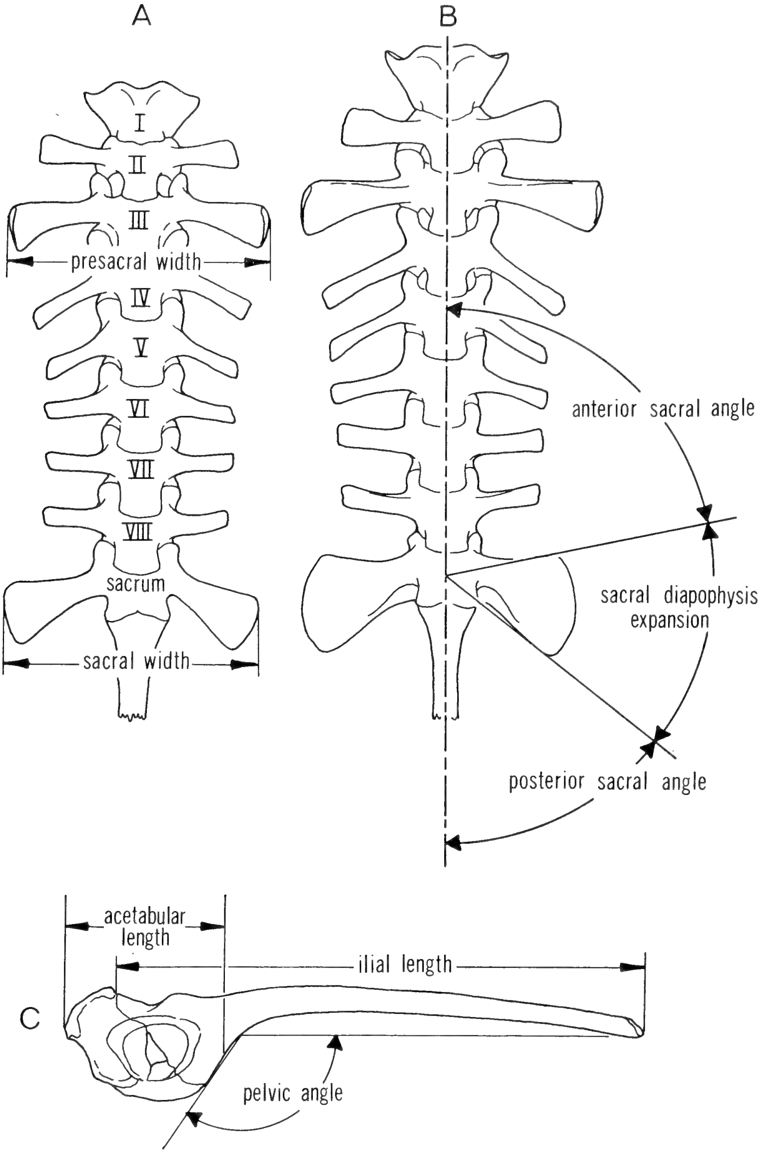

FIG. 2. Graphical explanation of postcranial osteological measurements. A. Ventral view of vertebral column of *Hyla vasta.* B. Ventral view of vertebral column of *Osteopilus brunneus.* C. Lateral aspect of pelvic girdle of *Osteopilus septentrionalis.*

portion of the ilium and the horizontal plane of the ilial shaft. In all cases, the values assigned this character are visual estimates—acute, nearly 90°, or obtuse.

Of the myological characters, the extrinsic musculature of the cloaca requires explanation here because these muscles previously have not been employed in anuran systematics. In fact, attention to the cloaca hitherto has been confined to descriptions of the musculature in such aberrant genera as *Ascaphus* (Du Toit, 1955) and *Rhinophrynus* (Noble, 1922).

The nomenclature that we adopt (see Fig. 3) differs from that of previous authors. The most proximal muscle, for which we propose the name *Musculus ischeococcygeus* is the *M. compressor cloacae* of Noble (1922) and some previous authors. We propose

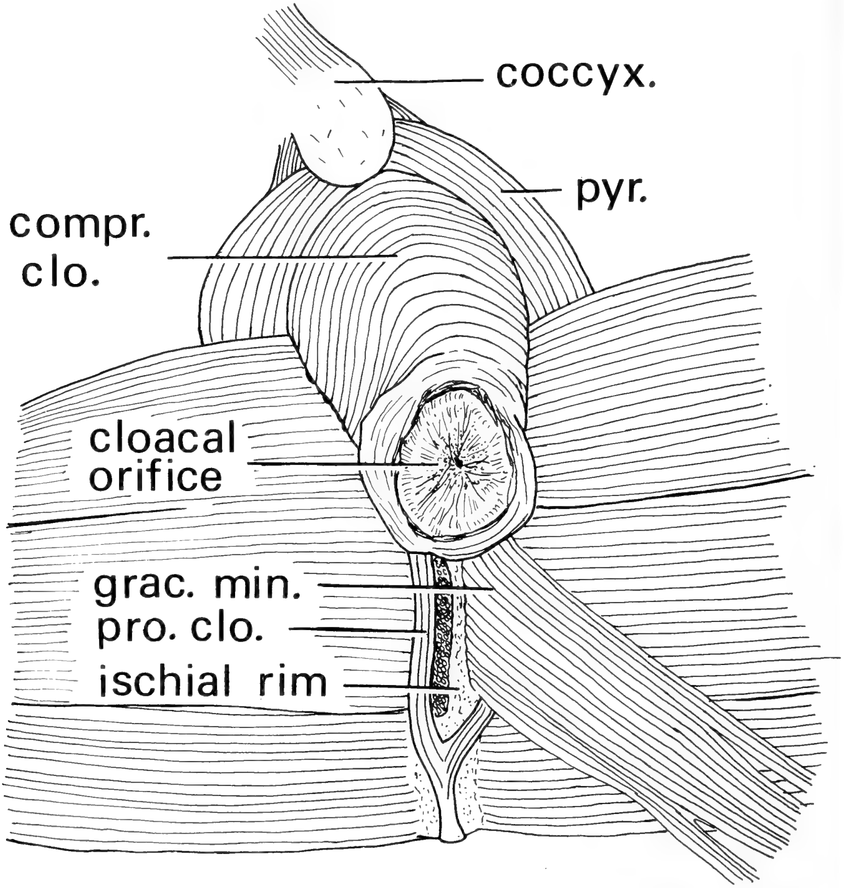

FIG. 3. Posterior aspect of thighs of *Osteopilus septentrionalis*. Superficial portion of *M. gracilis minor* removed from left side. Abbreviations: *compr. clo., M. compressor cloacae; grac. min., M. gracilis minor; pro. clo., M. protractor cloacae; pyr., M. pyriforms.*

this new name because this muscle occupies a pre-cloacal position and does not in any way compress the cloaca. The adjacent muscle is a genuine cloacal compressor and our use of compressor cloacae for it is in agreement with the actions of Du Toit (1955). A previously unreported muscle which we find occurs in many hylid species we name the *M. protractor cloacae.*

Studies of musculature were assisted by the use of iodine/potassium iodide staining technique described by Bock and Shear (1972).

We express the vocal sac aperture as a fraction of the mandible length. This was obtained from the maximal diameter of the vocal sac aperture (usually on a longitudinal axis), and the distance between the mandibular symphysis and the postarticular extremity of the mandible.

DISTRIBUTION OF THE GREATER ANTILLEAN HYLID FAUNA

At the risk of over-simplification, the Greater Antilles and Bahama Islands may be subdivided arbitrarily into five geographical subunits according to the distributions of the resident treefrogs (Fig. 1). These are: 1) Jamaica, 2) Hispaniola (Haiti and the Dominican Republic), 3) Cuba and the Isle of Pines, 4) the Bahama Islands, and 5) Puerto Rico. The following accounts are extremely brief and simplified, and intended only to introduce the reader to the habits, habitats, and distributions of the resident treefrogs. We also hope these accounts will serve as a modest, if superficial, summary of the principal topographical and vegetational features of the geographical subunits. Information on the latter was derived from inspection of a variety of topographic and vegetation maps and the accounts of Verdoorn (1945), and Rabb and Hayden (1957).

It is important to note that all the islands of the Greater Antilles are very diverse ecologically, each ranging from arid lowland deserts to high, upland deciduous or pine forests. The islands differ principally in their physiographic complexity. Hispaniola is the most complex (see Schwartz, 1973), whereas Puerto Rico and Jamaica are smaller and more simple. Each of these islands consists mainly of a central mountain mass surrounded by lowlands. In contrast to Jamaica and Puerto Rico, the largest island, Cuba, is characterized by three isolated mountain masses with surrounding lowlands.

Jamaica.—The four endemic hylids which occur on this relatively small island (*ca.* 224 x 80 km) are *Hyla lichenata, H. brunnea, H. marianae,* and *H. wilderi.* Topographically, the island is diverse. It is bisected longitudinally by a highland mass, the peaks of which lie between elevations of 1500 and 2100 m. The western and central three-fourths of the island comprise a plateau reaching elevations of 900 m. On the southern margin of Jamaica, there is an irregular coastal plain (maximally 24 km in width). A typically insular climate prevails, with the northeast sector receiving the highest annual precipitation, the central plateau somewhat less, and the southern coastal plain the least. The dry coastal plain is characterized by cactus, thorn bush, and dry scrub. In contrast, the northern aspect of the island is heavily wooded, with tropical rainforest on the more remote slopes. The southern aspect of the island supports a drier, sclerophyllous vegetation consisting of park-savanna with scattered palms, pines, and scrub. The extensive central plateau is thickly wooded on its northern side and at higher elevations. Parkland and pasturage characterize lower elevations. The central and southern parts of the plateau are cultivated.

Hyla brunnea is the most widespread of the four species; it occurs over almost the entire island at elevations below 1500 m (Schwartz and Fowler, 1973). This moderately large, casque-headed frog (adults attain 76 mm snout-vent length; Schwartz and Fowler, 1973) is found most often in arboreal and terrestrial bromeliads in open woods. *Hyla wilderi* seems to be widely distributed over the central plateau at elevations between 122 and 610 m (*op. cit.*). This species is small (adults reach about 30 mm snout-vent length) and is not casque-headed; it occurs sympatrically with *brunnea* and frequents arboreal and terrestrial bromeliads in open woods. *Hyla lichenata* is the largest (adults reaching 122 mm snout-vent length; Gosse, 1851) of the four species and is distinguished by its rugose patterned, casqued cranium. Although documentation is poor, the frog seems to be rather widely distributed throughout most of the island at low to moderately high elevations. In contrast to *brunnea* and *wilderi*, *lichenata* is reported to be an inhabitant of more densely wooded forests, where it has been observed to perch in hollows in branches 1.2 to 3.6 m above the ground (Dunn, 1926). *Hyla marianae* is moderately small (adults reaching 39 mm snout-vent length) and inhabits bromeliads in dense and scattered deciduous forests between elevations of 122 and 895 m (Schwartz and Fowler, 1973). It is at least partially sympatric with each of the three other species. All four species deposit their eggs exclusively in the water-filled leaf bases of bromeliads. Although they have been reported to inhabit both terrestrial and arboreal bromeliads, eggs have been found only in arboreal bromeliads. Apparently, none of the species occurs on the xeric, southern coastal plain.

Hispaniola.—Although Hispaniola is larger (*ca.* 640 x 288 km) and more diverse topographically and vegetationally than Jamaica, again, only four species of hylids occur on the island—*Hyla dominicensis, H. vasta, H. heilprini,* and *H. pulchrilineata;* all are endemic. Hispaniola is the second largest Antillean island and probably the most complex physiographically. There is a central east-to-west mountain mass, the highest peak of which lies at an elevation of 3175 m. The mountains are fragmented into a number of spurs and parallel chains. At higher elevations, the mountains support a mixed pine and broadleaf forest. Extensive areas of tropical rainforest occur at lower elevations in the central, northeastern and eastern portions of the island, whereas the peripheral, low elevations and coastal plains are characterized by park-savanna with palms and scrub. Xeric lowland dry scrub associations exist along the northwestern coast and south-central coastal areas.

Apparently, *Hyla dominicensis* is the most common and widespread of the resident hylids. The distribution of this relatively large frog (adults attain 99 mm snout-vent length) seems to be island-wide from the coastal lowlands to moderate elevations in the foothills. The species is principally an inhabitant of parkland-savanna and tropical rainforest environments. It is known to deposit its eggs in stagnant pools of rainwater in the forest and along the edge of stream banks (Noble, 1927). The second large treefrog of Hispaniola is *Hyla vasta* (adults reach 137 mm in snout-vent length). This non-casque-headed species is considerably scarcer in collections than *dominicensis* and perhaps, therefore, less common. It occurs sympatrically with *dominicensis* at moderate to low elevations and has been observed to lay its eggs in small gravel and stone depressions in quiet pools along streams (Noble, 1927). Schwartz (pers. com.) indicated that *vasta* is also partially sympatric with *Hyla heilprini* which breeds in torrenial streams. *Hyla pulchrilineata* is the smallest member of the Hispaniolan hylid fauna. Adults attain a snout-vent length of 43 mm, and the cranium bears no dermal modifications. Published locality records for this species are scarce, but Schwartz (pers. com.) indicated that *pulchrilineata* is widespread on the island, occurring from the coastal lowlands to an elevation of about 636 m; thus, *pulchrilineata* seems to be sympatric with *dominicensis, vasta,* and *heilprini.* Nothing has been reported concerning the larvae and reproductive behavior of this species. The fourth species, *Hyla heilprini,* is moderate in size (adults reaching 54 mm snout-vent length) and lacks cranial ornamentation. The limited locality records for this frog indicate that it inhabits the central Hispaniolan highlands; however Schwartz (pers. com.) reported that the species is more widespread than suggested in the literature and implied that *heilprini* is not limited to the highlands. Noble (1927) reported that *heilprini* was found along streams at places where the water fell in cascades over rocks.

Cuba and the Isle of Pines.—Cuba, the largest of the Antillean islands, and its small insular associate, the Isle of Pines, have only one treefrog, the moderately large (adults up to about 75 mm snout-vent length), casque-headed *Hyla septentrionalis.* In contrast to the other Greater Antillean treefrogs, this species is not endemic to a single island; it occurs in the Bahamas, southern

Table 1. Tabulation of means and ranges of body sizes and proportions of smaller members of the Greater Antillean hylid fauna. Abbreviations: HL, head length; HW, head width; IOD, interorbital distance; SVL, snout-vent length; TIB, tibia length; and TYMP, tympanum diameter.

Species	SVL (mm)	Tib/SVL (%)	HL/SVL (%)	HW/SVL (%)	IOD/HW (%)	Tymp/Eye (%)
Hyla pulchrilineata						
♂ (N=20)	31.6 (28.7-39.5)	50.5 (46.3-54.1)	34.2 (32.2-36.0)	32.0 (30.3-34.2)	29.4 (27.8-31.0)	61.6 (54.8-67.6)
♀ (N=6)	40.1 (37.6-42.8)	50.8 (48.4-53.0)	33.4 (31.7-35.1)	32.0 (31.2-32.6)	29.7 (27.4-31.1)	57.3 (48.9-62.8)
Hyla heilprini						
♂ (N=12)	49.4 (47.0-54.3)	53.1 (49.1-57.0)	35.7 (33.9-37.6)	35.9 (34.0-38.4)	28.2 (23.4-30.6)	59.9 (55.5-65.3)
♀ (N=4)	49.3 (46.2-52.0)	51.5 (49.6-53.7)	35.0 (33.9-36.4)	36.2 (34.5-37.2)	28.1 (26.9-28.8)	53.4 (51.7-56.6)
Hyla marianae						
♂ (N=3)	28.0 (23.4-33.1)	52.8 (51.3-53.8)	38.0 (36.9-38.9)	38.0 (34.2-37.9)	33.8 (33.3-34.1)	50.5 (47.1-52.6)
♀ (N=2)	38.7 (37.7-39.6)	51.3 (50.1-52.5)	36.2 (35.3-37.1)	36.0 (37.6-38.4)	30.8 (30.7-31.0)	50.4 (47.5-53.3)
Hyla wilderi						
♂ (N=15)	25.8 (23.8-27.3)	52.6 (49.2-55.8)	34.4 (31.7-36.0)	35.8 (34.1-37.5)	32.3 (28.7-37.8)	51.5 (46.4-56.0)
♀ (N=7)	27.3 (25.4-28.7)	52.1 (50.2-54.0)	33.4 (32.1-34.1)	35.1 (34.5-35.6)	32.2 (31.3-33.0)	52.5 (50.0-54.5)

TABLE 2. Tabulation of means and ranges of body sizes and proportions of larger members of the Greater Antillian hylid fauna. Figures marked by asterisks represent means of a sample of two. In those instances in which ranges are absent, the means are based on a literature report in which ranges were not provided (Duellman and Schwartz, 1958). See table 1 for abbreviations.

Species	SVL (mm)	Tib/SVL (%)	HL/SVL (%)	HW/SVL (%)	IOD/HW (%)	Tymp/Eye (%)
Osteopilus brunneus						
♂ (N=6)	45.5 (41.0-48.1)	47.3 (45.1-51.8)	37.3 (36.2-39.0)	36.8 (35.4-38.1)	39.4 (32.8-45.0)	71.9 (63.6-76.8)
♀ (N=6)	60.5 (52.5-70.0)	46.7 (44.7-49.1)	35.6 (33.0-38.4)	35.6 (33.7-38.1)	43.8 (40.5-46.6)	75.5 (72.7-80.6)
Osteopilus dominicensis						
♂ (N=20)	57.8 (52.6-63.8)	51.3 (47.9-55.3)	32.3 (30.9-33.8)	30.8 (29.0-32.1)	39.9 (34.6-44.2)	63.6 (57.1-69.0)
♀ (N=19)	76.8 (70.2-98.7)	54.5 (49.0-56.3)	34.8 (31.8-36.4)	33.7 (31.8-35.8)	44.5 (41.5-48.4)	63.6 (66.7-83.1)
Osteopilus septentrionalis						
♂ (N=40)	55.3	*45.8	*33.4 (31.9-34.8)	31.8	*30.8 (30.4-31.2)	*66.4 (62.8-70.0)
♀ (N=17)	75.2	*46.9	*35.2 (34.5-35.9)	33.3	*39.7 (34.4-45.0)	*77.1 (75.8-78.4)
Hyla vasta						
♂ (N=12)	96.7 (87.5-108.8)	53.4 (49.3-56.4)	31.7 (30.3-34.1)	33.4 (31.7-35.3)	26.2 (24.8-27.8)	58.4 (51.0-71.0)
♀ (N=2)	136.9 (131.8-141.9)	51.0 (49.8-52.2)	30.0 (29.5-30.4)	32.2 (31.8-32.6)	34.1 (33.9-34.2)	57.8 (57.6-58.0)
Calyptahyla lichenata						
♂ (N=1)	92.6	--------	35.4	39.0	35.1	68.2
♀ (N=1)	104.0	53.9	38.4	41.8	34.5	84.8

peninsular Florida and Puerto Rico. Cuba differs from the smaller islands of Hispaniola and Jamaica in lacking a central highland mass; its mountainous areas are disjunct. A relatively low chain occurs on the western end of the island with peaks reaching elevations of 728 m. South-centrally, the peaks of a small mountain mass reach 1156 m. The most extensive montane area lies along the southeastern coast and on the eastern end of the island where peaks reach elevations above 2000 m. There are restricted areas of mixed pine and broadleaf forests in the extreme eastern and western montane areas. Two low, isolated highland masses (*ca.* 310 m elevation) occur on the Isle of Pines. Tropical rainforest occurs principally in the south-central montane area of Cuba, whereas the southeastern coast supports xeric-adapted vegetation. Save for coastal mangrove and xeric scrub areas, most of Cuba is characterized by park-savanna vegetation of scattered palms and scrub. *Hyla septentrionalis* is widespread on Cuba and the Isle of Pines at low to moderate elevations, where it inhabits old cisterns, axils of palm leaves, banana plants, and drain pipes; eggs are laid in temporary drainage ditches, flooded basements, and old cisterns (Carr, 1940). Little is known concerning its habits in natural situations.

The Bahamas.—The Bahama archipelago consists of some 29 major islands extending about 1128 km northwest to southeast. The relief of the islands is below about 67 m. Some of the larger islands are characterized by lengthwise ranges of hills, whereas others (*e.g.*, the large island, Andros) have virtually no topographical relief. Running streams are rare and availability of fresh water is seasonal, depending upon rainfall. Vegetationally, the islands are characterized by coppice thorn bush and dry scrub. *Hyla septentrionalis* is the only treefrog occurring naturally in the Bahamas; it has been reported from the Cayman Islands in addition to Little Bahama Bank, Grand Bahama Bank, San Salvador, Rum, Crooked and Acklin's Islands. The species was introduced recently to Great Inagua Island (Schwartz, 1968). *Hyla septentrionalis* has become well established in southern peninsular Florida, where it occurs sympatrically with several North American hylids (Duellman and Schwartz, 1958).

Puerto Rico.—The island of Puerto Rico has no native treefrogs. *Hyla septentrionalis* and *H. cinerea* are recent adventives (Duellman and Crombie, 1970; Schwartz, pers. com.). The island, although small (*ca.* 160 x 48 km), is topographically diverse. The elevation of the central highlands reaches approximately 1220 m. A relatively narrow area of savanna-parkland occurs along the margin of Puerto Rico. Mixed pine and broadleaf forests predominate in the central hills and tropical rainforest is restricted to the higher, central elevations.

ANALYSIS OF CHARACTERS

External morphology.—Tables 1 and 2 summarize data on the sizes and proportions of nine species of the West Indian hylid fauna. Although the quality of these data vary with respect to sample size and uniformity, they are sufficient to substantiate several observations on the physical features of these frogs. The species (*wilderi, marianae, pulchrilineata,* and *heliprini*) included in table 1 are small to moderate-sized frogs which range in mean size from 27.3 to 49.4 mm snout-vent length. The species (*brunneus, dominicensis, septentrionalis, vasta,* and *lichenata*) listed in table 2 are moderate to large frogs with snout-vent lengths between 60.5 to 136.9 mm. Ratios of tibia to snout-vent length are remarkably uniform among all species, with values lying between 46.9 and 54.5 percent; similarly the ratios of head length and width to snout-vent length vary little (30.0-39.0%). In contrast to the proportional uniformity of the foregoing measurements, the ratio of interorbital distance to head width parallels the pattern evident in overall size of frogs. The smaller species included in table 1 have relatively narrower interorbital areas (28.1-33.8%) than do the larger species (*brunnea, dominicensis, septentrionalis, vasta,* and *lichenata*) of table 2 (30.8-44.5%). Likewise, relative to the diameters of the eyes, the tympana of the smaller species are smaller (50.4-61.1%) than those of the larger species (57.8-77.1%). Among the group of larger frogs, the tympanum-eye ratio of *Hyla vasta* is noticeably lower (*ca.* 58%) than the other species (63.6-77.1%). Visual inspection shows the tympanum of *vasta* to be small; the eye is not distinctly large.

The dorsal skin of *wilderi, pulchrilineata, marianae,* and *heilprini* is smooth. That of *dominicensis* and *brunnea* is smooth; however the latter has scattered, small, round tubercles on the forearm. *Hyla septentrionalis* and *vasta* have similar tubercles scattered over the entire dorsum. In contrast to the other species, the dorsum of *lichenata* is strongly tubercular. The ventral skin of all species is granular to some degree. It is weakly granular on the abdomen and thighs of all the smaller species, except *heilprini,* in which it is coarsely granular; *wilderi* and *marianae* are distinguished by the presence of tubercles around the cloaca and *heilprini* by the presence of a large, dermal submental gland. Granulation is moderately developed on the posterior abdomen and around the cloaca in *brunnea.* In *septentrionalis* it extends over the thighs and entire abdominal area, but is absent around the cloaca. The ventral regions of *dominicensis, lichenata,* and *vasta* are both coarsely granular; *lichenata* is further distinguished by tubercular skin around the cloaca.

Fringes are absent from the limbs of all species except *vasta* and *lichenata.* In the latter, a distinct dermal fringe is present along the outer edge of the forearm and tarsus. *Hyla vasta* bears more extensive fringes along the forearm and the hind limb, extending the length of the tarsus and foot. In addition, it has a distinct series of tubercles on the mandible and a proliferation of tubercles at the tibia-tarsal joint. Dermal wrist folds are absent in all of the smaller species except *septentrionalis.*

The tympanum is distinct in each species except *wilderi,* in which it is not obvious externally, and *heilprini,* in which it is "concealed." Similarly, the supratympanic folds are scarcely evident in these two species, whereas they are distinct in the others. The nostrils are terminal in all species, but vary in their degree of protuberance. In most the nostrils are not protuberant. They are slightly protuberant in *dominicensis, lichenata,* and *brunnea,* and noticeably protuberant in *vasta.* The cloacal opening lies posteriorly at the upper level of the thighs in all species. Dermal modifications in the cloacal region are absent in all species, except *lichenata, vasta,* and *heilprini.* A small horizontal supracloacal flap characterizes *lichenata,* whereas longitudinal folds of skin lie adjacent to the cloaca in *heilprini.* A profusion of tubercular skin growths distinguish *vasta.*

Hands and feet.—Hand morphology varies considerably among the West Indian hylids. All species have well-developed digital pads which are larger on the fingers than on the toes. *Hyla heilprini* is unique in having a prepollex which is evident externally, and a well-developed prepollical spine. Webbing is absent from the hand in *wilderi* and present basally between the fingers in *marianae, pulchrilineata,* and *septentrionalis.* Of the remaining species, the fingers of *brunnea, dominicensis* and *lichenata* are approximately one-fourth webbed, whereas those of *heilprini* are one-half webbed and those of *vasta* three-fourths webbed. Subarticular tubercles are distinct and round on inner digits with a tendency toward becoming flattened and bifid on outer fingers in all species except *wilderi,* in which all subarticular tubercles are low, round, and barely evident. Supernumerary tubercles vary from total absence in *marianae* and *pulchrilineata,* to presence of a few indistinct tubercles in *vasta* and *wilderi,* a moderate number of low, round tubercles in *lichenata* and *septentrionalis,* and presence of numerous tiny tubercles in *brunnea, dominicensis,* and *heilprini.* All species have inner palmer tubercles which are more or less elliptical in shape. Distinct outer palmar tubercles are absent in five species; whereas in the remaining four (*wilderi, dominicensis, vasta,* and *pulchrilineata*) two outer palmar tubercles are present. Males of at least seven of the species bear nuptial excrescences; these vary from flat horny pads in *marianae, pulchrilineata, dominicensis, septentrionalis* and *vasta,* to a proliferation of small, keratinous granules in *brunnea,* and the presence of large keratinous spines in

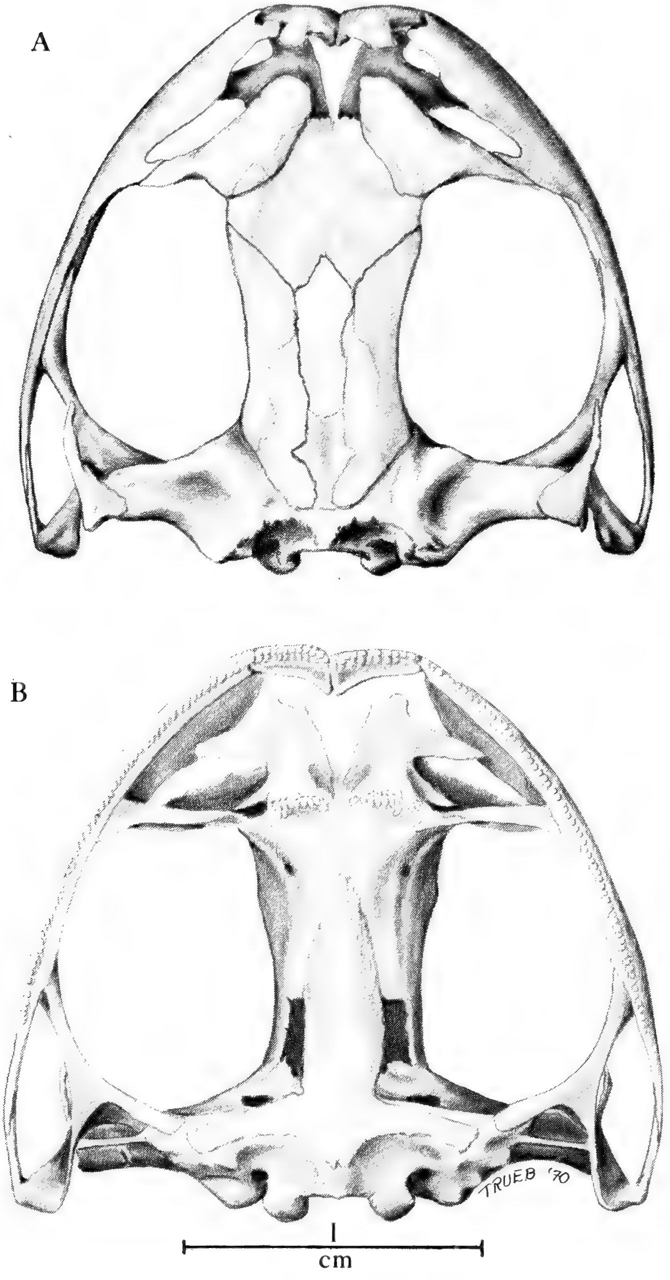

FIG. 4. Skull of *Hyla vasta* (University of Kansas, Museum of Natural History 84711). A. Dorsal view. B. Ventral view.

wilderi. Nuptial excrescences are absent in *heilprini;* their presence or absence has not been noted in *lichenata.*

Webbing is present between the toes and more extensively developed in all species than finger webbing. The toes of *wilderi* are about one-fourth webbed, those of *marianae* one-third and *pulchrilineata* and *septentrionalis* two-thirds webbed. The feet of *brunnea, dominicensis,* and *lichenata* are three-fourths webbed, whereas those of *vasta* and *heilprini* are fully webbed. Subarticular tubercles are round; they have a tendency to be flattened and bifid on the outer toes of *dominicensis, heilprini,* and *lichenata.* Plantar supernumerary tubercles are absent in *vasta* and *heilprini,* and few in number in all other species except *brunnea* and *lichenata,* in which their numbers are moderate. Inner metatarsal tubercles are present and vary between ovoid and flat, and elliptical and elevated in shape. Outer metatarsal tubercles are absent or scarcely evident in all species except *pulchrilineata, marianae* and *lichenata;* the tubercles are small and round in the latter species.

Cranial Osteology.—On the basis of cranial characteristics, the West Indian hylid fauna is easily subdivided into the small-sized and large-sized groups observed in tables 1 and 2. Although the observed classes correlate with body size, they are predicated on structural features of the skulls and will be discussed separately. Among the larger species there are three groups. The first is composed of *septentrionalis, dominicensis,* and *brunnea,* whereas the second and third groups each contain only one species, *lichenata* and *vasta,* respectively.

Despite being the largest of the West Indian frogs (Table 2), *vasta* has the least well ossified skull (Fig. 4); it is only slightly wider than long and has no dermal modifications. The skulls of the moderate-sized *septentrionalis*-group also are slightly wider than long but, are distinguished by exostosis, casquing, and co-ossification (Fig. 5). A moderate development of dermal sculpturing resulting in patterns of pits, ridges, and bony tubercles is associated with this group. *Hyla lichenata* is distinctively different from both *vasta* and the *septentrionalis* group. The skull (Fig. 6) is distinctly wider than long and heavily exostosed, casqued, and co-ossified. Dermal sculpturing consists of a distinctive pattern of peripheral, radial ridges which grade into a central pattern of pits and ridges.

The skull of *vasta* is minimally roofed and delicate in structure (Fig. 4A). A dermal sphenethmoid is absent. Although nasals are moderately large, they are widely separated and barely overlap the anterior margin of the sphenethmoid. Similarly, the frontoparietals are minimally developed. They are not peripherally expanded and do not articulate with the maxillary. The palatines (Fig. 4B) are well developed, anteriorly convex, and articulate with the lateral edge of the sphenethmoid. The parasphenoid is large. The cultri-

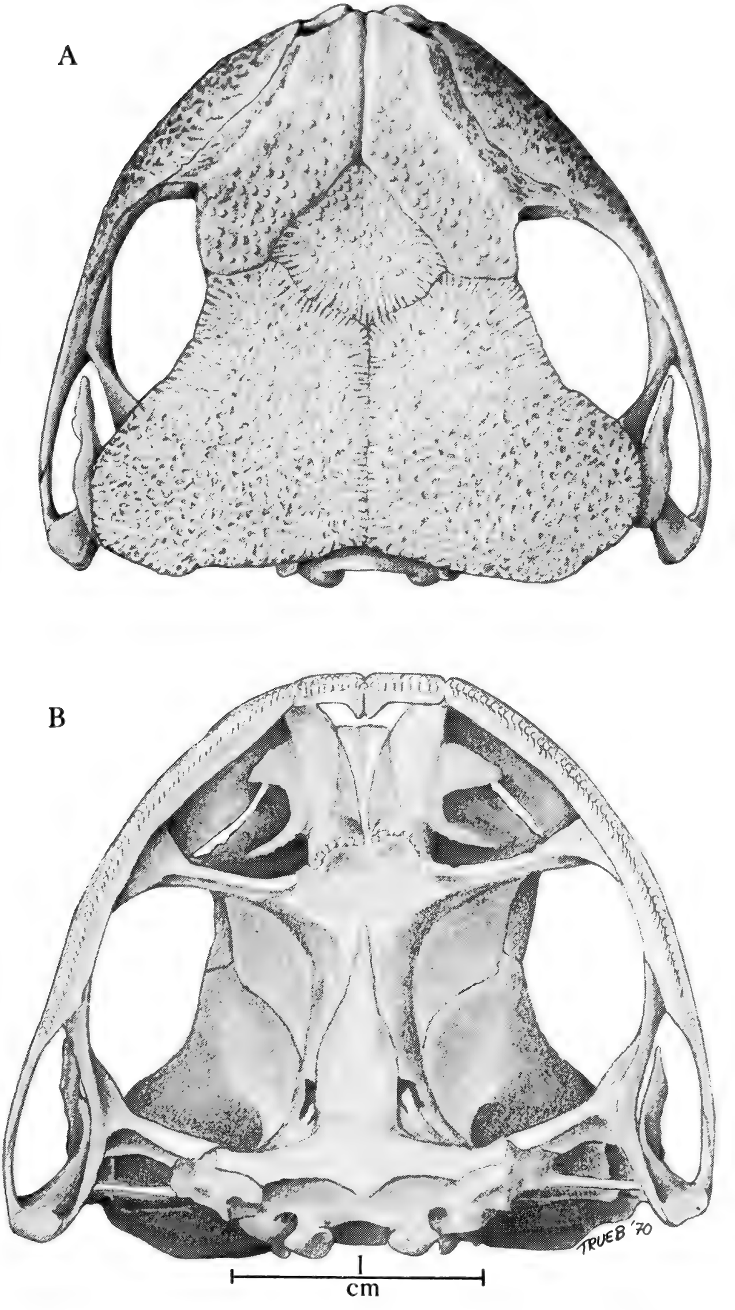

FIG. 5. Skull of *Osteopilus brunneus* (University of Kansas, Museum of Natural History 84693). A. Dorsal view. B. Ventral view.

form process of this element is edentate and extends to the forepart of the orbit. The alae are posterolaterally inclined; their distal ends are widely separated from the medial rami of the pterygoid bones. The pterygoids are robust, triradiate and fully articulated; the anterior rami articulate with the maxillaries at the mid-level of the orbits. The prevomers are widely separated from the maxillary arch. Prevomerine teeth are situated on moderately broad, curved elevations and occur in a double row laterally.

Cranially, *dominicensis, septentrionalis* and *brunnea* represent a group of broadly casqued, moderately exostosed, co-ossified hylids. Each species is characterized by a pattern of dermal sculpturing which consists of irregularly shaped pits and ridges, and proliferations of small, bony tubercles (Fig. 5A). Along the margins of the dermal roofing bones and the maxillae, the tubercles tend to be aligned in series to produce patterns of low radial ridges. A dermal sphenethmoid is present in each species. The frontoparietals are extensively developed; a broad supraorbital flange is present and the paired elements articulate medially, completely obscuring the frontoparietal fontanelle. Posterolaterally, the frontoparietal completely roofs the prootic region in mature females of each species. In *septentrionalis* and *dominicensis* the frontoparietal articulates with the otic arch of the squamosal, whereas no articulation is established between these elements in *brunnea.* The occipital margins of the frontoparietals are strongly convex in *dominicensis* and *brunnea,* but tend to be straight in *septentrionalis.* The nasals are extensive and with all adjacent elements articulated in all three species. The canthal ridges are straight in *dominicensis,* very slightly concave in *septentrionalis,* and markedly concave in *brunnea.* Furthermore, *brunnea* has a much longer medial nasal articulation than the other two species. In *dominicensis* and *septentrionalis,* the zygomatic arch of the squamosal articulates with the maxillary, whereas the arch is incomplete in *brunnea.* Palatines are well developed in *brunnea* and *septentrionalis,* but very poorly developed in *dominicensis.* In contrast to the condition of *vasta,* the palatines of the *septentrionalis* group tend to be straight or to have their proximal ends turned anteriorly (Fig. 5B). The cultriform process of the parasphenoid is edentate and extends to the anterior level of the orbit in each species. The parasphenoid alae are perpendicularly oriented in *dominicensis* and *brunnea* and slightly inclined posterolaterally in *septentrionalis.* Likewise, the distal ends of the alae are narrowly separated from the medial pterygoid ramus in *dominicensis* and *brunnea* and widely separated in *septentrionalis.* The pterygoid is best developed in *brunnea,* in which the anterior arm articulates with the maxillary at the mid-level of the orbit and the medial arm articulates firmly with the otic capsule. The element is less robust and articulates with the maxillary at the

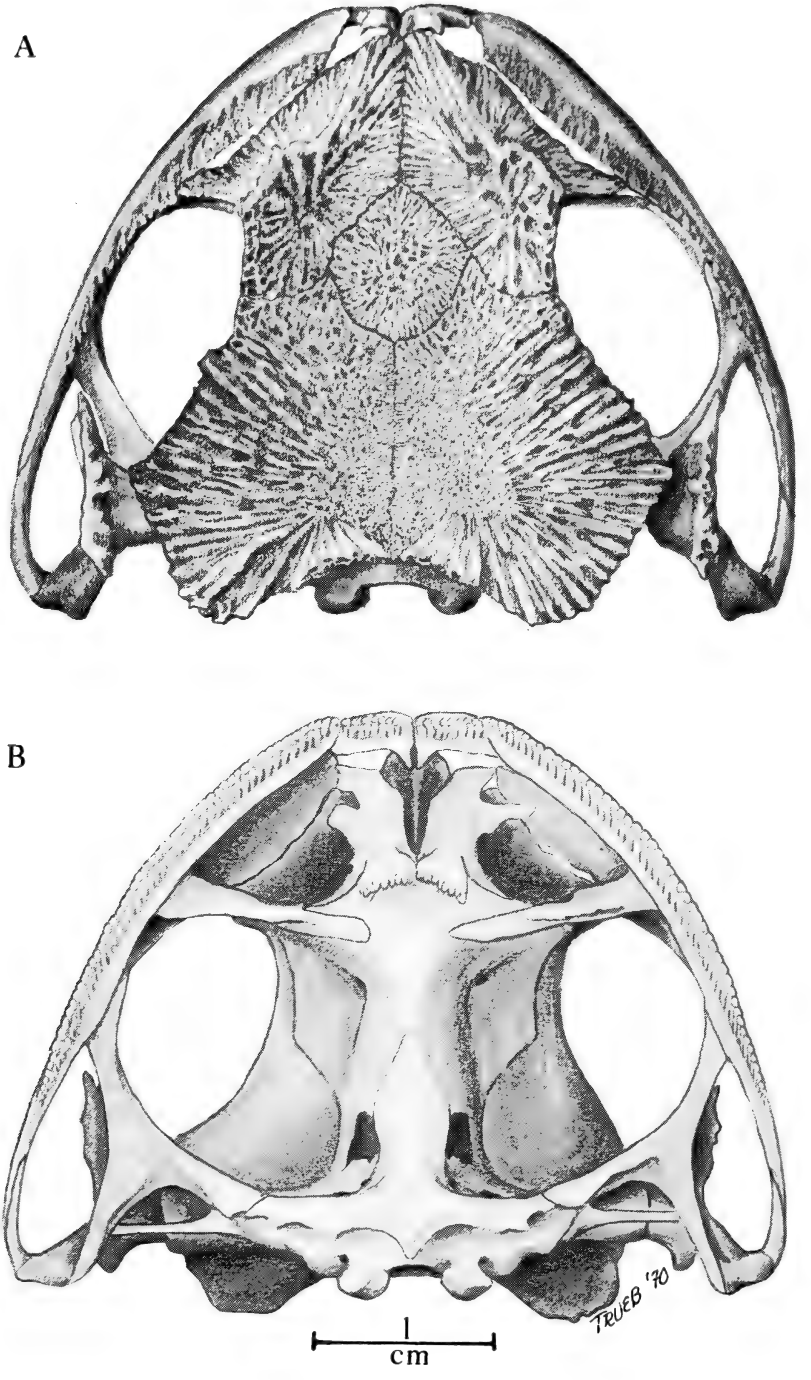

FIG. 6. Skull of *Calyptahyla lichenata* (British Museum of Natural History 52.12.1). A. Dorsal view. B. Ventral view.

posterior level of the orbit in *dominicensis* and *septentrionalis.* In the latter species the medial pterygoid ramus is weakly articulated with the otic capsule, whereas in *dominicensis* the articulation is absent. The prevomers of the three species are similar in having single rows of teeth situated on broad, curved elevations. The prevomers are small and widely separated from the maxillary arch in *dominicensis,* whereas they are large and articulate with the maxillary arch in *septentrionalis* and *brunnea. Hyla brunnea* is further distinguished by the strong curvature of the prevomerine tooth row (Fig. 5B).

The skull of *lichenata* is distinctly different from those of the other four species. Like the *septentrionalis*-group, it bears a dermal sphenethmoid and is broadly casqued and co-ossified. However, the skull is considerably broader than long and the pattern of exostosis (Fig. 6A) consists of rugose peripheral ridges which grade into a central pattern of bony pits and ridges. Although the skull is heavily casqued, it is less well developed than in the *septentrionalis* group. The nasals are not completely articulated with the maxillaries. The frontoparietals extend posterolaterally over the otic region but are widely separated from the squamosal. The zygomatic arch of the squamosal does not articulate with the maxillary. The palatines are robust and straight (Fig. 6B). The cultriform process of the parasphenoid is edentate and exceptionally short, extending only to the mid-level of the orbit. The parasphenoid alae are oriented perpendicularly and articulate distally with the medial rami of the pterygoids. The pterygoids are extremely robust and fully articulated; the medial ramus articulates with the maxillary at the mid-level of the orbit. The prevomers are moderate-sized bones separated from the maxillary arch. They bear single rows of teeth on elevations which are only slightly curved and oriented at a slight angle to one another.

The cranial characteristics of the smaller members of the Western Indian hylid fauna (*wilderi, marianae, heilprini,* and *pulchrilineata*) clearly represent the cumulative effect of different kinds of adaptive trends than those evident among the larger frogs. Correlated with their smaller body sizes (*ca.* 25-50 mm), the dimensions of the skulls are decreased, and ossification is reduced. The latter is especially evident in the absence of dermal modifications (including the absence of the dermal sphenethmoid), and the moderate to minimal development of dermal roofing bones; the frontoparietal foramen is evident in each species. The mandibles are incompletely articulated and, similarly, suspensory and bracing elements (squamosal, palatine, and pterygoid) tend to be reduced in size and incompletely articulated. Three different patterns of cranial architecture are evident among these smaller hylids. The skulls of *marianae* (Fig. 8) and *wilderi* (Fig. 9) are characterized by the most

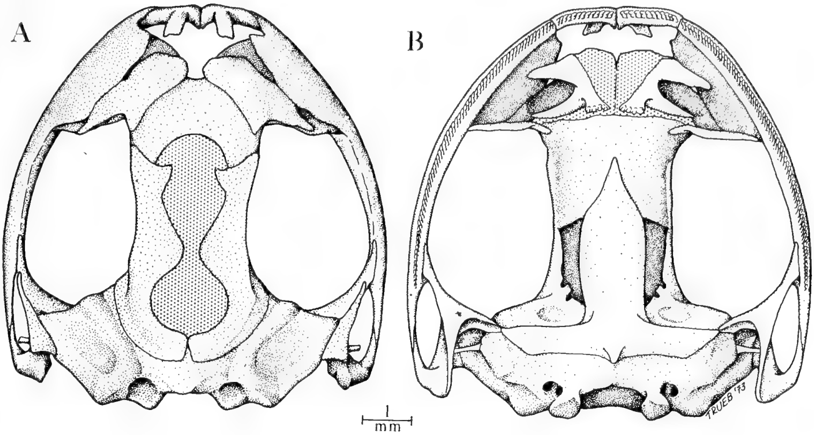

FIG. 7. Skull of *Hyla pulchrilineata* (University of Kansas, Museum of Natural History 84709). A. Dorsal view. B. Ventral view.

marked reduction in ossification and by snouts which (in dorsal view) are broadly rounded. The skull of *pulchrilineata* (Fig. 7) is easily distinguished by its length and narrowness, and that of *heilprini* (Fig. 10) by its truncate snout.

The narrow skull of *pulchrilineata* (Fig. 7A) is the most distinctive of these four species. The nasals are approximately rectangular in dorsal view and about twice as long as wide; their longitudinal axes nearly parallel those of the maxillary arch. About one-third of the length of the nasal projects anterior to the sphenethmoid. The premaxillary bears long, dorsolaterally divergent alary processes, but only a reduced palatine projection vetromedially. The prootic is narrow and laterally, abuts (but is not overlapped by) the otic ramus of the squamosal. The zygomatic ramus of this element extends approximately one-third the distance to the maxillary. The palatines are reduced, non-articulate and anteriorly concave (Fig. 7B). The parasphenoid bears a large cultriform process; the anterior end of the process is truncate and lies at the forelevel of the orbit. The pterygoid is small; the anterior ramus articulates with the maxillary at the posterior level of the orbit, whereas the medial arm does not bear a bony articulation with the otic capsule. The prevomers are small but bear moderately large dentigerous processes. These processes are curved (anteriorly concave), and narrowly separated; each bears a single row of approximately nine teeth.

The relatively greater breadth of the skulls of *wilderi* and *marianae* (Figs. 8 and 9) readily distinguishes them from *pulchrilineata*. The nasals are only slightly longer than wide, and their longitudinal axes parallel the maxillary arch. One-third (*wilderi*) to one-half

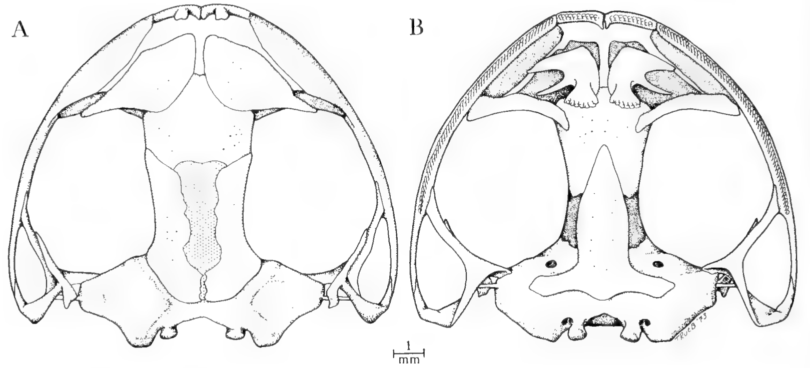

FIG. 8. Skull of *Hyla marianae* (University of Kansas, Museum of Natural History 146838, female). A. Dorsal view. B. Ventral view.

(*marianae*) the length of the nasal lies anterior to the sphenethmoid. The nasals of both species differ from those of *pulchrilineata* in having convex medial margins which broadly overlap the sphenethmoid. The alary processes of the premaxillary are moderately long in *marianae* as contrasted with *wilderi;* the processes are nearly vertical in both species. The palatine projection of the premaxillary is small in *wilderi* and minute in *marianae.* Like *pulchrilineata,* both *marianae* (Fig. 8A) and *wilderi* (Fig. 9A) have reduced prootics; but unlike the former, the otic rami of the squamosals in *marianae* and *wilderi* do not articulate with the prootics. Moreover, the zygomatic rami of the squamosals are longer, extending about one-half the distance to the maxillaries. The palatines of *wilderi* and *marianae* are anteriorly convex in contrast to those of *pulchrilineata.* Those of *wilderi* (Fig. 9B) are reduced; they articulate with neither the maxillary nor the sphenethmoid, whereas the palatines of *marianae* (Fig. 8B) extend from the maxillary to articulate firmly with the sphenethmoid. The parasphenoids of both species are similar. The cultriform process of this element is edentate, acuminate anteriorly, and terminates at a level in the anterior third of the length of the orbit. The parasphenoid alae are widely separated from the medial rami of the pterygoid. The pterygoid of *marianae* is moderate in size and fully articulated; in contrast, that of *wilderi* is small and lacks a medial articulation with the otic capsule. The anterior rami of the pterygoids of both species articulate with the maxillaries at the posterior levels of the orbits. The prevomers of *marianae* are relatively larger than those of *wilderi.* The bones are widely separated from the maxillary arches in both species and bear similar dentigerous processes which are straight, widely separated elevations. The processes bear single rows of teeth totaling 7-8 per row in *marianae* and 4-5 per row in *wilderi.*

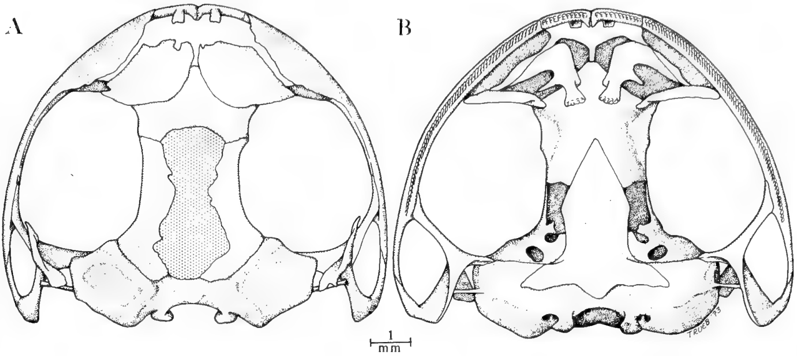

FIG. 9. Skull of *Hyla wilderi* (University of Kansas, Museum of Natural History 84713, female). A. Dorsal view. B. Ventral view.

Several features set apart the skull of *heilprini* (Fig. 10). Most apparent is its blunt, truncate snout. Unlike the other three species, the nasals are long and narrow (at least three times as long as the greatest width). Furthermore, the nasals are acuminate anteriorly with their anterior ends converging at the margin of the sphenethmoid. The longitudinal axes of the nasals are not parallel to the maxillary arch. The frontoparietals of *heilprini* are poorly developed; thus a large part of the frontoparietal fontanelle is evident, particularly posteriorly. The premaxillary differs in several respects from those of the other small hylids. The alary processes are moderately small, dorsomedially convergent, and posteriorly inclined; the palatine processes are well developed. The prootics are wide in contrast to those of *pulchrilineata, marianae,* and *wilderi.* The squamosals overlap the prootics dorsolaterally and the zygomatic rami extend approximately one-half the distance to the maxillaries. The palatines are delicate, anteriorly convex, and articulate with the sphenethmoid medially. The parasphenoid is similar in structure to those of *marianae* and *wilderi,* differing from the latter and *pulchrilineata* in having alae which are only narrowly separated from the medial rami of the pterygoids. The pterygoids of *heilprini* are moderately large and fully articulated. The anterior pterygoid rami are much longer than those of the other species; they articulate with the maxillaries at approximately the midlevel of the orbit. The prevomers are moderately large and not closely associated with the maxillary arch. Each element bears a single row of teeth (5-6 per row) on a slightly curved elevation.

Axial osteology.—The vertebral columns of the West Indian hylids are uniformly characterized by eight procoelous, presacral vertebrae, none of which is fused. The cervical cotyles are widely separated, and there are no dermal modifications. The sacral vertebrae bear bicondylar articulations with unmodified coccyges. Within

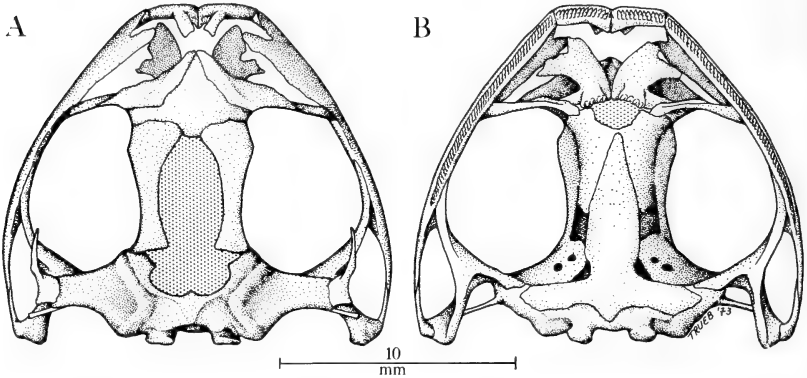

FIG. 10. Skull of *Hyla heilprini* (University of Kansas, Museum of Natural History 90838, male). A. Dorsal view. B. Ventral view.

these generalized limitations, there are morphological patterns (Fig. 2 A and B) which corroborate the species groups established on the basis of cranial structure. The presence of neural spines on the presacral vertebrae of the larger species distinguishes them from the smaller frogs.

Among the larger members of the West Indian frogs, *lichenata* and *vasta* show the most specializations in the vertebral column associated with a trend towards advanced terrestrialism (*i.e.*, arboreality); in general, these modifications are most pronounced in *lichenata*. Although the neural spines are best developed on presacrals I-V, they are present on all presacrals of *lichenata*. In *vasta*, the neural spines are obvious on presacrals I-IV and barely visible on the remaining presacrals. In both of these species (in contrast to the other frogs) the sacral diapophyses are wider than the widest transverse processes (presacral III); the diapophyses are proportionately widest in *lichenata*. The transverse processes are of nearly uniform width in *lichenata;* presacral III comprises 87 percent of the width of the sacral diapophyses, and each of presacrals IV-VIII, 75 percent of the sacral width. The pattern is less uniform in *vasta* (III—95% of the sacral width, IV—81%, and V-VIII—71%). In both species the transverse processes of presacral II and III are expanded distally. *Hyla lichenata* differs from *vasta* in bearing a small flange on the anterior margin of the transverse process of presacral II and a similar flange on the posterior margin of the transverse process of presacral III. The sacral diapophyses are only slightly dilated in *vasta* (*ca.* 20° and *lichenata* (*ca.* 31°). The differential expansion is the result of the orientation of the anterior margin of the sacral diapophyses. The orientation may be measured by calculating the angle between the anterior edge of the sacral diapophysis and the longitudinal axis of the body. The angle approximates 80° in *lichenata* and 103° in *vasta.*

The vertebral columns of the *septentrionalis*-group (*septentrionalis, dominicensis,* and *brunnea*) show fewer advanced terrestrial specializations than those of *vasta* and *lichenata* (Fig. 2). Neural spines are best developed in *dominicensis,* in which they are evident on presacrals I-V; in *brunnea,* spines are present on presacrals I-IV, whereas in *septentrionalis* they are invariably present only on presacrals I-III. The sacral diapophyses of all three species are narrower than the widest transverse process of the presacrals (III), in contrast to *vasta* and *lichenata.* The transverse processes of the presacrals tend to be subequal in width. In *brunnea,* presacral III comprises 109 percent of the width of the sacral diapophyses, IV—89 percent, each of V and VI—79 percent, VII—75 percent, and VIII—72 percent. The pattern is nearly the same in *dominicensis* except that presacral VIII is slightly wider than VII. *Hyla septentrionalis* demonstrates the strongest tendencies towards terrestrial modifications of the axial skeleton in this group; the transverse processes are more nearly equal in width (III—113% of sacral width, IV—100%, V—93% VI—87%, VII and VIII—85%). All three species are characterized by distal expansion of the transverse processes of presacral II and III. A minute anterior flange is present on the transverse process of presacral II in *brunnea;* a similar, but much larger flange is present in *septentrionalis.* The sacral diapophyses are more broadly dilated in all three species than in *vasta* or *lichenata.* The angle of expansion is about 41° in both *brunnea* and *dominicensis,* and approximately 57° in *septentrionalis.* The corresponding anterior sacral angles are 70°, 74°, and 82° in *septentrionalis, dominicensis,* and *brunnea,* respectively.

The vertebral columns of the smaller hylids tend to show fewer specializations and greater uniformity of pattern than those of the larger frogs. In each of the four species, neural spines are absent and the width of the transverse processes of presacral III is greater than the width of the sacral diapophyses. The transverse processes lack flanges, and the sacral diapophyses are moderately dilated (43-48°). In *pulchrilineata,* which probably has the most generalized axial structure of the groups, the width of presacral III comprises 117 percent of the width of the sacral diapophyses. The widths of the transverse processes of the presacrals are subequal except those of VII and VIII (III—117%, IV—98%, V—85%, VI—80%, and VII and VIII—73%). The transverse processes of presacrals II, III, and IV are slightly expanded distally. The angle between the anterior edge of the sacral diapophysis and the longitudinal axis of the body is 77°; the corresponding posterior angle is 55°.

In the remaining three species (*heilprini, wilderi,* and *marianae*), only the transverse processes of presacral III are expanded distally.

Of the three, the axial morphology of *heilprini* is most similar to *pulchrilineata,* although the two are readily distinguishable. The presacrals of *heilprini* are clearly subequal in width (III—111% of sacral width, IV—96%, V—87%, VI—86%, VII—80%, and VIII—75%). The sacral diapophysis expansion is nearly the same as *pulchrilineata* (anterior angle, 77°; angle of expansion, 45°). Of the smaller species, *marianae* and *wilderi* show the highest degree of axial specialization. The relative widths of the transverse processes are slightly subequal in *marianae* (III—110% of sacral width, IV—97%, V—86%, VI—84%, VII—83%, and VIII—79%) and more nearly uniform in *wilderi* (III—105% of sacral width, IV—90%, and V-VIII—80%). The orientation and expansion of the sacral diapophyses is similar in both species. The anterior sacral angles are 75° and 80° in *marianae* and *wilderi,* respectively. Corresponding angles of sacral expansion are 43° and 48°.

Pelvic osteology.—In general, the pelvic structure of the West Indian hylids is quite generalized (Fig. 2C). The ilium and ischium are ossified and the pubis is cartilaginous or secondarily calcified in larger species. Dorsal acetabular expansion is minimal. Ilial protuberances are present, but moderately developed in all species. The ilium is devoid of dorsal crest and lateral expansions in all species except *marianae* in which a low crest is present.

Values for relative ilial length (measured as a function of the length of the acetabular portion of the girdle) are *pulchrilineata,* 3.8; *dominicensis,* 3.7; *septentrionalis* and *brunnea,* 3.6; *vasta,* 3.5; *lichenata,* 3.3; *wilderi,* 2.9; and *marianae,* 2.1. One pattern emerges which apparently is independent of body size. Among the smaller frogs, the species with the least specialized vertebral column structure (*pulchrilineata*) has the longest ilium. Similarly, the more generalized of the larger species (*septentrionalis* group) tend to have longer ilia than the more specialized *vasta* and *lichenata.* The *septentrionalis* group is characterized by obtuse angles between the ilial shaft and the preacetabular margin; that of *vasta* approaches 90°, whereas the angle is acute in *lichenata. Hyla heilprini* has an obtuse preacetabular angle; the angles of *pulchrilineata* and *wilderi* approximately 90° and that of *marianae* is acute.

Throat musculature and vocal sac structure.—All members of the West Indian hylid fauna have vocal sacs except *marianae.* The larger frogs are uniformly characterized by: 1) a posterolateral attachment of the fibers of the intermandibularis upon the ventral surface of the submentalis; 2) vocal sacs which are confined to a position above the interhyoideus muscle; and 3) presence of the adductor mandibulae externus superficialis. The *septentrionalis*-group is distinguished from *vasta* and *lichenata* by the differentiation of the intermandibularis to form a supplementary, apical element (Fig. 11). Most hylids, like *vasta* and *lichenata,* have an

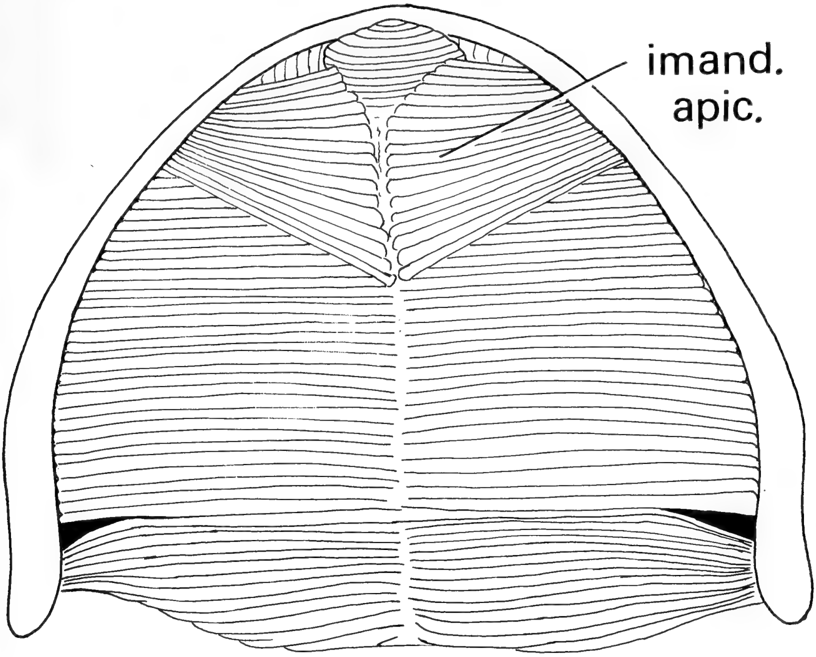

FIG. 11. Superficial mandibular musculature of *Osteopilus brunneus.* Abbreviations: *imand. apic.,* supplementary apical element of *M. intermandibularis.*

undifferentiated intermandibularis (Tyler, 1971). The interhyoideus muscle shows some variation in the development of lateral lobes. The lobes are absent in *brunnea* and *lichenata;* they are present and located posterior to the mandible in *dominicensis* and *vasta.* In *septentrionalis,* the lobes are present, small in size, and situated above the mandible. Similarly, the nature of the medial attachment of the intermandibularis muscle varies. In *dominicensis* and *septentrionalis,* the muscles meet at a tendinous raphe, whereas a slender aponeurosis is present in *lichenata* and *brunnea,* and a broad aponeurosis in *vasta.*

In *brunnea* the vocal sac apertures are present as slits of moderate length, each being equivalent to approximately one-third of the length of the mandible. The remaining large species are characterized by vocal sac apertures which are small, circular orifices equivalent to one-eighth to one-tenth of the length of the mandible. This condition occurs infrequently in hylid frogs and represents a specialization over the moderate-sized slit.

There are only two features common to all of the smaller species: (1) Absence of differentiation of the intermandibularis; (2) absence of the *adductor mandibulae externus superficialis.* Posterolateral attachment of the fibers of the intermandibularis upon the ventral surface of the submentalis occurs in *marianae, pulchrilineata,* and *wilderi* but not *heilprini,* where *pulchrilineata* is the only species lacking a median aponeurosis of the intermandibularis. The interhyoideus is least developed in *marianae,* which is unique in lacking a vocal sac, and most highly developed in *pulchrilineata,* in which there is a distinct, posterior, bilobular, supramandibular orientation. The remaining species have developed unilobular, postmandibular vocal sacs. In all species the vocal sac apertures are slit-like and approximately one-third of the length of the mandibles.

Hyla heilprini is unique in possessing a dermal, submental gland comparable to that occurring in *H. colymba,* which is illustrated by Duellman (1970).

Extrinsic musculature of the cloaca.—The cloaca of all West Indian hylids is characterized by the presence of the protractor cloacae (Fig. 3). The muscle constitutes a bilateral extension of the ventral lip of the cloacal orifice, functionally permitting protraction of the orifice. The muscle occurs in all North American hylids examined, all casque-headed hylids, is present or absent in *Hyla* from Middle and South America, and does not occur in any from Australia and New Guinea.

The only observed variation among the West Indian species is the inferior boundary of the protractor cloacae, and the nature of its attachments to the ischial ridge. In the larger species either a few muscle fibers or the median tendon extend to the ventral surface of the ischial ridge (Fig. 3). In the smaller species the muscle always terminates at the position posterior to the gracilis minor where the lateral halves of the protractor cloacae unite. From that site a very short tendon attaches to the posterior face of the ischial ridge.

Breeding sites and larval morphology.—The four Jamaican species (*brunnea, lichenata, wilderi,* and *marianae*) are known to breed only in bromeliads. None of the remaining species has been observed to utilize bromeliads for breeding. *Hyla septentrionalis* is apparently restricted to ponds and cisterns, whereas *vasta* and *dominicensis* utilize streams as well as pools. *Hyla heilprini* breeds in torrential streams. No observations are recorded in the literature on either the breeding site or the larvae of *pulchrilineata.*

The tadpoles of these frogs are diverse morphologically and easily distinguishable. The most generalized larvae are associated with the pond breeders. Noble (1927) reported that *dominicensis* laid its eggs in stagnant pools of rainwater in the forest or along the edge of a stream bank. The larva of *dominicensis* is characterized by a short tail with well-developed fins, an interrupted labial disc and a 2/5 tooth row pattern. The tadpole of *septentrionalis* is similar, save for a 2/4 tooth row pattern. *Hyla vasta* lays its eggs in basins in gravel and stones on the edges of stream pools (Noble, 1927); subsequent to hatching, the larvae move from the basins over wet stones into the stream. The larvae of *vasta* have a short, thick, muscular tail with deep fins, an uninterrupted labial disc, and minimally, a 4/6 tooth row pattern. The larvae of *heilprini* are the most obviously stream adapted with extremely thick, muscular tails, deep fins, uninterrupted labial disc and a 6/9 tooth row pattern. Relative to the non-bromeliad tapoles, the bromeliad larvae have longer tails, reduced fins, and reduced numbers of toothrows. The larvae of both *brunnea* and *lichenata* have incomplete labial discs and a tooth row pattern of 1/0; the tail of the *lichenata* larva is somewhat shorter than that of *brunnea.* The labial discs are complete in the larvae of *marianae* and *wilderi;* furthermore, tooth rows are absent and the lower beaks are unnotched in contrast to the remaining species. The tadpole of *wilderi* can be distinguished from that of *marianae* by the relatively shorter tail and presence of keratinous structures around the margin of the labial disc in the former.

RELATIONSHIPS OF THE WEST INDIAN HYLIDS

Our previous understanding of the West Indian hylids has been based principally on the work of Dunn (1926) and subsequent commentary by Noble (1927, 1931) and Williams *et. al.* (1963) who focused attention on the apparently complex and peculiar relationships of these frogs. Careful perusal of Dunn's (1926) discussion of the West Indian hylids yields several interesting observations. Dunn considered *brunnea, septentrionalis,* and *dominicensis* to be closely related; he was the first to recognize them as the *septentrionalis* group. Similarly, he implied a relatively close relationship between *wilderi* and *marianae.* Dunn obviously was perplexed by the distributional symmetry of the small and large species (*i.e.,* the occurrence of two large species in combination with two smaller species on both Jamaica and Hispaniola), in contrast to the insular divergence of breeding habits (*i.e.,* bromeliad breeders on Jamaica as opposed to the more generalized pond and stream breeders of Hispaniola). It is implicit, although not directly stated in his discussion, that Dunn was reluctant to assume more than one invasion of the West Indies by an ancestral hylid stock. Although the assumption is parsimonius in terms of historical zoogeography, it severely restricted his corollary conclusions on the evolutionary relationships of the nine taxa. He implied that the *septentrionalis* group represented the most primitive derivative of an ancestral stock; thus, *septentrionalis* (*sensu stricto*) represented a Cuban derivative, *brunnea* the Jamaican derivative, and *dominicensis* the Hispaniolan derivative. Dunn postulated that *lichenata, wilderi,* and *marianae* represented derivative of *brunnea,* which diversified with respect to size while maintaining a specialized arboreal mode of reproduction. He suggested that on Hispaniola *vasta, heilprini,* and *pulchrilineata* evolved from a *dominicensis*-like ancestor. The Hispaniolan derivatives diversified with respect to size, but unlike their Jamaican counterparts, they also diversified with respect to breeding site (*i.e.,* pond and stream) within the more generalized aquatic reproductive mode.

Noble (1927) commented at some length on Dunn's proposal in his discussion of the significance of life history data in the evolution of the Amphibia. He suggested that the tadpoles of the Hispaniolan hylids seemed to represent an orthogenetic series progressively modified to life in a mountain stream, thus strengthening Dunn's argument in favor of a monophyletic origin for the group. Although, on the whole, Noble seemed to have agreed with Dunn's conclusions, he did question the high degree of parallelism involved in the evolution of the two insular faunas.

On the basis of the comparative morphological evidence presented herein, Dunn's implied monophyletic origin of the West Indian hylids is an untenable hypothesis. The four smaller species—*pulchrilineata, heilprini, marianae,* and *wilderi*—are similarly distinguished from the members of the *septentrionalis*-group and *vasta* and *lichenata,* by their size, generalized cranial structure, absence of dermal modification to the skull, and generalized pattern of throat musculature. Dunn (1926) suggested that *marianae* and *wilderi* might represent "neotenic" derivatives of a *brunnea*-like ancestor. Were this so, one would expect a striking resemblance in the pattern of osteological features between the smaller species and *brunnea.* Morphologically, *brunnea* unquestionably is distinct from *marianae* and *wilderi;* however, comparison of the two latter species suggests a close relationship between them. Myologically, *marianae* and *wilderi* differ in only three of the ten characters considered. Both are characterized by skulls with greatly reduced ossification and bluntly rounded snouts. The species share similar body proportions (Table 1), many features of soft morphology, and axial specializations such as short ilia, obtuse pelvic angles, expanded sacral diapophyses and transverse processes of nearly uniform width. Both are inhabitants of the central highlands of Jamaica, where they breed in bromeliads. *Hyla marianae* inhabits arboreal bromeliads in deciduous forest; its known altitudinal range is 122 to 895 m (Schwartz and Fowler, 1973). In contrast, the smaller species, *Hyla wilderi,* is known to inhabit both terrestrial and arboreal bromeliads in dense and scattered woodlands at elevations between 122 and 610 m (*op. cit.*).

There seems to be no evidence linking either *pulchrilineata* or *heilprini* to *marianae* and *wilderi.* Osteologically, both Hispaniolan species are far more generalized than the Jamaican species; they are characterized by longer ilia, vertebral processes of subequal length, and more heavily ossified skulls. The resemblance of *pulchrilineata* and *heilprini* is limited to an absence of arboreal specializations in these species. Cranially, *pulchrilineata* is distinctly different from any other West Indian hylid. *Hylid heilprini* is uniquely distinguished by its dermal submental gland and specializations adapting it to life along mountain streams of Hispaniola; included among these specializations are the presence of a propollical spine, well-developed palmar and plantar webbing, and extensive development of subarticular and supernumerary tubercles.

Dunn was correct in his assessment of *septentrionalis, brunnea* and *dominicensis.* These three species comprise a closely related complex of moderately large frogs characterized by uniquely specialized throat musculature (differentiated intermandibularis muscle). The skulls are heavily ossified (exostosed, casqued, and co-ossified) and share many structural details in common, including presence of a dermal sphenethmoid and similar prevomerine morphology. In contrast to the specializations of the skull, the axial osteology of these three species is quite generalized. Sacral diapophysis expansion is moderate, and the transverse processes are distinctly subequal in length. The ilia of each of these species are long and the pelvic angle is obtuse.

Although it is not at once obvious, *lichenata* and *vasta* are more similar to one another in many respects than either is to the *septentrionalis* group. Both are extremely large frogs, sharing a generalized pattern of throat musculature (*i.e.,* differentiated intermandibularis muscle) and many arboreal specializations. The latter include dermal fringes along the outer margins of the fore- and hind limbs, and certain characteristics of the axial and pelvic skeleton. The ilia are somewhat shorter than those of the *septentrionalis* group and the anterior pelvic angle is acute or perpendicular, instead of obtuse. These two species are unique among the West Indian hylids in having very slightly dilated sacral diapophyses, the total width of which is greater than that of the third presacral vertebrae. Furthermore, in both *lichenata* and *vasta,* the transverse processes of the vertebrae are long and nearly uniform in length. We are not implying that these two species are closely related; there is a host of morphological differences distinguishing them. On the other hand, the structural characteristics which they share make it seem highly unlikely that either species could have been derived from the *septentrionalis* group as proposed by Dunn. The most distinctive feature of *lichenata* is its heavily casqued, co-ossified skull. Although this would seem to indicate a relationship to the *septentrionalis* group, the basic cranial architecture is distinctly different and certainly not derived from the pattern of these frogs; furthermore, the undifferentiated intermandibularis sets it further apart from members of that group. Similarly, the vacuous, poorly ossified skull of *vasta* could only have arisen from the *septentrionalis* group by heterochronous arrestment of bone deposition, which is not commensurate with the size attained by this species.

On the basis of the accumulated evidence, there seem to be minimally six phylogenetic lines represented among the West Indian hylids—three having given rise to the four smaller species and three others ancestral to the five larger species. Of the smaller species, *marianae* and *wilderi* are the only species for which a common ancestor can be postulated. Unfortunately, at this time there is no clear evidence linking *wilderi* and *marianae* to any particular group of hylids currently known from South or Central America. Although both species are highly specialized for an arboreal mode of existence, *marianae* is the more generalized. It is larger, and possesses fewer morphological specializations than *wilderi*. Presumably, the ancestral stock was similar to *marianae*—a moderate-sized bromeliad breeder inhabiting the central highlands of Jamaica. *Hyla marianae* may represent a species closely related to the ancestral stock; the only obvious specializations of *marianae* are loss of the vocal sac and vocal slit aperture, and reduction of ilial length. In contrast, *wilderi* is clearly a more highly derived species which has retained a vocal sac and become adapted to life in smaller bromeliads. The transverse processes of the vertebrae are more uniform in width than those of *marianae*, but the ilia are somewhat longer. The skulls of the two species are nearly identical, save for the reduced ossification of *wilderi*, which can be interpreted as developmental arrestment associated with overall reduction of size in this species. Palmar and plantar webbing is reduced in *wilderi*, but retained in *marianae*. The nuptial excrescense of *marianae* is a flat horny pad, whereas that of *wilderi* is modified into a patch of keratinous spines. The larvae of both are highly specialized for their existence in bromeliads. The tadpole of *marianae* has a somewhat longer, slimmer tail with more reduced caudal fins than *wilderi*, but the larval mouth of the latter is much smaller and characterized by a distinctive ring of keratinous spines at its perimeter (Dunn, 1926).

The presence of *pulchrilineata* and *heilprini* on Hispaniola must result from two separate invasions of that island by forms unrelated to one another and the *marianae-wilderi* complex. Although nothing has been reported concerning the breeding habits and larvae of *pulchrilineata*, the species seems to represent a generalized, wide-spread Hispaniolan hylid. *Hyla heilprini*, on the other hand, is a specialized stream-side inhabitant whose morphological characters are highly reminiscent of the wide-spread, South American *Hyla* *albomarginata* group (see Duellman, 1970, for a résumé of this species group).

The *septentrionalis* group, *vasta,* and *lichenata* seem to us to represent three distinct phylogenetic lines. Morphologically, *Hyla vasta* seems to be related to the *Hyla boans* group of Central and South America. Members of the *boans* group are large species inhabiting lowland forests, and like *vasta,* they are characterized by extensive digital webbing. They have moderately or poorly ossified skulls which are very similar in structure to that of *vasta* (see Duellman, 1970, for a résumé of this species group). The vertebral columns in this group tend to have uniform transverse processes and narrowly dilated sacral diapophyses similar to those of *vasta.* The intermandibularis muscle always bears a vast, median aponeurosis which represents a derived condition as in *vasta.* Perhaps the most intriguing similarity involves breeding behavior. Males of some members of the *boans* group (*boans, faber,* and *rosenbergi*) build stream-side, water-filled nests of mud or gravel in which eggs are deposited and tadpoles develop. At localities where the substrate is not amenable to these nest building habits, *boans* has been observed (Duellman, pers. com.) to utilize water-filled depressions adjacent to streams exactly as reported for *vasta* by Noble (1927).

Hyla brunnea, dominicensis, and *septentrionalis* form a very closely related species group characterized by their moderately large size and casqued, co-ossified crania. As a group, they are distinguished from *vasta* and *lichenata* by their differentiation of the intermandibularis to form an apical element, their obtuse pelvic angles, and generalized vertebral column structure in which the sacral diapophyses are narrower than the third presacral. These frogs seem to be highly adaptable, ecological generalists occurring over a wide elevational range (0-1500 m), in a variety of habitats. Although *brunnea* apparently breeds only in bromeliads, *septentrionalis* and *dominicensis* breed wherever standing water is available.

Of the three species, *septentrionalis* and *dominicensis* are the most closely allied and probably more closely related to an ancestral type than *brunnea.* Externally, *septentrionalis* and *dominicensis* are almost indistinguishable, differing only slightly with regard to skin tuberculation, presence of a tarsal fold and less digital webbing in *septentrionalis.* The skulls of the two species differ in only minor details involving the shape of the occipital margin, orientation of the parasphenoid alae, and articulation of the medial rami of the pterygoids. The vertebral column of *septentrionalis* tends to have transverse processes of more uniform width than *dominicensis.* *Hyla brunnea* differs distinctly from both *septentrionalis* and *dominicensis* in its cranial architecture and throat myology.

Osteologically, the *septentrionalis* group seems to be most closely allied with *Osteocephalus,* a widespread Amazonian genus recently reviewed by Trueb and Duellman (1971). Members of this genus tend to be moderately large, lowland generalists, which are primarily found at elevations below 500 meters, but do ascend the Amazonian slopes of the Andes to elevations of 1800 meters. Like the *septentrionalis* group, members of *Osteocephalus* are characterized by broad skulls which are exostosed with a tendency towards co-ossification. The basic cranial architecture of the two groups is the same; many details are similar, including the patterns of dermal sculpturing, the pterygoids, prevomers and dermal sphenethmoids. The body proportions are similar, as is the hand and foot morphology. Two principal differences prevail between these two groups. *Osteocephalus,* like the majority of Neotropical hylids, has an undifferentiated intermandibularis muscle. Unlike most other hylids, including the *septentrionalis* group, the vocal sacs of *Osteocephalus* are paired, posterior in position and when inflated, protrude posteroventral or posterolateral to the angles of the jaws. It has been suggested that both paired vocal sacs and the development of a supplementary apical slip to the intermandibularis represent evolutionary specializations which are restricted in occurrence (Tyler, 1971). In view of the similarities of *Osteocephalus* and the *septentrionalis* group, it seems plausible to suggest that they may have had a common South American ancestor characterized by generalized throat musculature and moderately heavy cranial ossification with a tendency toward exostosis and casquing. Such an ancestor may have invaded the West Indies and evolved the derived pattern of throat musculature characteristic of the *septentrionalis* group. Subsequent isolation and evolution of an ancestral stock on Jamaica, Hispaniola, and Cuba may well have given rise to each of these three closely related species.

The extra- and intra-Antillean relationships of *lichenata* are perplexing. The species shares a great many external features and characters of axial morphology as well as some features of the vocal apparatus with *vasta,* as pointed out above. However, the cranial architecture of *lichenata* is completely unlike that of *vasta.* Furthermore, these two species are widely divergent ecologically; *lichenata* is a tree cavity dweller which breeds exclusively in bromeliads. The skull of *lichenata* is most similar to those of the genus *Trachycephalus,* a South American group which apparently is allied closely with the generalized and widespread *Osteocephalus* (Trueb, 1970). The similarities of cranial structure of *lichenata* and *Trachycephalus* are striking. Both have broad skulls which are heavily casqued and co-ossified with the same pattern of dermal sculpturing. The prevomers are similar, bearing teeth on curved elevations. The palatines are well developed, and each bears a prominent transverse ridge. The anterior pterygoid ramus has a broad maxillary articulation which tends to extend to the midlevel of the orbit, and the parasphenoid alae are perpendicularly oriented to the long axis of the bone. The principal area of difference involves cranial ossification. The dermal roofing bones of *Trachycephalus* are heavily ossified; consequently internal suspensory and bracing elements (pterygoid and palatine) tend to be reduced (*e.g.*, no medial articulation of the pterygoid). In contrast, the dermal roofing elements of *lichenata* are less well developed and the palatine and pterygoid are robust, fully articulated bones. Furthermore, the cultriform process of the parasphenoid is exceedingly short in *lichenata* (see Trueb, 1970, for figure and osteological descriptions of *Trachycephalus*). The vertebral columns of *Trachycephalus* are characterized by subequal lengths of transverse processes and widely expanded sacral diapophyses in contrast to *lichenata.* Like the latter species, the intermandibularis muscle is undifferentiated in *Trachycephalus,* but basically similar to *Osteocephalus* and, unlike *lichenata,* the vocal sacs are paired and lateral.

In view of these conflicting suites of characters, the following conclusions can be drawn concerning the relationships of *lichenata.* 1) Because of differences in throat myology and axial morphology (see Analysis of Characters), *lichenata* cannot be derived from the *septentrionalis* group. To assume that *lichenata* may have been derived from an ancestral stock of this group would require that either the differentiated intermandibularis was independently evolved three times or that *lichenata* developed an undifferentiated intermandibularis from the specialized, differentiated muscle. Neither assumption is especially parsimonius. 2) The structure of the vocal sac apparatus in *lichenata* precludes its being derived from either *Osteocephalus* or *Trachycephalus;* however, the structure of the intermandibularis links *lichenata* more closely with these genera than to members of the *septentrionalis* group.

Apparently, *lichenata* represents a separate invasion of the West Indies by a primitive stock related to the *Osteocephalus-septentrionalis* complex. Although both the *septentrionalis* and *lichenata* ancestral lines retained the primitive subgular vocal sacs, the ancestral *septentrionalis* line was distinguished by differentiation of the intermandibularis. The resemblances of the crania of *Trachycephalus* and *lichenata* may be accounted for by a common ancestral stock and parallel evolution of the frogs which have taken up a similar arboreal mode of existence.

SYSTEMATIC ACCOUNTS

The close affinities of the members of the *septentrionalis* group and their distinctiveness from all other Neotropical hylids suggest that these frogs have undergone considerable evolution in the isolation of the Greater Antilles and should be warranted generic recognition apart from *Hyla.* Fitzinger (1843) applied the generic name *Osteopilus* to *Trachycephalus marmoratus* Duméril and Bibron. Because *Osteopilus* is the earliest available name, the members of the *septentrionalis* group are herewith allocated to this genus.

Osteopilus Fitzinger, 1843

Osteopilus Fitzinger, 1843:30 [Type species.—*Trachycephalus marmoratus* Bibron, 1842, in Ramón de la Sagra (=*Hyla septentrionalis* Duméril and Bibron), by monotypy; *nec Hyla marmorata* (Laurenti, 1768)].

Diagnostic definition.—1) Skull slightly longer than broad, or as long as broad; 2) dermal roofing bones of skull well ossified, exostosed, and co-ossified; 3) prenasal and internasal bones absent; 4) dermal sphenethmoid present; 5) dentigerous processes of prevomers large, curved, moderately to closely positioned, and bearing a single row of teeth; 6) cultriform process of parasphenoid of normal length, terminating anteriorly just posterior to the level of the palatines; 7) vocal sac single and subgular, confined to position above interhyoideus muscle; 8) submentalis muscle moderate in size and araphic; 9) intermandibularis muscle differentiated to form supplementary apical elements; 10) fibers of intermandibularis muscle attach to posterolateral portions of submentalis muscle; 11) protractor cloacae muscle fibers extend inferiorly to ventral surface of ischial ridge; 12) tympanum large, 63-77 percent of diameter of eye; 13) finger and toe discs large and round; 14) nuptial excrescences present in breeding males; 15) inner metatarsal tubercle not modified for digging; 16) no fringes on hind or forelimbs; 17) total width of sacrum less than total width of presacral vertebra III; 18) sacral diapophyses moderately dilated; 19) transverse processes of posterior presacral vertebrae subequal in width; 20) angle between ilial shaft and preacetabular margin obtuse.

Content.—As defined here, the genus contains three known species—*Osteopilus brunneus* (Gosse), *O. dominicensis* (Tschudi), and *O. septentrionalis* (Duméril and Bibron).

Description.—Refer to section on comparative morphology.

Distribution.—The Greater Antilles, including Cuba, Jamaica, Hispaniola, Puerto Rico, and Isle of Pines, southern penisular Florida, and the Bahama islands. The genus is most common at lowland localities, although it does occur at moderate elevations (1500 m) in the highlands of Jamaica and Hispaniola.

Osteopilus brunneus (Gosse) new combination

Hyla brunnea Gosse, 1851:361 [Type not designated; type locality Savanna-la-Mar, Parish of Westmoreland, Jamaica].

Trachycephalus scutigerus Cope, 1863:45 [Holotype.—United States National Museum 6268 (now apparently lost) from "Jamaica"; Prof. C. B. Adams, collector]. Synonymy *fide* Dunn (1926:125).

Hyla septentrionalis brunnea—Barbour, 1937:81.

Diagnosis.—1) Size moderate, sexual dimorphism extreme; maximum observed snout-vent length in males 48.1 mm (mean 45.5 mm), in females, 70.0 mm (mean 60.5 mm); 2) skin on dorsum smooth except for scattered, small, round tubercles on forearm; 3) ventral skin finely granular on posterior half of abdomen; scattered, small tubercles around cloaca; 4) fingers one-fourth webbed; 5) numerous tiny supernumerary tubercles present on hand; 6) outer palmar tubercle absent; 7) nuptial excrescence of males a proliferation of small, keratinous granules; 8) tarsal fold absent; 9) toes three-quarters webbed; 10) moderate number of plantar supernumerary tubercles; 11) nostrils slightly protuberant; 12) skull longer than broad; 13) parasphenoid alae posterolaterally oriented to longitudinal axis of skull; 14) medial ramus of pterygoid narrowly separated from parasphenoid ala and with firm articulation with otic capsule; 15) anterior ramus of pterygoid articulating with maxillary at mid-level of orbit; 16) prevomerine dentigerous processes strongly curved, narrowly separated medially; 17) sacral diapophyses moderately dilated (*ca.* 41°; anterior sacral angle *ca.* 82°; posterior sacral angle *ca.* 57°); 18) interhyoideus muscle without lobes; 19) intermandibularis muscle with slender, median aponeurosis; 20) vocal sac aperture a moderate slit; 21) anterior cornu of hyoid lacking anterolateral lobe; 22) larvae with long tail, reduced caudal fins, incomplete labial disc, notched lower beak, and toothrow pattern of 1/0.

Osteopilus brunneus can be distinguished readily from the other two species in the genus by the shape of its snout, which is clearly truncate in lateral profile, terminal nostrils, smooth gular skin, finely granular abdominal skin, and absence of clearly defined transverse bars on the forearms.

Distribution.—This species is endemic to Jamaica where it is widespread at elevations below 1500 m.

Remarks.—Although *Osteopilus brunneus* has been mentioned frequently in the literature, useful accounts are few and widely scattered. Gosse (1851:361) provided notes on the natural history of the species; these were summarized and augmented by Barbour (1910:288) and Dunn (1926:125). Dunn described the call, preferred habits and sites of egg deposition, and figured the larvae and larval mouthparts (1926: Pl. 1, Fig. 2; Pl. 2, Fig. 2). The best systematic accounts are those of Barbour (*loc. cit.*) and Lynn, in Lynn and Grant (1940:19-22). Included in the latter is information on colors in preservative and in life and their variation, comments on size, variation, and statements of habits, habitat, and distribution. Lynn, in Lynn and Grant (1940:Pl. 1) also provided semidiagrammatic drawings of *brunneus.* The species was illustrated also by Noble (1931:89, Fig. 28B). Discussion and comment on the relationships of *brunneus* are available in Dunn (1926), Noble (1927), and Duellman (1970). The most recent account of *brunneus* is provided by Schwartz and Fowler (1973). Although they acknowledged that specimens of this species are found most frequently in bromeliads, the authors also reported collecting individuals from leaves of shrubs and sides of trees (up to 2.1 m above the ground), and from the ground itself. The maximum snout-vent length they observed in male *brunneus* is 50.6 mm (mean, 45.6 mm; n=25), and in female *brunneus*, 78.5 mm (mean, 65.7 mm; n=25).

Osteopilus dominicensis (Tschudi) new combination

Hypsiboas dominicensis Tschudi, 1838:30 [Syntypes.—Museum National d'Histoire Naturelle (Paris) 4614 (four specimens) from "Saint-Dominque"; presented by M. Alexandre Ricord].
Trachycephalus dominicensis—Duméril and Bibron, 1841:540.
Trachycephalus ovatus Cope, 1863:44 [Holotype.—Museum of Comparative Zoology (Harvard) 1518 from near Jérémie, Haiti; purchased from D. F. Weinland, 1859]. Synonymy *fide* Boulenger (1882:369).
Hyla ovata—Boulenger, 1882:369 (part).
Hyla dominicensis—Boulenger, 1882:370 (part).
Hyla (Trachycephalus) ovata—Fischer, 1888:44.
Hyla (Trachycephalus) dominicensis—Meerwarth, 1901:40.
Hyla septentrionalis dominicensis—Barbour, 1937:81.
Hyla dominicensis dominicensis—Mertens, 1938:332.
Hyla dominicensis—Cochran, 1941:13.

Diagnosis.—1) Size moderately large, sexual dimorphism extreme; maximum observed snout-vent length in males 63.8 mm (mean 57.8 mm), in females 98.7 mm (mean 76.8 mm); 2) skin on dorsum smooth; 3) ventral skin of throat, abdomen, and posteroventral surfaces of thighs coarsely granular; 4) fingers one-fourth webbed; 5) numerous, tiny supernumerary tubercles present on hand; 6) outer palmar tubercle present; 7) nuptial excrescence of males a flat, keratinous pad; 8) tarsal fold absent; 9) toes three-quarters webbed; 10) few plantar supernumerary tubercles; 11) nostrils slightly protuberant; 12) skull slightly longer than broad; 13) parasphenoid alae perpendicularly oriented to longitudinal axis of skull; 14) medial ramus of pterygoid narrowly separated from parasphenoid, but not articulating with otic capsule; 15) anterior ramus of pterygoid articulating with maxillary at posterior level of orbit; 16) prevomerine dentigerous processes moderately curved, narrowly separated medially; 17) sacral diapophyses moderately dilated (*ca.* 41°; anterior sacral angle *ca.* 74°; posterior sacral angle *ca.* 65°); 18) interhyoideus muscle with postmandibular lobes; 19) intermandibularis muscle without median aponeurosis; muscles meet at tendinous raphe; 20) vocal sac aperture a small orifice; 21) anterior cornu of hyoid with anterolateral lobe; 22) larvae with short tail, extensive caudal fins, incomplete labial disc, notched lower beak, and tooth-row pattern of 2/5.

Osteopilus dominicensis can be distinguished from *O. brunneus* by the shape of its snout, which is sloping in lateral profile, and by the coarse granularity of its gular and abdominal skin. It differs from *septentrionalis* in having more webbing between the fingers and toes, and from both *septentrionalis* and *brunneus* in the presence of a distinct outer palmar tubercle.

Distribution.—This species is endemic to Hispaniola where it is found from the coastal lowlands to moderate elevations (up to 1500 m) in the foothills and on the plateaus.

Remarks.—Although *dominicensis* was named by Tschudi (1838), the first useful description to appear was that of Duméril and Bibron (1841:540-541). Save for an illustration of the adult (Noble, 1931:89, Fig. 28 D) and the larva and larval mouthparts (Noble, 1927, Pl. IX, Fig. A), no new information was published on *dominicensis* until Mertens (1939:34-35) reported on color variation, distribution, habitat, life history, and larval characteristics. A brief account of this species, including the description of an adult female, remarks on variation in adults and a diagnostic series of illustrations was provided by Cochran (1941:13-17, Fig. 3). Lynn (1958:154-155) commented on color variation in adults and the production of irritating skin secretions by *dominicensis,* and Williams, *et. al.* (1963:315) reported phragmotic behavior in the species. Egg deposition and tadpoles were described by Noble (1927:95). Discussion of the relationships of *dominicensis* are available in Dunn (1926), Noble (1927), Myers (1950), and Duellman (1970).

Osteopilus septentrionalis (Duméril and Bibron) new combination

Trachycephalus marmoratus Duméril and Bibron, 1841:538. [Holotype.—Museum National d'Histoire Naturelle (Paris) 4612, adult female from "Cuba"; donated by Ramón de la Sagra and Henri Delaroche]. Preoccupied by *Hyla marmorata* (Laurenti, 1768:29).

Hyla septentrionalis Duméril and Bibron, 1841:538. Substitute name for *Trachycephalus marmoratus.*

Trachycephalus insulsus Cope, 1863:43 [Syntypes.—United States National Museum 12166 (adult male) and 167237 (adult female, formerly USNM 6266) from "Cuba"; collected by Felipe Poey]. Synonymy *fide* Boulenger (1882:368).

Trachycephalus wrightii Cope, 1863:45 [Holotype.—United States National Museum 5174 (adult female) from "District of Guantanamo, southeastern Cuba" (Oriente Province); collected by Charles Wright]. Synonymy *fide* Boulenger (1882:368).

Hyla schebestana Werner, 1917:36 [Holotype.—presumably destroyed in World War II, formerly Zoologisches Museum (Hamburg), no number, an adult female from "Cuba"; donated by "Herrn Apotheker Sebesta"]. Synonymy *fide* Duellman and Cromble (1970:1).

Hyla septentrionalis septentrionalis.—Barbour, 1937:81.

Hyla dominicensis septentrionalis.—Mertens, 1938:333.

Hyla dominicensis insulsa.—Mittleman, 1950:26.

Hyla dominicensis.—Peterson, Garrett, and Lantz, 1952:63.

Hyla insulsa.—Jaume, 1966:15.

Hyla septentrionalis.—Duellman and Crombie, 1970:92.1.

Diagnosis.—1) Size moderately large, sexual dimorphism extreme; average snout-vent length in males 55.3 mm, in females, 75.2 mm; 2) skin on dorsum with scattered tubercles; 3) ventral surfaces granular, tubercles absent around cloaca; 4) fingers basally webbed; 5) moderate number of low, round supernumerary tubercles present on hand; 6) outer palmar tubercle absent; 7) nuptial excrescence of males a flat, horny pad; 8) weak tarsal fold present; 9) toes about two-thirds webbed; 10) few plantary supernumerary tubercles; 11) nostrils slightly protuberant; 12) skull slightly longer than broad; 13) parasphenoid alae posterolaterally oriented to longitudinal axis of skull; 14) medial ramus of pterygoid widely separated from parasphenoid and bearing only a weak articulation with the otic capsule; 15) anterior ramus of pterygoid articulating with maxillary at posterior level of orbit; 16) prevomerine dentigerous processes moderately curved and separated medially; 17) sacral diapophyses dilated (*ca.* 57°; anterior sacral angle *ca.* 70°; posterior sacral angle *ca.* 53°); 18) interhyoideus muscle with small, supramandibular lobes; 19) intermandibularis muscle without median aponeurosis; muscles meet as tendinous raphe; 20) vocal sac aperature a small orifice; 21) anterior cornu of hyoid with anterolateral lobe; 22) larvae with moderately long tail, extensive caudal fins, incomplete labial disc, notched lower beak, and tooth-row pattern of 2/4.

Osteopilus septentrionalis is distinguished from both *dominicensis* and *brunneus* by its tuberculate dorsal skin and basal webbing between the fingers. The species differs from *brunneus* by the shape of the snout, which is sloping in lateral profile in *septentrionalis.* It differs from *brunneus* by the shape of the snout, which is sloping in lateral profile in *septentrionalis.* It differs from *dominicensis* by the absence of an outer palmar tubercle.

Distribution.—The species is widespread at low and moderate elevations throughout Cuba and on the Isle of Pines. *Osteopilus septentrionalis* also occurs on the Cayman Island (Grand Cayman, Little Cayman, and Cayman Brac) and on some of the Bahama Islands northwest of the Mayaguana Passage (Little Bahama Bank, Grand Bahama Bank, San Salvador, Rum, Crooked, and Acklin's islands). The species occurs on southern, peninsular Florida and has been introduced to Great Inagua Island and Puerto Rico.

Remarks.—A complete review of the nomenclatural history, and pertinent literature including a description of the species, its fossil record and distribution was provided by Duellman and Crombie (1970:92.1-92.4). See Cochran (1961) for black and white and color photographs of *septentrionalis.*

It is clear that *lichenata* is a highly specialized and distinctive frog which is neither closely allied to any member of the West

Indian hylid fauna nor any known representative from Central or South America. Because of its peculiar characteristics and endemism to Jamaica, we feel that this species should be accorded generic recognition.

Calyptahyla new genus

Type species.—Trachycephalus lichenatus Gosse, 1851.

Diagnostic definition.—1) Skull broader than long; 2) dermal roofing bones of skull well ossified, exostosed, and co-ossified; 3) prenasal and internasal bones absent; 4) dermal sphenethmoid present; 5) dentigerous processes of prevomers large, straight, narrowly separated medially and bearing a single row of teeth; 6) cultriform process of parasphenoid short, terminating anteriorly at mid-level of orbit; 7) vocal sac single and subgular; confined to position above interhyoideus muscle; 8) submentalis moderate in size and araphic; 9) intermandibularis muscle not differentiated; 10) fibers of intermandibularis muscle attach to posterolateral part of submentalis muscle; 11) protractor cloacae muscle fibers extend inferiorly to ventral surface of ischial ridge; 12) tympanum large, 68 percent or more of diameter of eye; 13) finger and toe discs large and round; 14) presence or absence of nuptial excrescences in males unknown; 15) inner metatarsal tubercle not modified for digging; 16) fringes present on hind and forelimbs; 17) total width of sacrum greater than total width of presacral vertebra III; 18) sacral diapophyses narrowly dilated; 19) transverse processes of posterior presacral vertebrae uniform in width; 20) angle between ilial shaft and preacetabular margin acute.

Content.—One species, *Trachycephalus lichenatus* Gosse.

Description.—Refer to section on comparative morphology.

Distribution.—This genus is endemic to Jamaica.

Etymology.—The generic name is derived from the Greek word *kalypto,* meaning to conceal or hide, and the Greek name *Hylas* from which the vocative *Hyla* is derived. Thus the name *Calyptahyla* (feminine) alludes to the secretive nature of this frog which has been heard to call so often in the dense woodlands of Jamaica and has been collected so infrequently.

Calyptahyla lichenata (Gosse) new combination

Hyla crucialis Harlan, 1826:64 [Type not designated; type locality "Jamaica"]. *Nomen oblitum.*

Trachycephalus lichenatus Gosse, 1851:362 [Type not designated; type locality "the summit of Bluefields Mountain, Jamaica"].

Trachycephalus anochlorus Gosse, 1851:364 [Type not designated; type locality "Jamaica"]. Synonymy *fide* Boulenger (1882:370).

Hyla lichenata.—Boulenger, 1882:370.

Diagnosis.—1) Size large, sexual dimorphism extreme; maximum observed snout-vent length in males, 92.6 mm, in females, 122 mm; 2) skin on dorsum heavily tuberculate; 3) ventral skin granular with paracloacal folds; 4) fingers one-fourth webbed; 5) moderate number of low, round supernumerary tubercles on hand; 6) outer palmar tubercle absent; 7) presence or absence of nuptial excrescence unknown; 8) tarsal fold absent; 9) toes three-fourths webbed; 10) plantar supernumerary tubercles few in number; 11) nostrils slightly protuberant; 12) skull broader than long; 13) parasphenoid alae perpendicularly oriented to longitudinal axis of skull; 14) medial ramus of pterygoid articulating with otic capsule and distal edge of parasphenoid ala; 15) anterior ramus of pterygoid articulating with maxillary at mid-level of orbit; 16) prevomerine dentigerous processes straight, oriented at a slight angle to one another; and narrowly separated medially; 17) sacral diapophyses narrowly dilated (*ca.* 31°; anterior sacral angle *ca.* 81°; posterior sacral angle *ca.* 68°); 18) interhyoideus muscle without lobes; 19) intermandibularis muscle with slender, median aponeurosis; 20) vocal sac aperture a small orifice; 21) anterior cornu of hyoid without anterolateral lobe; 22) larva with relatively short tail, reduced caudal fins, incomplete labial disc, notched lower beak and tooth-row pattern of 1/0.

Calyptahyla lichenata can be distinguished from any other known species of Neotropical hylid by the following combination of characters: 1) single subgular vocal sac; 2) rugosely sculptured, co-ossified cranium lacking labial flanges; and 3) heavily tuberculate dorsum.

Distribution.—This species is endemic to Jamaica and widely distributed in dense forest throughout the island at low and moderate elevations.

Remarks.—Little is known about this immense casque-headed frog. The most complete account of the natural history and habits of *lichenata* was given by Dunn (1926:127-129). His descriptions were based largely on observations of Mr. E. Stuart Panton who described the call of *lichenata* and noted the preferred perch of this species in hollow trees or hollow branches of trees. The tadpole and larval mouthparts were illustrated by Dunn (1926:Pl. 1, Fig. 1; Pl. 2, Fig. 1). The adult was figured by Noble (1931:89, Fig. 28 A). The best illustrations and only complete systematic account available is that of Lynn, in Lynn and Grant (1940:22-24, Pl. II, Fig. 3). Included in the latter work are complete descriptions, comments on variation, and summaries of earlier literature. Discussion of the relationships of *Calyptahyla lichenata* may be found in Dunn (1926), Noble (1927), Myers (1950), and Duellman (1970). It should be noted that an application has been submitted to the International Commission on Zoological Nomenclature (Trueb, 1972) requesting suppression of the specific name *crucialis*, a *nomen oblitum* of 145 years. For the most recent account of this species refer to Schwartz and Fowler (1973).

The remaining five species of Greater Antillean hylids seem to be allied closely with the mainland *Hyla.* This suggests that either these frogs are more recent derivatives of mainland ancestors, or that in isolation, evolutionary change has had less dramatic effects on these phylogenetic lines than on *Osteopilus* and *Calyptahyla.* We think that until new evidence suggests otherwise, *vasta, marianae, wilderi, heilprini,* and *pulchrilineata* should be retained in the genus *Hyla.* A diagnostic definition of the Greater Antillean *Hyla* is provided below to distinguish members of this group from *Osteopilus* and *Calyptahyla.* For a synonymy of the genus *Hyla,* refer to Duellman (1970:173), whose arrangement has been modified only by the resurrection of *Litoria* Tschudi (Tyler, 1971).

Hyla Laurenti, 1768

Diagnostic definition.—1) Skull longer than broad, as long as broad, or broader than long; 2) dermal roofing bones poorly to moderately well ossified; not exostosed, casqued or co-ossified; 3) prenasal and internasal bones absent; 4) dermal sphenethmoid absent; 5) dentigerous processes of prevomers widely separated or not, large or small, curved or straight, usually bearing a single row of teeth; 5) cultriform process of parasphenoid of normal length, terminating anteriorly between the mid-level of the orbit and the level of the palatines; 7) if present, vocal sac single and subgular; 8) submentalis moderate in size and araphic; 9) intermandibularis not differentiated; 10) fibers of intermandibularis with or without attachment to posterolateral part of submentalis muscle; 11) protractor cloacae muscles extending inferiorly, or not, to ventral surface of ischial ridge; 12) tympanum moderately large, 50.5-61.0 percent of diameter of eye; 13) finger and toe discs large and round; 14) nuptial excrescences usually present in breeding males; 15) inner metatarsal tubercle not modified for digging; 16) no fringes on hind or forelimbs; 17) total width of sacrum more or less than total width of presacral vertebra III; 18) sacral diapophyses slightly or moderately dilated; 19) transverse processes of posterior presacral vertebrae uniform or subequal in width; 20) angle between ilial shaft and preacetabular margin varying from obtuse to acute.

Content.—As defined here, *Hyla* includes five Greater Antillean species—*Hyla vasta* Cope, *H. pulchrilineata* Cope, *H. heilprini* Noble, *H. marianae* Dunn, and *H. wilderi* Dunn.

Description.—Refer to section on comparative morphology.

Distribution.—Within the Greater Antilles, members of this genus are known only from Jamaica (*marianae* and *wilderi*) and Hispaniola (*vasta, pulchrilineata,* and *heilprini*).

Hyla vasta Cope

Hyla vasta Cope, 1871:219 [Holotype.—Academy of Natural Sciences (Philadelphia) 2097 from "Haiti, San Domingo"; collected by Dr. William M. Gabb].

Diagnosis.—1) Size large, sexual dimorphism extreme; maximum observed snout-vent length in males 108.8 mm (mean 96.7 mm), in females 141.9 mm (mean 136.9 mm); 2) skin on dorsum strongly tuberculate; 3) ventral skin coarsely granular; tubercles around cloaca; 4) fingers three-fourths webbed; 5) very few, indistinct supernumerary tubercles on hand; 6) outer palmar tubercle present; 7) nuptial excrescence in breeding males a flat, keratinous pad; 8) tarsal fold absent; 9) toes fully webbed; 10) plantar supernumerary tubercles absent; 11) nostrils strongly protuberant; 12) skull broader than long; 13) parasphenoid alae posterolaterally oriented to longitudinal axis of skull; 14) medial ramus of pterygoid articulating with otic capsule, widely separated from parasphenoid ala; 15) anterior ramus of pterygoid articulating with maxillary near mid-level of orbit; 16) prevomerine dentigerous processes large, slightly curved, having a moderate medial separation and a single row of teeth medially and a double row laterally; 17) sacral diapophyses narrowly dilated (*ca.* 20°; anterior sacral angle *ca.* 103°; posterior sacral angle *ca.* 57°); 18) interhyoideus muscle with postmandibular lobes; 19) intermandibularis muscle with broad, median aponeurosis; 20) vocal sac aperture a small orifice; 21) anterior cornu of hyoid without anterolateral lobe; 22) larva with short, thick tail, extensive caudal fins, complete labial disc, notched lower beak, and tooth-row pattern of 2/5.

Hyla vasta is distinguished easily from all other West Indian hylids by its size, tuberosity, and lack of a casqued, co-ossified cranium. It is unique among the Greater Antillean *Hyla* in having a sacrum which is wider than the third presacral vertebra.

Distribution.—This species is endemic to Hispaniola where it occurs from sea level to an elevation of approximately 1728 m (Schwartz, pers. com.).

Remarks.—Although Noble (1923a; 1923b) wrote two popular accounts describing his quest for the giant tree frog, *Hyla vasta,* the first noteworthy information published about this frog, its habits, habitats and life history is that of Mertens (1939:35-36). A standardized systematic account and illustrations of the species appeared in Cochran (1941:19-22, Fig. 5). Photographs of this remarkable frog in life were provided by Noble (1923a; 1923b). A drawing of the species appeared in Noble (1931:89, Fig. 28C), and the tadpole and larval mouthparts were illustrated by Noble (1927: Pl. IX, Fig. B). Discussion of the relationships of *Hyla vasta* may be found in Dunn (1926), Noble (1927), Myers (1950), and Duellman (1970).

Hyla pulchrilineata Cope

Hyla pulchrilineata Cope, 1869:163 [Holotype.—Academy of Natural Sciences (Philadelphia) 14495 from "east St. Domingo"; collected by Dr. William M. Gabb].

Diagnosis.—1) Size moderately small, some sexual dimorphism; maximum observed snout-vent length in males 39.5 mm (mean 31.6 mm), in females 42.8 mm (mean 40.1 mm); 2) skin on dorsum smooth; 3) ventral skin slightly granular on belly and thighs; no tubercles around cloaca; 4) fingers webbed basally; 5) palmar supernumerary tubercles absent; 6) two round, outer palmar tubercles present; 7) nuptial excrescence in breeding males a flat, horny pad; 8) tarsal fold absent; 9) toes two-thirds webbed; 10) few plantar supernumerary tubercles; 11) nostrils not protuberant; 12) skull longer than broad; 13) parasphenoid alae slightly posterolaterally oriented to longitudinal axis of skull; 14) medial ramus of pterygoid not articulating with otic capsule, and widely separated from parasphenoid ala; 15) anterior ramus of pterygoid articulating with maxillary at posterior level of orbit; 16) prevomerine dentigerous processes moderate sized, straight, and having a narrow medial separation and a single row of teeth; 17) sacral diapophyses dilated (*ca.* 48°; anterior sacral angle *ca.* 77°; posterior sacral angle *ca.* 55°); 18) interhyoideus muscle with small, supramandibular lobes; 19) intermandibularis muscles lacking aponeurosis, muscles meet at tendinous raphe; 20) vocal sac aperture a moderate slit; 21) anterior cornu of hyoid with anterolateral lobe; 22) larva unknown.

The absence of a dermal submental gland and prepollical spine, and the smaller size of *pulchrilineata* readily distinguish this species from *heilprini.* The characteristic dorsal pattern of stripes and the narrow head of *pulchrilineata* differentiate it from *marianae* and *wilderi.*

Distribution.—Hyla pulchrilineata is endemic to Hispaniola where it is widespread occurring from the coastal lowlands to an elevation of approximately 636 m on the island (Schwartz, pers. com.).

Remarks.—There is a paucity of published information on *pulchrilineata.* Although the calling sites and voice of this species are known (Schwartz, pers. com.), no tadpoles have been associated with the species. The best available systematic account of *pulchrilineata* is that provided by Cochran (1941:17-19 and Fig. 4). She included a description, comments on variation and an illustration. A photograph appeared in Noble (1923a:115).

Hyla heilprini Noble

Hyla heilprini Noble, 1923c:1 [Holotype.—American Museum of Natural History 11401, adult male, from Lo Bracita, Prov. Pacificador, Dominican Republic; collected on August 20, 1922, by G. K. Noble].

Diagnosis.—1) Size moderate, no sexual dimorphism in size noted; maximum observed snout-vent length in males 54.3 mm (mean 49.4 mm), in females 52.0 mm (mean 49.3 mm); 2) skin on dorsum smooth; 3) ventral skin coarsely granular on belly and thighs; no tubercles around cloaca; 4) fingers one-half webbed; 5) numerous small, palmar supernumerary tubercles; 6) outer palmar tubercles absent; 7) breeding males lacking a nuptial excrescence; but having an extruding prepollex and propollical spine; 8) tarsal fold absent; 9) toes fully webbed; 10) plantar supernumerary tubercles absent; 11) nostrils not protuberant; 12) skull broader than long; 13) parasphenoid alae posterolaterally oriented to longitudinal axis of skull; 14) medial ramus of pterygoid articulating with otic capsule and separated from parasphenoid; 15) anterior ramus of pterygoid articulating with maxillary at mid-level of orbit; 16) prevomerine dentigerous processes moderate sized, slightly curved, and having a wide medial separation and a single row of teeth on each; 17) sacral diapophyses dilated (*ca.* 45°; anterior sacral angle *ca.* 77°; posterior sacral angle *ca.* 58°); 18) interhyoideus muscle without separate lobes; 19) intermandibularis muscles with broad median aponeurosis; 20) vocal sac aperture an elongate slit; 21) anterior cornu of hyoid without anterolateral lobe; 22) larva with thick, short, muscular tail, extensive caudal fins, complete labial disc, notched lower beak and tooth-row pattern of 6/9.

Hyla heilprini is distinguished uniquely from all other West Indian hylids by either one of two characters—presence of a dermal submental gland and/or presence of a prepollical spine. Moreover, it is the only species having an elongate vocal slit aperture and cloacal musculature characterized by a short protractor muscle which terminates above the proximal end of the gracilis minor.

Distribution.—The species is endemic to Hispaniola, where it is widespread (occurring near torrential streams) between elevations of sea level and approximately 1728 m (Schwartz, pers. com.).

Remarks.—Noble's (1923c) original description of *Hyla heilprini* is probably the most comprehensive of the type descriptions provided for any of the Greater Antillean species. In her account of *heilprini,* Cochran (1941:22-24) offered only brief remarks on variation in addition to Noble's description, which is quoted in a large part. She also illustrated the adult (Cochran, 1941:23; Fig. 6). The larva and larval mouthparts are figured by Noble (1927:Pl. IX, Fig. C), and a photograph of the adult appeared in Noble (1923b: 119). Discussion of the relationships of *heilprini* may be found in Dunn (1926) and Noble (1927).

Hyla marianae Dunn

Hyla marianae Dunn, 1926:129 [Holotype.—Museum of Comparative Zoology (Harvard) 11122 from Spauldings, Clarendon Parish (altitude 2900 feet); collected in August, 1925, by E. R. Dunn].

Diagnosis.—1) Size moderately small, sexual dimorphism marked; maximum observed snout-vent length in males 33.1 mm (mean 28.0 mm), in females 39.6 mm (38.7 mm); 2) skin on dorsum smooth; 3) ventral skin weakly granular; tubercles present around cloaca; 4) fingers basally webbed; 5) palmar supernumerary tubercles absent; 6) outer palmar tubercle absent; 7) nuptial excrescence in breeding males a flat, horny pad; 8) tarsal fold absent; 9) toes one-third webbed; 10) few, round, plantar supernumerary tubercles present; 11) nostrils not protuberant; 12) skull as broad as long; 13) parasphenoid alae posterolaterally oriented to longitudinal axis of skull; 14) medial ramus of pterygoid articulating with otic capsule, and widely separated from parasphenoid; 15) anterior ramus of pterygoid articulating with maxillary at level of posterior half of orbit; 16) prevomerine dentigerous processes moderately small, straight, and having a wide medial separation and a single row of teeth on each; 17) sacral diapophyses moderately dilated (*ca.* 43°; anterior sacral angle *ca.* 75°; posterior sacral angle *ca.* 62°); 18) interhyoideus muscle without postmandibular lobes; 19) intermandibularis muscles with slender, median aponeurosis; 20) vocal sac aperture absent; 21) anterior cornu of hyoid with anterolateral lobe; 22) larva with long tail, reduced caudal fins, complete labial disc, unnotched lower beak and toothrow pattern of 0/0.

Hyla marianae most closely resembles *H. wilderi* from which it can be distinguished by its larger size, distinct tympanum, and presence of basal webbing between the fingers and a distinct outer metatarsal tubercle on the foot. The absence of a dermal submental gland and prepollical spine differentiate this species from *heilprini.* Superficially, *marianae* might be most easily confused with *pulchrilineata* which, in contrast to *marianae,* is characterized by a pattern of narrow dorsal stripes and a head which is distinctly longer than broad.

Distribution.—This species is endemic to Jamaica where it is found in dense and scattered deciduous forest between elevations of 122 and 895 m (Schwartz and Fowler, 1973).

Remarks.—Apart from Dunn's (1926:129) brief species description and the systematic account of Lynn, in Lynn and Grant (1940: 27-28), there is virtually no published information on *marianae.* The larva and larval mouthparts were illustrated by Dunn (1926: Pl. 1, Fig. 3; Pl. 2, Fig. 3) and semidiagrammatic drawings of the adult were provided by Lynn and Grant (1940:Pl. III, Fig. 5). Discussion of the relationships of *marianae* may be found in Dunn (1926) and Noble (1927). More recently, Schwartz and Fowler (1973) provided a systematic account of this species.

Hyla wilderi Dunn

Hyla wilderi Dunn, 1925:161 [Holotype.—Museum of Comparative Zoology (Harvard) 10500, an adult male from Moneague, Saint Ann Parish, Jamaica (altitude 1200 feet); collected in March, 1925, by Dr. and Mrs. H. H. Wilder].

Hyla shrevei Taylor, 1952:1 [Holotype.—Museum of Comparative Zoology (Harvard) 26769, male, from "La Loma, Chiriquicito, Republica de Panama" (apparently in error); collected by E. R. Dunn and C. Duryea]. Synonymy *fide* Goin (1959:340).

Diagnosis.—1) Size small, little sexual dimorphism; maximum observed snout-vent length in males 27.3 mm (mean 25.8 mm), in females 28.7 mm (mean 27.3 mm); 2) skin on dorsum smooth; 3) ventral skin weakly granular; tubercules present around cloaca; 4) fingers not webbed; 5) few palmar supernumerary tubercles; 6) two outer palmar tubercles present; 7) nuptial excrescence in breeding males a group of keratinous spines; 8) tarsal fold absent; 9) toes one-fourth webbed; 10) few, low, rounded plantar supernumerary tubercles present; 11) nostrils not protuberant; 12) skull broader than long; 13) parasphenoid alae posterolaterally oriented to longitudinal axis of skull; 14) medial ramus of pterygoid not articulating with otic capsule, and widely separated from parasphenoid; 15) anterior ramus of pterygoid articulating with maxillary at posterior level of orbit; 16) prevomerine dentigerous processes small, patch-like, and having a wide medial separation and single row of teeth on each; 17) sacral diapophyses dilated (*ca.* 48°; anterior sacral angle *ca.* 80°; posterior sacral angle *ca.* 52°); 18) interhyoideus muscle without postmandibular lobes; 19) intermandibularis muscles with slender, median aponeurosis; 20) vocal sac aperture a moderate slit; 21) anterior cornu of hyoid without anterolateral lobe; 22) larva with relatively short tail, reduced caudal fins, complete labial disc with keratinous "spines" arranged around perimeter, unnotched lower beak, tooth-row pattern of 0/0.

Hyla wilderi can be distinguished from *marianae* by the smaller size, indistinct tympanum, absence of webbing between the fingers, and absence of an outer metatarsal tubercle in the former. Absence of a chin gland and prepollical spine differentiates this species from *heilprini*. The broader head and absence of dorsal stripes distinguishes *wilderi* from *pulchrilineata*.

Distribution.—This species is endemic to Jamaica where it is widely distributed in open woodlands between elevations of 122 and 610 m (Schwartz and Fowler, 1973).

Remarks.—A complete systematic account of *Hyla wilderi* is provided by Lynn, in Lynn and Grant (1940:25-26); he also illustrated the species (Pl. III, Fig. 4). The larva and larval mouthparts are figured by Dunn (1926:Pl. 1, Fig. 4; Pl. 2, Fig. 4). Relationships of this species are discussed by Dunn (1926) and Noble (1927). The most recent account of *wilderi* is that of Schwartz and Fowler (1973). They reported finding individuals in both arboreal and terrestrial broemliads and observed a maximum snout-vent length in males of 27.9 mm (mean, 25.5 mm; n=25) and 29.2 mm in females (mean, 26.4 mm; n=25).

ORIGIN OF THE GREATER ANTILLEAN HYLID FAUNA

Graham (1972) summarized the paleophysiography of the Caribbean Basin and noted that there is no evidence that the Greater or Lesser Antilles either were rafted to their present positions or connected to continents in the past. In the absence of contrary evidence, he assumed that the islands have maintained their characteristic arc-configuration (extending from the Yucatan Peninsula to Venezuela) throughout the Tertiary, although the spatial relationships between individual islands may have varied considerably during middle and late Tertiary times. The variation in spatial relationships supports Williams's (1969) statement that the lowest islands of the Lesser Antilles may have been submerged several times during the Pleistocene. Graham (1972) proposed that the flora of the Antilles is derived from 1) long distance dispersal of floral elements from Yucatan-northern Central America, and 2) from northern South America. In the probable absence of any inter-island land connections among the Greater Antilles, and the absence of sustained connections among the islands of the Lesser Antilles, inter-island dispersal of most forms would then depend, at least in part, upon waif dispersal by wind and water. The relatively high frequency with which rafts of sufficient size to transport plants and small animals occur in the Caribbean has been documented by King (1962).

Among the reptiles and amphibians of the Antilles, three groups have been studied extensively; these are the hylid and leptodactylid frogs, and the anoline lizards. The extensive publications of Schwartz on leptodactylid frogs are taxonomic and are not concerned with the distributional patterns, ecology, and zoogeographic history of the group. In contrast, the studies of Williams (*e.g.*, 1969, 1972) delve into the phylogenetic relationships and zoogeographic history (particularly as it relates to inter-island dispersal, colonization, competition, coexistence, and speciation) of the numerous anoline lizards of the Antilles. In view of Williams' work especially, we are tempted to compare our zoogeographic conclusions with his. As these conclusions relate to our hypothesis, Williams states (pers. com.) that with respect to anoline lizards he believes, ". . . that the Greater Antilles have received relatively few invaders, usually one per major group [see Williams, 1969] and that complex radiations involving considerable island interchange have occurred." He further postulates that there have been only two invasions of *Anolis*—"From two colonists—one to Puerto Rico or Hispaniola—I would derive a fauna of *ca.* 70 species. I would indeed recognize two other anoline invasions, one to provide Cuba with the two species of *Chamaeleolis* and another to provide Hispaniola with *Chamaelinorops*." In considering Williams' statements with respect to our conclusions, there are several basic differences in the faunas under study that should be noted. First, we are dealing with amphibians, not reptiles. Although both groups can, and undeniably have, dispersed over water, the chances for successful dispersal and subsequent colonization in anurans are less than those for lizards for obvious structural and physiological reasons. Furthermore, among anurans of the Antilles (bufonids, leptodactylids, and hylids) the hylids are the least likely to be able to disperse successfully over water for reasons discussed beyond. Finally, we are dealing with a much smaller extant fauna, and have no way of estimating possible or probable extinctions if, in fact, they occurred. Given these limitations, we have attempted to construct a zoogeographic model compatible with the available paleophysiographic evidence, morphological evidence, and systematic conclusions resulting from this study.

The Greater Antillean hylids may have been derived reasonably from three sources—North America, northern Central America, and South America. As a possible source, North America merits the least consideration. Other than the occurrence of the Puerto Rican adventive, *Hyla cinerea,* no North American hylids occur in the Greater Antilles. Doubtless, this is a result of the fact that during much of the Cenozoic, peninsular Florida was submerged, thus greatly increasing the distance between the North American land mass and the Greater Antilles. *Osteopilus septentrionalis* apparently is a recent immigrant to southern peninsular Florida. The species may have rafted to Florida from nearby Cuba and/or the Bahamas, or it may have been introduced by man; both alternatives are feasible, and perhaps both occurred.

As Graham (1972) pointed out, the historical association of the Greater Antilles with Yucatan-Central America is enigmatic. Because of certain floral and faunal similarities, it is thought currently (Khudoley and Meyerhoff, 1971) that there was a connection between Cuba and northern Central America and that this connection may have been in the form of closely spaced island "stepping stones." If this is so, then frogs, like plants, may have dispersed by means of rafts to Cuba from Central America. Of those species for which related, mainland forms may be postulated, only *Hyla* *vasta* and *Hyla heilprini* have related taxa occurring in Central America. We have proposed that *vasta* is related to the *Hyla boans* group. The greatest diversity of this group is in South America, although three species (*boans, crepitans,* and *rosenbergi*) range into Central America as far as eastern Panamá and southeastern Costa Rica; there is an isolated population of *Hyla crepitans* at Tela, Honduras (Duellman, 1970). Similarly, a representative of the *Hyla albormarginata* group, to which *heilprini* may be related, occurs in Central America. Of the nine species comprising this group, one species, *Hyla rufitela,* occurs in the Caribbean lowlands from east-central Nicaragua to Panamá; the remaining species are South American. Thus, it is possible to assume the existence of lines ancestral to *heilprini* and *vasta* in Central America. If these ancestral anurans did disperse from Central America into the Greater Antilles, then inter-island dispersal progressed from the Yucatan-northern Central America area to Cuba or Jamaica, and thence eastward to Hispaniola. Given this dispersal route, we might anticipate finding one or more of these or related species on Jamaica or Cuba. Although such forms are unknown, it is possible that they existed from Puerto Rico, which is inhabited by only two recently introduced hylids, *Osteopilus septentrionalis* and *Hyla cinerea.* Probably the strongest argument against this proposed route of dispersal is found in the prevailing wind and ocean currents which are generally east-west rather than west-east. Under these conditions, it is highly improbable that the frogs could have successfully rafted from Central America to the Greater Antilles. However, the possibility exists that dispersal took place during the separation of North and South America at the Atrato (Bolivar) Trough at a time when ocean currents may have been substantially different. Thus ancestral *heilprini* and *vasta* may have successfully colonized Hispaniola and been excluded from Puerto Rico either by competition or inter-island ocean currents which precluded their rafting westward from Hispaniola to Puerto Rico.

A third available alternative is that some, or all, of the Greater Antillean hylids originated in South America and rafted by way of the Lesser Antilles into the Greater Antilles. At least two facts favor this hypothesis. Of all the species for which related mainland forms can be postulated (*i.e.,* all except *marianae, wilderi,* and *pulchrilineata*), the related mainland groups are most diverse in tropical South America; this includes the *Hyla boans* group, *Hyla albomarginata* group, *Osteocephalus* and *Trachycephalus.* Furthermore, the existence of substantial rafts which originated from the Orinoco and reached Barbados and St. Vincent has been documented (King, 1962). Ocean currents are such that they would favor waif dispersal in a northward or northwestward direction throughout the West Indies and Bahama Islands. This seems to be the simpler of the two possible hypotheses, save for the absence of any of the Greater Antillean frogs or related forms on the Lesser Antilles and Puerto Rico (except for *Osteopilus septentrionalis,* a recent adventive). Because of the small sizes of the Lesser Antillean islands and the presence of leptodactylids on these islands, we must assume that the hylids have been, for the most part, unsuccessful colonists (except for the member of the *Hyla rubra* complex as noted in the Introduction). For the present we must assume that competition has excluded this diverse group of species from Puerto Rico, although it seems unlikely. Despite the difficulties with this alternative, we favor South American origins of the Greater Antillean hylid fauna because the hypothesized dispersal routes are amenable with ocean and wind currents as we know them today, and because of the richness of the tropical South American frog fauna as contrasted with that of the Yucatan-northern Central American area.

Although not the largest island in the Greater Antilles, Hispaniola has extremely diverse habitats. If we assume a South American origin of the Greater Antillean hylid fauna, then Hispaniola is also nearer the mainland source of frogs than Jamaica, Cuba, or the Bahamas. Because of its size, relative distance from the mainland, and variety of habitats, we should expect a more diverse anuran fauna on Hispaniola than on the remaining islands. This, in fact, turns out to be the case. Hispaniola support 2 species of *Bufo* (Bufonidae), 1 species of *Leptodactylus* (Leptodactylidae), at least 42 species of *Eleutherodactylus* (Leptodactylidae), and 4 hylid species. Because of the degree of their morphological distinctiveness (see Analysis of Characters), the hylid species which occur on Hispaniola seem to represent four distinct phylogenetic lines, and therefore, four separate, successful invasions. Although there is distributional sympatry, the species differ in size and/or habitat preference so that interspecific competition would appear to be minimal or non-existent. There seems to be a co-adjustment of species pairs by size (Fig. 1) reminiscent of Schoener's Second Rule as stated by Williams (1972:57-58) in his discussion of the anoles of the West Indies. Both *Osteopilus dominicensis* and *Hyla pulchrilineata* appear to be generalists most common at lower elevations; however, *dominicensis* is about half again as large as *pulchrilineata. Hyla vasta* is between two and three times as large as *Hyla heilprini;* both use streams as breeding sites, although *heilprini* breed in swifter parts of the streams than *vasta.* It would seem that competition might occur between *vasta* and *dominicensis;* however, *vasta* is about one-third larger than *dominicensis,* and *dominicensis* breeds in quiet, rather than moving water.

Jamaica is much smaller than Hispaniola and, based on the suggested dispersal scheme, more distant from the mainland; thus, we should expect it to have a lower immigration rate, and therefore, fewer species (MacArthur and Wilson, 1967:22-23). Only one species of *Bufo* (Bufonidae) occurs on Jamaica, and it is an adventive (Schwartz and Fowler, 1973). In addition to the four hylids, there are 15 species of *Eleutherodactylus* (Leptodactylidae), three of which have been introduced (*op. cit.*). Although Jamaica supports the same number of hylid species as Hispaniola, the species represent three distinct phylogenetic lines and therefore, separate invasions; one of the species (*brunneus*) is closely related to *Osteopilus dominicensis* of Hispaniola. Perhaps an ancestral stock of *Osteopilus* successfully colonized Hispaniola and subsequently Jamaica, evolving into *dominicensis* and *brunneus*, respectively. Because of the distinctiveness of *Calyptahyla lichenata* from all other Antillean anurans, we think it represents a separate invasion, as does the ancestral stock of *marianae* and *wilderi*. The hylids of Jamaica are much more restricted ecologically than those of Hispaniola, although the same kind of size differential prevails (Fig. 1). Williams *et al.* (1963) suggested that at some time in the past absence of standing water on Jamaica forced the resident treefrogs to breed in bromeliads. Regardless of the operant selective factor, these four species have adapted successfully to this limited resource. The two larger species, *brunneus* and *lichenata*, use larger bromeliads for breeding. *Calyptahyla lichenata* is about one-third larger than *Osteopilus brunneus* and frequents tree-hole cavities, a habit not observed in *brunneus*. *Hyla marianae* and *H. wilderi* are one-half to one-third the size of the larger hylids and therefore use smaller bromeliads for breeding than does *lichenata* or *brunneus*. Of the two smaller hylids, *wilderi* is smaller than *marianae*. We suggest that *wilderi* evolved from a *marianae*-like ancestor in the process of adapting to life in smaller bromeliads.

Cuba is much larger than Hispaniola and Jamaica, and has far more extensive arid to semi-arid lowlands than either. Although Cuba is somewhat farther from South America than Jamaica, it is, as pointed out, much larger and has an interesting anuran fauna relative to Jamaica and Hispaniola. Five species of *Bufo* (Bufonidae), about 24 species of *Eleutherodactylus*, and one species of *Sminthillus* (Leptodactylidae) occur on Cuba in addition to the single hylid representative. In view of its position, extensive lowland habitat, and anuran fauna, it is not surprising that Cuba (and the Isle of Pines) has only one hylid, *Osteopilus septentrionalis*. *Osteopilus septentrionalis* is very similar in habits and morphology to *O. dominicensis* of Hispaniola; this suggests that their common ancestor successfully invaded Cuba from Hispaniola. The ability of this group to colonize successfully is substantiated by the occurrence of *O. septentrionalis* in southern Florida and the Bahamas, and by its apparent success on Great Inagua Island and Puerto Rico where it has been introduced recently.

Parenthetically we note that, except for the absence of naturally occurring hylids, Puerto Rico supports an anuran fauna about as diverse as that of Jamaica: two species of *Bufo* (Bufonidae), one *Leptodactylus,* and about 12 species of *Eleutherodactylus* (Leptodactylidae). Thus, of the anurans inhabiting the Greater Antilles, the leptodactylids seem to have been the most successful in inter-island colonization and subsequent adaptive radiation and speciation. This success may be related to the relative independence from fresh water these taxa have achieved by the evolution of specialized breeding habits—namely, the utilization of foam nests and more commonly, the direct development of young from eggs deposited in terrestrial situations. Bufonids, on the other hand, seem to have been the least successful colonists. They are more diverse on Cuba with five species, whereas only two species each occur on Hispaniola and Puerto Rico, and none occurs naturally on Jamaica (a distributional disparity which may relate, in part, to the relative abundance of lowland habitats on the various islands). At first thought, it would seem that a typical bufonid is hardier and less susceptible to the possible inequitable conditions encountered in waif dispersal than the smaller eleutherodactyline. However, larger size may inhibit bufonid dispersal; the smaller frog is more apt to find suitable protective cover (*e.g.*, bromeliads) in which to secret itself than the larger frog. Furthermore, bufonids have not developed the breeding specializations typical of their leptodactylid relatives. As a rule, bufonids (and, in particular, *Bufo*) deposit their small, pigmented eggs in rosary-like strings in ponds or other temporary fresh water sources. Thus, whereas a founding leptodactylid population might be established by overwater dispersal of terrestrial eggs, the possibility of a similar mode of dispersal in *Bufo* is negligible. The diversity of hylids in the Greater Antilles closely parallels that of the bufonids, except that the hylids have achieved their greatest diversity (at both generic and specific levels) on Jamaica and Hispaniola instead of Cuba—a fact which we believe is explained most logically by two facts: 1) Ecologically, the greatest area of Cuba is more suitable to habitation by bufonids than by hylids. 2) There have been multiple invasions of the Greater Antilles by hylids from South America and subsequent competition with the more numerous and adaptively leptodactylids.

The fact that we postulate more numerous invasions and far less speciation and inter-island dispersal than does Williams with respect to anoline lizards necessarily relates to several significant factors. Systematic study has shown the West Indian anoline lizards to be a closely related group, whereas our results reflect a great amount of morphological diversity, indicating that the Antillean hylids represent several diverse phylogenetic stocks—a fact which is incontrovertible in our minds. Given that frogs probably are less successful in overwater dispersal than lizards, how do we account for the disparity in the number of postulated invasions? One possible explanation centers on extinction. The anoles have been extraordinarily successful in radiating into available niches (Williams, 1969, 1972) on the various islands. The question arises then, how many invasions of lizards, other than anolines, may have resulted in unsuccessful colonization because of competition with resident anoles? The apparent minimal amount of speciation of the various lines of hylids is probably related to 1) the limited number of niches available to them, and 2) competition with the more numerous and adaptively labile leptodactylids.

SUMMARY

A comparative study is undertaken of nine species of hylids inhabiting the Greater Antilles and Bahamas. Although information from the literature concerning the habits, habitats, breeding sites and larvae is included, we concentrate on morphological comparison of these frogs. Included in the morphological analysis of characters are sizes and proportions, characteristics of the skin, and features of the hands and feet. Osteological data on the cranium, vertebral column, and pelvic girdle are provided for each species, and in addition, data on throat and cloacal myology are presented.

On the basis of our findings, we conclude that the nine species, all of which were allocated heretofore to the genus *Hyla,* are best placed in more than one genus. *Hyla lichenata* has been assigned to a new genus, *Calyptahyla,* which is similar to *Trachycephalus* of South America. *Hyla septentrionalis, H. dominicensis,* and *H. brunnea* have been allocated to *Osteopilus* Fitzinger, 1843. These frogs differ in various myological and osteological features from *Hyla* and probably are related most closely to *Osteocephalus* of South America. The remaining five taxa are retained in the genus *Hyla,* although, with the exception of *H. marianae* and *H. wilderi,* they do not appear to be related closely to one another. *Hyla vasta* may be related to the *Hyla boans* group of South America, and *Hyla heilprini* to the *Hyla albomarginata* group, also of South America. We are unable to postulate any close mainland relative for *Hyla pulchrilineata,* or *H. marianae* and *H. wilderi* at this time.

We propose that the present hylid fauna of the Greater Antilles has been established by at least five separate invasions from the mainland. Although other possibilities are discussed, we favor a hypothetical colonization of the Greater Antilles by frogs which have dispersed northward through the Lesser Antilles from the South American mainland. In this way we account for the greater diversity of hylids of the nearest island, Hispaniola, as compared

to Jamaica and Cuba. Jamaica is far more diverse with respect to its resident hylids than Cuba which is farther from the South American mainland. By analyzing the sites and habitat preferences of the hylids residing on any given island we find an interesting conformity to the model of co-adjustment of species pairs by size applied recently to the Antillean anoles.

RESUMEN

Hemos emprendido un estudio comparativo de nueve especies de los hílidos que habitan las Bahamas, Cuba, Hispaniola, Puerto Rico y Jamaica. Aunque incluimos información sobre la literatura tocante a los hábitos, las habitaciones, los lugares de criar, y las larvas, concentramos en una comparación morfológica de estas ranas. Incluimos en el análisis morfológico de caracteres las dimensiones y proporciones, las características de la piel, y los semblantes de las manos y los pies. Proveemos datos osteológicos sobre el cráneo, la columna vertebral, y la pelvis para cada especie, y además presentamos datos de músculos de la garganta y de la cloaca.

A base de nuestras observaciones, concluimos que las nueve especies, todas las cuales se han atribuido previamente al género *Hyla,* representan más de un género. Nosotros asignamos *Hyla lichenata* a un género nuevo, *Calyptahyla,* que es similar a *Trachycephalus* de Sudamérica *Hyla septentrionalis, H. dominicensis* y *H. brunnea* han atribuido a *Osteopilus* Fitzinger, 1843. Estas ranas difieren substancialmente en algunos semblantes morfológicos y osteologicos de *Hyla,* y estas están emparentados probablemente más estrechamente a *Osteocephalus* de Sudamérica. Retenemos los cinco especies restantes en el género *Hyla,* aunque, con la excepción de *H. marianae* y *H. wilderi,* que no parecen estar emparentados unos con otros. Posiblemente, *Hyla vasta* este emparentada con el grupo *Hyla boans* de Sudamérica, y *Hyla heilprini* con el grupo *Hyla albomarginata* de Sudamérica también. No podemos postular ningún pariente cercano del continente para *Hyla pulchrilineata, H. marianae,* y *H. wilderi.*

Proponemos que la fauna corriente de los hílidos de las islas mayores de las Antillas se ha establecido por cinco invasiones del continente por lo menos. Aunque discutimos otra posibilidades, preferimos una colonización hipotética de las islas majores de las Antillas con ranas que hayan dispersado hacia el norte por las islas menores de las Antillas del continente de Sudamérica. De este modo, explicamos la diversidad mayor de los hílidos de la isla más cercano Hispaniola, comparado con Jamaica y Cuba. Jamaica es más diversa con respecto a los hílidos residentes que Cuba, que queda más lejos del continente de Sudamérica. Mediante análisis de los tamaños y las preferencias en habitaciones de los hílidos que viven en alguna isla particular, hallamos una conformidad notable al modelo (Williams, 1972:57-58) que ha aplicado a los lagartillos del género *Anolis* de las Antillas.

LITERATURE CITED

BARBOUR, T.
1910. Notes on the herpetology of Jamaica. Bull. Mus. Comp. Zool., 52(15):273-301, pls. 1-2.
1937. Third list of Antillean reptiles and amphibians. Bull. Mus. Comp. Zool., 82(2):77-166.

BIBRON, G.
1842. *In* Ramón de la Sagra. Historia física, politica y natural de la Isla de Cuba. Part 2, Historia natural [not seen].

BOCK, W. J. and C. R. SHEAR
1972. A staining method for gross dissection of vertebrate muscles. Anat. Anz. 130:222-227.

BOULENGER, G. A.
1882. Catalogue of the Batrachia Salientia s. Ecaudata in the collection of the British Museum, ed. 2, London, xvi + 655 pp.

CARR, A. F., JR.
1940. A contribution to the herpetology of Florida. Univ. Florida Publ., Biol. Sci. Ser., 3(1):1-118.

COCHRAN, D. M.
1941. The herpetology of Hispaniola. Bull. U.S. Natl. Mus., viii + 398 pp.
1961. Living amphibians of the world. Doubleday & Co. Inc., New York. 199 pp.

COPE, E. D.
1863. On Trachycephalus, Scaphiopus, and other Batrachia. Proc. Acad. Nat. Sci. Philadelphia. 15:43-54.
1869. Seventh contribution to the herpetology of tropical America. Proc. Acad. Nat. Sci. Philadelphia, 11:147-169.
1871. Ninth contribution to the herpetology of tropical America. Proc. Acad. Nat. Sci. Philadelphia, 23 (part 2):200-224.

DUELLMAN, W. E.
1970. The hylid frogs of Middle America. Monog. Mus. Nat. Hist., Univ. Kansas, 1:xi + 753 pp.

DUELLMAN, W. E. and R. I. CROMBIE
1970. Hyla septentrionalis. Cat. Amer. Amph. Rept., 92:1-4.

DUELLMAN, W. E. and A. SCHWARTZ
1958. Amphibians and reptiles of southern Florida. Bull. Florida State Mus., Biol. Sci., 3(5):181-324.

DUMÉRIL, A. M. C. and G. BIBRON
1841. Erpetologie generale ou histoire naturelle complete des reptiles. vol. 8. Paris, vi + 792 pp.

DUNN, E. R.
1925. A new tree-toad from Jamaica. Occas. Papers Boston Soc. Nat. Hist., 5:161-162.
1926. The frogs of Jamaica. Proc. Boston Soc. Nat. Hist., 38(4):111-130, pls. 1-2.

DU TOIT. C. A.
1955. The "tail" of *Ascaphus:* A historical resume and new histological-anatomical details. Ann. Univ. Stellenbosch. 31: A (1):1-71.

Fischer, J. G.
1888. Herpetologische Mitteilungen IV. Über eine Kollektion Reptilien und Amphibien von Hayti. Jahrb. hamb. wiss. Anstalt. 5, S. 23-45.

Fitzinger, L.
1843. Systema reptilium. Vienna, ix + 106 pp.

Goin, C. J.
1959. A synonym and a homonym in the frog genus *Hyla.* Copeia, 1959 (4):340-341.

Gosse, P. H.
1851. A naturalist's sojourn in Jamaica. London [not seen in entirety].

Graham, A.
1972. Some aspects of Tertiary vegetational history about the Caribbean Basin. Mem. I Congr. Latinoamericano Bot.:97-117.

Harlan, R.
1826. Descriptions of several new species of Batrachian Reptiles, with observations on the larvae of frogs. Amer. Jour. Sci. and Arts, 10 (Art. 7):53-65.

Jaume, M. L.
1966. Catalogo de los anfibios de Cuba. Mus. "Felipe Poey" Acad. Cien. Cuba, Trab. Divulg., 35:1-21.

Khudoley, K. M. and A. A. Meyerhoff
1971. Paleogeography and geological history of Greater Antilles. Geol. Soc. Amer. Mem., 129:199 pp. [not seen].

King, W.
1962. The occurrence of rafts for dispersal of land animals into the West Indies. Quart. Jour. Florida Acad. Sci., 25(1):45-52.

Laurenti, J. N.
1768. Specimen medicum, exhibens synopsin Reptilium emendatum cum experimentis circa venena et antidota reptilium Austriacorum. Vienna, 214 pp., pls. 1-5.

Lynn, W. G.
1958. Some amphibians from Haiti and a new subspecies of *Eleutherodactylus schmidti.* Herpetologica, 14:153-157.

Lynn, W. G. and C. Grant
1940. The herpetology of Jamaica. Bull. Inst. Jamaica, Sci. Ser., 1:1-132.

MacArthur, R. H. and E. O. Wilson
1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, xi + 203 pp.

Meerwarth, H.
1901. Die westindischen Reptilien und Batrachier des naturhistorischen Museums in Hamburg. Mitth. Naturh. Mus. Hamburg, 18:1-41 [not seen].

Mertens, R.
1938. Amphibien und Reptilium aus Santo Domingo, gesammelt von Prof. Dr. H. Boker. Senckenbergiana, 20(5):332-342.
1939. Herpetologische Ergebnisse einer Reise nach der insel Hispaniola, Wesindien. Abhandl. Senckenberg. Naturforsch. Gesellsch., 449: 1-84, 10 pls.

Mittleman, M. B.
1950. Miscellaneous notes on some amphibians and reptiles from the southeastern United States. Herpetologica, 6(1):20-24.

Myers, G. S.

1950. The systematic status of *Hyla septentrionalis,* the large tree frog of the Florida Keys, the Bahamas and Cuba. Copeia, 1950(3):203-214.

Noble, G. K.

1922. The phylogeny of the Salientia. I. The osteology and the thigh musculature; their bearing on classification and phylogeny. Bull. Amer. Mus. Nat. Hist., 46(1):1-87.

1923a. In pursuit of the giant tree frog. Nat. Hist., 23(2):105-116.

1923b. Field studies of Dominican tree frogs and their haunts. Nat. Hist., 23(2):117-121.

1923c. Six new batrachians from the Dominican Republic. Amer. Mus. Novitates, 61:1-6.

1927. The value of life history data in the study of the evolution of the Amphibia. Ann. New York Acad. Sci., 30:31-128, pl. 9.

1931. The biology of the Amphibia. McGraw-Hill Book Co., Inc., New York, xiii + 577 pp.

Peterson, H. W., R. Garrett, and J. P. Lantz

1952. The mating period of the giant tree frog *Hyla dominicensis.* Herpetologica, 8(3):63.

Rabb, G. B. and E. B. Hayden, Jr.

1957. The Van Voast-American Museum of Natural History Bahama Islands Expedition Record of the expedition and general features of the islands. Amer. Mus. Novitates, 1836:1-53.

Schwartz, A.

1968. The geckos (*Sphaerodactylus*) of the southern Bahama Islands. Ann. Carnegie Mus., 39(17):227-271.

1973. Six new species of *Eleutherodactylus* (Anura, Leptodactylidae) from Hispaniola. Jour. Herpetology, 7(3):249-273.

Schwartz, A. and D. C. Fowler.

1973. The Anura of Jamaica: a progress report. Studies on the Fauna of Curaçao and other Caribbean Islands, 43(142):50-142.

Taylor, E. H.

1952. A new Panamanian treefrog. Breviora, (1):1-3.

Trueb, L.

1966. Morphology and development of the skull in the frog *Hyla septentrionalis.* Copeia, 1966(3):562-573.

1970. The evolutionary relationships of casque-headed treefrogs with co-ossified skulls (family Hylidae). Univ. Kansas Publ., Mus. Nat. Hist., 18:547-716, pls. 1-12.

1972. *Hyla crucialis* Harlan, 1826 (Amphibia): Proposed suppression under plenary powers. A.N.(S). 1892. Bull. Zool. Nomencl., 29 (1):39-40.

Trueb, L. and W. E. Duellman

1971. A synopsis of Neotropical hylid frogs, genus *Osteocephalus.* Occas. Papers Mus. Nat. Hist., Univ. Kansas, 1:1-47.

Tschudi, J. J.

1838. Classification der Batrachier mit Berucksichtigung der fossilien Thiere dieser Abtheilung. Memb. Soc. Sci. Nat. Neuchatel, 2:1-100.

Tyler, M. J.

1971. The phylogenetic significance of vocal sac structure in hylid frogs. Univ. Kansas Publ., Mus. Nat. Hist., 19:319-360.

VERDOORN, F.

1945. Plants and plant science in Latin America. Frans Verdoorn, editor. Chronica Botanica Co., Waltham, Massachusetts, vol. 16: xxxvii + 381 pp.

WERNER, F.

1917. Uber einige neue Reptilien und einin neuen Frosch des Zoologischen Museums in Hamburg. Mitt. Zool. Mus. Hamburg, 34:31-36.

WILLIAMS, E. E.

1969. The ecology of colonization as seen in the zoogeography of anoline lizards on small islands. Quart. Rev. Biol., 44(4):345-389.

1972. The origin of faunas. Evolution of lizard congeners in a complex island fauna: A trial analysis. *In* Evolutionary Biology. Th. Dobzhansky, M. K. Hecht, and W. E. Steere Eds., Appleton-Century-Crofts, Vol. 6:47-89.

WILLIAMS, E. E., B. SHREVE, and P. S. HUMPHREY

1963. The herpetology of the Port-au-Prince region and Gonave Island, Haiti. Parts I-II. Bull. Mus. Comp. Zool., 129(5):293-342, pls. 1-5.

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THE MAMMALS OF CARTER COUNTY, SOUTHEASTERN MONTANA

By

RICHARD P. LAMPE,[1] J. KNOX JONES JR.,[2]
ROBERT S. HOFFMANN,[3] AND ELMER C. BIRNEY[4]

This report treats the more than 50 species of mammals occurring in a segment of the Northern Great Plains defined by the political boundaries of Carter County, Montana, the southeasternmost county in the state. The mammalian fauna of this area has, until now, been relatively poorly documented.

Carter County (Fig. 1), organized in 1917 and named after Thomas Henry Carter, Montana's first Congressional representative, has an area of approximately 3300 square miles and slopes northeastward on the average at 10 feet to the mile (Bauer, 1924:233). The county is characterized by gently rolling hills, extensive flats, steep ridges, and occasional "badlands." The Boxelder Creek Valley drains northeastward through the center of the county. This valley varies in elevation from 3200 to 3500 feet above sea level and generally is featureless except for the intermittent tributaries of Boxelder Creek that flow either northwestward or southeastward. The northern portion of the valley, referred to as Alkali Flats, is bordered by

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[1] Bell Museum of Natural History, University of Minnesota, Minneapolis, 55455. This paper is based in part on research accomplished while the senior author was a graduate student at the Museum of Natural History and Department of Systematics and Ecology, The University of Kansas.

[2] Associate Vice President for Research and Dean of the Graduate School, Texas Tech University, Lubbock, 79409

[3] Curator of Mammals, and Professor of Systematics and Ecology, Museum of Natural History, The University of Kansas, Lawrence, 66045

[4] Curator of Mammals, Bell Museum of Natural History, University of Minnesota, Minneapolis, 55455

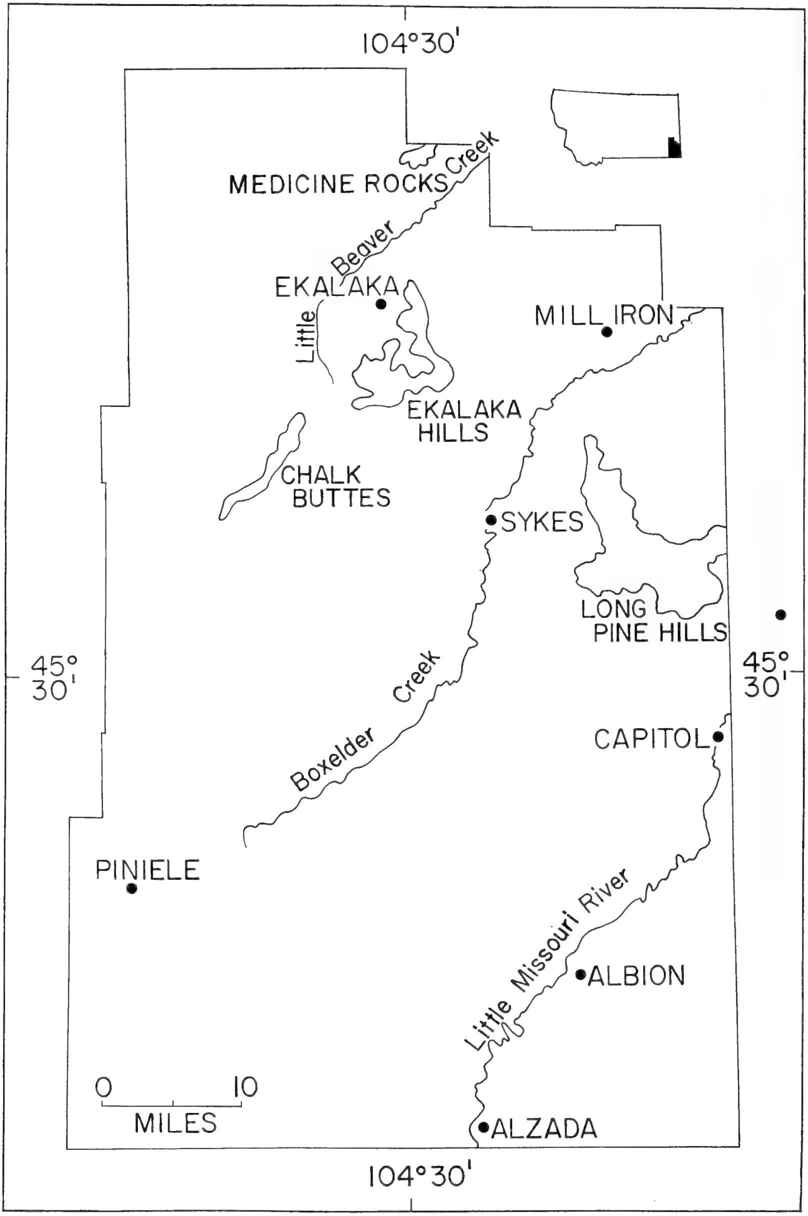

Fig. 1. Map of Carter County, Montana, showing location of place-names mentioned in text. Camp Crook, Harding Co., South Dakota, is located at the black dot on the right-hand margin of the map.

three disjunct pine-clad ridges, Chalk Buttes to the west (maximum elevation, 4215), Ekalaka Hills to the north (maximum elevation, 4115), and Long Pine Hills to the east (maximum elevation, 4130). The Long Pine Hills and Ekalaka Hills are separated by Boxelder Creek, whereas the latter and Chalk Buttes are separated by a small valley drained by the intermittent Little Beaver Creek. Little Beaver and Boxelder creeks are tributaries of the Little Missouri River, which traverses the southeastern corner of the county. The extreme western part of the county lies in the Powder River drainage.

Largest of the three pine-clad ridges are the L-shaped Long Pine Hills, which extend north and south for approximately 18 miles with an east-west base of 11 miles. Lillegraven (1970:832) described the Long Pine Hills as part of a system of ". . . Tertiary erosional remnants standing above the Late Cretaceous rocks of northwestern South Dakota, southwestern North Dakota, and southeastern Montana." The southern and western sides of these ridges tend to have more cliffs and support less vegetation than do the eastern and northern slopes, which slope gradually onto the plains (Bauer, 1924:233; Lillegraven, 1970:832). Landslides of Tertiary rocks in the Long Pine Hills and Finger Buttes have been part of the erosional sequence of the area (Gill, 1962:731).

South of Boxelder Creek Valley, the rolling landscape is broken by numerous, sparsely vegetated buttes. Formations such as Chimney Butte, Sheep Mountains, and Finger Buttes extend as a chain southwestward from the Long Pine Hills, forming the divide between the drainages of Boxelder Creek and the Little Missouri River.

Soils of Carter County are of four types (Kellogg, 1938). Chestnut soils of the Williams-Morton-Bainville series have developed over glacial tills, sandstone, and shale and are found in the northern and southwestern parts of the county. In the extreme northwestern corner, brown soils have developed over shale and sandstone. Lithosols of the Pierre type, with parent material of Cretaceous shale, occur in southeastern Carter County. The rough, eroded areas or "badlands" of the north-central part of the county have developed over clay and shale of Tertiary formation. Banks and washes of the many dry stream beds found throughout the county are sandy. Underlying or partially exposed sedimentary rocks of Cretaceous deposits include Benton (shale), Niobrara (shale), Pierre (shale), and Fox Hill (sandstone). Tertiary deposits include the Ludlow and Hell Creek members of the Lance formation, the Tongue River member of the Fort Union formation, the White River formation, and the Arikaree formation (Bauer, 1924; for additional information on geologic formations see also Alden, 1932, and Perry, 1962).

Much of Carter County is covered by mixed-grass prairie, complemented by pine-clad ridges and sagebrush flats. Part of the Sioux Division of Custer National Forest, the Chalk Buttes, Ekalaka Hills (known also as the Ekalaka Forest), and Long Pine Hills support predominantly ponderosa pine *(Pinus ponderosa).* Mature stands of this pine are relatively open; they usually are restricted to ridges and slopes, only seldom extending onto the grassy lower valleys that dissect the ridge formations. Northern and eastern slopes generally support denser stands than do southern and western slopes, which tend to be steeper and have more cliffs. Sawlog and pole stands generally accommodate an understory of mixed grasses, forbs, and woody shrubs, whereas stands of saplings have a poorly developed understory in response to the greater density of young trees and consequent minimal sunlight penetration. Park-like stands of pine commonly occur on lower slopes and subordinate ridges along with snowberry *(Symphoricarpos racemosus),* various grasses, shrubs, and forbs. Juniper *(Juniperus scopulorum)* occurs irregularly and small stands of aspen *(Populus tremuloides)* occupy some slopes.

Thickets of common snowberry, fleshy hawthorne (*Crataegus* sp.), wild plum (*Prunus* sp.), chokecherry *(P. melanocarpa),* buffalo-berry (*Shepherdia* sp.), gooseberry and currant (*Ribes* sp.), serviceberry *(Amelanchier alnifolia),* and rose (*Rosa* sp.) occupy some of the wetter ravines. Boxelder *(Acer negundo),* green ash *(Fraxinus pennsylvanica),* and some ponderosa pine are found in the drainageways leading from the ridges. The grassland drainages support discontinuous stands of deciduous trees—mainly cottonwood *(Populus sargentii),* willow (*Salix* sp.), boxelder, and green ash—characterized as the Northern Floodplain Forest (Küchler, 1964); the Little Missouri River is lined with a heavier growth of riparian forest than that found along smaller streams throughout the county.

Grasslands of the county are of the wheatgrass-needle grass community (Küchler, 1964) with dominants of western wheatgrass *(Agropyron smithii),* blue grama *(Bouteloua gracilis),* needle-and-thread grass *(Stipa comata),* and green needle-grass *(Stipa viridula).* Grasslands occupying the valleys and meadows of the Long Pine Hills are characterized as a sedge-blue grama-bluestem-wheatgrass community (Jonas, 1966:7) but ". . . under more favorable conditions needle-and-thread grass would possibly replace wheatgrass in importance." Flats in the northern and central areas of the county are commonly vegetated by fringed sagebrush *(Artemisia frigida),* big sagebrush *(A. tridentata),* and silver sagebrush *(A. cana),* with an understory of short grasses and prickly pear *(Opuntia humifusa).*

Carter County has a semiarid continental climate (Table 1) that is shielded from the northward flow of precipitation-laden air by the Black Hills. Slightly more than half of the mean annual precipitation falls in May, June, and July. Seasonal fluctuation in temperature is great and fluctuations are common from day to day. The contrast between summer and winter temperatures is exemplified by an average of 34 days with a maximum temperature above 90°F and

TABLE 1. Climatological data from Ekalaka, Montana (1931-1952), and Camp Crook, South Dakota (1896-1967). Temperature is recorded in degrees Fahrenheit and precipitation is measured in inches.

	Ekalaka, Montana	Camp Crook, South Dakota
Temperature		
Mean annual	44.1	43.8
Mean January	17.6	17.3
Mean July	71.8	71.2
Record high	108	114
Record low	–43	–57
Precipitation		
Mean annual	13.27	13.71
Record maximum	21.97 (1963)	24.07 (1927)
Record minimum	6.35 (1936)	4.73 (1936)
Mean annual snowfall	22.3	33.2

an average of 33 days with a minimum temperature below zero. During winter, prevailing northwest winds often accompany snow storms, creating drifts in protected areas and leaving open fields bare. It is noteworthy that weather conditions in July, 1972, were unseasonably cold and wet, including temperatures below 32°F and freezing rains.

Our interest in the mammals of Carter County stemmed from studies by one of us (Jones) conducted in Harding County, South Dakota, during the 1960's as well as previous work in Montana by Hoffmann. Kenneth Andersen visited the Long Pine Hills briefly in May of 1968 and obtained a small collection of mammals. Subsequently, in the period 29 June to 24 July 1970, a field party from The University of Kansas made extensive collections from the Long Pine Hills and other localities in northern and eastern Carter County, and Jaime Pefaur, a graduate student at The University of Kansas, studied populations of small mammals on a north-facing slope at the eastern edge of the Long Pine Hills until mid-August of the same year. Birney and Lampe collected mammals for the University of Minnesota in the Long Pine Hills, Ekalaka Hills, and Chalk Buttes in July 1971. Merlin Tuttle and Larry Heaney made additional collections for Minnesota in Carter County in July 1972.

Early reference to the mammals of Carter County was made by Captain W. F. Reynolds (1868) during his brief passage through the area in 1859. Subsequent military explorations in this area, such as General George Custer's expedition to the Black Hills in 1874, were concerned primarily with matters other than faunal observations (see also Turner, 1974). E. A. Preble, in an undated manuscript, probably written about 1910, listed mammals from eastern Montana and briefly commented on the habitat preference and abundance of 57 species. Other references in the literature to mammals of Carter County are those of Visher (1914), Couey (1946), Tryon (1947), Hoffmann *et al.* (1969a,b), Andersen and Jones (1971), Pefauer and Hoffmann (1971), and Jones *et al.* (1973). Several specimens from Carter County have been incorporated in revisionary studies such as those by Nelson (1909), Bailey (1915), Hollister (1916), Jackson (1928), Howell (1929, 1938), and Goldman (1944).

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ACCOUNTS OF SPECIES

The following accounts treat the 53 species of mammals presently on record from Carter County, Montana. Additionally, comments on 15 species of unverified occurrence are appended. Specimens examined (a total of 488) are listed in telegraphic style and are ordered first from north to south and, secondarily, from west to east. All specimens examined are deposited in the Museum of Natural History at The University of Kansas or in the Bell Museum of Natural History at the University of Minnesota (noted as MMNH). All measurements used are in millimeters (lengths of embryos are for crown-rump) and weights are expressed in grams. In certain cases, measurements are given as means, with extremes in parentheses.

ORDER INSECTIVORA

Sorex cinereus haydeni Baird, 1858

Masked Shrew

Specimens examined (26).—3 mi S, 1.75 mi E Ekalaka, 6 (MMNH); 5.5 mi N, 10 mi W Camp Crook, 3500 ft, 20 (17 MMNH).

The masked shrew evidently is a common inhabitant of protected, mesic habitats in the pine-covered portions of the study area. Only three specimens, all adults, were captured during approximately four weeks of intensive trapping in summer of 1970. Most trapping efforts were with break-back traps, although buried can traps were tried unsuccessfully in several areas in the Long Pine Hills that seemed suitable for shrews. Three additional specimens, two adult females and a shrew of unknown sex, were captured in 1971 in break-back traps in the mesic draw at Lantis Spring and in lush vegetation around a nearby beaver pond fed by the spring, the site of capture of two males in 1970. The third specimen from 1970, a female, was taken above the draw on snowbrush-covered ground near a clearing.

On 10 July 1972, five can-traps were set near water at Lantis Spring. Four of these contained masked shrews the following morning. Eleven more can-traps and 75 Museum Specials then were set in mesic habitat along the spring and near the beaver pond. No shrews were captured in the Museum Specials, but six more were taken from the cans. Even after an additional 50 Museum Specials, baited with a mixture of rolled oats and peanut butter, were set near the spring, all four shrews subsequently captured were taken from the 16 buried cans. A few days later, two *Sorex* were among the animals taken from 202 Museum Specials set in tall grass and reeds near a marsh in the Ekalaka Hills. Seventeen can-traps set near the marsh yielded four additional masked shrews.

Brown (1967) and Spencer and Pettus (1966) demonstrated the efficiency of can-trapping for shrews. Our studies indicate that the masked shrew is not uncommon in Carter County. Instead, it seems to be common in isolated or semi-isolated populations associated with permanent sources of water and relatively undisturbed habitats. Genoways and Jones (1972:5) trapped *Sorex cinereus* at seven localities in southwestern North Dakota, but Andersen and Jones (1971:388) did not report shrews from adjacent Harding County, South Dakota, although can-traps were not employed there. Three specimens from 5 mi SE Ekalaka were recorded by Jackson (1928: 53), and were probably those mentioned by Preble (MS) from the Sioux National Forest, near Ekalaka.

Testes of 12 males taken in mid-July 1972 were 4 mm in mean length. One of eight females collected at that time carried four embryos, each 12 mm in length; another had placental scars but apparently had completed lactation.

Sorex merriami leucogenys Osgood, 1909

Merriam Shrew

Specimen examined (1).—5 mi N, 3.5 mi W Camp Crook, 3400 ft, 1.

Our specimen of Merriam's shrew, the fifth to be recorded from Montana (Pefaur and Hoffmann, 1971:247), was trapped on 22 July on a north-facing grassy slope at the eastern edge of the Long Pines. An adult male with enlarged flank glands and testes 5 mm in length, it had the following selected external and cranial measurements: total length, 101 mm; tail length, 39 mm; hind foot length, 11 mm; weight, 4.8 gms; condylobasal length, 16.5 mm; palatal length, 7.2 mm; cranial breadth, 8.3 mm; least interorbital breadth, 3.7 mm; maxillary breadth, 5.2 mm; maxillary toothrow length, 6.2 mm. Owing to the large size of this shrew, especially apparent in the cranial dimensions, we assign it to the subspecies *leucogenys* (see Long, 1965, and Hooper, 1944, for representative measurements of *S. m. leucogenys* and *S. m. merriami*), even though the type locality of *S. m. merriami* lies only approximately 150 miles to the west.

ORDER CHIROPTERA

Seven species of bats were collected in Carter County in 1970. Collections were made principally in the Long Pine Hills, but a few bats were obtained in adjacent areas and at Medicine Rocks. Specimens obtained during that summer were reported by Jones *et al.* (1973) together with comments on habitat, reproduction, molt, activity, dietary habits, and ectoparasites of these seven bats. Included in the present accounts are specimens obtained in the Long Pine Hills, Ekalaka Hills, and Chalk Buttes in 1971 and 1972. One species, *Plecotus townsendii,* was not captured in Carter County until July 1972 and thus was not treated by Jones *et al.* (1973).

Myotis evotis evotis (H. Allen, 1864)

Long-eared Myotis

Specimens examined (7).—4 mi S, 1 mi E Ekalaka, 4 (MMNH); 5.5 mi S, 1 mi E Ekalaka, 1 (MMNH); 7 mi N, 10 mi W Camp Crook, 3800 ft, 2 (MMNH).

All specimens are adults, and were netted over reservoirs in the Long Pine Hills and the Chalk Buttes and in a campground clearing in the Ekalaka Hills. At Stagville Spring, 4 mi S and 1 mi E Ekalaka, 11 long-eared myotis were collected over a spring-fed watering tank located in a brush-lined ravine. Seven of these were banded and released. Three of four banded females were lactating; the three males gave no external evidence of reproductive activity.

Four adult males taken in mid-July had testes that were 3, 3, 4, and 5 mm in length, and three were in the process of seasonal molt.

Myotis leibii ciliolabrum (Merriam, 1886)

Small-footed Myotis

Specimen examined (1).—4 mi S, 1 mi E Ekalaka, 1 (MMNH).

A lactating female in the process of seasonal molt was netted 18 July above a livestock tank in the Ekalaka Hills. This specimen is the only small-footed myotis known from the county outside of the Long Pine Hills, where six were obtained in 1970 (Jones *et al.*, 1973).

Myotis lucifugus carissima Thomas, 1904

Little Brown Myotis

No specimens of the little brown myotis were captured in 1971 or 1972. Jones *et al.* (1973) reported 12 individuals that had been netted or shot over water in the Long Pines in 1970.

Myotis volans interior Miller, 1914

Long-legged Myotis

Specimens examined (7).—4 mi S, 1 mi E Ekalaka, 2 (MMNH); 5.5 mi S, 1 mi E Ekalaka, 3 (MMNH); 7 mi N, 10 mi W Camp Crook, 2 (MMNH).

We found the long-legged myotis to be common in most areas of buttes and ridges in Carter County although none was taken in the Chalk Buttes. All specimens collected in mid-July are adults. One female was lactating and two males had testes that were 3 and 4 mm in length. Seven adults were netted over a livestock tank near Stagville Spring in the Ekalaka Hills on 17 July 1971; of five subsequently banded and released, two were reproductively active females, one lactating and the other pregnant.

Lasionycteris noctivagans (Le Conte, 1831)

Silver-haired Bat

Although found to be common in the Long Pine Hills in 1970 (Jones *et al.*, 1973), only a single silver-haired bat was captured in the subsequent two summers. This specimen, an adult male netted over a beaver pond at Slick Creek Spring, 7 mi N, 10 mi W Camp Crook, was banded and released.

Eptesicus fuscus pallidus Young, 1908

Big Brown Bat

Specimens examined (4).—11 mi S, 7.5 mi W Ekalaka, 1 (MMNH); 7 mi N, 10 mi W Camp Crook, 3800 ft, 3 (MMNH).

Two adult male big brown bats were banded and released at the locality (Slick Creek Spring) listed above, and an additional two adult females and one adult male were preserved. An adult male (testes 8 mm in length) was netted over a small reservoir in the Chalk Buttes in 1971. We failed to capture this species in southeastern Montana in 1972.

Lasiurus cinereus cinereus (Palisot de Beavois, 1796)
Hoary Bat

Specimens examined (6).—4 mi S, 1 mi E Ekalaka, 1 (MMNH); 11 mi S, 7.5 mi W Ekalaka, 2 (MMNH); 7 mi N, 10 mi W Camp Crook, 3800 ft, 3 (MMNH).

Volant juvenile hoary bats were netted in mid-July in both 1971 and 1972. Two adults, a lactating female and a male, also were captured. Testes of the male were 8 mm in length on 13 July. One juvenile female was banded and released in the Long Pines in 1971.

Plecotus townsendii pallescens (Miller, 1897)
Townsend's Big-eared Bat

Specimen examined (1).—7 mi N, 10 mi W Camp Crook, 1 (MMNH).

A reproductively inactive, adult female *Plecotus* was captured in a mist net stretched over a beaver pond in the Long Pine Hills on 12 July 1972. Preble (MS) reported the species from adjacent Powder River County and Hoffmann *et al.* (1969b:741) considered it widespread in Montana. Andersen and Jones (1971:372) considered big-eared bats uncommon in Harding County, South Dakota. The absence of this bat in our 1970 collections (Lampe, 1971; Jones *et al.*, 1973) and in 1971 and the paucity of specimens from adjacent areas attest to the apparent rarity of the species in this portion of its range.

ORDER LAGOMORPHA

Lepus townsendii campanius Hollister, 1915
White-tailed Jackrabbit

Specimens examined (9).—12 mi E Ekalaka, 3200 ft, 1; 6.5 mi N, 5.5 mi W Camp Crook, 3400 ft, 1; 5.5 mi N, 3 mi W Camp Crook, 1; 2 mi N, 14 mi W Camp Crook, 1; 2 mi N, 4.5 mi W Camp Crook, 3700 ft, 1; 2.5 mi S, 3 mi W Camp Crook, 3200 ft, 1; 5.5 mi S, 3.5 mi W Camp Crook, 1; 6 mi S, 3 mi W Camp Crook, 3200 ft, 1; 12 mi S, 4 mi W Camp Crook, 1.

White-tailed jackrabbits are common in the grasslands of Carter County, particularly in the meadows and broad valleys within the Long Pine Hills. All of our specimens were collected in 1970 from along roads or roadside ditches.

An adult female taken on 3 July carried three embryos, each of which was 48 mm in length. Another examined on 7 July was lactating; both females were actively molting. Three subadult males collected in early and mid-July had testes that were 24, 18, and 15 mm in length, whereas an adult male obtained on 5 July had testes 55 mm long. One jackrabbit was parasitized by ticks, *Dermacentor andersoni.*

Sylvilagus audubonii baileyi (Merriam, 1897)
Desert Cottontail

Specimens examined (2).—17 mi E Ekalaka, 3200 ft, 2.

This cottontail was seen on sagebrush flats and in grasslands as well as on the pine-covered ridges of the Long Pine Hills. Two S. *audubonii* were obtained from a small formation in the "badlands" north of the Long Pines. Preble (MS) listed specimens from the "head of Boxelder Creek," no doubt the same individuals reported by Nelson (1909:234) as simply from "Boxelder Creek." Additionally, Andersen and Jones (1971:373) reported a specimen obtained on a sparsely covered pine ridge at the extreme eastern edge of the Long Pines in Harding County, South Dakota.

A subadult male examined on 8 July had testes 14 mm in length. An adult female shot on 9 July was actively molting and carried six embryos (three in each uterine horn) in addition to a seventh in the right uterine horn that, in light of its smaller size (9 mm in length as compared to 14 mm for the others), was apparently being resorbed.

Sylvilagus floridanus similis Nelson, 1907
Eastern Cottontail

Specimens examined (4).—5.5 mi N, 10 mi W Camp Crook, 1 (MMNH); 2 mi N, 4.5 mi W Camp Crook, 3700 ft, 1; 8 mi S, 3 mi W Camp Crook, 3200 ft, 2.

The eastern cottontail occurs in Montana only in Carter County, where it is restricted to riparian habitats. One specimen was shot along a small spring-fed stream at the southeastern edge of the Long Pine Hills and a juvenile was trapped in a thicket on high ground at Lantis Spring; the other two were collected in dense, woody vegetation along the Little Missouri River. Hall and Kelson (1951:52) reported specimens of *S. f. similis* from Boxelder Creek (25 mi SW Sykes—Hall, 1951:159), Capitol, and the Little Missouri River (7 mi NE Albion—Hall, *loc. cit.*) in southern Carter County.

It is of interest that our four specimens and those cited by Hall and Kelson *(loc. cit.)* all were collected in the eastern third of Carter County. The apparent absence of *S. floridanus* in western Carter County may be of importance with respect to the distribution of *S. nuttallii,* which evidently has been displaced by *S. floridanus* in adjacent states (Genoways and Jones, 1972:11; Turner, 1974:61).

A female taken on 30 June carried six embryos. Two males shot in early July had testes 40 and 55 mm in length. These three specimens, all adults, were actively molting from winter to summer pelage.

ORDER RODENTIA

Eutamias minimus pallidus (J. A. Allen, 1874)
Least Chipmunk

Specimens examined (15).—17 mi E Ekalaka, 3200 ft, 1; 4 mi S, 1 mi E Ekalaka, 2 (MMNH); 4.5 mi S, 1 mi E Ekalaka, 2 (MMNH); 4 mi N, 8 mi W Camp Crook, 3650 ft, 4; 4 mi N, 7.5 mi W Camp Crook, 3800 ft, 1; 2 mi N, 4.5 mi W Camp Crook, 3700 ft, 3; 1.5 mi N, 5 mi W Camp Crook, 4100 ft, 2.

Chipmunks are common in the pine-covered hills of southeastern Montana. Specimens were obtained from ridges and roadsides where fallen logs and rocks provided suitable cover. Two adult males were collected at Capitol Rock, a large butte along the southern edge of the Long Pine Hills, 1.5 mi N and 5 mi W Camp Crook, that is characterized by gullies, steep and eroded slopes, and pale-colored soils. An adult male obtained from a similar, but smaller area of "badlands" isolated in the grasslands of northeastern Carter County, 17 mi E Ekalaka, was markedly grayer than specimens collected in the Long Pines and Ekalaka Hills. This animal was actively molting on 8 July. A chipmunk was observed running over a bare, vertical cliff-facing at the crest of Trenk Pass, 11 mi S, 6.5 mi W Ekalaka, in July 1971, but no specimens were collected in the Chalk Buttes.

An adult female obtained in late June and one taken in July were lactating and still retained winter pelage. Eleven subadults taken in July were molting. A young individual, one of four obtained on 25 July from 4 mi N and 8 mi W Camp Crook, had a scar, no doubt caused by a cuterebrid larva, on the right shoulder.

Preble (MS) mentioned specimens from the Sioux National Forest and Alzada and commented that chipmunks inhabited "indifferently the evergreen forests, bushy canyons, and even sections almost without forest cover. . . ." Howell (1929:44) reported specimens from Alzada, Ekalaka, 8 mi E Sykes, and 5 mi E Sykes.

Spermophilus tridecemlineatus pallidus J. A. Allen, 1874
Thirteen-lined Ground Squirrel

Specimens examined (33).—11.5 mi N, 3 mi E Ekalaka, 5; 16 mi E Ekalaka, 2; 1 mi S, 1 mi W Ekalaka, 1 (MMNH); 3.5 mi S, .25 mi W Ekalaka, 2 (MMNH); 3.75 mi S, 2.25 mi W Ekalaka, 3 (MMNH); 4 mi S, 1.5 mi W Ekalaka, 1 (MMNH); 5 mi N, 3.5 mi W Camp Crook, 3400 ft, 18; 6 mi S, 4.5 mi W Camp Crook, 3200 ft, 1.

This ground squirrel is common in short grass and sagebrush throughout the area of study. Juveniles represented more than half of the total number of specimens obtained. Eight of eleven specimens collected in an upland meadow along the eastern edge of the Long Pine Hills during the period 8 to 13 July were juveniles, and only one of seven individuals from southwest of Ekalaka was adult.

Preble (MS) commented on the destruction of crops caused by thirteen-lined ground squirrels, "especially in the southeastern part of the state." Howell (1938:114) reported specimens from Albion, Capitol, and Medicine Rocks.

An adult female taken on 14 July had seven placental scars and eight corpora albicantia. The testes of eight adult males obtained in mid-July had a mean length of 5.8 mm; those of eight juveniles collected on comparable dates averaged 4.9.

Fleas, *Thrassis* sp., and ticks, *Ixodes sculptus,* were found on these thirteen-lined ground squirrels.

Cynomys ludovicianus ludovicianus (Ord, 1815)
Black-tailed Prairie Dog

Specimens examined (4).—5 mi N, 6 mi E Ekalaka, 3400 ft, 3; 1 mi S, 13 mi E Ekalaka, 3200 ft, 1.

Once a common inhabitant of grasslands throughout Carter County, the prairie dog was found in areas overgrazed by herds of bison and other ungulates. With the decline of native herbivore populations, the prairie dog became associated with domestic livestock, often becoming a "pest," particularly in areas overgrazed by cattle and sheep. Visher (1914:89) reported the existence of large "towns" in Harding County, South Dakota, in the early 1900's, one of which covered "several sections . . . west of the Little Missouri River." Such colonies most likely occurred also in Carter County. Rather than directly treating the cause of poor range condition, rodent control campaigns tended to treat only symptoms—that is, large populations of prairie dogs. The efficiency of programs designed to eradicate this sciurid is attested to by the fact that *Cynomys* now occurs only in relatively small, disjunct populations in Carter County and adjacent regions.

Three prairie dogs were shot in mid-day from a colony of approximately 200 individuals northeast of Ekalaka. The colony was located on flat ground covered with sagebrush *(Artemesia tridentata),* below the dam of a farm pond. Another specimen was obtained from a half-grown badger that was observed crossing a road with a prairie dog in its mouth. As members of our field party approached the badger, it dropped the prey and took shelter in a nearby burrow.

Hollister (1916:14) reported a specimen from Boxelder Creek and Andersen and Jones (1971:375) noted two specimens from the grasslands of northwestern Harding County, South Dakota, bordering the eastern Long Pine Hills.

An adult female taken on 14 July contained eight placental scars and eight corpora albicantia. Two males, an adult and subadult, collected on 14 July both had testes 8 mm in length. Fleas, *Opisocrostis hirsutus,* and ticks, *Ixodes kingi,* were found on one of three individuals collected northeast of Ekalaka.

Sciurus niger rufiventer É. Geoffroy St.-Hilaire, 1803
Fox Squirrel

Specimens examined (2).—Sec. 16, T 5 S, R 62 E, 2.

Although fox squirrels are known to occur in the riparian cottonwood forests of the Yellowstone and Big Horn rivers in central Montana (Hoffmann *et al.,* 1969a:589), their presence in southeastern Montana has not been documented previously. Hibbard (1956:525) discussed the westward spread of fox squirrels in North Dakota along the Missouri and James rivers as well as their wooded tributaries in the south-central part of that state. Our specimens verify the occurrence of fox squirrels in the Little Missouri drainage. Because we know of no introductions of this species in this area of Montana, our records probably indicate a southward migration from the valley of the Missouri River.

Both specimens are adult males in winter pelage, collected along the Little Missouri River in east-central Carter County on 14 January 1971 by John Teigen, Jr. In this area, the banks and flood plain of the Little Missouri support riparian stands of boxelder, green ash, plains cottonwood, and willows.

Selected external and cranial measurements of our specimens are: total length, 490, 488 mm; tail length, 212, 208 mm; hind foot length, 68, 68 mm; ear length, 28, 28 mm; weight, 645, 623 gms; condylobasal length, 56.8, 58.8 mm; palatal length, 32.1, 32.5 mm; zygomatic breadth, 35.2, 35.2 mm; mastoid breadth, 27.6, 27.2 mm; postorbital breadth, 19.2, 19.1 mm; maxillary toothrow length, 11.4, 11.5 mm; testes length, 23, 25 mm.

Tamiasciurus hudsonicus dakotensis (J. A. Allen, 1894)

Red Squirrel

Specimens examined (14).—5.5 mi S, 1 mi E Ekalaka, 2 (MMNH); 7 mi N, 10 mi W Camp Crook, 3800 ft, 1; 6 mi N, 10 mi W Camp Crook, 1 (MMNH); 5.5 mi N, 10 mi W Camp Crook, 2 (MMNH); 4 mi N, 9 mi W Camp Crook, 3950 ft, 5; 3.75 mi N, 7.75 mi W Camp Crook, 2 (MMNH); sec. 1, T 3 S, R 61 E, 1.

Red squirrels were collected in moderately dense stands of ponderosa pine. Two were taken in the Ekalaka Hills in 1972 and others were collected in the central part of the Long Pine Hills in all three years of field work. Red squirrel "sign" was noted by Lampe and Birney in the Chalk Buttes, but no individuals were seen. Five squirrels were obtained in 1970 from an immature pine stand of 10 to 15 acres located on a gentle westward-facing slope marked by small ravines. Additional areas were hunted thoroughly, but only two other specimens were taken; a third was sighted 6 mi N and 10 mi W Camp Crook. Three individuals were feeding on ponderosa pine cones when shot, but no indication of regular feeding stations was observed in 1970.

Three red squirrels were shot and numerous others were seen during a two-day visit to the central Long Pine Hills in 1971. A midden with a surface area of approximately 60 square feet was found on a small north-facing slope at a place 8.5 mi N and 11 mi W Camp Crook. The midden was extremely moist as a result of its proximity to a nearby spring. Smaller caches and middens were seen elsewhere in the Long Pines around fallen and hollow trees.

The scarcity of caches on the forest floor in stands of ponderosa pine was discussed by Finley (1969:238). The dryness of sites occupied by this pine, the increased circulation of air and penetration of sunlight caused by the lack of lower limbs, and the open nature of stands create conditions unsuitable for the storage of cones. Caches seen in the Long Pines were associated with mesic or sheltered conditions, whereas those observed in the Chalk Buttes were small, shallow subterranean chambers. The marked variability in cone production of ponderosa pine (Finley, 1969:261) may account for much of the variation in red squirrel population density noted in the three years of our study.

Preble (MS) mentioned that red squirrels were fairly common near Ekalaka and east of Sykes and that specimens from these places appeared to be typical *T. h. dakotensis.* Visher (1914:88) reported a specimen shot in the Long Pines in July of 1910, and Miller and Kellogg (1955:263) included southeastern Montana in the range of *dakotensis.* Andersen and Jones (1971:375) commented that specimens from the Long Pine Hills were clearly assignable to *dakotensis* on the basis of color (see also Hoffmann and Jones, 1970:374, fig. 7; and Turner, 1974:80).

Average (and extreme) external and cranial measurements of 12 adults (five females, seven males) are: total length, 343.4 (322-365) mm; tail length, 133.9 (115-144) mm; hind foot length, 53.9 (50-58) mm; ear length, 28.0 (25-30) mm; condylobasal length (four females, seven males), 47.6 (46.7-49.1) mm; palatal length, 26.7 (26.0-27.3) mm; zygomatic breadth (four females, five males), 29.2 (28.9-30.4) mm; mastoid breadth (three females, six males), 24.1 (23.3-24.5) mm; postorbital breadth (four females, seven males) 14.2 (13.5-14.7) mm; maxillary toothrow length, 9.0 (8.8-9.2) mm.

Five of seven females collected from late May through July were lactating; two contained three placental scars each. Two females obtained on 18 and 20 July were young of the year. Seven adult males taken during July had testes that had an average length of 14.2 (10-20) mm.

Thomomys talpoides bullatus Bailey, 1914

Northern Pocket Gopher

Specimens examined (34).—16 mi E Ekalaka, 1; .5 mi S, 12 mi E Ekalaka, 1; 3 mi S, 1 mi E Ekalaka, 1 (MMNH); 3 mi S, 1.75 mi E Ekalaka, 3 (MMNH); 12 mi S, 16 mi E Ekalaka, 3600 ft, 3; 8 mi N, 8 mi W Camp Crook, 2; 7 mi N, 3 mi W Camp Crook, 3400 ft, 1; 6 mi N, 10 mi W Camp Crook, 1; 6 mi N, 9 mi W Camp Crook, 4000 ft, 1; 5.5 mi N, 10 mi W Camp Crook, 1 (MMNH); 5.5 mi N, 9.5 mi W Camp Crook, 1; 5 mi N, 6 mi W Camp Crook, 3500 ft, 2; 5 mi N, 3.5 mi W Camp Crook, 3400 ft, 12; 2 mi N, 4.5 mi W Camp Crook, 3700 ft, 1; 6 mi S, 4.5 mi W Camp Crook, 3200 ft, 3.

The northern pocket gopher is common in Carter County. Our specimens were collected primarily in the Long Pine Hills from roadside ditches, sparsely pine-clad ridges, and meadows. Four individuals were trapped in similar habitats in the Ekalaka Hills and adjacent areas. Three were taken along a sandy arroyo located 6 mi S and 4½ mi W Camp Crook.

Bailey (1915:102) referred a specimen from Alzada to *Thomomys talpoides bullatus,* the type locality of which is just to the west of Carter County at Powderville, Powder River County. Swenk (1941:3) later included this specimen in his description of *T. t. pierreicolus,* a subspecies supposedly delimited by the distribution of soils of the Pierre series. Andersen and Jones (1971:376) examined a specimen from Harding County, also referred by Swenk (1941:3) to *pierreicolus,* and found it clearly referable to *bullatus.*

Five adults collected in early and mid-July and a subadult taken in early July were molting. Two adult males obtained on 8 July had testes that were 10 and 13 mm in length, whereas those of a subadult taken the same day were 4 mm. An adult and a subadult collected on 18 July had testes that were 6 and 5 mm, respectively. An adult female taken on 8 July and two obtained 12 July contained, respectively, 13, 10, and six placental scars.

The following ectoparasites were found on our specimens of *Thomomys talpoides:* a flea, *Foxella ignota albertensis;* four mites, *Androlaelaps geomys, Androlaelaps fahrenholzi, Haemogamasus* sp., and *Hirstionyssus* sp.; two ticks, *Ixodes kingi* and *I. sculptus;* and two lice, *Geomydoecus thomomus* and *G. wardi.* Fleas, mites, ticks and lice were found together on one specimen from the Long Pine Hills.

Perognathus fasciatus olivaceogriseus Swenk, 1940

Olive-backed Pocket Mouse

Specimens examined (30).—11.5 mi N, 3 mi E Ekalaka, 1; 17 mi E Ekalaka, 3200 ft, 1; 4.5 mi S, 1 mi E Ekalaka, 1 (MMNH); 5.5 mi N, 3.5 mi W Camp Crook, 3400 ft, 22; 6 mi S, 4.5 mi W Camp Crook, 3200 ft, 5.

The olive-backed pocket mouse was found to be common in grazed and ungrazed meadows on sandy soils. A series of 11 adults and 11 young was collected from a north-facing slope at the eastern edge of the Long Pine Hills. Five individuals were obtained in an area of short grass and sage 6 mi S and 4.5 mi W Camp Crook, along a sandy arroyo. Specimens from 8 mi NE Albion were mentioned by Preble (MS).

Adult females taken on 7 and 8 July carried embryos (five measuring 11 mm and nine measuring 13 mm, respectively). A female bearing three placental scars was obtained on 9 July and one of two adult females taken on 10 July carried three embryos and had seven placental scars, whereas one of two taken on 11 and 12 July contained five embryos in addition to six placental scars. Two females trapped on 16 and 17 July carried seven and six embryos, respectively, the latter also containing five placental scars. One taken on 19 July had four corpora lutea and one obtained on 25 July was nonparous. An adult female examined on 29 July contained 11 placental scars of at least two ages. One obtained on 1 August was lactating and had nine placental scars, and another trapped on 5 August carried five embryos and had six placental scars. Two adult males taken on 8 and 11 July had testes that were 11 and 6 mm in length, respectively.

Average and extreme external and cranial measurements for 10 adults (two males, eight females) are: total length, 128.9 (125-136) mm; tail length, 59.7 (55-65) mm; hind foot length, 16.9 (16-18) mm; ear length, 6.6 (6-8) mm; basal length, 17.6 (17.2-18.3) mm; occipitonasal length (one male, six females), 11.9 (11.3-12.2) mm; interorbital breadth, 4.7 (4.5-5.0) mm; depth of cranium, 8.5 (8.3-8.8) mm.

Jones (1953:522) assigned an olive-backed pocket mouse from 8 mi NE Albion to *P. f. olivaceogriseus.* Andersen and Jones (1971: 376) and Genoways and Jones (1972:16) considered specimens from northwestern South Dakota and southwestern North Dakota, respectively, to be intergrades between the subspecies *fasciatus* and *olivaceogriseus,* but in both cases assigned specimens to *fasciatus,* mostly on the basis of color. Specimens from Carter County average slightly smaller and paler in color than do mice from those two adjacent areas. Therefore, we use the name *olivaceogriseus* to represent olive-backed pocket mice from southeastern Montana, although they undoubtedly are intergrades between the two races.

Our specimens of *P. fasciatus* were parasitized by a flea, *Meringis* sp., and three species of mites, *Androlaelaps fahrenholzi, Haemogamasus* sp., and *Hirstionyssus* sp.

Perognathus hispidus paradoxus Merriam, 1889
Hispid Pocket Mouse

Specimen examined (1).—5 mi N, 3.5 mi W Camp Crook, 1.

A nulliparous, subadult female, the first record of this species from Montana (Pefaur and Hoffmann, 1971:247), was trapped on a grassy slope at the eastern edge of the Long Pines. Mammals trapped in the same or adjacent trap lines included *Sorex merriami, Spermophilus tridecemlineatus, Thomomys talpoides, Reithrodontomys megalotis, Peromyscus maniculatus, Microtus ochrogaster, Microtus pennsylvanicus, Mus musculus,* and *Zapus hudsonius.* The hispid pocket mouse has also been recorded from adjacent Harding County, South Dakota (Andersen and Jones, 1971:377; Birney and Lampe, 1972:466), and northwestern Crook County, Wyoming (Long, 1965:618).

Dipodomys ordii terrosus Hoffmeister, 1942
Ord's Kangaroo Rat

The kangaroo rat evidently is uncommon in southeastern Montana, being found in sandy areas along dry streams as well as on flats. We obtained no *D. ordii,* but its presence was reported to us, and Preble (MS) mentioned specimens from the Sioux National Forest near Ekalaka. Additionally, this rat is known from adjacent Harding County, South Dakota (Andersen and Jones, 1971:377), and Bowman County, North Dakota (Genoways and Jones, 1972: 18), and from but a few miles west of the Carter County boundary at Powderville, Powder River County, Montana (KU 14885-86 and 14912-13).

Castor canadensis missouriensis Bailey, 1919
Beaver

Beaver dams and freshly cut trees were noted along many of the streams and springs in the Long Pine Hills. An adult was observed at dusk on a large pond at Slick Creek Spring, 7 mi N and 10 mi W Camp Crook, 3800 ft, a place where numerous dams (the largest 35 feet long and 10 feet high) had been built across steep ravines, the sides of which were clad with mature stands of ponderosa pine. The bark of some pines in an area up to 150 feet away from the ponds had been girdled to a height of about two feet. Pines nearest the ponds bore old scars and many were dead, whereas those on the periphery of the girdled area were freshly cut. No lodges were observed, although a cache of deciduous limbs and saplings was noted on a pond below Slick Creek Spring. Active dams also were found at other localities in the Long Pine Hills, as follows: Wickham Gulch, 2 mi N and 4.5 mi W Camp Crook, 3700 ft; Lantis Springs, 5.5 mi N and 10 mi W Camp Crook, 3500 ft; 4 mi N and 7.5 mi W Camp Crook, 3800 ft.

Visher (1914:89) and others have reported beaver activity in Harding County, South Dakota—on Boxelder Creek and along the Little Missouri River. Beaver probably occur in these drainages in Carter County as well.

Reithrodontomys megalotis dychei J. A. Allen, 1895
Western Harvest Mouse

Specimens examined (2).—5 mi N, 5.5 mi W Camp Crook, 3500 ft, 1; 5 mi N, 3.5 mi W Camp Crook, 3400 ft, 1.

This harvest mouse evidently is uncommon in southeastern Montana. Our only two specimens, a subadult male and an adult male (testes 8 and 9 mm in length, respectively) were trapped in July from dense grassy areas in the eastern Long Pine Hills.

Peromyscus maniculatus nebrascensis (Coues, 1877)
Deer Mouse

Specimens examined (152).—11.5 mi N, 3 mi E Ekalaka, 23; 16 mi E Ekalaka, 3150 ft, 3; 17 mi E Ekalaka, 3200 ft, 15; 2 mi S, 1.5 mi E Ekalaka, 1 (MMNH); 3 mi S, .75 mi E Ekalaka, 7 (MMNH); 3 mi S, 1.75 mi E Ekalaka, 2 (MMNH); 3.75 mi S, 2.25 mi W Ekalaka, 4 (MMNH); 4.5 mi S, 1 mi E Ekalaka, 2 (MMNH); 11 mi S, 7.5 mi W Ekalaka, 2 (MMNH); 11 mi S, 7 mi W Ekalaka, 2; 11 mi S, 6.5 mi W Ekalaka, 3 (MMNH); 10.5 mi N, 5 mi W Camp Crook, 3400 ft, 1; 9 mi N, 11 mi W Camp Crook, 3600 ft, 1; 9 mi N, 3 mi W Camp Crook, 3400 ft, 2; 8.5 mi N, 8 mi W Camp Crook, 1; 7 mi N, 3 mi W Camp Crook, 3300 ft, 1; 5.5 mi N, 10 mi W Camp Crook, 3950 ft, 8 (6 MMNH); 5 mi N, 6 mi W Camp Crook, 3500 ft, 14; 5 mi N, 3.5 mi W Camp Crook, 3400 ft, 31; 4 mi N, 8 mi W Camp Crook, 3650 ft, 7; 3.75 mi N, 7.75 mi W Camp Crook, 1 (MMNH); 2 mi N, 4.5 mi W Camp Crook, 3700 ft, 7; 8 mi S, 3 mi W Camp Crook, 3200 ft, 14.

The deer mouse was by far the most common and widely distributed mammal in Carter County. We obtained specimens from all terrestrial habitats except dense stands of ponderosa pine having a sparse understory.

Adults, subadults, and young (in juvenile pelage) were obtained in various stages of seasonal and maturational molt throughout July and in early August. A pregnant female was still in worn winter pelage on 25 July and an adult male and a pregnant female were molting to summer pelage as late as 22 July. Adults of both sexes were taken in fresh summer pelage as early as 1 July, but most individuals obtained early in July still were in winter pelage.

In the first half of July, 12 females carried an average of 5.2 (3-7) embryos, the crown-rump length of which ranged from 3 to 14 mm. Eight individuals collected at this same time had an average of 6.1 (4-9) recent placental scars and two individuals were lactating. One captured during this period in 1972 had 11 placental scars of at least two age categories. In the second half of July, nine females carried an average of 5.0 (3-6) embryos that varied from 3 to 18 mm in length. An average of 4.5 placental scars was noted for four individuals. Thirty-five adult males collected in the first half of July had testes with a mean length of 9.6 (8-11) mm, and 15 taken in the last half of July had testes whose average length was 9.9 (8-13) mm.

Additionally, we obtained two females on 30 June that had four and five recent placental scars. Five males obtained on that date had testes that were 10.2 (10-11) mm in mean length. A subadult female taken on 1 August carried three 2 mm embryos.

Peromyscus maniculatus were parasitized by the following ectoparasites: a mite, *Androlaelaps fahrenholzi;* ticks, *Dermacentor andersoni* and *Ixodes sculptus;* a louse, *Hoplopleura hesperomydis;* and fleas, *Callistopsyllus terinus, Monopsyllus eumolpi eumolpi, Monopsyllus wagneri,* and *Monopsyllus* sp. Three specimens were parasitized by cuterebrid larvae.

Onychomys leucogaster missouriensis (Aubudon and Bachman, 1851)
Northern Grasshopper Mouse

Specimen examined (1).—11.5 mi N, 3 mi E Ekalaka, 1.

A subadult male was trapped in a sandy draw bordered by short grass in Medicine Rocks State Park, an area of massive rock outcroppings in northern Carter County from which Preble (MS) also listed specimens. Although 240 traps were set on three consecutive nights in this area in mid-July, no additional *Onychomys* were obtained; however, *Peromyscus maniculatus, Spermophilus tridecemlineatus,* and *Perognathus fasciatus* were obtained from the same or adjacent trap lines. The rarity of grasshopper mice in eastern Montana was earlier mentioned by Preble (MS).

Our male, taken on 15 July, was molting actively as evinced by patches of new pelage on both shoulders and rump. The testes were 12 mm in length.

Neotoma cinerea rupicola J. A. Allen, 1894
Bushy-tailed Woodrat

Specimens examined (3).—11 mi S, 6.5 mi W Ekalaka, 1 (MMNH); 7 mi N, 3 mi W Camp Crook, 3400 ft, 1; 3.75 mi N, 7.75 mi W Camp Crook, 1 (MMNH).

Our three bushy-tailed woodrats were nulliparous females, apparently young of the year. One, trapped on 5 July under a rock ledge, was molting on the sides and rump. The other two, taken on 12 and 17 July, were completing molt into adult pelage. One was trapped under a large rock near the summit of Trenk Pass in the Chalk Buttes. The other was removed from an abandoned building. Nests and old fecal pellets of woodrats were found frequently in the Long Pine Hills; Merlin Tuttle examined contents of owl pellets (thought to be those of a great horned owl) from an abandoned farm in the Ekalaka Hills that contained remains of these woodrats. Andersen and Jones (1971:380) recorded a specimen from 7 mi N and 2.5 mi W Camp Crook, South Dakota, at the extreme eastern edge of the Long Pine Hills.

Although none of our specimens was fully adult, we assign them to the subspecies *rupicola* rather than *orolestes*. They are indistinguishable from a series assigned to *rupicola* by Andersen and Jones (1971), which includes several individuals of comparable age from Harding County, South Dakota. We are convinced that woodrats living in the several hills and buttes of this tri-state area are of a single taxon.

Microtus ochrogaster haydenii (Baird, 1858)

Prairie Vole

Specimens examined (6).—9 mi N, 3 mi W Camp Crook, 3300 ft, 3; 5 mi N, 3.5 mi W Camp Crook, 3400 ft, 3.

Three specimens were trapped in an ungrazed upland meadow, 5 mi N and 3.5 mi W Camp Crook, and the remaining three were collected from the semi-marshy banks of a small stream in a lightly grazed pasture of sweet clover. *M. pennsylvanicus* and *M. ochrogaster* were taken together at the former locality; however, 600 trap nights in the vicinity of the stream at the latter locality produced no specimens of *pennsylvanicus.* Jones (1964:228), Turner (1974:116), and others have noted that the prairie vole occupies riparian habitats in the absence of *pennsylvanicus* but is excluded from such habitats when both species are present.

One praire vole harbored a flea, *Orchopeas leucopus,* and a chigger, *Euschoengastia setosa.*

Microtus pennsylvanicus insperatus (J. A. Allen, 1894)

Meadow Vole

Specimens examined (71).—1.75 mi S, 1 mi E Ekalaka, 1 (MMNH); 2 mi S, 1.5 mi E Ekalaka, 2 (MMNH); 3 mi S, 1.75 mi E Ekalaka, 27 (MMNH); 8.5 mi N, 8 mi W Camp Crook, 3400 ft, 1; 5.5 mi N, 10 mi W Camp Crook, 10 (MMNH); 5 mi N, 10 mi W Camp Crook, 2; 5 mi N, 6 mi W Camp Crook, 3500 ft, 1; 5 mi N, 3.5 mi W Camp Crook, 3400 ft, 5; 3.75 mi N, 7.75 mi W Camp Crook, 18 (MMNH); 2 mi N, 4.5 mi W Camp Crook, 3700 ft, 1; 8 mi S, 3 mi W Camp Crook, 3200 ft, 3.

The meadow vole was the most abundant microtine in Carter County. It was found in grasslands and lush riparian habitats in the Long Pine Hills as well as along the Little Missouri River. Although we have no specimens from within the Ekalaka Hills, many of these voles were trapped along streams that flow northward from there. The number of specimens collected was small in comparison to the density of runways observed in many areas that were trapped. Preble (MS) earlier mentioned specimens from Medicine Rocks, Ekalaka, Capitol, and Albion.

Of 26 females obtained in July, 10 carried an average of 6.7 embryos (5-9) that ranged in length from 4 to 29 mm. Four females were recorded as lactating in early and mid-July; three other individuals had recent placental scars. Testes of 34 adult and subadult males taken in mid-July were 14.6 (9-20) mm in average length and those of an adult taken in early August were 18 mm. Molt was observed in adult, subadult, and juvenile individuals collected in July and early August.

Our specimens of meadow voles were parasitized by a mite, *Laelaps kochi,* and a louse, *Hoplopleura acanthopus.*

Lagurus curtatus pallidus (Merriam, 1888)

Sagebrush Vole

Specimen examined (1).—16 mi E Ekalaka, 3150 ft, 1.

An adult male, trapped on 8 July on a sagebrush flat in the northeastern part of the county, was the only sagebrush vole obtained. Fecal pellets and runways occasionally were found under large clumps of sagebrush in this area, but extensive trapping, employing both break-back and can traps, produced no additional individuals. *Peromyscus maniculatus* and *Spermophilus tridecemlineatus* were obtained in this habitat. Bailey (1927:101) earlier commented on the difficulty of collecting sagebrush voles in North Dakota. The species evidently is relatively rare and of localized occurrence along the eastern edge of its range.

Preble (MS) mentioned specimens from Medicine Rocks, 15 mi N Ekalaka [probably 11.5 mi N and 3 mi E Ekalaka], and from 5 mi SE Ekalaka. Birney and Lampe (1972:466) reported the only specimens of sagebrush voles known from South Dakota. The species also is known adjacent to Carter County in southwestern Powder River County (Hoffmann *et al.*, 1969a:592) and southwestern Bowman County, North Dakota (Genoways and Jones, 1972:24).

Our specimen was molting as evinced by small irregular patches of new pelage on head, back, and sides, and had testes that were 11 mm in length. External and cranial measurements are: total length, 139 mm; tail length, 19 mm; hind foot length, 16 mm; ear length, 12 mm; weight, 38.2 gms; condylobasal length, 25.9 mm; palatal length, 14.8 mm; interorbital breadth, 3.1 mm; zygomatic breadth, 15.5 mm; maxillary toothrow length, 7.0 mm.

Mus musculus Linnaeus, 1758

House Mouse

Specimens examined (3).—3 mi S, 1.75 mi E Ekalaka, 1 (MMNH); 5 mi N, 3.5 mi W Camp Crook, 3400 ft, 2.

Two adult house mice, a male and a female, were collected on a north-facing slope of a grassy meadow at the eastern edge of the Long Pine Hills. Both were taken on a grid that previously had been live-trapped for 10 days in a trap-release program, then snap-trapped. No house mice were obtained in live-traps on this grid nor were any taken in either live-traps or snap-traps on two adjacent grids. Our third specimen, an adult male, was trapped in a marsh along with *Zapus hudsonius, Microtus pennsylvanicus,* and *Peromyscus maniculatus.*

Preble (MS) commented that house mice generally were distributed in eastern Montana in the proximity of railroads. Andersen and Jones (1971:381) recorded a single individual, trapped along a fencerow, from adjacent Harding County, South Dakota.

Zapus hudsonius campestris Preble, 1899

Meadow Jumping Mouse

Specimens examined (33).—3 mi S, 1.75 mi E Ekalaka, 21 (MMNH); 5.5 mi N, 10 mi W Camp Crook, 3 (MMNH); 5 mi N, 5.5 mi W Camp Crook, 3500 ft, 2; 5 mi N, 3.5 mi W Camp Crook, 3400 ft, 2; 4 mi N, 8 mi W Camp Crook, 3650 ft, 2; 3.75 mi N, 7.75 mi W Camp Crook, 1 (MMNH); 2 mi N, 4.5 mi W Camp Crook, 3700 ft, 1; 8 mi S, 3 mi W Camp Crook, 3200 ft, 1.

Twenty-one of our specimens were trapped from a large marsh at the north edge of the Ekalaka Hills. The remainder were obtained from riparian and marshy habitats in the Long Pine Hills, along the Little Missouri River, and on a grassy upland slope at the eastern edge of the Long Pines. Of our 33 specimens, all caught in July, 25 were adult, and only eight were juvenile or subadult (see Krutzsch, 1954:377, for criteria of age classes). Testes of 13 adult males were 6.1 mm in mean length whereas those of six young males were 4.7 mm. Of the 14 females in our sample, six were carrying embryos that ranged in length from 6 to 19 mm. Mean and modal number of embryos per pregnant female was 6.0 and 7, respectively. Three adult and five young females were neither pregnant nor lactating. Preble (MS) recorded specimens from Ekalaka and the Sioux National Forest.

Intergradation between the subspecies *campestris* and *intermedius* has been suggested in Harding County, South Dakota (Andersen and Jones, 1971:382), and in Dawson County of east-central Montana (Krutzsch, 1954:448). Average and extreme cranial measurements of 19 adults (11 males, 8 females) are: condylobasal length, 21.2 (20.1-22.2) mm; occipitonasal length, 23.3 (22.3-24.0) mm; palatal length, 10.1 (9.7-10.5) mm; mastoidal breadth, 10.3 (10.0-10.7) mm; maxillary toothrow length, 3.7 (3.5-4.1) mm. In their more ochraceous color, our specimens more closely resemble *campestris* from Harding County, South Dakota and the Black Hills, than *intermedius* from North Dakota.

Erethizon dorsatum bruneri Swenk, 1916

Porcupine

Specimen examined (1).—7 mi N, 3 mi W Camp Crook, 3400 ft, 1.

An adult male weighing 27 pounds was shot in the late afternoon of 4 July in a den located under a rock ledge on a pine-clad ridge along the eastern edge of the Lone Pine Hills. In addition, we observed an individual in a meadow, 5 mi N and 3.5 mi W Camp Crook, and two others on a road near Lantis Spring, 5.5 mi N and 10 mi W Camp Crook. Fresh sign of porcupines was seen elsewhere in the Long Pines. The species evidently is fairly common there and, presumably, in adjacent pine-covered areas.

ORDER CARNIVORA

Canis latrans latrans Say, 1823
Coyote

The coyote population of Carter County was apparently extremely low at the time of our studies, perhaps as a result of active predator control practices, including 1080 poison. This compound is currently banned, and coyotes are reported increasing in many places. Our field parties neither saw nor heard coyotes. Visher (1914:90) reported that during the winter of 1910-11 one trapper collected 102 coyotes in the Ekalaka Forest. During the period July 1970 to June 1971, bounties were paid on four coyotes purportedly taken in Carter County. Andersen and Jones (1971:382) listed two specimens obtained by a federal trapper during the winter of 1961-62 along the eastern edge of the Long Pine Hills, 6 mi N and 4 mi W Camp Crook, Harding County, South Dakota.

Canis lupus nubilus Say, 1823
Wolf

The wolf, although now extirpated (Goldman, 1944:442), once ranged throughout Carter County. Bailey (1907:10) reported that in 1893 "wolves were common at Alzada and Powderville, and were very destructive to stock, especially calves and colts." Visher (1914:90) noted that during the winter of 1909-10 a trapper took four wolves in the Ekalaka Forest, and Goldman (1944:444) listed a specimen from Ekalaka.

Extirpation of the wolf in Carter County most likely paralleled in time its disappearance from Harding County, South Dakota (see Andersen and Jones, 1971:383). Populations may have remained slightly longer than elsewhere in the Long Pine Hills and forested areas near Ekalaka, although such areas were exploited heavily by commercial trappers.

Vulpes vulpes regalis Merriam, 1900
Red Fox

We took no specimens of this fox in Carter County, but an immature female, captured approximately 5 mi W Camp Crook, was held as a pet by a local family. An adult was sighted on the night of 26 July 1970 on a sagebrush flat just north of the Long Pines and another was seen on the night of 17 July 1971 on a U.S. Forest Service road in the Ekalaka Hills. Visher (1914:90) reported the red fox as "not rare about the Long Pines" in the early part of the century.

During the period 1 July 1970 to 16 July 1971, Carter County paid bounties on 958 red foxes. The extent to which predator control programs have affected red fox populations is unknown, but Andersen and Jones (1971:383) reported that in adjacent Harding

County, South Dakota, this fox "seems to maintain considerably higher populations than does the coyote," in spite of control pressure.

Ursus arctos horriblilis Ord, 1815

Grizzly Bear

The skull of a grizzly bear displayed in the Carter County Museum in Ekalaka, was found in 1920 on Cottonwood Creek, T 5 S and R 61 E, in southern Carter County. The specimen evidently had been shot inasmuch as there appears to be a bullet hole above the orbits. Visher (1914:91) noted that during the early 1890's a grizzly bear was killed a short distance southwest of Camp Crook. Additionally, a cave wall in the Cottonwood Creek area carries the inscription "Killed Bear in nest" (M. E. Lambert, pers. com.), which may refer to this or the following species.

Ursus americanus americanus Pallas, 1780

Black Bear

Visher (1914:91) reported that "Bears have been recently killed in the Long Pine and Ekalaka forests, but their day of extermination is here near at hand." Preble (MS) indicated that black bears formerly were widely distributed in eastern Montana.

Procyon lotor hirtus Nelson and Goldman, 1930

Raccoon

Our only records of the raccoon in Carter County are of tracks found in the Long Pines along the edge of a beaver pond, 4 mi N and 8 mi W Camp Crook, and a specimen from 3 mi W Alzada (Hoffmann *et al.,* 1969a:595). An adult was observed on several nights in July, however, on a ridge at the extreme eastern edge of the Long Pine Hills just inside Harding County, South Dakota, and Andersen and Jones (1971:384) reported a litter of five young found in May in this same area. They noted that this species "evidently is one of the commonest carnivores" in northwestern South Dakota and raccoons likely occur along the Little Missouri River and in other suitable riparian habitats in Carter County.

Mustela frenata longicauda Bonaparte, 1838

Long-tailed Weasel

Specimens examined (2).—3 mi S, 1.75 mi E Ekalaka, 1 (MMNH); 7 mi N, 4 mi W Camp Crook, 1.

The mummified body of a long-tailed weasel in winter pelage was found on a sparsely forested ridge at the eastern edge of the Long Pine Hills. From size and cranial characters, we judge this specimen to be a female. A second weasel, a young male, was captured in a hand-held rat trap by Larry Heaney at the entrance to a pocket gopher burrow on 17 July. A partially eaten gopher had been removed from the burrow minutes before following a minor tug-of-war with the weasel. The rat trap was then baited with meat of the dead gopher. Preble (MS) noted that this species ". . . appears generally distributed but nowhere abundant" in southeastern Montana.

Mandibular formation is anomalous in the mummy; the length of the right mandible is 25.8 mm whereas the length of the left mandible is 28.1. Extension of the left mandible caused a slight labial curve in the distal portion of the right mandible, nonalignment of the left upper and lower canines, and malocclusion of upper and lower incisors. The lower left canine does not occlude with the upper, but is directed more anteriorly and occludes with the left i2 and i3, which in turn have been pushed posteriorly toward the upper left canine. Both second lower incisors are situated posterior to i1 and i3.

Mustela nigripes (Aububon and Bachman, 1851)
Black-footed Ferret

Specimen examined (1).—Piniele, 1.

Cahalane (1954:419) reported that an adult male black-footed ferret was killed on 3 November 1953 on a highway north of Alzada, in southern Carter County. Additionally, Henderson *et al.* (1969) listed seven localities of record in Harding County, South Dakota, two of which are in townships adjoining Carter County (T 19 N, R 1 E, and T 15 N, R 1 E), and we have examined museum specimens from Custer County, Montana, adjacent to Carter County to the northwest.

A skin and partial skeleton (KU 14411) of an adult mentioned by Hoffmann *et al.* (1969a:597) was obtained in October 1944 at Piniele in southwestern Carter County. In view of its small size, this specimen most likely represents a female. Selected cranial measurements are: condylobasal length, 66.8 mm; palatal length, 30.8 mm; mastoid breadth, 33.8 mm; least interorbital breadth, 16.7 mm; postorbital breadth, 10.7 mm; maxillary toothrow length, 19.1 mm.

Close dependence of the black-footed ferret on prairie dogs as a major food source no doubt has had a serious impact on the current status of this mustelid, although it may never have been abundant. Efforts to reduce or extirpate prairie dogs continue in Carter County and elsewhere in southeastern Montana.

Taxidea taxus taxus (Schreber, 1778)
Badger

Specimen examined (1).—8 mi S, 3 mi W Camp Crook, 3700 ft, 1.

Badgers probably occur throughout Carter County. A subadult male with testes that were 49 mm in length was trapped on 8 July at a den located in the north face of a gulley along the Little Missouri River. The stomach of this specimen contained the remains of three *Thomomys talpoides,* a small bird, five bees, and unidentified plant material. A subadult observed crossing a road in the sagebrush flats to the north of the Long Pine Hills, 1 mi S and 13 mi E Ekalaka, 3200 ft, in the late afternoon of 14 July escaped to a nearby burrow after it dropped an immature prairie dog that it carried in its mouth. Our one specimen harbored a tick, *Ixodes kingi.*

Mephitis mephitis hudsonica Richardson, 1829

Striped Skunk

Specimens examined (4).—8.5 mi N, 8.5 mi W Camp Crook, 3400 ft, 2; 6 mi N, 9 mi W Camp Crook, 2.

Striped skunks evidently are common in the Long Pine Hills and surrounding areas. Two of our four specimens were collected from a densely wooded slope in the Long Pines—one trapped along a game trail and the other picked up in the field as a skeleton. The other two specimens, a young male (testes 2 mm in length) and an adult female (six placental scars), were shot on the night of 16 July along a road in rolling grasslands just to the north of the eastern part of the Long Pines.

Striped skunks were observed frequently in the Long Pine Hills. Our only sight record other than from that area was of a young animal killed on a road in the vicinity of Sheep Mountain, 4 mi S and 11 mi W Camp Crook. Andersen and Jones (1971:385) reported an observation from just east of the Long Pines at a place 6 mi N and 2.5 mi W Camp Crook, Harding County, South Dakota.

The young male shot on 16 July was parasitized by a tick, *Ixodes kingi.*

Felis concolor hippolestes Merriam, 1897

Mountain Lion

Mountain lions, "formerly of quite general distribution over the eastern part of Montana" (Preble, MS), have been extirpated in the southeastern part of the state. Visher (1914:91) noted that the mountain lion that visited Harding County, South Dakota, during the winter of 1910-11 "was doubtless a roamer from the Long Pines or Ekalaka Forests." The presence of this cat in Carter County probably now is limited to an occasional transient.

ORDER ARTIODACTYLA

Cervus elaphus canadensis Erxleben, 1777

Wapiti or Elk

Prior to the appearance of homesteaders and hunters, elk were common on the plains of eastern Montana. In a summary of historical accounts of big game in Montana, Koch (1941:368) noted "that they [elk and bison] occurred in vastly greater numbers in the plains country, with some timber or mountain shelter, than they did in the higher mountain country. . . . " Preble (MS) mentioned that elk formerly were distributed over southeastern Montana and Visher (1914:87) reported that the "last [elk] were killed in 1879 when a large crew cut trees for the N.P.R.R. in the Long Pines." A fragment of an elk antler was found (M. E. Lambert, pers. com.) in "a timbered area of the Chalk Buttes about twenty miles south of Ekalaka."

Odocoileus hemionus hemionus (Rafinesque, 1817)

Mule Deer

Mule deer commonly were seen in meadows and occasionally along ridges in the Lone Pine Hills and Chalk Buttes. Preble (MS) reported this deer to be generally distributed throughout eastern Montana in the early part of this century. Mule deer may be more numerous in Carter County than are white-tailed deer; in the Long Pines, however, we found the latter to be the more numerous. Sight records other than from the Long Pine Hills are from 1.5 mi N and 5.5 mi E Ekalaka (six bucks) and 4 mi SE Ekalaka (four does and one fawn).

Odocoileus virginianus dacotensis Goldman and Kellogg, 1940

White-tailed Deer

Specimens examined (6).—8.5 mi N, 13 mi W Camp Crook, 2 (MMNH); 5.5 mi N, 10 mi W Camp Crook, 3400 ft, 1; 5 mi N, 3.5 mi W Camp Crook, 3400 ft, 1; 4 mi N, 9 mi W Camp Crook, 3950 ft, 2.

We frequently observed white-tailed deer in the Long Pine Hills, mainly along the pine-covered ridges and in meadows adjacent to such ridges. Our only observation of white-tails outside the Long Pines was of a doe, accompanied by a fawn, resting among deciduous brush along the Little Missouri River at a place 8 mi S and 3 mi W Camp Crook. Preble (MS) reported white-tailed deer " . . . to be more commonly met with in the southeastern part of the State than elsewhere [in eastern Montana]."

No group of more than five deer was observed. Several does with fawns repeatedly were seen grazing in grassy draws in early and mid-July. All of our specimens are skulls picked up in the Long Pines.

Antilocapra americana americana (Ord, 1815)

Pronghorn

Pronghorns regularly were seen in the grasslands, and occasionally in meadows, along the margin of the Long Pines in the summer of 1970. Beer (1944:45) reported that in 1941 Carter County had the largest number of pronghorns, an estimated 2500, of any county in Montana. He also noted that in severe winters pronghorns migrated into the area from South Dakota, seeking shelter among the breaks and ridges along the Little Missouri River. Andersen and Jones (1971:387) reported sighting herds of up to 50 individuals in adjacent Harding County, South Dakota; all of our observations, however, were of groups of five or less.

While conducting an aerial census of pronghorns in Carter County on 28 January 1948, Thompson (1949:313) observed an adult golden eagle attacking a single adult male pronghorn near the rear of a herd of 64 individuals. In three consecutive attacks, the eagle grasped the back of the animal and rode with outspread wings as the pronghorn fled with the herd across open grassland. We have no such observations of predation, but golden eagles were sighted in the Long Pines as well as over adjacent grasslands.

An analysis of pronghorn stomach contents, conducted in Carter County from September through December of 1944 and 1945 (Couey, 1946:367), revealed that sagebrush (*Artemisia tridentata* and *A. cana*), snowberry (*Symphoricarpos* sp.), and snakeweed (*Guterriezia* sp.) composed 75 per cent of the diet by volume.

Bison bison bison (Linnaeus, 1758)

Bison

Vast herds of bison are known to have occurred along the Missouri and Yellowstone rivers as well as across the prairies of what is now Carter County until the middle of the 19th century. During the exploration of the Yellowstone River and its tributaries in 1859, Captain W. F. Raynolds and his party crossed the extreme southwestern corner of Carter County. While camped near the present border between Carter County, Montana, and Crook County, Wyoming, on 21 June, he noted (1868:33): "We are now in the buffalo region, and small herds are to be seen in all directions. Their presence may explain some of the prevalent barrenness, as they consume all the grass in their paths." During an expedition to the Black Hills in July 1874, Custer traveled down the Little Missouri River and entered southeastern Carter County, then part of the Montana Territory. Custer found (1875:1) "this valley [of the Little Missouri River] almost destitute of grazing . . ." a condition perhaps attributable to bison.

J. A. Allen (1877:545) noted that by 1877, between the Platte and Missouri rivers, bison were confined to the area of the Bighorn, Tongue, and Powder rivers. Indian hostilities, which prevented exploitation of the eastern Montana herds, were curtailed in the mid-1870's, opening the territory to "civilization" and the extirpation of the remaining bison. Visher (1914:88) reported "a small bunch" in

Harding County, South Dakota, in 1886 and commented on the occurrence of numerous bullet-riddled skulls testifying to the activities of "market shooters."

Ovis canadensis auduboni Merriam, 1901
Bighorn Sheep

Bighorn sheep once were abundant in eastern Montana (Preble, MS) and specimens were collected in the late 1800's in the badlands and high plateaus along the Little Missouri River in North Dakota (Buechner, 1960:20).

The mounted head of a bighorn displayed in the Carter County Museum, Ekalaka, Montana, was obtained by Dan Bowman in 1893 from the Powder River near Locate, Custer County, Montana. The only record of bighorn in Carter County consists of two pairs of horn cores, one "dug out of a spring twenty miles west of Ekalaka on Spring Creek," and the other "found on Tie Creek south of the Long Pines" (M. E. Lambert, pers. com.). The specimens are tentatively assigned to *O. c. auduboni*, a subspecies now considered extinct (Cowan, 1940:542).

OTHER SPECIES

Three additional species, the muskrat *(Ondatra zibethicus)*, the mink *(Mustela vison)*, and the bobcat *(Lynx rufus)* most assuredly are found in Carter County as indicated by the availability of suitable habitats and the presence of recent records (Andersen and Jones, 1971) from nearby areas. Although we obtained neither specimens nor sight records of these species, all three were reported by local residents. Additionally, during the fiscal year 1970-71, bounties were paid in Carter County for 130 bobcat and lynx. Individuals were not identified to species, but we believe that most, if not all, were *Lynx rufus.*

Species of Unverified Occurrence

Twelve species listed below may occur (or in the recent past probably occurred) in Carter County. The possible presence of 10 species is inferred by their distribution and habitat preference in areas adjacent to Carter County. A published account of migration of the Norway rat (Tryon, 1947) and the mention of lynx in an unpublished manuscript by Preble also are noted. Preble's mention of *Lepus americanus* from the forested areas near Ekalaka almost certainly was in error as this hare now occurs no nearer Carter County than in the Killdeer Mountains of North Dakota (Genoways and Jones, 1972:9), Richland County, Montana (Hoffmann *et al.*, 1969a:584), and the Bighorn Mountains of Wyoming (Long, 1967: 548).

Sylvilagus nuttallii grangeri (J. A. Allen, 1895).—Although this cottontail is not presently known from Carter County, it may be found along the wooded and brushy streams in the hills along the western and southern edge of the county. Specimens have been taken a short distance to the south in Crook County, Wyoming (Long, 1965:544).

Marmota flaviventris dacota (Merriam).—The yellow-bellied marmot is known to occur in the Black Hills (Turner, 1974:68) and adjacent regions in Wyoming (Long, 1965:570). Hoffmann *et al.* (1969a:568) reported marmots from Rosebud County, Montana, which is west of Carter County. The presence of yellow-bellied marmots among rocky outcrops in Carter County is possible, although we observed no sign of the species.

Reithrodontomys montanus albescens Cary, 1903.—The plains harvest mouse has been reported (Andersen and Jones, 1971:378) from adjacent Harding County, South Dakota, where it was rare in upland grassy habitats. In northeastern Wyoming, it is known from northern Campbell County (Long, 1965:626). The species has not been reported from Montana.

Peromyscus leucopus aridulus Osgood, 1909.—The white-footed mouse may be present in the county in small discontinuous populations, similar to the isolated population reported by Andersen and Jones (1971:378) in adjacent Harding County, South Dakota. The species is known from Crook County, Wyoming (Long, 1965:634), and elsewhere in Montana (Hoffmann *et al.*, 1969a:590). However, we trapped unsuccessfully for this species in a variety of habitats.

Rattus norvegicus (Berkenhout, 1769).—Tryon (1947:188) included northeastern Carter County within the range of migration of rats that had reached eastern Montana in the late 1940's from North Dakota. Migrational routes in eastern Montana followed highways and railroads, and therefore, were primarily in valleys. We know of no specimens of the Norway rat from Carter County.

Vulpes velox (Say, 1823).—The swift fox no doubt occurred in Carter County within historic times, but there are no actual records of its presence. Hoffmann *et al.* (1969a:594) regarded the species as "now probably extinct in the state." However, it is noteworthy that a specimen was taken in nearby Slope County, North Dakota, on 20 February 1970 (Pfeifer and Hibbard, 1970:835).

Urocyon cinereoargenteus ocythous Bangs, 1899.—Although no records of the gray fox are known from Montana, an adult male has been recorded (Jones and Henderson, 1963:283) from 43 miles east of Carter County at Deer Ear Buttes, Butte Co., South Dakota. This record constituted a considerable westward extension of the then known range and possibly is indicative of a trend in dispersal of this species.

Mustela erminea muricus (Bangs, 1899).—No specimens of this weasel have been reported from eastern Montana. However, the proximity of a recent record (Long, 1965:692) from Crook County, Wyoming, at a place 40 miles south of Carter County, suggests the possible occurrence of the ermine in the southeastern part of the state.

Gulo gulo luscus (Linnaeus, 1758).—The wolverine, although probably never abundant, likely occurred in southeastern Montana within historic time.

Spilogale putorius interrupta (Rafinesque, 1820).—Southeastern Montana was included in the distribution of the spotted skunk by Hoffmann and Pattie (1968:117), although no specimens have been reported from the area. Visher (1914:91) commented that the spotted skunk was more abundant than the "large skunk" in northwestern South Dakota, but Andersen and Jones (1971:385) more recently reported the species as rare there.

Lontra canadensis pacifica (Schreber, 1776).—Preble (MS) commented that the otter once occurred in small numbers in eastern Montana, and Visher (1914:91) reported a specimen taken on the Little Missouri River in Harding County, South Dakota. We follow van Zyll de Jong (1972) in the use of generic and subspecies names of the otter.

Lynx canadensis canadensis Kerr, 1792.—Lynx populations in Montana have recently shown a marked increase, but this cat is uncommon in the southeastern part of the state (Hoffmann *et al.*, 1969a:598). No records of the species are known from Carter County, where it no doubt once occurred and may again be found. Although it has been suggested that *L. canadensis* is conspecific with *L. lynx* of the Old World, we follow Kurtén and Rausch (1959: 41) in regarding them as specifically distinct.

ZOOGEOGRAPHIC COMMENTS

Faunal Components

The 50 native North American species known as recent inhabitants of southeastern Montana exhibit five distributional patterns, the implications of which have been discussed by Hoffmann and Jones (1970). The largest faunal grouping consists of species having widespread distributions. These species either occupy much of temperate North America, or have distributions that do not coincide with any major faunal unit. The 23 species so categorized are: *Myotis leibii, Myotis lucifugus, Lasionycteris noctivagans, Eptesicus fuscus, Lasiurus cinereus, Castor canadensis, Peromyscus maniculatus, Erethizon dorsatum, Canis latrans, Canis lupus, Vulpes vulpes, Ursus arctos, Ursus americanus, Procyon lotor, Mustela frenata, Taxidea taxus, Mephitis mephitis, Felis concolor, Cervus elaphus, Odocoileus hemionus, Odocoileus virginianus, Antilocapra americana,* and *Bison bison.* Many of these mammals are vagile and eurytopic species, or species with specializations that are met in more than a single biotope (for example, the beaver). The wolf, grizzly bear, black bear, mountain lion, elk, bison, and bighorn sheep have been extirpated in southeastern Montana directly or indirectly by man. The reduction of coyote populations elsewhere in Montana (Hoffmann *et al.*, 1969a:596) and in Wyoming (Robinson, 1961, and Linhart and Robinson, 1972) had been followed by increased populations of other carnivores, such as skunk, badger, lynx, and red fox; the last-mentioned species recently has extended its range westward in Montana (Hoffmann *et al.*, 1969a:594).

Although these wide-ranging carnivores occurred in grasslands, the mountain lion and black bear were more likely to be found among rocky buttes and ridges and the raccoon is more typical of the floodplain forests. The porcupine, although associated principally with coniferous forests, herein is considered a "widespread species" because of its extensive distribution. The mule deer and pronghorn are essentially western species, whereas the white-tailed deer is a wide-ranging species. Although a common plains mammal, the bison had an extensive northern and eastern distribution. Three of the five bats are apparently permanent residents of the area, *Lasiurus* and *Lasionycteris* being migrants.

Boreomontane species.—Three bats, *Myotis evotis, Myotis volans, Plecotus townsendii,* as well as *Thomomys talpoides, Neotoma cinerea,* and *Ovis canadensis* are primarily montane species, although the first, second, third, and sixth species also have extensive southwestern distributions. Four species (*Sorex cinereus, Eutamius minimus, Tamiasciurus hudsonicus,* and *Microtus pennsylvanicus*) occur in boreal areas to the north as well as montane areas to the west. *Zapus hudsonius,* basically a boreal species, also inhabits much of the eastern deciduous forest. All of these species, except the three bats, have developed distinctive subspecies on the Northern Great Plains.

Steppe species.—Steppe species have evolved in close association with the grassland environment; they are characteristic of, and more or less restricted to, such areas. Steppe species occurring in southeastern Montana are *Lepus townsendii, Cynomys ludovicianus, Spermophilus tridecemlineatus, Perognathus fasciatus, Perognathus hispidus, Microtus ochrogaster,* and *Mustela nigripes.* Indicative of such autochthonous influence is the close predator-prey relationship of the prairie dog and the black-footed ferret.

Sonoran species.—Species that have invaded the area from the Southwest are *Sylvilagus audubonii, Dipodomys ordii, Reithrodontomys megalotis,* and *Onychomys leucogaster.* The last two species now inhabit much of the Northern Great Plains as well as areas of the Great Basin.

Great Basin species.—Two species have invaded the plains from the Great Basin. The sagebrush vole *(Lagurus curtatus)* most likely entered the Northern Great Plains through the Wyoming Basin (Hoffmann and Jones, 1970:370). Knowledge of the distribution of *Sorex merriami,* although this shrew is widespread in the Great Basin, is limited by a lack of specimens.

Eastern species.—The eastern cottontail *(Sylvilagus floridanus)* reaches its northwesternmost known distribution in Carter County, where it is closely associated with riparian habitats. Found primarily east of the Rocky Mountains, one subspecies of this rabbit, *S. f. similis,* has developed on portions of the Northern and Central Great Plains. Another eastern species, *Sciurus niger,* is a recent invader, and most likely entered the area from the northeast along the Little Missouri River, where it is restricted to the deciduous floodplain forest.

Unverified species.—Eleven of the 12 species of unverified occurrence in Carter County are native North American mammals. Of these 11, five *(Sylvilagus nuttallii, Marmota flaviventris, Mustela erminea, Gulo gulo,* and *Lynx canadensis* have boreal or montane affinities, two (*Peromyscus leucopus* and *Urocyon cinereoargenteus*) are associated with the easern forest, three (*Reithrodontomys montanus, Vulpes velox,* and *Spilogale putorius*) are steppe species, and one *(Lontra canadensis)* is a widespread species.

Faunal Comparisons

In order to add greater perspective to the zoogeographic relationships of the mammalian fauna of southeastern Montana, we have compared it with the faunas from two other sites on the Northern Great Plains. Southern Saskatchewan, a Transition and Upper Sonoran zone of parkland and prairie bordered on the east, south, and west by the Saskatchewan and Qu'Appelle rivers, is representative of the northern extent of the Great Plains. Northwestern Nebraska (Sioux, Dawes, and Sheridan counties) comprises a southern site that includes the Pine Ridge district of the High Plains and the Pierre Plains of the Missouri Plateau. Carter County, Montana, and adjacent Harding County, South Dakota, form a unit representing a central location on the Northern Great Plains.

The mammals of southern Saskatchewan have recently been examined by Beck (1958) and Soper (1961). The distributional records of Jones (1964) and McDaniel (1967) were used to compile a list of mammals of northwestern Nebraska. The foregoing accounts and those by Andersen and Jones (1971) for adjacent Harding County were combined for the mammalian fauna of the central site. The past and present distribution of many carnivores and artiodactyls is uncertain and members of these two orders thus are excluded from the following discussion.

Of a total of 51 species of small mammals found at the three sites, 24 species are common to all. Although the number of

TABLE 2. Composition of small mammal faunas of three regions on the Northern Great Plains; see text for discussion and sources of figures.

Taxa	Northwestern Nebraska	Northwestern South Dakota Southeastern Montana	Southern Saskatchewan
Insectivora	3	2	4
Chiroptera	7	8	6
Lagomorpha	4	3	4
Rodentia	23	22	23

species present at each site is similar (Table 2), the species composition varies considerably. Of the 11 species restricted to southern Saskatchewan, six (*Sorex vagrans, Microsorex hoyi, Sylvilagus nuttalii, Lepus americanus, Glaucomys sabrinus,* and *Clethrionomys gapperi*) are of boreal or montane distribution and three (*Blarina brevicauda, Lasiurus borealis,* and *Marmota monax*) have affinities with the eastern deciduous forest. Two sciurid rodents, *Spermophilus richardsonii* and *Spermophilus franklinii,* are restricted to the northern site and are, respectively, of Great Basin and (eastern) steppe affinities. A montane bat species, *Plecotus townsendii,* is, among the three faunas, the only species found only in the southeastern Montana-northwestern South Dakota area. The five species found only in northwestern Nebraska consist of two steppe species (*Geomys bursarius* and *Perognathus flavescens*), two Sonoran species (*Lepus californicus* and *Spermophilus spilosoma*), and one eastern species *(Scalopus aquaticus).* It is apparent, although not surprising, that the northern and southern sites support faunistic elements of somewhat different distributional affinities. It is interesting to note that but a single species is found solely at the central site.

The two species common only to the northern and central samples are the boreal *Tamiasciurus hudsonicus* and the invader from the Great Basin, *Lagurus curtatus.* Two steppe species (*Perognathus hispidus* and *Reithrodontomys montanus*), two Sonoran species (*Sylvilagus audubonii* and *Reithrondontomys megalotis*), two montane species (*Myotis evotis* and *Myotis volans*), one eastern deciduous woodland species *(Sciurus niger),* and one Great Basin species *(Sorex merriami)* are common to the central and southern sites. There are no species shared by the northern and southern sites to the exclusion of the Montana-South Dakota region.

As its geographic location suggests, the Montana-South Dakota sample represents an "intermediate" fauna inasmuch as all but one species is shared with either the northern or southern samples. The presence of eight species shared by the central and southern samples in comparison to two species common to the northern and central units is noteworthy. The boreomontane element, prevalent in southern Saskatchewan, is limited at the central site and to an even greater degree at the southern site, probably owing to such features as temperature, amount of precipitation, and nature and extent of forest habitats. Grassland invaders have been aided in their post-Wisconsin dispersal by the continuity of the grassland environment. Several of the steppe and grassland-associated species present at the southern site have reached the Montana-South Dakota area, but are absent in Saskatchewan.

SUMMARY

Fifty-three species of mammals are reported to have occurred in Carter County, Montana, within historical times. In addition, 12 species are noted as having a possible but unverified occurrence in the county. Annotated accounts of these 65 species provide comments on their distributional status and natural history in southeastern Montana. Zoogeographically, this part of Montana supports a mammalian fauna composed of widespread, boreomontane, steppe, sonoran, Great Basin, and eastern species. Species with widespread distributions comprise the largest single group.

LITERATURE CITED

ALDEN, W. C.
1932. Physiography and glacial geology of eastern Montana and adjacent areas. U.S. Geol. Surv., Prof. Paper, 174:viii + 133.
ALLEN, J. A.
1877. History of the American bison, *Bison americanus*. Ann. Rept. U.S. Geol. and Geogr. Surv. Territories, 9:443-587.
ANDERSEN, K. W., and J. K. JONES, JR.
1971. Mammals of northwestern South Dakota. Univ. Kansas Publ., Mus. Nat. Hist., 19:361-393.
BAILEY, V.
1907. Wolves in relation to stock, game and the national forest reserves. Bull. U.S. Forest Service, 72:1-31.
1915. Revision of the pocket gophers of the genus Thomomys. N. Amer. Fauna, 39:1-136.
1927. A biological survey of North Dakota. *Ibid.*, 49:vi + 1-226.
BAUER, C. M.
1924. The Ekalaka lignite field, southeastern Montana. Bull. U.S. Geol. Surv., 751:231-267.
BECK, W. H.
1958. A guide to Saskatchewan mammals. Spec. Publ. Saskatchewan Nat. Hist. Soc., 1:1-52.
BEER, J.
1944. Distribution and status of the pronghorn antelope in Montana. Jour. Mamm., 25:43-46.
BIRNEY, E. C., and R. P. LAMPE
1972. Sagebrush vole (Lagurus curtatus) in South Dakota. Amer. Midl. Nat., 88:466.
BROWN, L. N.
1967. Ecological distribution of six species of shrews and comparison of sampling methods in the central Rocky Mountains. Jour. Mamm., 48:617-623.

Buechner, H. K.

1960. The bighorn sheep in the United States, its past, present, and future. Wildlife Monogr., 4:1-174.

Cahalane, V. H.

1954. Status of the black-footed ferret. Jour. Mamm., 35:418-424.

Couey, F. M.

1946. Antelope foods in southeastern Montana. Jour. Wildlife Mgt., 10:367.

Cowan, I. McT.

1940. Distribution and variation in the native sheep of North America. Amer. Midl. Nat., 24:505-580.

Custer, G. A.

1875. A report of the expedition to the Black Hills. Exec. Doc., Senate, 2nd Sess., 43rd Congress, 32:1-9.

Finley, R. B., Jr.

1969. Cone caches and middens of Tamiasciurus in the Rocky Mountain region. Pp. 233-273, *in* Contributions in mammalogy (J. K. Jones, Jr., ed.), Misc. Publ. Mus. Nat. Hist., Univ. Kansas, 51:1-428.

Genoways, H. H., and J. K. Jones, Jr.

1972. Mammals from southwestern North Dakota. Occas. Papers Mus., Texas Tech Univ., 6:1-36.

Gill, J. R.

1962. Tertiary landslides, northwestern South Dakota and southeastern Montana. Bull. Geol. Soc. Amer., 73:724-736.

Goldman, E. A.

1944. Classification of wolves. Pp. 387-507, *in* The wolves of North America (S. P. Young and E. A. Goldman), Amer. Wildlife Inst., Washington, D.C., xvi + 636 pp.

Hall, E. R.

1951. A synopsis of the North American Lagomorpha. Univ. Kansas Publ., Mus. Nat. Hist., 5:119-202.

Hall, E. R., and K. R. Kelson

1951. Comments on the taxonomy and geographic distribution of some North American rabbits. *Ibid.,* 5:49-58.

Henderson, F. R., P. F. Springer, and R. Adrian

1969. The black-footed ferret in South Dakota. South Dakota Dept. Game, Fish and Parks, Pierre, 37 pp.

Hibbard, E. A.

1956. Range and spread of the grey and fox squirrel in North Dakota. Jour. Mamm., 37:525-531.

Hoffmann, R. S., and J. K. Jones, Jr.

1970. Influence of late-glacial and post-glacial events on the distribution of Recent mammals on the Northern Great Plains. Pp. 355-394, *in* Pleistocene and Recent environments of the central Great Plains (W. Dort, Jr., and J. K. Jones, Jr., eds.), Spec. Publ. Dept. Geol., Univ. Kansas, 3:1-433.

Hoffmann, R. S., and D. L. Pattie

1968. A guide to Montana mammals. . . . Univ. Montana, Missoula, x + 133 pp.

Hoffmann, R. S., P. L. Wright, and F. E. Newby

1969a. The distribution of some mammals in Montana. I. Mammals other than bats. Jour. Mamm., 50:579-604.

Hoffmann, R. S., D. L. Pattie, and J. F. Bell

1969b. The distribution of some mammals in Montana. II. Bats. *Ibid.,* 50: 737-741.

HOLLISTER, N.
1916. A systematic account of the prairie-dogs. N. Amer. Fauna, 40:1-37.
HOOPER, E. T.
1944. Additional records of the Merriam shrew in Montana. Jour. Mamm., 25:92.
HOWELL, A. H.
1929. Revision of the American chipmunks (genera *Tamias and Eutamias*). N. Amer. Fauna, 52:1-157.
1938. Revision of the North American ground squirrels, with a classification of the North American Sciuridae. *Ibid.,* 56:1-256.
JACKSON, H. H. T.
1928. A taxonomic review of the American long-tailed shrews (genera *Sorex* and *Microsorex*). N. Amer. Fauna, 51:vi + 1-238.
JONAS, R. J.
1966. Merriam's turkey in southeastern Montana. Tech. Bull., Montana Fish and Game Dept., 3:1-36.
JONES, J. K., JR.
1953. Geographic distribution of the pocket mouse, Perognathus fasciatus. Univ. Kansas Publ., Mus. Nat. Hist., 5:515-526.
1964. Distribution and taxonomy of mammals of Nebraska. *Ibid.,* 16:1-356.
JONES, J. K., JR., and F. R. HENDERSON
1963. Noteworthy records of foxes from South Dakota. Jour. Mamm., 44:283.
JONES, J. K., JR., R. P. LAMPE, C. A. SPENRATH, and T. H. KUNZ
1973. Notes on the distribution and natural history of bats in southeastern Montana. Occas. Papers Mus., Texas Tech Univ., 15:1-12.
KELLOGG, C. E. (ed.)
1938. Soils of the United States. Pp. 1019-1161, *in* Soils and Men, Yearbook of Agriculture, U.S.D.A., xvi + 1232 pp.
KOCH, E.
1941. Big game in Montana from early historical records. Jour. Wildlife Mgt., 5:357-370.
KRUTZSCH, P. H.
1954. North American jumping mice (genus Zapus). Univ. Kansas Publ., Mus. Nat. Hist., 7:349-472.
KÜCHLER, A. W.
1964. Potential natural vegetation of the conterminous United States. Spec. Publ., Amer. Geogr. Soc., 36:v + 1-39 + map + 116 plates.
KURTÉN, B., and R. RAUSCH
1959. Biometric comparisons between North American and European mammals. Acta Arctica, Fasc. XI. E. Munksgaard, Copenhagen, 44 pp.
LAMPE, R. P.
1971. The mammals of southeastern Montana. Unpubl. M.A. thesis, Univ. Kansas, Lawrence, ii + 68 pp.
LILLEGRAVEN, J. A.
1970. Stratigraphy, structure, and vertebrate fossils of the Oligocene Brule Formation, Slim Buttes, northwestern South Dakota. Bull. Amer. Geol. Soc., 81:831-850.
LINHART, S. B., and W. B. ROBINSON
1972. Some relative carnivore densities in areas under sustained coyote control. Jour. Mamm., 53:880-884.
LONG, C. A.
1965. The mammals of Wyoming. Univ. Kansas Publ., Mus. Nat. Hist., 14:493-758.

McDaniel, L. L.
1967. Merriam's shrew in Nebraska. Jour. Mamm., 48:489-493.

Miller, G. S., and R. Kellogg
1955. List of North American Recent mammals. Bull. U.S. Natl. Mus., 205:xii + 954.

Nelson, E. W.
1909. The rabbits of North America. N. Amer. Fauna, 29:1-314.

Pefaur, J. E., and R. S. Hoffmann
1971. Merriam's shrew and hispid pocket mouse in Montana. Amer. Midl. Nat., 86:247-248.

Perry, E. S.
1962. Montana in the geologic past. Bull. Montana Bur. Mines and Geol., 26:vi + 1-78.

Pfeifer, W. K., and E. A. Hibbard
1970. A recent record of the swift fox *(Vulpes velox)* in North Dakota. Jour. Mamm., 51:835.

Preble, E. A.
MS. List of the mammals of eastern Montana. On file, Dept. Zoology, Univ. Montana, Missoula, 12 pp.

Raynolds, W. F.
1868. Journal of Captain W. F. Raynolds. Pp. 18-127, *in* Report on the exploration of the Yellowstone River . . . , Exec. Doc., Senate, 2nd Sess., 40th Congress, 77:1-174. [erroneously printed as 1st Sess.]

Robinson, W. B.
1961. Population changes of carnivores in some coyote-control areas. Jour. Mamm., 42:510-515.

Soper, J. D.
1961. Field data on the mammals of southern Saskatchewan. Canadian Field-Nat., 75:23-40.

Spencer, A. W., and D. Pettus
1966. Habitat preferences of five sympatric species of long-tailed shrews. Ecology, 47:677-683.

Swenk, M. H.
1941. A study of subspecific variation in the Richardson pocket gopher (Thomomys talpoides) in Nebraska, with description of two new subspecies. Missouri Valley Fauna, 4:1-8.

Thompson, W. K.
1949. Predation on antelope. Jour. Wildlife Mgt., 13:313-314.

Tryon, C. A., Jr.
1947. Entrance and migration of the Norway rat into Montana. Jour. Mamm., 28:188-189.

Turner, R. W.
1974. Mammals of the Black Hills of South Dakota and Wyoming. Misc. Publ. Mus. Nat. Hist., Univ. Kansas, 60:1-178.

Van Zyll de Jong, C. G.
1972. A systematic review of the Nearctic and Neotropical river otters (genus *Lutra,* Mustelidae, Carnivora). Life Sci. Contrib., Royal Ontario Mus., 80:1-104.

Visher, S. S.
1914. Report on the biology of Harding County, northwestern South Dakota. Bull. South Dakota Geol. Surv., 6:1-103.

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